CHAPTER 15

Evolution

OVERVIEW

An introduction to the early development of evolutionary concepts is followed by a discussion of Charles Darwin and his contributions to the theory of evolution through natural selection. Evidence for evolution is given, and mechanisms of organic evolution, including mutations, migration, and genetic drift, are discussed. The roles of reproductive isolation and hybridization in the evolution of species are explored. The chapter concludes with a discussion of some aspects of past and present controversy surrounding evolution.

Some Learning Goals

1. Be able to summarize the early development of evolutionary concepts.
2. Know the contributions of Charles Darwin to the theory of organic evolution and the principles of natural selection as he understood them.
3. Know the various lines of evidence for evolution.
4. Explain the significance of natural selection, mutation, migration, and genetic drift to evolution.
5. Outline how reproductive isolation and hybridization contribute to the evolution of species.
6. Give reasons, past and present, for the controversy over evolutionary theory.

ew historical events since 1859 have had a greater impact on society in general and the biological sciences in particular than the publication of Charles Darwin's book *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life.* Darwin's theory of evolution through natural selection (the tendency of organisms with favorable adaptations to their environment to survive and produce new generations) has stimulated an enormous amount of thinking and research. It has also provided an explanation based on natural laws for the diversity of life around us.

There have been disagreements over the nature, mechanisms, and even the existence of evolution. These stemmed, in part, from a failure of people in diverse fields to define terms and to distinguish between fact and theory in matters of evolution. Evolution itself, for example, has been broadly defined by some as simply being synonymous with change. We are told that anything from cars to computers to cultures is evolving and that even our thought processes evolve. We need, therefore, to distinguish between change in inanimate objects or intangibles and *organic evolution,* which is the accumulation of genetic changes in populations of living organisms through many generations.

A BRIEF OVERVIEW OF THE EARLY DEVELOPMENT OF EVOLUTIONARY CONCEPTS

More than 2,300 years ago, Aristotle (384–322 B.C.), although not recognizing any processes of natural selection, did observe grand design in nature and arranged all organisms known to him from the simplest to the most complex in what he called the *Scala Naturae* (Scale of Nature). Aristotle's arrangement implied that all organisms were static and didn't evolve. These beliefs were widespread until at least the 17th century and were not extensively challenged before Darwin. *Fossils* (parts of previously existing organisms preserved in rocks or other substances) had been found many centuries before Darwin but were not properly identified until the 15th century when Leonardo da Vinci (1452–1519) correctly observed that they were parts of previously existing organisms that had become extinct.

Count de Buffon (1707–1788), a French naturalist, spent much of his adult life writing a natural history of 44 volumes in which he described all known plants and animals. In this work, Buffon (whose real name was Georges-Louis Leclerc) presented evidence of descent with modification in organisms and speculated on the mechanisms involved. However, he provided no theories on how evolution might take place.

Georges Cuvier (1769–1832), a French zoologist and *paleontologist* (one who studies fossils; fossils and fossilization are discussed in Chapter 21), used comparative anatomy toward the close of the 18th century to classify animals. Cuvier, however, firmly believed that organisms did not change over time. When geological finds showed apparent evolution of organisms in rock formations of certain regions, Cuvier tried to explain them away with what was called *catastrophism.* He theorized that mass extinctions or catastrophes had occurred whenever a new geological find revealed a different group of fossils, and the presence of the new fossils was due to repopulation of the region by species migrating in from surrounding areas.

By the end of the 18th century (before the principles of genetics were known), many prominent biologists had come to believe that hereditary changes in populations over long periods of time (evolution) occurred as a result of the inheritance of acquired characteristics. One of the more prominent supporters of this widespread idea was Jean Baptiste Lamarck (1744–1829). He believed, for example, that giraffes acquired their long necks over many generations as a result of the gradual increase in neck length as shorter-necked animals stretched to reach leaves on the branches of trees. Slight stretching of the neck was supposed to have been passed on to the offspring as it occurred, and eventually, numerous tiny increases due to individual stretching added up to the present great neck length of giraffes (Fig. 15.1).

