5 Evolution

Issues

- Did life evolve?
- Is science compatible with religion?
- How does evolution relate to genetics?
- How do new species originate?
- Is life still evolving?
- Will life continue to evolve?
- Is the science of evolution static or changing?

Biological Concepts

- Evolution (descent with modification, natural selection)
- Fossils and geologic time
- Environmental influences on species
- Adaptation
- Form and function
- Species and speciation
- Origin of life

Chapter Outline

5 Evolution

Ask any biologist to name the most important unifying concepts in biology, and the theory of evolution is likely to be high on the list. As geneticist Theodosius Dobzhansky explained, "nothing in biology makes sense, except in the light of evolution." However, many people in the United States are unaware of the importance of evolution as a unifying concept: public opinion surveys reveal that 25–40% of Americans either do not believe in evolution or think that evidence for it is lacking. (The percentage varies depending on how the question is worded.) In this chapter we examine both the theory of evolution and the opposition to it.

As explained in Chapter 1, scientists use the word 'theory' for a coherent cluster of hypotheses that has withstood many years of testing. In this sense, evolution is a thoroughly tested theory that has withstood nearly a century and a half of rigorous testing. Scientific evidence for evolution is as abundant as, and considerably more varied than, the evidence for nearly any other scientific idea. To refer to evolution as "just a theory" is thus a grave misunderstanding of both scientific theories in general and evolutionary theory in particular. When physicists speak of the atomic theory or the theory of relativity, or when medical professionals speak of the germ theory of disease, they are speaking of great unifying principles. These principles are now well established, but they have withstood repeated testing for somewhat fewer years than the theory of evolution has. Educated people no longer doubt the existence of atoms or of germs, and nobody refers to any of these concepts as 'just a theory.' In the way that the atomic theory is a unifying principle for much of physics and chemistry, the theory of evolution is a unifying principle for all of the biological sciences.

The Darwinian Paradigm Reorganized Biological Thought

Arguably the most influential biology book of all time was published in 1859. *On the Origin of Species by Means of Natural Selection*, written by the English naturalist Charles Darwin (1809–1882), contains at least two major hypotheses and numerous smaller ones, along with an array of evidence that Darwin had already used to test these hypotheses. Both hypotheses deal with **evolution**, the process of lasting change among biological populations. Together, these hypotheses offer explanations for the origins and relationships of organisms, the great diversity of life on Earth, the similarities and differences among species, and the adaptations of organisms to their surroundings.

The first major hypothesis, **branching descent**, is that species alive today came from species that lived in earlier times and that the lines of descent form a branched pattern resembling a tree (Figure 5.1). Darwin used this hypothesis, which he called "descent with modification," to explain similarities among groups of related species as resulting from common inheritance. The second major hypothesis is that parents having genotypes that favor survival and reproduction leave more offspring, on average, than parents having less favorable genotypes for the same traits in a given environment. Darwin called this process **natural selection**, and he hypothesized that major changes within lines of descent had been brought about by this process. Both of these two hypotheses are falsifiable, and they have been tested hundreds if not thousands of times, without being falsified, since Darwin first proposed them in 1859. Darwin's two hypotheses made sense of several previously noticed but unexplained regularities in anatomy, classification, and geographic distribution. As both a unifying theory and a stimulus to further research, Darwin's *Origin of Species* fits the concept of a scientific paradigm expounded by Thomas Kuhn and explained in Chapter 1 (p. 13). Modern evolutionary thought is still largely based on Darwin's paradigm of branching descent and natural selection, expanded to include the findings of genetics.

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Pre-Darwinian thought

Darwin's evolutionary theory was not the first. An earlier theory had been proposed by the French zoologist Jean-Baptiste Lamarck in 1809. Lamarck believed in what he called *la marche de la nature* (the parade of nature), a single straight line of evolutionary progress. This idea was based in part on the earlier idea of a scale of nature, called 'scala naturae' in Latin or 'chain of being' in English, an idea described on our Web site (under Resources: Scala naturae).

Lamarck also noticed that species were adapted to local environments. An **adaptation** is any feature that enables a species to survive in circumstances in which it could not survive as well without the adaptation. Adaptations had been observed since ancient times, but scientists of Lamarck's generation were among the first to propose hypotheses to explain adaptation. Along with several contemporaries, Lamarck was an environmental determinist, meaning that he believed in the almost limitless ability of adaptation to mold species to their environments and achieve a perfect match. Each environmental determinist favored a different explanation for adaptation. Lamarck's own explanation was based on the strengthening or increase in size of body parts through repeated use, or their weakening or decrease in size through disuse. Lamarck thought that such changes, acquired during the life of an individual, would be passed on to the next generation, but we now know that these **acquired characteristics** are not inherited and do not contribute to evolution. Other scientists, including Darwin, recognized adaptation to the local environment as an important phenomenon. However, Darwin differed from the determinists in seeing important limitations to the ability of adaptation to modify species.

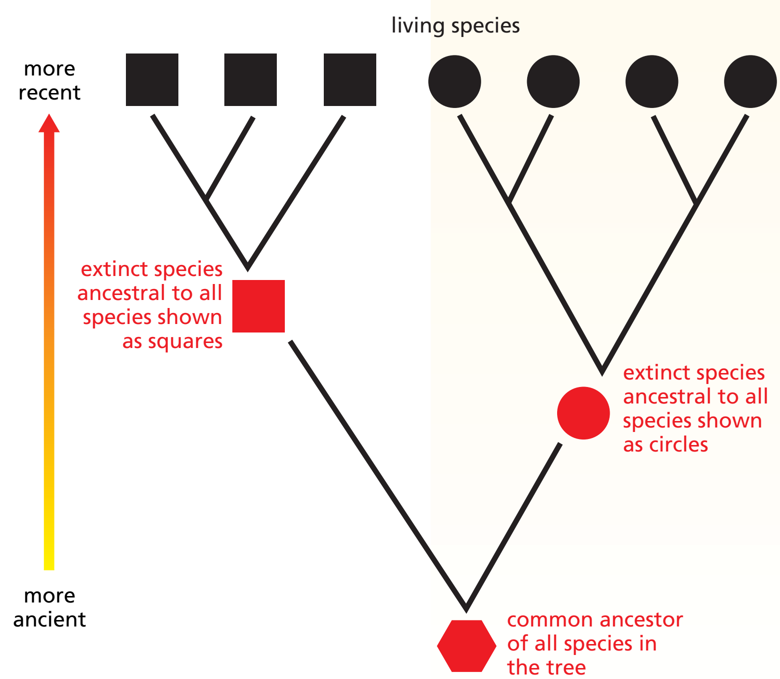

Figure 5.1

The pattern of branching descent. Living species in the top row are descended from the ancestors below them. The red circle represents the common ancestor to all other circles, and the red square is likewise ancestral to all the squares. The red hexagonal shape at the bottom is ancestral to all species shown in this family tree. In a classification, all the squares would be placed in one group and all the circles in another.

British naturalists had quite different explanations for adaptation. The Natural Theology movement, led by the Reverend William Paley, sought to prove the existence of God by examining the natural world for evidence of perfection. By careful examination and description, British scientists found case after case of organisms with anatomical structures so well constructed, so harmoniously combined with one another, and so well suited in every detail to the functions that they served that one could only marvel at the degree of perfection achieved. Such harmony, design, and detail, they argued, could only have come from God. Paley offered well-planned adaptation as proof of God's existence: "The marks of *design* are too strong to be gotten over. Design must have a designer. That designer must have been a person. That person is God." (Paley, *Natural Theology*, end of Chapter 23; page numbers vary among many editions.) In a nation in which many clergymen were also amateur scientists, it became fashionable to dissect organisms down to the smallest detail, all the better to marvel at the wondrously detailed perfection of God's design. A large series of intricate and sometimes amazing adaptations were thus described, which Darwin would later use as examples to argue for an evolutionary explanation based on natural selection.

The publication of *On the Origin of Species* challenged many scientific ideas, including those of Lamarck and Paley, and it thus caused controversy among scientists. Some people felt that it also challenged social and religious views that had been taught for centuries. Today, there are still people who are antievolutionists and we discuss their ideas later in this chapter.

The development of Darwin's ideas

From 1831 to 1836, Charles Darwin traveled around the world aboard the ship H.M.S. *Beagle*. His observations in South America convinced him that the animals and plants of that continent are vastly different from those inhabiting comparable environments in Africa or Australia. For example, all South American rodents are relatives of the guinea-pig and chinchilla, a group found on no other continent. South America also had llamas, anteaters, monkeys, parrots, and numerous other groups of animals, each with many species inhabiting different environments throughout the continent, but different from comparable species elsewhere (Figure 5.2). This was definitely not what Darwin had expected! Environmental determinist theories such as Lamarck's had led Darwin to expect that regions in South America and Africa that were similar in climate would have many of the same species. Instead, he found that most of the species inhabiting South America had close relatives living elsewhere on the continent under strikingly different climatic conditions. They had no relationship, however, to species living in parts of Africa or Australia with similar climates. The animals inhabiting islands near South America were related to species living on the South American continent. Fossilized remains showed that extinct South American animals were related to living South American species. "We see in these facts some deep organic bond, prevailing throughout space and time, over the same areas of land and water, and independent of their physical conditions. The naturalist must feel little curiosity, who is not led to inquire what this bond is. This bond, on my theory, is simply inheritance, that cause which alone, as far as we positively know, produces organisms quite like, or…nearly like each other." (Darwin. *Origin of Species*, 1859, p. 350.)

The Galapagos Islands. The Galapagos Islands are a series of small volcanic islands in the Pacific Ocean west of Ecuador. Darwin's visit to these islands proved especially enlightening to him. In this archipelago, a very limited assortment of animals greeted him: no native mammals or amphibians were present; instead there were several species of large tortoises and a species of crab-eating lizard. Most striking were the land birds, now often called 'Darwin's finches' (phylum Chordata, class Aves, order Passeres): a cluster of more than a dozen closely related species, each living on only one or a few islands (Figure 5.3). The tortoises also differed from island to island, despite the clear similarities of climate throughout the archipelago. Darwin hypothesized that each species cluster had arisen through a series of modifications from a single species that had originally colonized the islands. The islands, Darwin noted, were similar to the equally volcanic and equally tropical Cape Verde Islands in the Atlantic Ocean west of Senegal, which Darwin had also visited, but the inhabitants were altogether different. Darwin concluded that the Galapagos had received its animal colonists (including the finches) from South America, while the Cape Verde Islands had received theirs from Africa, so in each example the closest relatives were found on

Figure 5.2

An assortment of South American mammals. These species are very different from the mammals found on other continents, even where climates are similar.

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the nearest continent, not on geologically similar or climatically similar but distant islands. Geographic proximity, in other words, was often more important than climate or other environmental variables in influencing which species occurred in a particular place.

Descent with modification

As the result of his studies of species distribution on continents and on islands, Darwin concluded that each group of colonists had given rise to a cluster of related species through a process of branching descent. He called this process “descent with modification,” and he emphasized that each species in the cluster had been differently modified from a common starting point. Darwin was the first evolutionary theorist to emphasize that clusters of related species indicated a branching pattern of descent, a series of treelike branchings in which species correspond to the finest twigs, groups of species to the branches from which these twigs arise, larger groups to larger branches, and so forth (see Figure 5.1). In this diagram, each branch point represents a time of species formation and genetic divergence, and the base of the tree represents the common ancestor of all the species that arose from it. Darwin used a very similar treelike diagram, the only illustration in his book.

Darwin found many large groups of related animal species inhabiting each continent. These groups were unrelated to the very different groups inhabiting similar climates on other land masses. Several large land areas had flightless birds, but they differed strikingly from one continent or island to the next: rheas in South America, kiwis and extinct moas in New Zealand, emus and cassowaries in Australia, extinct elephant birds on Madagascar, and ostriches in Africa. Each land mass had its own distinct type of flightless bird, although they all lived in regions of similar climate. Theories of environmental determinism (such as Lamarck’s) could not explain these differences, nor could theories of divine creation explain why God had seen fit to create half a dozen distinct types of flightless birds where one might have sufficed.

Before Darwin’s time, biological classifications had already taken their modern hierarchical form, as described in Chapter 6, and as illustrated in Figure 6.1. Darwin explained this hierarchy as the natural result of branching descent with modification, a process that produces the similarities and differences that biologists have used in classifying organisms.

Figure 5.3

Some of Darwin’s finches from the Galapagos Islands.