If acquired characteristics could be inherited, we should be able to demonstrate it experimentally, and indeed, many researchers have attempted to do so, but all have failed. For example, one biologist surgically removed the tails of mice for many successive generations, but the average length of the tails of the last generation was exactly the same as that of the first generation. The experiment demonstrated that repeatedly removing tails in no way affects the hereditary characteristics carried in the genes within the cells. This is also the reason fruit trees that are pruned annually never produce seeds that grow into dwarfed trees, even after many generations.

CHARLES DARWIN

Although there are variations in some aspects of current organic evolutionary theory, that which pervades and unifies most biological thought today received its greatest impetus from the observations of Charles Darwin (1809–1882) (Fig. 15.2) and his contemporary, Alfred Wallace, who independently arrived at the same conclusions as Darwin.

Charles Darwin was born in Shrewsbury, England, in 1809. As a boy, he showed a keen interest in natural history, but in deference to his physician father's wishes, he enrolled in the University of Edinburgh medical school to study medicine; he later studied theology at Cambridge University, without, however, excelling in either subject. In 1831, when he was 22 years old, he graduated with a degree in theology but was not really sure what he wanted to do with his life.

Shortly after Darwin's graduation, King William IV of England commissioned a sailing vessel, the HMS *Beagle,* to undertake a voyage around the world to chart coastlines, particularly those of South America. Young Darwin, after a recommendation from a Cambridge biology professor, accepted an unpaid position as assistant naturalist and captain's companion on the voyage, which began December 27, 1831.

During the voyage, which lasted 5 years, Darwin read a geology book that made a profound impression on him. The book, authored by Charles Lyell, was based on a theory of John Hutton, who believed the earth was much older than the few thousand years it previously had been thought to be. Hutton suggested that the earth had been subjected to cycles of upheaval and erosion over great periods of time. The erosion resulted in rock fragments and weathered debris being washed down rivers into the oceans where the deposits gradually accumulated in thick layers. The thick layers, which slowly were converted into sedimentary rocks (many of which contained fossils), became land as they were elevated above sea level. Hutton believed that, given enough time, all geological changes could be attributed to slow, natural processes, and Lyell suggested the slow changes occurred at a uniform rate. Although some modern geologists incorporate many of Hutton's ideas about gradual change over long periods of time, they point to evidence that geological changes have not in the past always proceeded at a uniform rate. Darwin himself was not convinced geological changes occurred at a uniform rate, but he did agree with Lyell that the earth must be very old indeed and that large changes were due to gradual accumulation of small changes.

Today, we can estimate the age of the earth by determining in rocks the ratio of a radioactive element to the nonradioactive element it becomes. We know that a radioactive element gradually loses its radioactivity, although sometimes at a variable rate. The amount of time it takes for a radioactive element to lose half of its radioactivity is referred to as its **half-life.** The half-life for each radioactive element is unique. For example, uranium, which becomes lead as it loses its radioactivity, has a half-life of 4.5 billion years, while radioactive carbon has a half-life of 5,730 years, and radioactive nitrogen has a half-life of only 10 minutes. By checking ratios of uranium to the lead it becomes when it loses its radioactivity, we now know that the earth is probably at least 5 billion years old.

Darwin had many opportunities to collect plants and animals on both sides of South America, as well as in the Galápagos Islands and along the coasts of Australia and New Zealand. He kept a daily journal and spent countless hours alone on horseback collecting and observing the living world around him. This gave him ample opportunity to think about the forms and distribution of the myriad new organisms he encountered. His thoughts slowly led to the development of ideas that later blossomed into his theory of evolution through natural selection.

Upon his return to England in 1836, Darwin retired to the country and began working on his collections and journal. He also carried on extensive correspondence with other biologists and made many detailed investigations into pollinating mechanisms, earthworm ecology, geographical distributions of plants and animals, and several other areas of natural history.

Throughout all of his activities, Darwin was guided by a concept he had adapted from an essay on human populations and food supplies written by Thomas Malthus in 1798. Malthus observed that populations grow geometrically until food supplies (which, if they increase at all, do not increase geometrically), disease, wars, and other factors limit their growth. Darwin realized that although humans might artificially improve or increase their food supply through selective breeding and cultivation, wild plants and animals could not do so and were therefore vulnerable to a process of selection in nature, which would explain changes in natural populations. He was reluctant to publish his ideas, however, and did not begin putting together his book on the origin of species[1] until 1856.