Medium ground finch (*Geospiza fortis*)

Large cactus finch (*Geospiza conirostris*)

Warbler finch (*Certhidea olivacea*)

Natural selection

When Darwin returned to England, he began reading about the ways in which species could be modified. How, he wanted to know, could a single colonizing species produce a whole cluster of related species on a group of islands? To help find clues to answer this question, Darwin contemplated the results of plant and animal breeding in Britain. During the preceding hundred years, British breeders had produced many new varieties of plants, such as roses and apples, and animals, including dogs, sheep, and pigeons, by careful breeding practices. Through these same practices, the breeders had greatly improved wool yields in sheep, and milk yields in cattle. By methodically selecting the individuals in each generation with the most desired traits and breeding these individuals with each other, the breeders had modified a number of domestic species through a process that Darwin called **artificial selection**. This process simply took advantage of the natural variation that was present in each species, yet it produced breeds that were strikingly different from their ancestors. Darwin remarked that some of the domestic varieties of pigeons or dogs differed from one another as much as did natural species, despite the fact that the domestic varieties had been produced within a short time from a known group of common ancestors. Could a similar process be at work in nature?

At about the same time, Darwin read Thomas Robert Malthus' *Essay on Population* (see Chapter 9, p. 287). Malthus emphasized that, in the natural world, each species produces more young than are necessary to maintain its numbers. This overproduction is followed in each generation by the premature death of many individuals and the survival of only a few. When Darwin compared this process with the actions of the animal breeders, he concluded that nature was slowly bringing about change in each species. Individuals varied in every species, and those that died young in each generation differed from those that survived to maturity and mated to produce the next generation. In this 'struggle for existence,' he hypothesized that

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> …individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind…. On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favourable variations and the rejection of injurious variations, I call Natural Selection…. Natural selection…is a process incessantly ready for action, and is as immeasurably superior to man's feeble efforts, as the works of Nature are to those of Art. (Darwin. *Origin of Species*, 1859, pp. 61, 81.)

All modern descriptions of natural selection are stated in terms of the concepts of genetics outlined in Chapter 2. New genotypes originate by mutation and by recombination, both of which act prior to any selection. Darwin, of course, knew nothing of mutations or of modern genetics, but he did realize that heritable variation had to come first and that "any variation which is not heritable is unimportant to us."

Natural selection may be defined as consistent differences in what Darwin called "success in leaving progeny," meaning the proportion of offspring that different genotypes leave to future generations. The relative number of viable individuals that each genotype contributes to the next generation is called its **fitness**, and *natural selection favors any trait that increases fitness*. Darwin's theory of natural selection is the basis for all modern explanations of adaptation.

Many agents of natural selection operate in nature. Often, the selecting agents are predators. Selection by predators may be convenient to study, but many other agents of selection are known. Any cause of death contributes to natural selection if it reduces the opportunity for reproduction and if some genotypes are more likely to die. Some genotypes may be more susceptible to particular diseases or parasites, and die in greater numbers from these causes, while other genotypes might be more resistant and thus survive more readily. Starvation and weather-related extremes of cold, dryness, or precipitation may also be agents of selection if some genotypes can survive these conditions better than others. These and other causes of mortality are all agents of selection if there are differences in the death rates for different genotypes.

Not every agent of selection causes death, however. Natural selection also favors those genotypes that reproduce more and leave more offspring. A special type of selection, called **sexual selection**, operates on the basis of success (or lack of success) in attracting a mate and reproducing. For example, animals of many species attract their mates with mating calls (such as bird songs), visual displays (as in peacocks; see Figure 8.2, p. 253), or special odors (as in silkworm moths or many other invertebrate animals). Individuals that do not perform well enough to attract a mate may live long lives but leave no offspring.

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THOUGHT QUESTIONS

1 Darwin did not initially use the expression "survival of the fittest." The phrase was first used by the British social philosopher Herbert Spencer, and was popularized especially by those who saw Darwinism as a license for unbridled, cutthroat competition in the era of the 'robber barons.' (Darwin did adopt the expression in his later editions.) Do you think that this expression accurately reflects Darwinian thought regarding the animal and plant kingdoms?

In what ways does it not?

A Great Deal of Evidence Supports Darwin's Ideas

Darwin had proposed two major hypotheses: branching descent ("descent with modification") acting over long periods of time, and natural selection as a mechanism that explained how evolutionary change takes place. In the years since Darwin proposed these two hypotheses, many scientists have used scientific methods to conduct thousands of tests of both hypotheses. The results of these tests have yielded much evidence that supports the hypotheses, and none that falsifies them.

Mimicry

One of the earliest tests of Darwin's hypothesis of natural selection involved the phenomenon of **mimicry**, in which one species of organisms deceptively resembles another. In one type of mimicry, a distasteful or dangerous prey species, called the model, gives a very unpleasant and memorable experience to any predator that attempts to eat it. Predators always avoid the model after such an unpleasant experience. A palatable prey species, the mimic, secures an advantage if it resembles the model enough to fool predators into avoiding it as well.

Selection by predators explains mimicry rather easily. Any slight resemblance that might cause a predator to avoid the mimic as well as its model is favored by selection and passed on to future generations of the mimic species, while individuals not protected in this way would be eaten in greater numbers. Predator species differ greatly in their abilities to distinguish among prey species, so a resemblance that fools one predator might not fool another. Any advantage that increases the number of predators fooled is favored by selection, causing closer and closer resemblance to evolve with the passage of time.

Sometimes several species that resemble each other are all distasteful to predators. Predators learn to avoid distasteful species, but a certain number of prey individuals are killed for each predator individual that learns its lesson. Without mimicry, each prey species must sustain this loss separately. Mimicry allows predators to learn the lesson with fewer individuals of each prey species dying in the process. The mimicry therefore benefits each prey species and is thus favored by natural selection.

Mimicry often varies geographically. Some wide-ranging tropical species mimic different model species in different geographic areas. The deceptive resemblance is always to a species living in the same area, never to a far-away species. Environmentalist theories such as Lamarck's had no way to account for the evolution of mimicry, and the patterns of geographic variation could not be explained by either environmentalist theories or by Paley's natural theology. Natural selection, however, explains the variation as resulting from selection by predators.

In a well-known case of mimicry, the model is the monarch butterfly, a distasteful species that feeds on milkweed plants. An unrelated species, the viceroy, is similar in superficial appearance, and is thus avoided by many predators (Figure 5.4); some of these predators may find the viceroy distasteful as well.

Industrial melanism

The power of natural selection is also demonstrated by a phenomenon called **industrial melanism**, when darker colors evolve in areas polluted by industrial soot in species that are usually light in color elsewhere. In the British Isles, a species known as the peppered moth (*Biston betularia*) (phylum Arthropoda, class Insecta, order Lepidoptera) had long been recognized by an overall light gray coloration with a salt-and-pepper pattern of irregular spots. A black variety of this species was discovered in the 1890s. The black moths increased until they came to outnumber the original forms in some localities (Figure 5.5). The British naturalists E.B. Ford and H.B.D. Kettlewell studied these moths for several decades from about 1944 onward. Downwind from the major industrial areas, the woods had become polluted with black soot that killed the lichens grow-

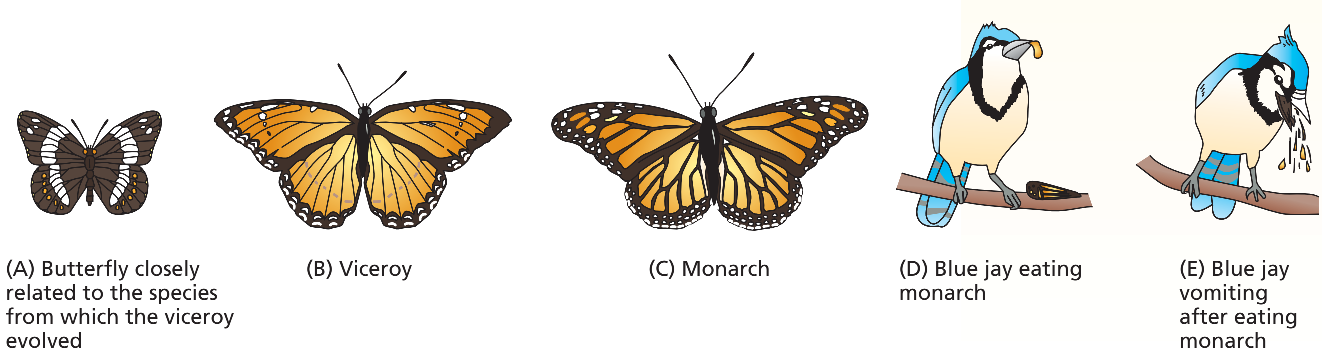


Figure 5.4

An example of mimicry. (A) *Limenitis arthemis*, a nonmimic relative of (B) *Limenitis archippus*, the viceroy. The viceroy resembles the unrelated monarch butterfly (C, *Danaus plexippus*), the model. The monarch is avoided by predators after just a single unpleasant experience (D, E). The warning color pattern of the monarch helps predators learn to avoid it; the viceroy is protected because its color pattern mimics that of the monarch.

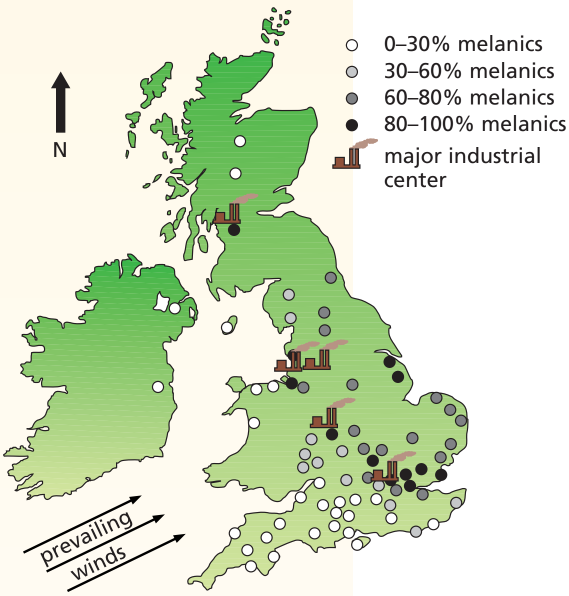
ing on the tree trunks. Most of the moths living on the darkened tree trunks in these regions were black. However, where the woods were untouched by the industrial soot, the tree trunks were still covered with lichens and the moths had kept the light-colored pattern. Ford and Kettlewell hypothesized that the moths resembling their backgrounds would be camouflaged and thus harder for predators to see. To test this hypothesis, they pinned both light and dark moths on dark tree trunks in polluted woods, and they also pinned both types on lichen-covered tree trunks in unpolluted woods. They observed that birds ate more of the dark moths in the unpolluted woods (favoring the survival of the light-colored pattern), but birds in the polluted woods ate more of the light-colored moths, not the dark ones. These observations and the geographical patterns of variation (see Figure 5.5) were easily explained in terms of natural selection by predators. In addition, since the experiments were first conducted, laws to control smokestack emissions and other forms of pollution were passed and enforced, and many of the woods affected by pollution have returned to their former state. In these woods, the lichens have returned to the tree trunks, and most of the moths in these places again have the original light-colored pattern.

Industrial melanism in insects demonstrates that species can change in response to changes in the environment and were not created with permanent, unalterable traits. Lamarckian mechanisms fail to explain industrial melanism because, in these species, the adult colors do not change once they are formed, and there is nothing that individuals can do that would alter their color. The experiments with birds as predators clearly show natural selection at work.

Figure 5.5

Industrial melanism in peppered moths in the British Isles.

Geographic variation in the frequency of melanic moths in the 1950s, which reached as high as 100% in polluted localities downwind from major industrial centers.



The melanic (black) variety and the original 'peppered' variety (below the right wing-tip of the melanic moth) on a light, lichen-covered tree trunk.

The same two varieties on a dark, soot-covered tree trunk.