Meanwhile, an English naturalist by the name of Alfred R. Wallace (1823–1913), who made major contributions to our knowledge of animal geography, independently concluded that natural selection contributed to the origin of new species and sent Darwin a brief essay on the topic in 1858. At the urging of Charles Lyell, Darwin and Wallace jointly presented a paper of their views to the Linnaean Society of London in 1858, and in 1859, Darwin's classic book *On the Origin of Species by Means of Natural Selection* was published.

EVIDENCE FOR EVOLUTION

Evidence in support of organic evolution is drawn from many areas, including similarities in the form and ecology of living organisms and the way they are related to each other today. Homologies (characteristics shared by different organisms) point to common ancestry. For example, members of the mustard family (Brassicaceae—2,500 species), which includes broccoli, cabbage, radish, and stocks, produce a pungent, watery juice that has the smell of sulfur when it breaks down. However, similarities are not always due to common ancestry. For example, a number of African spurges (species of *Euphorbia*) and American cacti have similar, succulent stems even though they are not closely related (Fig. 15.3). The plants do share similar arid habitats to which they have independently become adapted (an *adaptation* is a characteristic that makes an organism better suited to its environment). In other words, plants of very different ancestry have adapted in similar ways to common environmental conditions in different parts of the world. This type of evolution is called *convergent evolution.*

Other evidence comes from the structure and relationships of proteins, DNA, and other molecules, and the common use of ATP by living organisms. Cytochrome *c* oxidase, for example, is an enzyme that occurs universally in all living organisms, which suggests it appeared very early, probably in a single organism, and that it has been successively inherited by the myriad of organisms in existence today.

Fossils, which are remnants of previously living forms (Fig. 15.4), provide compelling evidence for descent with modification. The simplest fossils are generally found in the oldest geological strata, while more complex forms tend to be found in younger strata.

Still further evidence is drawn from the geographical distribution of organisms. Many groups are confined to a single continent or island. In some instances where similar organisms occur on more than one land mass, there is evidence that the land masses concerned were once linked, which would have permitted terrestrial migration. Other conclusions are drawn from the physiology and chemistry of the organisms.

MICROEVOLUTION—EVOLUTION WITHIN SPECIES

Natural Selection

Darwin observed that animal breeders, through a process of artificial selection, changed populations of domestic animals by retaining those with desirable traits and by destroying those with unwanted traits. Darwin also noted that in nature, some individual organisms do not go on to reproduce because all natural populations have a limited supply of food and other resources. In addition, the traits of organisms vary within populations. He reasoned that those best adapted to available resources would increase in number in succeeding generations, and those less well suited would decrease. Darwin also used comparative anatomy and embryology in developing his theory of descent with modification, which he called **natural selection,** and based it on four principles:

1. *Overproduction.* Many living organisms produce enormous numbers of offspring. For example, a single maple tree produces thousands of seeds each year, most being capable of becoming a new tree. A single mushroom can produce mil-

lions of spores, each with the potential to become a new mushroom-bearing fungus.

2. *Struggle for Existence.* All the germinating seeds, spores, and other reproductive structures of living organisms compete for available moisture, light, nutrients, and space. In nature, the amounts of these elements available are insufficient to support all of these organisms, and many die as a result.
3. *Inheritance and Accumulation of Favorable Variations.* All living organisms vary. Hereditary variations that have survival value or do not result in the death of the individual are inherited from generation to generation and accumulate with time, while other variations harmful to the survival and reproduction of the individual are gradually eliminated.
4. *Survival and Reproduction of the Fittest (Differential Survival and Reproduction).* Those forms of organisms best adapted to the environment ("fittest") have the best chance to survive and reproduce, while others less well adapted may die. A tree with thicker bark, for example, may have a higher probability of surviving cold temperatures to reproductive age and producing more offspring. The offspring of the thicker-barked tree may then bear its inherited features.

One of the criticisms of Darwin's theory, after it was published in 1859, was that it did not explain how hereditary variations originated and developed. It should be remembered, however, that Mendel's findings were not published until 1866, and the details of mitosis and meiosis did not become known until 1900 to 1906. Today, with our far greater knowledge of how variations occur and are inherited, we have come to understand the mechanisms of evolution in populations much better than was possible in Darwin's time.