Evidence for branching descent

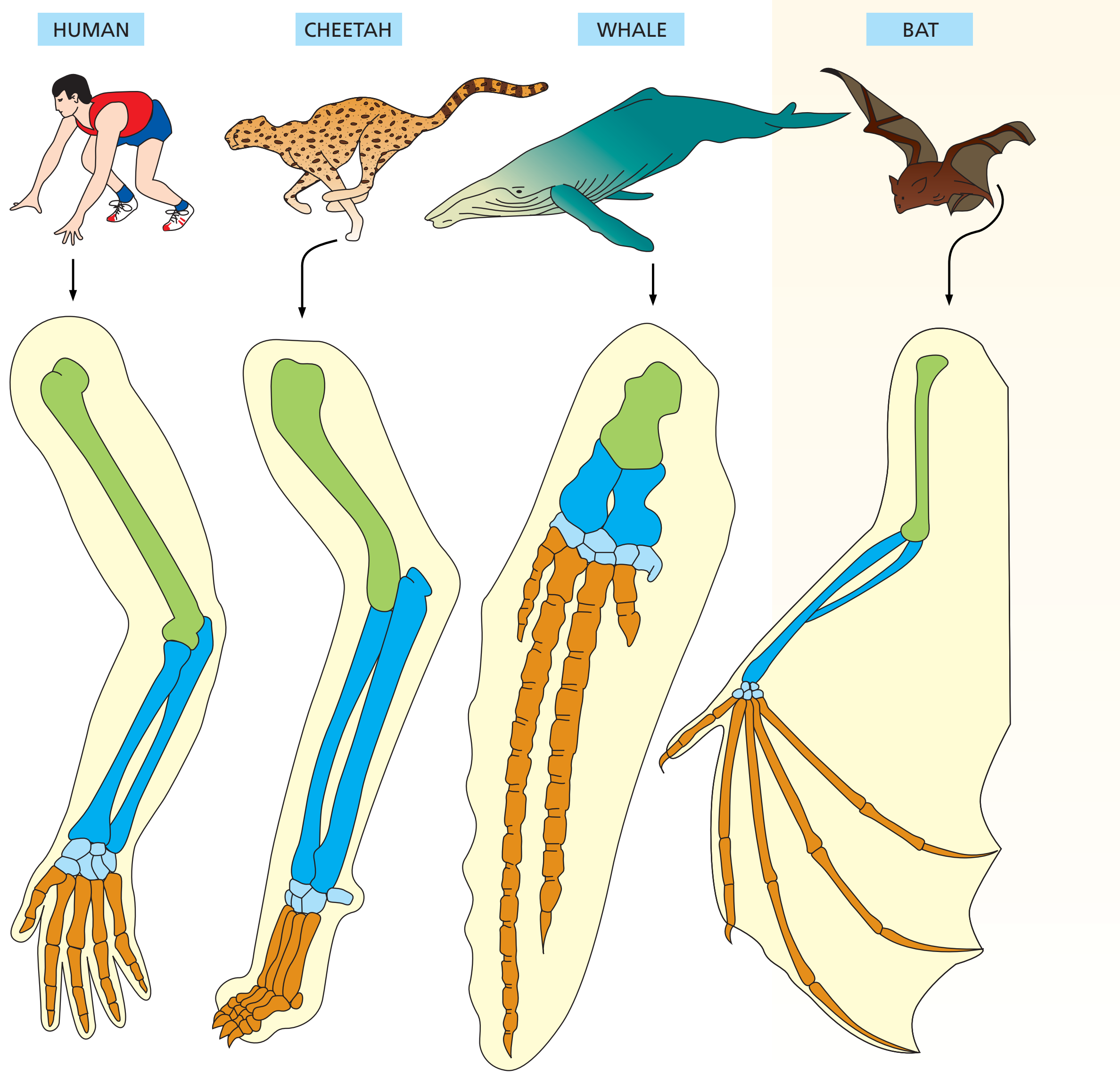
Darwin's contemporaries immediately recognized that his concept of "descent with modification" could be used to make sense out of a variety of observations not easily explained by other means. The branching pattern of descent explained the formation of groups or clusters of related species in particular geographic areas. Moreover, it explained the arrangement of these groups into a hierarchy of smaller groups within larger groups. Biologists before Darwin had been making classifications this way for about a century, but it was his theory of branching descent that explained why this type of classification made sense. Darwin predicted that biological classifications would increasingly become genealogies (that is, maps of descent similar to Figure 5.1) as more and more details about the evolution of each group of organisms became known. Darwin's prediction came true as scientists found more and more evidence showing that relationships among species arise in branching patterns of descent. Evidence for such relationships comes from the comparative study of the anatomy, biochemistry, physiology, and embryology of different species.

Homologies. The construction of family trees is based in large measure on the study of shared structures or gene sequences. Under Darwin's paradigm, shared similarities are evidence that the organisms in question share a common ancestry. In a sense, a shared similarity is a falsifiable hypothesis that the several species sharing it are related to one another by descent. By itself, one such similarity reveals very little, but a large number of similarities that fit together into a consistent pattern strongly suggest shared ancestry. When the evidence for shared ancestry is compelling, the similarity is called **homology**.

Darwin noted the similarities among the forelimbs of mammals: "what can be more curious than that the hand of a man, formed for grasping, that of a mole for digging, the leg of the horse, the paddle of the porpoise, and the wing of the bat, should all be constructed on the same pattern, and should include the same bones, in the same relative positions?" (Figure 5.6). Darwin wondered why similar leg bone structures appeared in the wings and legs of a bat, used as they are for such totally different purposes. Among the Crustacea (barnacles, crabs, shrimp, etc.), most species have a thorax region with eight pairs of leglike appendages

Figure 5.6

Homologies among mammalian forelimbs adapted to different functions.



used for locomotion, but the group that includes lobsters and crabs has the first three of these pairs modified into accessory mouthparts, leaving only five pairs of walking legs. Why, asks Darwin, should a crustacean that has more mouthparts have correspondingly fewer legs, or why should those with more legs have fewer mouthparts? Darwin's answer is that all these structures arose by modification of the same type of repeated part. Crustacean mouthparts and legs are derived from a common set of leglike appendages. When the structure of these appendages varied (through mutation and other causes), natural selection favored different structures for different uses. Individuals with better-functioning mouthparts near the mouth, or with better-functioning legs near the center of gravity, left more offspring, and the proportions of the responsible genotypes increased in each population. As a consequence, when more appendages were used around the mouth as food-handling structures, there were fewer appendages remaining to be used as legs. An omnipotent God, however, could have added mouthparts without taking away legs (without being limited by the total number of appendages), leaving Darwin to declare, "How inexplicable are these facts on the ordinary view of creation!" (Darwin. *Origin of Species*, 1859, p. 437.)

Vestigial structures. Structures whose function has been lost in the course of evolution tend to diminish in size. Often, they persist as small, functionless remnants, called **vestigial structures.** A good human example is the coccyx, a set of two or three vestigial tail bones at the base of the spinal column, homologous to the tails of other mammals. The Darwinian paradigm of natural selection and branching descent explains these vestigial structures as the remnants of structures that had once been functional. Neither Lamarck nor the creationists had any explanation for the presence of vestigial structures, and certainly not for the homologies of vestigial structures in many species with their functional counterparts in related species.

Convergence. Similarities that result from common ancestry (that is, true homologies) should also be similar at a smaller level of detail, and even similar in embryological derivation, meaning that they should grow from the same source tissues. A hypothesis of homology can thus be falsified if two similar structures turn out to be dissimilar in detailed construction or in embryological derivation. There are also cases in which several hypotheses of homology are in conflict because they require different patterns of relationship for different characters. In such cases, evolutionists examine all the similarities more closely and repeatedly to see whether a reinterpretation is possible for one set of similarities.

Convergence is an evolutionary phenomenon in which similar adaptations evolve independently in lineages not closely related. Similarities for which the hypothesis of homology is falsified by more careful scrutiny are often reinterpreted as convergent adaptations, meaning structures that evolved independently in unrelated lineages. Resemblance resulting from convergent adaptation is called **analogy**. Distinguishing homology from analogy is an ongoing aim of evolutionary classification. For example, the wings of bats and insects are analogous, rather than homologous, structures. They are constructed in different ways and from different materials, and their common shapes (which they also share with airplane wings) reflect adaptation to the aerodynamic requirements of flying. Although bat wings are not homologous to insect wings, they are homologous to human arms, whale flippers, and the front legs of horses and elephants. These all have similar bones, muscles, and other parts in similar positions despite their very different shapes and uses, while insect wings have no bones and their muscles are very differently located.

Cephalopods as an example. One frequent test of the hypothesis of branching descent is to identify a group of organisms that share some particular character, such as an anatomical or biochemical peculiarity. The general hypothesis of branching descent then gives rise to a more specific hypothesis, that these organisms all share a common descent from a common ancestor. An example of this type of reasoning can be illustrated by the Cephalopoda, a group of mollusks that includes the squids, octopuses, and their relatives. All cephalopods can be recognized by the presence of a well-developed head and a mantle cavity beneath (Figure 5.7). The mantle cavity contains the gills, the anus, and certain other anatomical structures. Other mollusks have mantle cavities, but only in the Cephalopoda is the mantle cavity located beneath the head and prolonged into a nozzlelike opening known as the hyponome. Knowing this, we can formulate the specific hypothesis that all cephalopods share a common descent.

If our hypothesis is true, then we should be able to find, as evidence, some additional similarities among cephalopods not shared with other mollusks. Such similarities do exist: all cephalopods have beaklike jaws at the front of the mouth, and a muscular part, called the foot in other mollusks, subdivided into a series of tentacles (see Figure 5.7). Moreover,

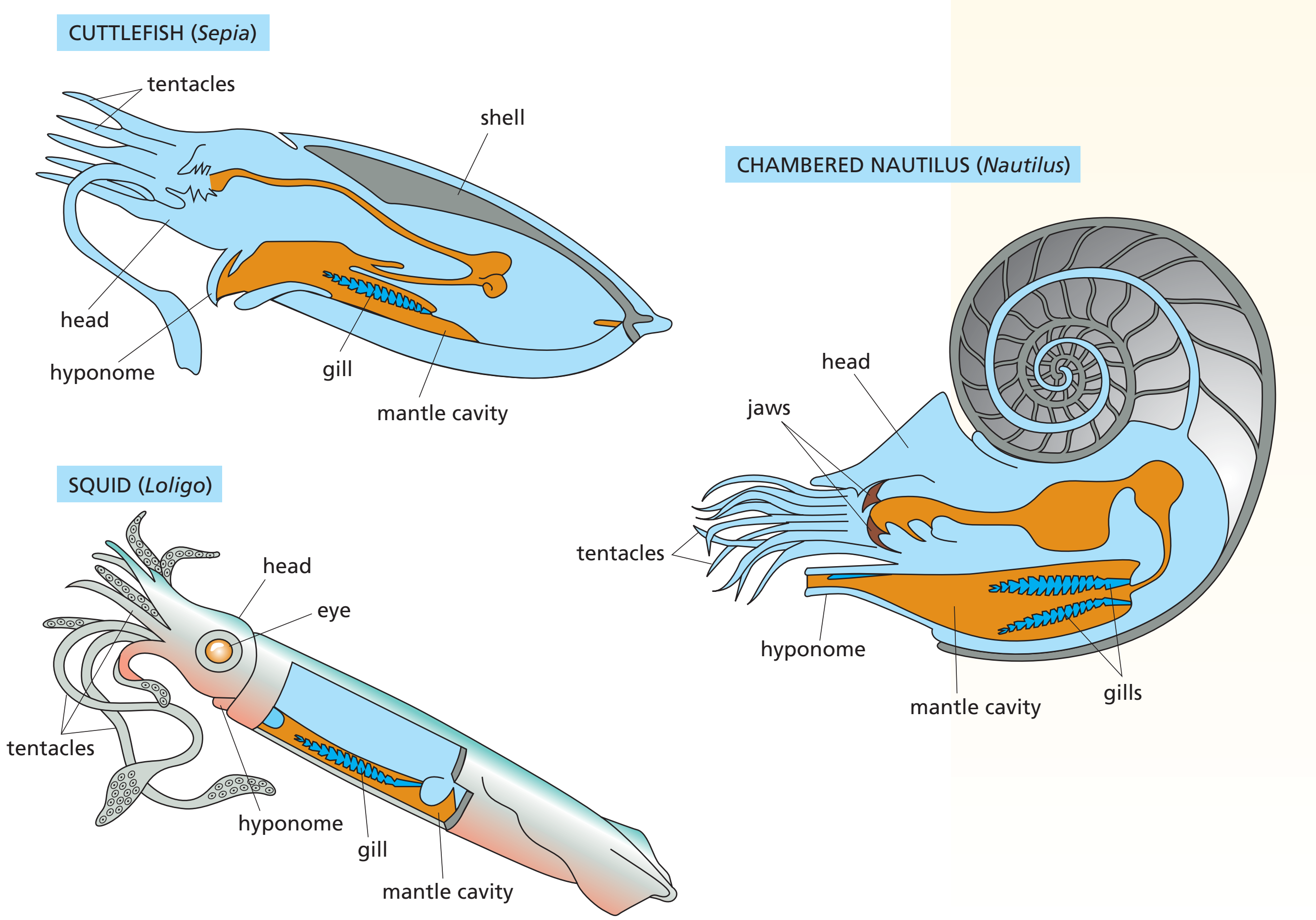


Figure 5.7

Three living types of cephalopod mollusks (kingdom Animalia, phylum Mollusca, class Cephalopoda): the cuttlefish, the squid, and the chambered nautilus.

all cephalopods have an ink gland that secretes a very dark, inky fluid. When a squid or octopus feels threatened by a predator, it releases this fluid into its mantle cavity and quickly squirts the contents of the mantle cavity forward through its nozzlelike hyponome. This action hides the animal and propels it backwards, in a direction not expected by its predator. The predator's attention is meanwhile held by the puff of inky fluid. By the time the color dissipates, the squid or octopus has vanished. All members of the Cephalopoda have this elaborate and unusual escape mechanism, including squids, cuttlefishes, octopuses, and the chambered nautilus. The hypothesis of a common descent for all the Cephalopoda is thus consistent with the known data, meaning that the hypothesis has been tested and not falsified.

Further comparisons among species. Since Darwin's time, many additional types of similarities have been discovered among organisms. The comparative study of embryonic development has resulted in the discovery of many new similarities among distantly related species, some of which are described in Chapter 6. Comparative genomics (Chapter 4) and comparative studies in biochemistry have revealed the detailed structure of protein chains, DNA and RNA sequences, and other large molecules of biological interest. As with anatomical similarities, similarities in biochemistry or in embryology group related species together, and small groups are contained within larger groups at many hierarchical levels. Each new type of similarity has brought new evidence of branching descent with modification: in most cases, the groups established by older methods are reaffirmed when newer methods result in the same groupings. In a few cases, new groupings are discovered, and sometimes these are later corroborated by further evidence such as new fossil discoveries.

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On the basis of anatomical, embryological, and biochemical comparisons, hypotheses of common descent have been tested and confirmed for cephalopod mollusks and for many other groups of animals and plants. This increases our confidence in the larger hypothesis that all species of organisms have evolved from earlier species in patterns of branching descent. The many facts of comparative anatomy, comparative physiology, embryology, biogeography, and animal classification are all consistent with the hypothesis that modern species have evolved from ancestors that lived in the remote past, and they make little sense otherwise.

Since Charles Darwin published his evolutionary ideas in 1859, thousands of tests have been made of his twin hypotheses of branching descent and natural selection. Because these thousands of tests have failed to falsify either hypothesis, both now qualify as scientific theories that enjoy widespread support. The Darwinian paradigm continues to this day as a major guide to scientific research.

Further evidence from the fossil record

The history of life on Earth is measured on a time scale encompassing billions of years. This geological time scale (Figure 5.8) was first established by studying **fossils**, the remains and other evidence of past life forms. Most fossils are formed from the burial of plants or animals in sediment. The soft parts of these organisms are often consumed or decomposed, but they may leave imprints in soft sediments if buried rapidly. Scientists had recognized since 1555 that most fossils were the remnants of species no longer living, thus providing clear-cut evidence for extinction. Comparisons of fossils with living species provide evidence of change over time and thus have a role in supporting the theory of descent with modification and the concept of evolution more generally.

Stratigraphy. The geological time scale was first established through the study of layered rocks (**stratigraphy**). One of the first principles established in the study of these rocks was that when rock layers have not been drastically disturbed, the oldest layers are on the bottom and successively newer layers are on top of them. Using this principle, geologists can identify the rock formations in a particular place as part of a local sequence, arranged chronologically from bottom to top.

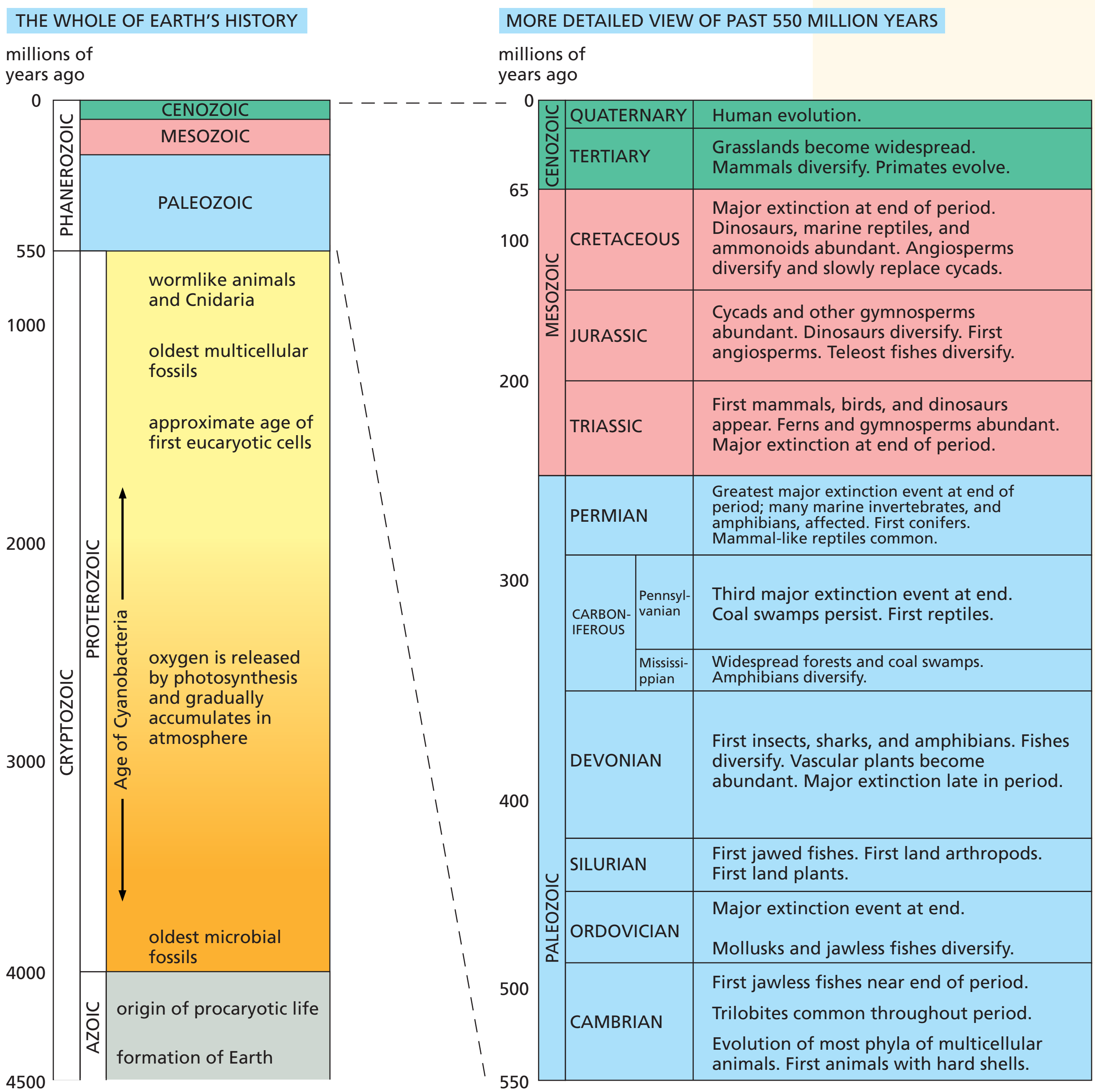


Figure 5.8

The geological time scale.

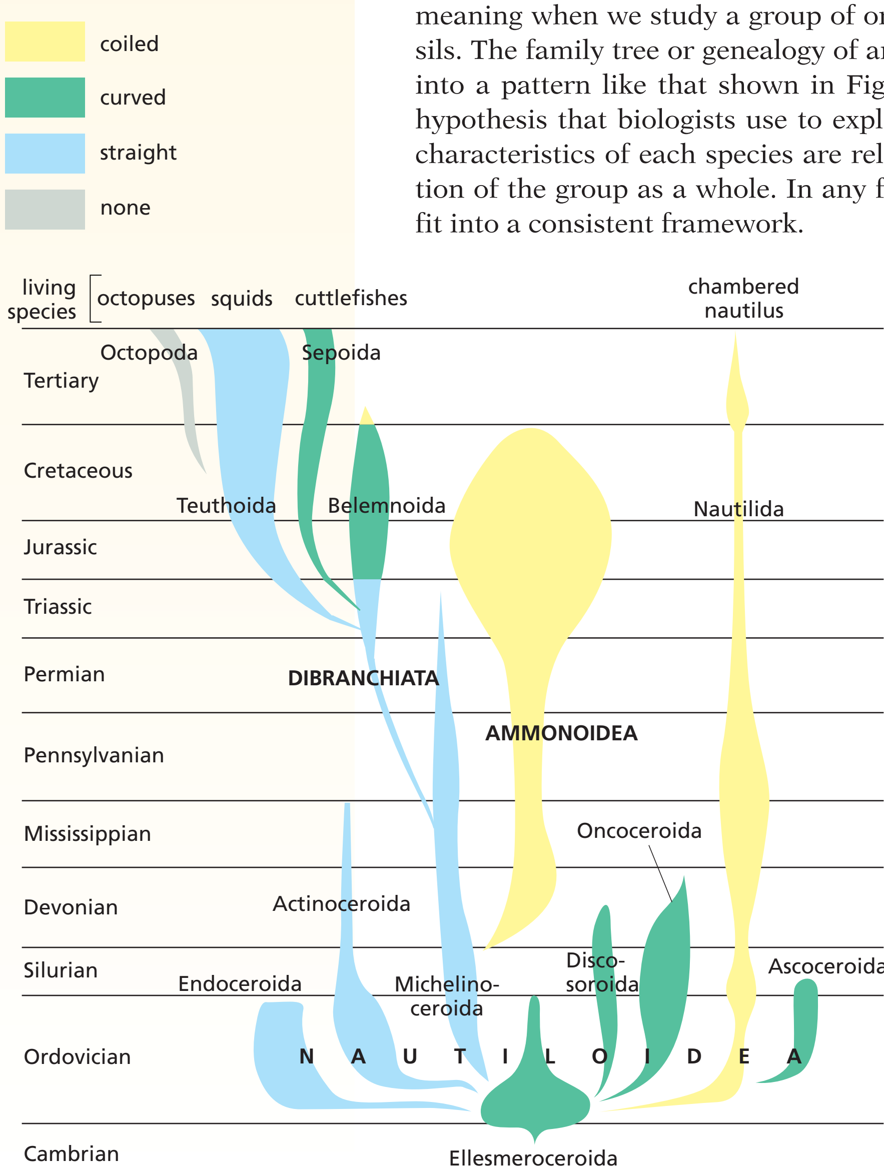
Local sequences from different places can be matched with one another in several ways, but the most reliable of these proved to be the study of their fossil contents. Two rock formations are judged to be from the same time period if they contain many of the same fossil species (the principle of **correlation by fossils**). The rocks do not need to be similar in composition or rock type—one can be a limestone and the other a shale—but if their fossil assemblages are similar, they are judged to be equally old. A single species of fossil is never sufficient; several fossil species are needed, and they must occur together with some consistency. Using this technique, paleontologists (scientists who study fossils) have been able to match up formations of the same age from many different localities, enabling them to assemble the world's various local sequences into a 'standard' worldwide sequence, which is the basis for the complete sequence of time periods shown in Figure 5.8. The dates assigned to these periods are determined by measuring the rate of radioactive decay in certain rocks.

Family trees. The age of a fossil, by itself, tells us very little about its place in any family tree. The relative ages of fossils only begin to have meaning when we study a group of organisms represented by many fossils. The family tree or genealogy of any group, called its **phylogeny**, fits into a pattern like that shown in Figure 5.1. Any such family tree is a hypothesis that biologists use to explain how the anatomical and other characteristics of each species are related, which leads to the classification of the group as a whole. In any family tree, the known fossils must fit into a consistent framework.

For example, there are many fossils of cephalopod mollusks, permitting further tests of the hypothesis of a common descent for all the Cephalopoda. Living and extinct cephalopods can be arranged into a family tree consistent with our knowledge of the characteristics of each species and the relations among them (Figure 5.9). Differences among the living cephalopods can be explained with reference to this family tree. The chambered nautilus is very different from other living cephalopods because it is fully housed within a coiled shell and has four gills, while the squids and octopuses have only two gills and a very small, reduced shell or else none at all. One would therefore imagine a family tree in which octopuses and squids have a common ancestor that the chambered nautilus does not share. The fossil

Figure 5.9

Family tree of the class Cephalopoda (phylum Mollusca), showing branching descent over time. Horizontal width represents number of species in each group; vertical distance represents time.



Cephalopoda conform to these expectations. The group of cephalopods with the oldest fossil record is the nautiloids, of which the chambered nautilus is the only living remnant. A second group of cephalopods, called the ammonoids (see Chapter 18, p. 351), flourished in Mesozoic times, during the age of dinosaurs. A small, third group had an internal shell that became reduced in size. When the ammonoids became extinct, this third group, the Dibranchiata, persisted and is represented today by the squids and octopuses. Thus, the fossil record of the cephalopod mollusks, including both the anatomy and age relationships of fossil forms, confirms the relationships hypothesized on the basis of the anatomy of the living forms.