Mutations

All wild organisms, from aardvarks to zinnias, occur in populations that are composed of a few to billions of individuals. Yet, even within very large populations, it is not possible to find two individuals that are identical down to the last molecule. As humans, we are well aware of this within our own species, but variation exists in all living organisms, even though in simpler one-celled forms the differences may be much less obvious. Whether the differences are obvious or subtle, the general characteristics of a population will eventually change if the environment or other factors favor certain hereditary variations and disfavor others.

In some instances, the environment may alter the phenotype without affecting the genetic constitution of an organism. Plants that grow relatively tall at sea level may become dwarfed when they are transplanted to cooler areas in the mountains or drier areas near deserts, yet they are capable of breeding freely with plants at the original location if they are returned to that area.

If we apply fertilizers to plants, stimulate their growth with hormones, or prune them, the changes are not passed on to the offspring because no permanent change occurs in a population unless there is *heritable variation.* The changes in transplanted, fertilized, or pruned plants are not transmitted to the offspring because the gametes of those plants will carry the same genetic information they would have carried if the transplanting, fertilizing, or pruning had not occurred. Despite this, however, dwarf fruit trees and short-tailed mice do occasionally occur, but for reasons quite different from those proposed by Lamarck and his contemporaries. They come about as a result of a sudden change in a gene or chromosome. Such a change is called a **mutation,** a term introduced in 1901 by the Dutch botanist Hugo de Vries.

Changes within chromosomes may occur in several ways. A part of a chromosome may break off and be lost (*deletion*), or a piece of a chromosome may become attached to another (*translocation*). In some instances, a part of a chromosome may break off and then become reattached in an inverted position (*inversion*) (Fig. 15.5). A mutation of a gene itself may involve a change in one or more nucleotide pairs (nucleotides are discussed in Chapter 13).

Mutation rates vary considerably from gene to gene, but mutations occur constantly in all living organisms at an average estimated to be roughly one mutant gene for every 200,000 produced. *Mutator genes,* if present, can increase the rate of mutation in other genes, but generally, the mutation rate for a specific gene remains relatively constant unless there are changes in the environment (e.g., an increase in cosmic radiation). Most mutations are harmful, many times to the point of killing the cell. However, about 1% of the mutations are either silent (have no effect on the survival of the phenotype) or produce a characteristic that may help the organism survive changes in its environment.

Migration

Gene flow between populations occurs when individuals or gametes migrate from one population to another. How much gene flow takes place depends on the size of the populations and the extent to which they may be isolated from one another. If there is a great deal of interbreeding over wide distances, as there might be in wind-pollinated plants, a single individual's genes can quickly be spread from one population to another. On the other hand, gene flow occurs at a much slower rate when interbreeding is more or less restricted to small, isolated populations. This is often the case with plants that occur only in specialized habitats, such as the vicinity of springs and seeps or on magnesium-rich serpentine soils. In general, a small amount of gene flow over longer distances can be expected to occur, even though most of the interbreeding takes place between closely associated individuals in a population.

Genetic Drift

As observed in Chapter 13, the Hardy-Weinberg law states that genes tend to remain at a constant frequency from generation to generation. However, by chance alone, genetic drift (a change in the genetic makeup of a population due to random events) may take place as the frequency of a given gene fluctuates from its statistical average in any generation due to the events that occur during meiosis and the production of gametes. In a large population, genetic drift is unlikely to make any significant difference. In a small population, however, the successes or failures of a single genotype to multiply may cause a marked change in its frequency and, in some cases, cause it to disappear altogether or, on the other hand, increase to a frequency of 100%. In other words, in a small population, the random shift in gene frequencies by chance may bring about evolutionary changes.