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The fossil record has repeatedly confirmed hypotheses of descent for particular living species. For example, Thomas Henry Huxley, one of Darwin's early supporters, studied the anatomy of birds and declared them to be "glorified reptiles." The interpretation of birds as descendants of the reptiles was strengthened by the discovery of *Archaeopteryx*, a fossil with many birdlike and also many reptilian features. Among these were a long tail, simple ribs, a simple breastbone, and a skull with a small brain and tooth-bearing jaws (Figure 5.10). Despite these reptilian features, *Archaeopteryx* had well-developed feathers and was probably capable of sustained flight. The discovery of transitional forms like *Archaeopteryx*, coupled with the fossils of other early birds and of feathered dinosaurs close to bird ancestry, strengthens our confidence in the hypothesis that birds evolved from reptiles. Other transitional forms are known, such as those between older and more modern bony fishes, between fishes and amphibians, between reptiles and mammals, and between terrestrial mammals and whales. Instead of being exactly intermediate in each trait, transitional forms usually exhibit a mix of some innovative characteristics and some ancestral characteristics.

Post-Darwinian thought

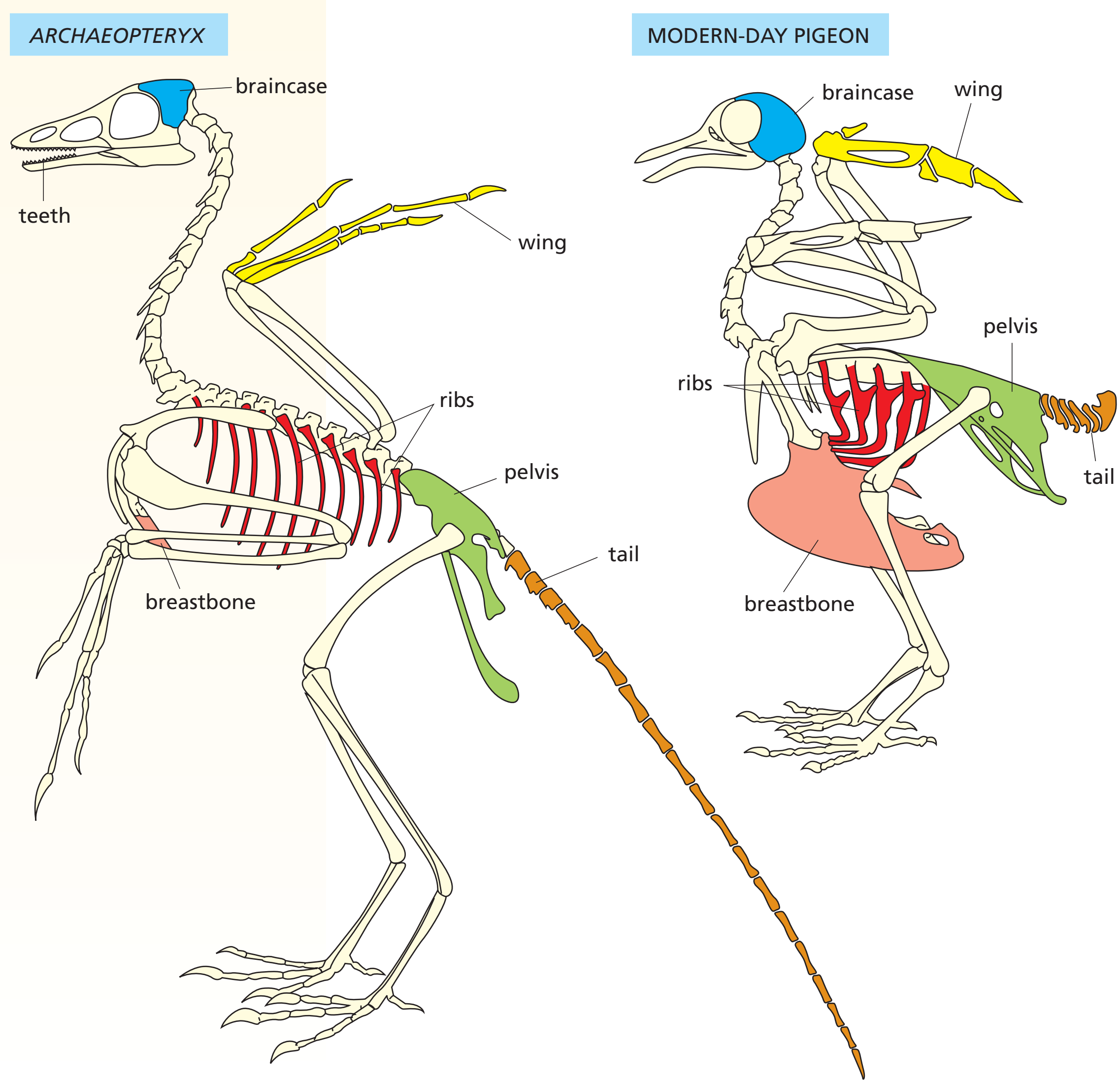
One of the hallmarks of science is that hypotheses are subjected to rigorous and repeated testing. Darwin's hypotheses have been thoroughly and repeatedly tested for nearly a century and a half, and the general outlines of branching descent and natural selection have been repeatedly and consistently confirmed. A second hallmark of science is that theories are extended and modified as new data are discovered. Here again, Darwin's ideas have been extended and supplemented by newer findings. Many additional details are now known, none of which contradict the basic concepts of natural selection and branching descent. A third hallmark of a scientific theory is that it acts as a spur to further research, and Darwin's two theories have stimulated more scientific research than just about any other theory in the history of biology, with the possible exception of Mendel's theories in genetics. Evolution guides our thinking in nearly every field of biology, which is why "nothing in biology makes sense, except in the light of evolution."

During the period 1860–1940, scientists who doubted the effectiveness of natural selection proposed many other hypotheses to explain evolutionary change. Our modern theory of mutations originated from one such hypothesis. In Czarist Russia, scientists of nearly every political stripe (from conservative monarchists to socialists and anarchists) found the British idea of competition very distasteful. They were therefore reluctant to embrace the concept of natural selection, which they felt was based on a model of competition. (Darwin had emphasized that he meant competition in a "large and metaphorical sense," but his Russian readers still found the similarity with capitalist economics distasteful.) As an alternative, the anarchist Petr Kropotkin, and the novelist and pacifist Leo Tolstoy, developed theories of "mutual aid" or **mutualism** as an important evolutionary mechanism. According to this view, organisms succeed (and leave more offspring) if they cooperate with one another instead of competing, as among social insects (see Chapter 8). Modern biologists now view mutualism as an adaptive interaction between species that may evolve as the result of natural selection. Natural selection favors any change that increases reproductive success, and this frequently includes changes that benefit other species directly. The theory of mutualism has thus been accepted into the mainstream of Darwinian evolutionary thought, and is no longer viewed as something incompatible with natural selection. Darwin himself gave several examples of cooperative interactions between species.

Although Darwin's theories of natural selection and branching descent continue to guide biological research to this day, the early 1940s saw the expansion of the evolutionary paradigm called the modern synthesis. Dar-

Figure 5.10

The early bird *Archaeopteryx*, compared with a modern-day pigeon. Modern birds lack teeth, and evolution has enlarged the braincase and strengthened other parts (wing, ribs, breastbone, pelvis, tail) highlighted here.



win's ideas are retained in this expanded paradigm, but the findings of genetics are also incorporated and are used to explain the source of heritable variation. Natural selection is well documented as an important cause of evolutionary change, but it is by no means the only cause. Chance alone (accidents of sampling which individuals die, which live, and which reproduce) can cause erratic changes in the allele frequencies of natural populations, especially small ones. This phenomenon, called **genetic drift**, is discussed further in Chapter 7. The changes produced by genetic drift are usually nonadaptive, and they increase the chances that a small population will die out. Later in this chapter we will also discuss the importance of geographic isolation, a nonselective force that sets up conditions that bring about the evolution of new species.

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Beginning in the 1970s, Niles Eldredge and Stephen Jay Gould advocated a theory that they viewed as alternative to Darwinian thought. Darwin had frequently emphasized that evolutionary change was gradual, but Eldredge and Gould claimed instead that species remain static for long periods and then change abruptly. The new species begins, they said, as a small, isolated population on the geographic periphery of the original species. The small size of the isolated population allows it to undergo rapid change, producing a new species. Once the new species becomes successful, its numbers and geographic range may increase to the point where it invades the geographic range of the original species from which it evolved. If the new species successfully outcompetes the original one, the original one may become extinct. What we often see in the fossil record is the abrupt replacement of one species by another rather than a gradual change. Gould always claimed that this **punctuated equilibrium** theory is an alternative to Darwin's gradualism, but certain other evolutionists (such as Ernst Mayr) view the two theories as fully compatible.

THOUGHT QUESTIONS

1 For a family tree such as that shown in Figure 5.9, what kinds of fossil evidence (be specific) would falsify the descent pattern shown? What kinds of evidence would cause paleontologists to modify the family tree but continue to believe in a process of descent with modification? What kinds of evidence would falsify the hypothesis of descent with modification?

2 One of the Galapagos finches studied by Darwin has woodpeckerlike habits and certain woodpeckerlike features: it braces itself on vertical tree trunks with stiff tail feathers in the manner of true woodpeckers and drills holes for insects with a chisel-like bill. However, it lacks the long, barbed tongue with which true woodpeckers spear insects; it uses cactus thorns for this purpose instead. How would Lamarck have accounted for this set of adaptations? How would Paley? How would Darwin? Which of these explanations accounts for the absence of the barbed tongue in the woodpecker finch? How would each hypothesis account for the absence of true woodpeckers on the Galapagos Islands?

3 Is the study of evolution static or changing? Find some recent news articles dealing with new fossil discoveries or other new findings that deal with evolution.

4 Explain antibiotic resistance in bacteria by using Darwin's concept of natural selection.

Creationists Challenge Evolutionary Thought

Opposition to the idea that life evolves has come from various quarters. Many opponents of evolution have been creationists, people who believe in the fully formed creation of species by God. In this section we discuss a variety of creationist ideas, along with the creationist opposition to evolution.

Creationists, by definition, believe that God created biological species. The majority of creationists believe that God created species much as we see them today, and that they did not evolve. Creationists are usually devout believers and most of them are Christian, but beyond these similarities creationists do not always share all of the same beliefs. Some creationists have been practising scientists who conduct research and follow scientific methodology, while others are strongly antiscience and may even seek the destruction of science and of scientific institutions.

Three major groups of creationists stand out:

1. Bible-based creationists, who insist on the biblical account of creation. These creationists work outside science and reject any scientific theory that conflicts with scripture; some of them are openly hostile to science.
2. Intelligent-design creationists, who try to work within the framework of science to find evidence of design in nature. They claim that biological systems are so complex and so well adapted to their functions that only an intelligent (and benevolent) designer could have made them.
3. Theistic evolutionists, who believe that God created the universe and all life, but that species evolved after that time and that evolution is one of God's creative processes. Several practising scientists and various clergy adhere to this view.

Bible-based creationism

In the United States, most creationists have based their beliefs on a literal interpretation of the Bible. Believing in the inerrant truth of their ideas, these creationists reject all science and all scientific evidence that contradicts their beliefs. Some of them are openly hostile to science. Almost all of these creationists are Protestant Christians, but they represent a small minority within the Protestant tradition. The large, established denominations accept the evidence for evolution as fully compatible with their religious beliefs.

Various shades of opinion divide the Bible-based creationists into separate groups. One group, the 'Young Earth' creationists, insists that the six days of creation mentioned in Genesis were each 24 hours in length. Another group, the 'Day–Age' creationists, seeks to reconcile science with biblical accounts by proposing that the six days of creation should be interpreted as six ages of indefinite duration. (The Hebrew word 'yom' is often used this way elsewhere in the Bible.) Many mainstream clergy of various faiths subscribe to this view. Somewhat similar in their views are the 'Gap' creationists, who reconcile biblical with geological time scales by claiming that a long, indefinite gap of time intervened between the events described in Genesis chapter 1 and Genesis chapter 2.

Early fundamentalism. In the early twentieth century, most opposition to evolution came from certain Protestants, mostly in the United States, who declared that evolution conflicted with the account of creation given in the Bible. These people founded a number of societies, including the Society for Christian Fundamentals (the origin of the term *fundamentalist*). The fundamentalists persuaded several state legislatures to pass laws restricting or forbidding the teaching of evolution in schools. Some of these state laws remained until the 1960s.

In 1925, a famous court case was brought in Tennessee by the fledgling American Civil Liberties Union. A teacher, John H. Scopes, was arrested for reading a passage about evolution to his high school class. The trial attracted worldwide attention. Scopes lost and was assessed a $100 fine. Upon appeal, the case was thrown out because of the way in which the fine had been assessed; the merits of the case were never really debated. The Scopes trial did, however, have a chilling effect on the textbook publishing industry: books that mentioned evolution were revised to take the subject out, and most high school biology textbooks published in the United States between 1925 and 1960 made only the barest reference, if any, to Charles Darwin or any of his theories.

Creationism in recent decades. The Soviet launch of the Earth-orbiting satellite Sputnik in 1958 set off a wave of self-examination in American education. Groups of college and university scientists began examining high school curricula with renewed vigor, and several new high school science textbooks were written. Most of the new biology texts emphasized evolution, or at least gave it prominent mention.

Alarmed in part by the new textbooks, a new generation of creationists began a series of attacks on the teaching of evolution. These new creationists tried to portray themselves as scientists, calling their new approach 'creation science' even though they never conducted experiments or tested hypotheses. Instead of making their studies falsifiable, the new creationists claimed that they held the absolute truth:

> Biblical revelation is absolutely authoritative.... There is not the slightest possibility that the *facts* of science can contradict the Bible and, therefore, there is no need to fear that a truly scientific comparison...can ever yield a verdict in favor of evolution.... The processes of creation...are no longer in operation today, and are therefore not accessible for scientific measurement and study. (H.M. Morris (Ed.). *Scientific Creationism*. San Diego: Creation-Life Publishers, 1974, pp. 15–16 and 104.)

> We do not know how the Creator created, what processes He used, for He used processes which are not now operating anywhere in the natural universe.... We cannot discover by scientific investigations anything about the creation process used by the Creator. (D.T. Gish. *Evolution: The Fossils Say No!*. San Diego: Creation-Life Publishers, 1978, p. 40.)

In contrast, Darwin knew that his theories were—rightly—subject to empirical testing and possible falsification (see the quotation on page 147).

Some creationist writings contain faulty explanations of scientific concepts. One such misinterpretation uses the second law of thermodynamics. According to this law, a closed system (one in which energy neither leaves nor enters) can only change in one direction, to that of less order and greater randomness. Thus, a building may crumble into a pile of stones, but a pile of stones cannot be made into a building without the expenditure of energy. Creationists have claimed that this law precludes the possibility of anything complex ever evolving from something simpler. The second law of thermodynamics does not, however, rule out the building up of complexity; rather, it states that making something complex out of something simple requires an input of energy. The second law of thermodynamics *does* apply to all biological processes. If the Earth were a thermodynamically closed system, life itself would soon cease. However, the Earth is not a thermodynamically closed system because energy is constantly being received from the Sun, and this energy allows life to persist and evolve. Creationist claims on this point may have originated as an innocent error, but the point has been so well refuted that its continued use can only be a deliberate misrepresentation that lies outside the bounds of science or of honest debate.

In the 1960s, because many of the laws in the United States forbidding the teaching of evolution had been declared unconstitutional, one group of creationists, led by Henry Morris, Duane Gish, and John Slusher, decided on a new approach. Evolution could be taught in the schools, they argued, but only if 'creation science' was taught along with it and given equal time. (The concept of 'equal time,' was originally a measure to ensure fairness in political campaigns.) A few state legislatures passed laws inspired by this new group of creationists. An Arkansas law known as the Balanced Treatment Act (Public Law 590) was finally declared unconstitutional in 1981, and a similar Louisiana law was declared unconstitutional a few years later. Interestingly, in the challenges to these laws, the scientific issues *were* raised in court, and prominent scientists were called upon to testify. Specifically, in the Arkansas and Louisiana cases, the U.S. Court of Appeals was asked to rule on what is scientific and what is not. The court finally ruled that evolution is a scientific theory and may be taught, whereas 'creation science' is not science at all because it involves no testing of hypotheses and because its truths are considered to be absolute rather than provisional. Instead, 'creation science' was found to be a religion, or to include so many religious concepts (creation by God, Noah's flood, original sin, redemption, and so forth) that it could not be taught in a public school without violating the U.S. Constitution's historic separation of church and state.

In the 1990s, a new group of creationists emerged, advocating the view that modern science, particularly evolution, is the basis for the materialistic philosophy that they claim is responsible for all that is wrong in today's society. The avowed aim of this group, called the 'Wedge group', is to destroy all of science, and evolution in particular, by driving in a thin 'wedge' and then continuing to drive it in deeper and deeper until the body of science is split asunder. Small but well-financed, this group is the guiding force behind the Discovery Institute and the Center for the Renewal of Science and Culture (CRSC), both of which support intelligent-design creationism.

Creationists continue to exert influence today. Despite state laws that have been declared unconstitutional, creationists continue to pressure local school boards and state education departments to support their approach. These efforts have sometimes been successful. In 1999, the Board of Education in Kansas approved, at the urging of creationists, a statewide science curriculum that included no mention of evolution. They also approved a statewide program for testing scientific knowledge and understanding, but decided that an understanding of evolution should not be part of this testing program. Two years later, after two of the officials who had voted for this curriculum had been voted out of office and a third had left voluntarily, the Board of Education reversed its earlier decision and restored evolution to the science curriculum in Kansas. This kind of opposition to the teaching of evolution is largely an American phenomenon. Biologists in most countries other than the United States have not faced similar opposition.

Intelligent design

In the eighteenth and nineteenth centuries, many creationists were also scientists who proposed and tested hypotheses. For example, Reverend William Paley and his supporters proposed that biological adaptations were the work of a benevolent God. In 1996, American biochemist Michael Behe resurrected Paley's preevolutionary arguments and revised them in the new language of cell biology and biochemistry.

Paley's Natural Theology. Paley sought to prove the existence of God by examining the natural world for evidence of perfection in design. The anatomical structures examined by Paley and his supporters were so well suited to the functions that they served and were, in his view, so perfectly designed that they could only have come from God. Paley's school of Natural Theology was very influential in Britain in the early nineteenth century, and the young Charles Darwin was educated in its lessons.

Paley and his supporters had paid much attention to complex organs such as the human eye. The eye, they pointed out, was composed of many parts, each exquisitely fashioned to match the characteristics of the other parts. What use would the lens be without the retina, or the retina without a transparent cornea? An eye, they argued, would be of no use until all its parts were present; thus it could never have evolved in a series of small steps, but must have been created, all at once, by God.

Paley pointed to the structure of the heart in human fetuses as containing features that adaptation to the local environment could not account for. In adult mammals, including humans, the blood on the left side of the heart is kept separate from the blood on the right side of the heart (see Chapter 10, pp. 353–354). In fetal mammals, the blood runs across the heart from the right side to the left, bypassing the lungs, which are collapsed and nonfunctional before birth. As the blood enters the left side of the heart, it passes beneath a flap that is sticky on one side. When the baby is born, its lungs fill, and blood flows through them. The blood returning to the heart from the lungs now builds up sufficient pressure on the left side that the flap closes. Because it is sticky on one side, it seals shut. No amount of adaptation to the environment, said Paley, could endow a fetus with a valve that was sticky on one side so that it would seal shut at birth. Only a power with foresight could have realized that the fetus would need a heart whose pattern of blood flow would change at birth, and thus designed the sticky valve. Paley attributed the

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foresight to God, and he insisted that no other hypothesis could explain such an adaptation to future conditions.

What is most interesting is that Paley and his many supporters understood the nature of science and used the methods of science to argue their case. Paley in particular sought scientific proof of God's existence and benevolence by arguing that no other hypothesis could explain the evidence as well. This example shows that good science is certainly compatible with a belief in God or a rejection of evolution. In fact, the best scientists of the period from 1700 to 1859 were, with few exceptions, devout men who rejected the pre-Darwinian ideas of evolution on scientific grounds.

Darwin's response. Darwin was quite familiar with Paley's arguments, and he offered evolutionary explanations for many of the intricate and marvelous adaptations that Paley's supporters had described. In each case, Darwin argued that the hypothesis of natural selection could account for the adaptation as well as the hypothesis of God's design.

To counter Paley's argument about complex organs such as the eye, Darwin pointed out that the eyes of various invertebrates can be arranged into a series of gradations, ranging in complexity from "an optic nerve merely coated with pigment" to the elaborate visual structures of squids, approaching those of vertebrates in form and complexity. A large range of variation in the complexity of visual structures is found within a single group of organisms, the Arthropoda, which includes barnacles, shrimps, crabs, spiders, millipedes, and insects. All the visual structures, regardless of their degree of complexity, are fully functional adaptations, advantageous to their possessors. It would therefore be quite reasonable, argued Darwin, to imagine each more complex structure to have evolved from one of the simpler structures found in related animals. Eyes, in other words, could have evolved through a series of small gradations.

As an additional argument against Paley, Darwin also pointed out several adaptations that were *less* than perfect, or that seemed to be 'making do' with the materials at hand. The gills in barnacles are modified from a brooding pouch that once held the eggs. The milk glands of mammals are modified sweat glands. The giant panda, evolved from an ancestor that had lost the mobility of its thumb, developed a new thumb-like structure made from a little-used wrist bone. (This last example was not known in Darwin's time, but fits well into his argument.) These many adaptations seem more easily explained by natural selection than by God's design because the design is imperfect and God could presumably have 'done better.' Natural selection is limited to the use of the materials at hand, and then only if there is variation; an omnipotent God could have made barnacle gills from entirely new material without taking away the brood pouches, and could have given pandas a true thumb instead of modifying a wrist bone. Darwin and his supporters used examples like these to show that the evolutionary explanation fitted the available evidence better than Paley's explanation of divine planning. For example, natural selection perpetuates only those hearts whose flaps seal properly at birth.

'Irreducible complexity.' With today's knowledge of cell biology and biochemistry has come a return to Paley's argument from design at the molecular level. The major proponent of this argument is biochemist Michael Behe. He begins with the claim that every living cell contains many sophisticated molecular systems that he calls "irreducibly complex." An irreducibly complex system, according to Behe, is any system that is nonfunctional unless all of its parts are present and functional. Behe's argument, which echoes Paley's, is that no irreducibly complex system could evolve by small, piecemeal steps. According to this creationist argument, natural selection can only improve upon a functioning system, so could never create a system that requires many parts in order to function at all. Thus, if a complex system cannot function without a minumum of five components, then natural selection could never bring about the evolution of a second component when only one existed, or a third component when only two existed, because none of these changes would improve anything if the system remained nonfunctional with fewer than all five of the required components. Paley had earlier made the same argument with regard to the several parts of the eye, as did the British zoologist St. George Mivart in Darwin's time. Darwin himself realized the power of this argument, for he wrote:

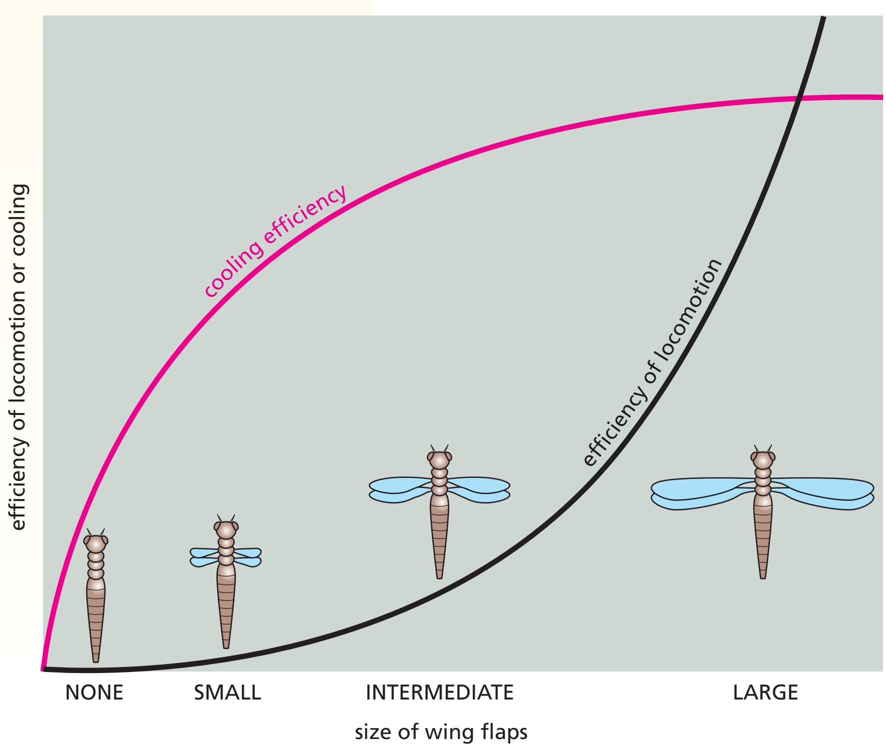
> If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous successive, slight modifications, my theory would absolutely break down. (Darwin. *Origin of Species*, 1859, p. 189.)

There are at least two responses to counter the argument of irreducible complexity. One is to show that the system is not, in fact, irreducibly complex, and that a partial system with only one or a few of its components does function in some capacity and represents an improvement over the same system with fewer components or none at all. If one component is an improvement over none, and two are an improvement over one, then the entire system can evolve piecemeal, step by step, because each step is an improvement over the previous ones, and natural selection favors each small, successive change.