RATES OF EVOLUTION

Darwin believed that evolution by natural selection was a slow and gradual process. A number of contemporary biologists, however, favor the *punctuated equilibrium* model, which holds that major changes have taken place in spurts of maybe 100,000 years or less, followed by periods of millions of years during which changes have been minor. They base their hypotheses on fossils, which, when arrayed according to their ages, reveal large gaps in the record. Although missing-link fossils are occasionally discovered, the record does little to support Darwin's concept of gradual, long-term change, even though it is believed that possibly as few as one organism in a million may have become a fossil. Others opposed to hypotheses of evolution through sudden change argue that because probably only a tiny percentage of organisms became fossilized and usually only the harder parts of organisms (e.g., bones, teeth, wood) are preserved, drawing definite conclusions from fossil evidence about evolution through either gradual or sudden change may be -speculative.

The conditions necessary for an organism to become a fossil are very specialized and limited in occurrence (see Chapter 21) and probably also were in the past. This makes it quite improbable that large numbers of missing-link fossils will ever be found. Proponents of evolution through periods of rapid change argue that under conditions of changing climates or other situations exerting strong selection pressures on forms with adaptive mutations, new species of organisms could arise in less than 100 generations, making 100,000 years ample time for considerable evolution to occur. Since it is not possible to prove or disprove the various theories experimentally, the debate on whether evolution has occurred through gradual or sudden change will undoubtedly continue indefinitely until, or unless, new evidence convincingly supports one theory more than another.

MACROEVOLUTION—HOW SPECIES EVOLVE

Reproductive Isolation

If new genes are produced in a freely interbreeding population, they may gradually be spread throughout the population, and the nature of the whole population will change in time. If some barrier divides the population, however, the two new populations eventually may become distinct from each other, sometimes in a relatively short period of time.

The log of a Portuguese sailing vessel of more than 600 years ago indicates that, for unknown reasons, some rabbits native to Portugal were released on one of the Canary Islands during a visit. When 20th-century biologists examined the island descendants of those rabbits, which, in Portugal, forage during the day, they found them to be smaller than their continental ancestors, to be nocturnal in foraging habits, and to have larger eyes. In addition, attempts at breeding them back to their European ancestors failed because, in the short space of 600 years, a new species of rabbit had evolved. Although there is evidence that new plant species have evolved in as little as 50 years, it should be emphasized that the 600 years involved in the evolution of the Canary Island rabbits appears to be much less time than is typical for the evolution of many other plant or animal species.

Geographic Isolation

How do two populations of organisms that initially have the same gene pool come to have gene pools different enough to prevent their interbreeding? Geographic or other isolation of the two populations from each other prevents the flow of genes between the two populations, and random mutations, which are rarely identical, then spread only throughout the population in which they arise. Imagine, for example, that a population of white-flowered daisies occurs throughout a wide valley that is bounded on both sides by high mountains. If a mutation occurs that results in the white part of the flower becoming red, the new color may, in time, if other environmental conditions permit, spread throughout the entire population. If, however, before the mutation occurs, there is a volcanic eruption that blocks off part of the valley, we would then have two populations of white-flowered daisies isolated from one another. If the same mutation for red color should then occur, it would spread only through one population. Meanwhile, if a mutation for hairy leaves occurs in the other population, that characteristic could spread throughout the second population but be prevented by the geographic barrier from spreading to the population of red-flowered daisies. In time, the genetic changes may become so great that even if the isolation is removed, gene flow between the two populations no longer can occur, and two distinct species of daisies would be the result.

In the United States, there are two closely related species of small trees or shrubs called redbuds (*Cercis*) that look very much alike. The eastern redbud (*Cercis canadensis*) occurs on the borders of streams, mostly east of the Mississippi River between the Canadian border and Florida, where some form of precipitation occurs throughout the year. The western redbud (*Cercis occidentalis*) is native to stream areas in California, Utah, Nevada, and Arizona, where most of the precipitation occurs in the winter and spring. The two species can be artificially hybridized, but each is so adapted to its own wild habitat and associated climate that specimens of either species die when transplanted to the other's wild habitat (Fig. 15.6). Presumably, a single species of redbud once occupied riparian sites throughout much of temperate North America. When the eastern populations became geographically isolated from those of the west, however, random mutations arose independently in the east and the west, and with free gene flow between the two populations no longer possible, two species now exist where formerly there was only one.

Several other factors contribute to the development of new species from geographically isolated populations with a common ancestry. When separation first occurs, it is most unlikely that both populations will have genes that are identical in all respects, and a small population will have only a small percentage of the genetic variation present throughout the original population. In addition, geographically isolated populations normally will be subjected to selection pressures from numerous subtle to conspicuous differences in environment. The Canary Island rabbits, for example, initially probably found it difficult to compete with other animals for food during the day. Although we don't know what changes at the molecular level actually took place, it may be that mutations or recombinations for improved night vision occurred, with those acquiring new alleles or combinations being able to survive, while those without them perished.

Ecological Isolation

Isolation leading to the development of new species is not limited to physical barriers such as mountains or oceans. Ecological factors such as climate or soils may play a role, as do time and mechanical isolating factors. As a result, related species can be *sympatric* (occupy overlapping ranges of territory) without genes being exchanged. Serpentine soils, for example, have a magnesium content not tolerated by many species of flowering plants. Plants that are unable to compete with species excluded from such soils, but can, however, tolerate serpentine soils, find a niche in which they can thrive and evolve independently.

A mutant form within a population may flower at a different time, preventing exchange of genes between it and nonmutant forms. In the temperate deciduous woods of eastern North America and in the Columbia River basin in the Pacific Northwest, there are many populations of early spring-flowering herbs called *Dutchman's breeches* (*Dicentra cucullaria*), which are discussed further in Chapter 16. Dutchman's breeches and *squirrel corn* (*Dicentra canadensis*), a close relative, often grow together in the eastern deciduous forest. Both species have highly dissected leaves that are so similar in appearance many early botanists and lay persons assumed Dutchman's breeches and squirrel corn were one and the same species (Fig. 15.7).

It is believed, however, that at some point in geological history, a mutation or mutations occurred that caused some plants to begin flowering after other plants had already set seed. As a result, one group became reproductively isolated from the other group. In due course, other mutations affecting the form and fragrance of the flowers and the shape and pigmentation of food-storage bulblets beneath the surface also occurred, but the plants continued to occupy the same habitats. In short, we now have two closely related but distinct species growing together without interbreeding, simply because it is no longer possible for them to do so.

Mechanical Isolation

Other isolating mechanisms may be mechanical. In orchids, for example, the pollen is usually produced in little sacs called *pollinia* (Fig. 15.8) that stick to the heads or bodies of visiting insects. If pollination is to occur, the pollinia must be inserted within a concave stigma. Each species of orchid is constructed so that it is highly unlikely that a pollinium of one species will be inserted within the stigma of another species. As a result, many species of related orchids can be sympatric without genes being exchanged.

Four closely related sympatric species of Peruvian *Catasetum* orchids, which can be artificially hybridized very easily, have no known natural hybrids, despite their being pollinated by a single species of bee. Microscopic examination of the pollinators has shown that the pollinium of one species is attached to the insect's head, that of another is attached to the insect's back, that of a third to the abdomen, and that of the fourth only to the left front leg. Even after visits to hundreds of flowers, none of the pollinia are misplaced (Fig. 15.9)!

Other Isolating Mechanisms

Even if pollen from one species is placed on or within the stigma of another species, however, fertilization frequently does not follow because the sperm is chemically (by incompatibility) or mechanically prevented from reaching the egg. Other isolating mechanisms include the failure of embryos to develop, and failure of hybrids to survive or breed.

THE ROLE OF HYBRIDIZATION IN EVOLUTION

When *hybridization* (the production of offspring from different populations by parents that differ in one or more characteristics) takes place, the hybrids may be significant or important in evolutionary change, depending on how the characteristics of the parents were combined. If, for example, the environment changes (e.g., average temperatures drop or annual precipitation increases), hybrids may have gene combinations that are better or worse suited to the new environment than those of either parent. Two related species may hybridize occasionally, and when they do, *introgression* (backcrossing between the hybrids and the parents) may occur. If the backcrossing occurs repeatedly, some characteristics of the parents may eventually disappear from the population if the new combinations of genes in the offspring happen to be better suited to the environment than those of the parents and as natural selection favors the offspring. Both parents and hybrids may, however, also evolve in other ways.