The other response to irreducible complexity is to recognize the role played by changes in function. A system may be incapable of its present function unless fully formed, and thus be described as irreducibly complex. However, the system, or some of its parts, may originally have served a different function, and thus could have evolved by a series of small steps as long as each step improved some ability to serve some function. This can be illustrated by the evolution of insect wings, which developed from external folds of the thoracic wall. By building models of insects with no folds, tiny folds, medium-size folds, and folds large enough to function as wings, scientists were able to show that an increase in the size of the fold from none to small or from small to medium would hardly have improved flying ability. Natural selection would probably not have been able to bring about the early increases in the size of the folds, based upon their usefulness in flying. On the other hand, the function of the folds in cooling the body was also considered. Muscular activity generates heat, and an animal would be in danger of cooking its own tissues if it exercised vigorously without somehow dissipating heat. The efficiency of the flaps in cooling the body also varies with size, as shown in Figure 5.11. Most of the improvement comes in the smaller sizes, with medium flaps dissipating more heat than small ones, which in turn dissipate more heat than none

Figure 5.11

The evolution of insect wings. The efficiency of thoracic folds in primitive insectlike arthropods was measured according to two criteria: efficiency in cooling the body down by dissipating heat, and efficiency in airborne locomotion by adding to downward air resistance and to lift. Up to a certain size, increments in the size of the folds improved cooling ability but had little effect on locomotion. Thus, early increases in fitness among small to moderate wing sizes depended on improved cooling; however, later increases in fitness depended more on improvements in flying ability.



at all. Large flaps, on the other hand, are scarcely any more efficient than medium-size flaps in their cooling ability. Thus, the early stages in the evolution of the wing flaps are thought to have been selectively favored because they improved the body's ability to exercise more without overheating. Only after the flaps had reached a certain medium size, their function as wings became more important than their function in dissipating heat. Thus, the early stages were selectively improved because they helped dissipate heat, while the later stages were selectively improved because they functioned as wings.

As this example shows, the early stages in the evolution of a structure may have been useful for a totally different function than the one they now serve. Half-built structures, or systems with only a few components, may have improved the ability of their possessors to pass on their genes even without fulfilling their present function. Many structures are now known to have changed their function in the course of evolution.

With these evolutionary counter-arguments in mind, we can now examine Michael Behe's claims of irreducible complexity for several systems that function within cells. All of them could have evolved gradually, step by step, despite Behe's insistence to the contrary. For example, the clotting of blood is a multi-step process that Behe argues is "irreducibly complex" because none of it would work unless all of it were present. In fact, blood can clot upon exposure to air, and the many chemicals that improve clotting ability could certainly have evolved one at a time, each representing a piecemeal improvement. Natural selection would favor the evolution of any protein or other compound that aided in the clotting process and reduced the chances of bleeding to death. Because blood chemistry does not fossilize, we have no proof of how blood clotting evolved, but a gradual evolution is certainly plausible.

Another of Behe's examples discusses complement proteins and antibody production. A somewhat detailed explanation of how this system works, and how various parts of the system can and do function apart from the rest, can be found on our Web site (under Resources: Complement). If parts of the system are useful without the remainder (and, in fact, functional in species known to lack the complete system), then they certainly could have evolved in small steps by natural selection.

Conclusions. It is important to note that Behe has conducted no research and provided no scientific evidence to support his claims of irreducible complexity or to test any other hypothesis. Perhaps we should describe his claims as philosophical rather than scientific. One important measure of a scientific theory is the amount of research that it stimulates. Behe's concept of irreducible complexity has stimulated no research that supports any of his claims, but many arguments have been offered to show that the systems that Behe discusses are not, in fact, irreducibly complex.

All of the systems that Behe claims to be irreducibly complex can be explained as the products of gradual, step-by-step evolution, especially if changes in function are considered. Various biologists have examined Behe's claims and none, to our knowledge, support them. Of the systems that Behe describes, none withstands scrutiny as an argument against evolution.

Despite the many criticisms that have been raised against Behe's arguments, the state of Ohio in 2002 seriously considered a proposal to add intelligent design to the science curriculum as an alternative to evolution by natural selection, even though there is no evidence (produced by hypothesis testing) to support the idea. Irreducible complexity is not a scientific theory, and does not qualify as science in the minds of most scientists.

Reconciling science and religion

A majority of scientists are religious, and a majority of devout people of all religions also accept scientific findings. There are many ways of reconciling religious and scientific viewpoints, and a majority of theological seminaries of all faiths teach that science and religion are fully compatible. The following are examples of the ways in which some people have reconciled religious beliefs and science.

René Descartes was the originator of a dualistic philosophy that separates science and religion as operating in different spheres. In this view, science informs us about the physical world, including the human body, while religion informs us about the spiritual world, including both God and the human soul. Questions about the body can be answered by science, while questions about the soul or about God can be answered only theologically. A separation between science and religion, based on this dualism, has become the official view of the Roman Catholic Church.

The Protestant theologian Reinhold Niebuhr defines religion as the study of the "ultimately unknowable." In this view, advances in science have expanded the frontiers of knowledge—the study of what is knowable, but religion is the study of what remains—the ultimately unknowable. Thus, religion and science operate in separate spheres, and there is no possibility of an incompatibility between them.

Various scientists have expressed the view that God should be excluded from scientific theories whenever it is possible to do so. One such scientist was the early nineteenth century French astronomer and mathematician Pierre Simon LaPlace, one of the authors of the idea that galaxies and solar systems form from swirling masses as the result of natural gravitational forces. When he published his book on this 'nebular hypothesis,' he presented a copy to the emperor Napoleon, who asked him why he had not mentioned God in his book. LaPlace replied, "I have no need of that hypothesis." A similar attitude caused the British geologist Charles Lyell to exclude all miracles from his geological theories.

According to some twentieth-century versions of a theory called 'operationalism,' God's presence in certain scientific explanations may not be needed. Thus, the statement, "The Grand Canyon was formed by the action of running water over long periods of time" is indistinguishable from the statement, "God formed the Grand Canyon by the action of running water over long periods of time." Any evidence that could support either of these statements would also support the other, and any evidence against either statement would also be evidence against the other. The two statements are operationally equivalent (or indistinguishable) because no evidence could possibly distinguish between them. According to this view, God is not a necessary part of the explanation, in line with the view that LaPlace had expressed earlier.

A number of scientists and religious thinkers have reconciled science with their religious beliefs by accepting the findings of science as an explanation of the ways that God operates. God created the world along with the natural laws that govern it, and science attempts to discover these natural laws. Isaac Newton, William Paley, and Albert Einstein all expressed views along these lines. One version of this approach is that God set natural laws in place but then withdrew to allow the universe to unfold according to the workings of these natural laws. Another version is that God occasionally intervened to set things right by making exceptions to natural laws. Einstein, who favored the non-interventionist interpretation, ridiculed this second approach in his statement, "I can't believe that God plays dice with the world."

Theistic evolution represents an attempt along these lines to reconcile evolution with a creationist viewpoint, either with or without divine intervention. The Jesuit philosopher and paleontologist Pierre Teilhard de Chardin believed that evolution, including human evolution, was part of God's method of creation in accordance with natural law. Charles Lyell, a geologist who had inspired Darwin's early thinking, and Alfred Russell Wallace, a naturalist who discovered natural selection independently of Darwin, both came late in life to the belief that evolution was the consequence of natural laws, but that divine intervention had been necessary to bring about the evolution of human beings. Most scientists, however, see no need for any such exceptions to explain human evolution.

THOUGHT QUESTIONS

1. In what ways did William Paley use scientific evidence? Did he use testable hypotheses? Which of today's creationists use falsifiable hypotheses to support their claims?
2. How much time should be devoted in science classes to alternative explanations or theories that have been tested and rejected? Should time be given to explanations that are not testable? Should all explanations be given equal time? How much (if any) of a science curriculum would you devote to divine creation as an alternative to evolution? To astrology as an alternative to astronomy? To the theory that disease is caused by demons or evil spirits?
3. Does the teaching of unpopular or rejected theories encourage students to think critically? Does it encourage attitudes of fairness? Does it increase students' understanding of what science is and how science works?
4. Do you think that the concept of intelligent design should be taught in high schools as an alternative to evolution by natural selection? Why or why not?

Species Are Central to the Modern Evolutionary Paradigm

The evolutionary paradigm known as the modern synthesis was based largely on the fusion of genetics with Darwinian thought. The cornerstone of the modern synthesis paradigm is a theory of speciation, the process by which one species branches into two species.

Populations and species

A biological **population** consists of those individuals within a species that can mate with one another in nature. If we look backward in time, we realize that any two individuals in a population share at least some of their alleles because of common descent. If we look into the future, we see that any two opposite-sex individuals in a population are potential mates. Membership in a population is determined by descent and by the capacity to interbreed.

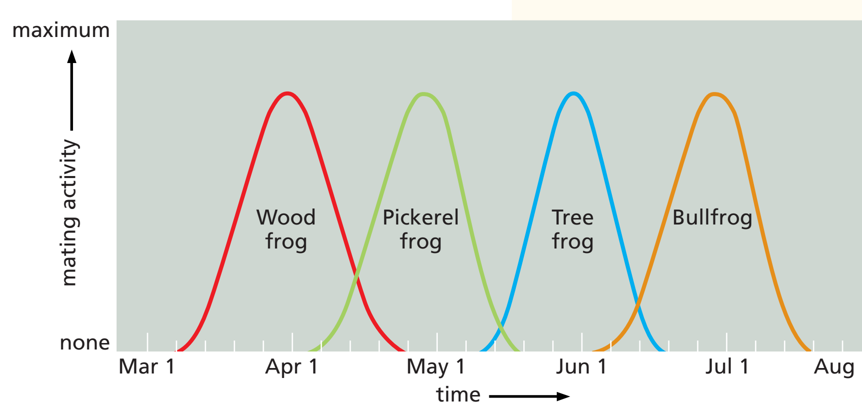
Biological populations within a species may exchange hereditary information (alleles) with one another. The combining of genetic information from different individuals or the exchange of genetic information between populations is called **interbreeding**. The existence of biological barriers to such exchange is called **reproductive isolation**. Interbreeding between populations of the same species takes place when members of different populations mate and produce offspring; reproductive isolation inhibits such matings to varying degrees.

Species are defined as *reproductively isolated groups of interbreeding natural populations*. There are several points to note in this definition. Physical characteristics (morphology) are not part of the definition of species; species are defined by breeding patterns instead. Populations belonging to the same species will interbreed whenever conditions allow them to. Populations belonging to different species are reproductively isolated from one another and will thus not interbreed. Any biological mechanism that hinders the interbreeding of these populations is called a **reproductive isolating mechanism**, as explained below. Species are composed of natural populations, not of isolated individuals. Thus, the mating behavior of individuals in captivity can only serve as *indirect evidence* of whether *natural populations* would interbreed under natural conditions.

The many reproductive isolating mechanisms fall into two broad categories: those that prevent mating and those that interfere with development after mating has occurred. Mating is prevented when potential mates never encounter each other, possibly because they live in different habitats, or because they are active at different times of day or in different seasons, or because they are not physiologically capable of reproduction at the same time. Figure 5.12 shows that wood frogs

Figure 5.12

Reproductive isolation of several frog species by season of mating, an ecological means of preventing mating between species.



are fully isolated ecologically from tree frogs and bullfrogs by breeding at different seasons; they are partly isolated from pickerel frogs because the breeding seasons overlap only slightly. Mating can also be prevented by differences in behavior, allowing potential mates with different courtship rituals to live together in the same place without mating. For example, different species of fireflies (phylum Arthropoda, class Insecta, order Coleoptera, family Lampyridae) use different flashing patterns and flight patterns (Figure 5.13) as mating signals. In addition, insects and some other animals have hardened and inflexible sexual parts (genitalia); mating of these animals requires a 'lock and key' fit, and mating is prevented if the parts do not fit together properly.

There are other isolating mechanisms in which mating occurs but the offspring do not develop. In animals, sperm from a male of another species may die before fertilization takes place. In plants, the pollen may fail to germinate on the flowers of another species. If a mating takes place between species, the fertilized egg may die after fertilization. Incompatible chromosomes may disrupt cell divisions and developmental rearrangements, leaving the embryo or larva to die. Alternatively, hybrid individuals may live for a while but not reach reproductive age, or they may be sterile. For example, a mule is a sterile hybrid between a horse and a donkey. The sterility of mules keeps the gene pools of horses and donkeys separate, so they remain separate species.

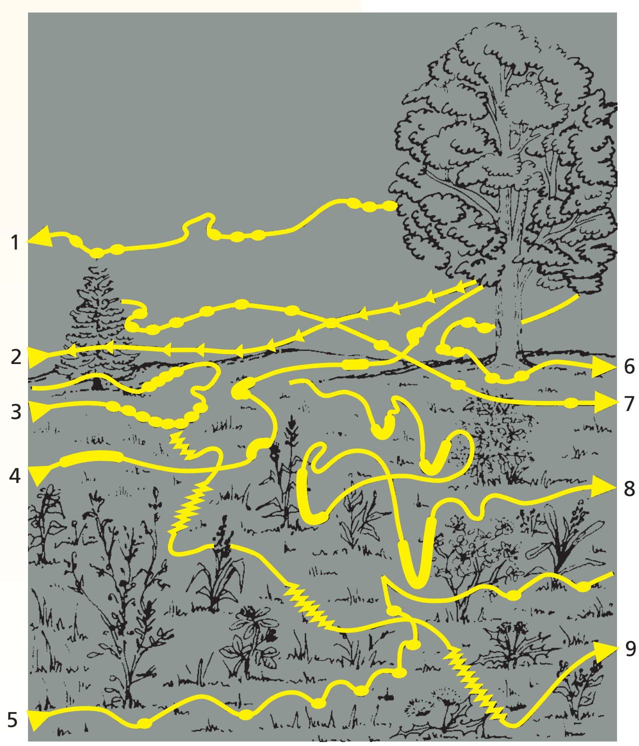


Figure 5.13

Flashing patterns used as mating signals by different species of fireflies. The species 1 to 9 are reproductively isolated from one another by the behavioral differences shown in these patterns. Details in this form of behavioral isolation include the duration of each flash, the number of repetitions, and the location of the insect when it flashes. A firefly will respond only to the flashing pattern of its own species.

How new species originate

To explain how a new biological species has come into existence, we need to explain how it has become reproductively isolated from closely related species. The origin of a species is thus the origin of one or more reproductive isolating mechanisms.

In the vast majority of cases, new species have come into existence through a process of **speciation** that includes a period of **geographic isolation** in which populations are separated by some sort of barrier such as a mountain range or simply an uninhabited area that the organisms do not cross. The essence of the theory is that reproductive isolating mechanisms originate during times when such barriers separate populations geographically. Geographic isolation is not by itself considered to be a reproductive isolating mechanism; rather, it sets up the conditions under which the separated populations may evolve along different lines, resulting in reproductive isolation.

What happens depends in part on the length of time for which the populations are geographically isolated—more time allows more chances for reproductive isolating mechanisms to evolve. Another factor is that natural selection must favor different traits on the two sides of the geographic barrier. That is, conditions must be different enough for one set of traits to increase fitness in one locale and for a different set of traits to increase fitness in another locale. If the populations on opposite sides of the barrier are selected differently for a long enough period, then one or more reproductive isolating mechanisms may evolve between the two groups of populations and separate them into different species (Figure 5.14). If the populations later come into geographical contact again, the reproductive isolating mechanisms that have evolved during their separation will keep them genetically separate as two species. For example, frog or cricket populations isolated on opposite sides of a mountain chain or a large body of water may develop different mating calls. Because the animals respond only to the mating calls of their own population, the two populations will be reproductively isolated and thus become separate species.

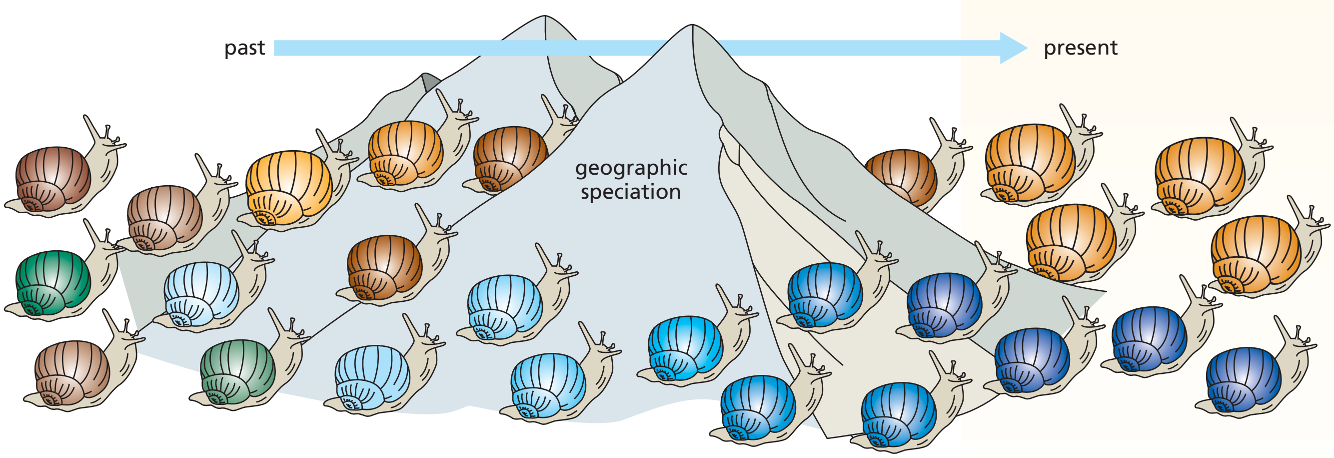
CONNECTIONS CHAPTER 6

The geographic theory of speciation predicts that examples of incomplete speciation may be discovered. If two populations are separated for a very long time (or if selective forces on opposite sides of a barrier differ greatly), then the populations are likely to split into two species. If the separation is brief, then speciation is unlikely. These two situations lie at opposite ends of a continuum. Somewhere along this continuum lies the situation in which populations have been separated by a geographic barrier long enough for reproductive isolation to begin evolving, but not yet long enough for the reproductive isolation to be perfected. Partial or imperfect reproductive isolation between two populations would lessen the chances of interbreeding between them, but not prohibit it entirely. Such situations have indeed been found, for example, among the South American fruitflies known as *Drosophila paulistorum*. Crosses between divergent populations of *Drosophila paulistorum* produce fertile hybrid females but sterile hybrid males. The geneticists studying these flies referred to them as “a cluster of species *in statu nascendi*” (in the process of being born).

People intuitively group similar species together and give names to many collective groups: birds, snakes, insects, pines, orchids, and so forth. Biologists organize these collective groups into a classification that reflects the degree of evolutionary relatedness among species, using methods described in Chapter 6.

Figure 5.14

Geographic speciation: the evolution of reproductive isolation during geographic isolation. Genetically variable populations that spread geographically can develop locally different populations that are capable of interbreeding with one another initially. If the populations are separated for a long enough time by a barrier such as a mountain range or a deep canyon, they may develop differences that prevent interbreeding even after contact is resumed.



THOUGHT QUESTIONS

1 What kinds of reproductive isolating mechanisms might prevent related species of antelopes from interbreeding? Answer the same question for related species of birds, related species of trees, and related species of butterflies.

2 Several kinds of organisms reproduce asexually, producing offspring without combining gametes from two parents. Can asexually reproducing organisms belong to species? Can the definition of species be modified to apply to asexually as well as sexually reproducing organisms?

Life on Earth Originated by Natural Processes and Continues to Evolve

In addition to explaining how species change and how new species arise, modern evolutionary theory also accounts for the origins of life on Earth. The origin of life, the early history of life on Earth, and the effects of life on Earth's atmosphere will all be discussed in Chapter 19.

Evolution as an ongoing process

Evolution is a process that takes place within species as well as between species, and the process continues in the present as it has in the past. The evolutionary changes in populations and the changes that create new species can be studied as they occur. Within the twentieth century, the peppered moths of some locations in England changed from predominantly light-colored to almost all dark and back again. In one species of Galapagos ground finches, *Geospiza fortis*, the average bill size changes back and forth. Small-beaked birds that eat soft seeds survive and produce the most offspring in years when rainfall is adequate, but birds with larger beaks are at an advantage in drought years because they can open large, tough old seeds. The average bill size of birds within the population thus increases in drought years and decreases in wet years. In fruitflies, different chromosomal variations (inversions) are favored in different seasons. We see that evolution responds adaptively to fluctuating environmental conditions. Different alleles are selected by different environmental conditions at different times because their phenotypes are more adaptive in those conditions.

CONNECTIONS CHAPTERS 7, 17, 19

Selection also continues to operate in human populations and in bacteria. For example, infant mortality is much higher among babies born under about 3 kg (7 lb) in weight, even with all that modern medicine can offer. Natural selection thus favors birth weights close to this optimum value. Selection also favors certain human genotypes in certain environments (Chapter 7) and during epidemics (Chapter 17). The use of antibiotics has favored the evolution of resistance to these drugs among bacteria (Chapter 17).

Concluding Remarks

Considerable evidence now shows that evolution has taken place in the past and that organisms continue to evolve today, though often slowly. The ways in which species resemble one another and are related to one another reflect branching patterns of descent. Evolutionary change is brought about by natural selection, a process that operates whenever some genotypes leave more offspring than others. Species are reproductively isolated from one another, and the splitting of a species therefore requires the evolution of a new reproductive isolating mechanism. All species, including humans, arose by speciation and are products of evolution. Our attempts to classify the resulting diversity of species are explained in Chapter 6.

CONNECTIONS
CHAPTER 6

Chapter Summary

- **Evolution** is the central, unifying concept of biology.
- Darwin's major contributions included his theories of **branching descent** ("descent with modification") and **natural selection**.
- Only inherited traits contribute to evolution and bring about **adaptation**; acquired characteristics do not.
- **Evolution** operates through **natural selection**: there is heritable variation in all **species**, and different genotypes differ in **fitness** by leaving different numbers of surviving offspring.
- Forces of **natural selection** include predators, disease, and **sexual selection**.
- **Mimicry** is easily explained by natural selection but not by any alternative hypothesis.
- Branching descent with modification accounts for **homology** between species. **Fossils** provide important evidence for evolution, as does the comparative study of anatomy, biochemistry, and embryological development.
- The modern synthesis combines Mendelian genetics with Darwinian evolution. It describes the evolution of genes and phenotypes in populations, and it includes a theory for the formation of species through geographic isolation.
- **Speciation** occurs through the build-up of genetic differences between **populations** arising primarily during times of geographic isolation. Over time, this results in **reproductive isolation**, which prevents **interbreeding** between species**.**
- **Evolution** continues today in all species. In many cases, we can detect ongoing change from year to year.

CONNECTIONS TO OTHER CHAPTERS

Chapter 1	Darwinian evolution and modern evolutionary theory are both good examples of successful paradigms.
Chapter 1	Presenting creationist ideas in school classrooms raises several social policy issues.
Chapter 2	Gene mutations provide the raw material for evolution.
Chapter 4	Comparative genomics reveals evolutionary patterns of descent.
Chapter 6	Branching descent and other evolutionary processes have produced a great diversity of species that have been described and classified, and many others that await discovery and description.
Chapter 7	Differences have evolved and continue to evolve both within and among human populations.
Chapter 8	Social behavior and reproductive strategies are, in part, products of evolution.
Chapter 9	Successful species may increase so rapidly in numbers that they outstrip the available resources.
Chapter 11	Plant characteristics resulting from evolution include the presence of chloroplasts and vascular tissues.
Chapter 13	Differences in brain anatomy in different species provide good evidence of evolution.
Chapter 16	Viruses and other microorganisms may evolve disease-causing strains, as well as strains resistant to certain medicines.
Chapter 17	Bacteria often evolve antibiotic resistance through natural selection.
Chapter 18	Speciation increases biodiversity, whereas extinction diminishes biodiversity.
Chapter 19	The evolution of life has changed the entire Earth, including the atmosphere and all habitats.

PRACTICE QUESTIONS

1. Match the ideas in the first list with the people in the second. One name needs to be used twice.

a. Evolution is a branching process.

b. Adaptations should be studied carefully as a way of understanding God's creation.

c. Evolution should never be taught.

d. New species originate by a process that includes geographic isolation.

e. Adaptation occurs by use and disuse.

f. Organisms with successful adaptations will be perpetuated, whereas those with unfavorable characters will die out.

g. Evolution and creation science should be given equal time in science classes.

i. Creationist supporters of the 'balanced treatment act'

ii. Creationists of the period 1890–1940

iii. Charles Darwin

iv. Jean Baptiste Lamarck

v. William Paley

vi. Modern evolutionary biologists

2. The Bahamas are a group of islands in the Atlantic, made mostly of coral fragments. The closest mainland is North America, but political ties are to Great Britain. According to Darwin's reasoning, the birds and other species living on these islands should have their closest relatives in:

   a. other islands of similar composition in the Pacific

   b. islands such as the Canary Islands, in the Atlantic at a similar latitude

   c. North America

   d. England

3. Which theory had no way of explaining the sticky flap in the fetal heart?

   a. Darwin's

   b. Paley's

   c. Lamarck's

4. In mimicry, the mimics and their models always:

   a. live in similar climates, although they may be far away

   b. live close together

   c. taste the same to predators

   d. are camouflaged to resemble their backgrounds

5. Which of these is NOT considered a reproductive isolating mechanism?

   a. two geographically separated species

   b. two species breeding in different seasons

   c. two species that produce infertile hybrids when they mate

   d. two species with different mating calls

   e. two species whose external genitalia cannot fit together

6. Give a clear definition of the term *species*.

7. What is the basic argument used by supporters of intelligent design? What kinds of evidence can be used against this argument?