Polyploidy occurs occasionally in nature when, during mitosis or meiosis, a new cell wall fails to develop between two daughter cells, even though the chromosomes have divided. This results in the production of cells with more than two complete sets of chromosomes. During our discussion of plant breeding in Chapter 14, we noted that this situation can result in a cell with twice the original number of chromosomes. If mitosis were to occur normally after such a cell was formed and the cell divided repeatedly until a complete organism resulted, that organism would have double the original number of chromosomes in all its cells. Most polyploid plants have arisen as a result of a failure of -meiosis to halve the chromosome number in gametes. Polyploids are produced when these gametes participate in fertilization.

The hybrids resulting from a cross between two diploid species are often sterile because the chromosomes do not pair up properly in meiosis. If polyploidy does occur in such a hybrid, however, the extra set of chromosomes present from each parent provides an opportunity for any one chromosome to pair with its homologue in meiosis, possibly overcoming the problem of sterility. This type of polyploidy apparently occurred frequently in the past (in terms of geological time), and it is believed that more than 40% of flowering plants that exist today originated this way (Fig. 15.10).

Apomixis

Sterile hybrids also may reproduce asexually. One form of asexual propagation, called **apomixis,** includes the production of seeds without fertilization. For example, a cell may divide by mitosis, forming an embryo. Asexual propagation also includes other forms of vegetative reproduction that are discussed in Chapters 4 through 7, Chapter 14, and Appendix 4.

When species reproduce mainly by apomixis but sometimes also hybridize so that new combinations of genes are occasionally produced, they can be highly successful in nature. Dandelions and wild blackberries, for example, are among the most successful plants known. They reproduce apomictically, as well as sexually through fertilization, and also by natural vegetative propagation (Fig. 15.11).

DISCUSSION

Darwin's theory of evolution through natural selection initially caused a great deal of controversy because even though Darwin believed to his death in a Divine Creator, he also believed that the Creator had used natural laws to bring all living things into being gradually over long periods of time. Most of his contemporaries, however, were guided by a literal interpretation of the biblical account of creation and were evidently convinced that all living things had been created in 6 days and had existed unchanged since the beginning.

If we now know and understand most of the mechanisms of organic evolution, why are there still any disagreements about the broad subject itself? Obviously, lack of objective analysis of the evidence is a factor, but it is not the sole reason. Science deals with tangible facts and evidence that can be measured or experimentally tested; beliefs stemming from metaphysics or religion are outside the realm of science to prove or disprove.

When the popular *Scofield Reference Bible* was first published in 1909, it included in the margin opposite the account of creation "4004 B.C.," a date arrived at by the 17th-century Irish archbishop James Ussher, who based his calculation on faulty interpretation of biblical genealogies. Ussher's date has been deleted from the margins of the Scofield Reference Bible editions published since 1967, and the editors have observed that little evidence exists for fixing dates of biblical events prior to

2100 B.C.

A group composed mostly of non-biologists, and calling themselves *scientific creationists*, have sought since the 1970s to include a non-evolutionary interpretation of the living world in public-school biology textbooks. Scientific creationists do not necessarily believe the earth was created in 4004 B.C., and they recognize the existence of minor variations in living organisms. The majority, however, believe the earth is less than 30,000 years old and reject the foundations of evolution as incompatible with a literal interpretation of the biblical account of creation. In doing so, scientific creationists reject the evidence for the age of the earth provided by radioactive elements, and for evolution, including that which has accumulated since Darwin.

Objective scientists freely acknowledge that some problems concerning the interpretation of the geological past and the pathways of organic evolution exist, but they ask their detractors to suggest more plausible alternatives. At this point, some people apply the tenets of religious faith, which like history, is not subject to scientific experimentation. Others, including those who subscribe to the theory of *Intelligent Design*, see no conflict between science and religion. Intelligent Design proponents accept much of the evidence for organic evolution but don't believe it was possible for living cells to have arisen by chance alone. They observe that some of the complex biochemical systems of living cells, with their numerous interrelated parts, would have had to have arisen at the same time, since if only one part arose, it would not have been functional and would not have been advantageous to the organism possessing it. Their Intelligent Design theory proposes that such complex systems were designed, presumably by a supernatural power.

Others are convinced that science and religion are mutually exclusive. An impasse may result when persons of different persuasions become dogmatic. Virtually no objective thinkers will deny the extraordinary impact that the Theory of Evolution has had on our concept of the living world. Nearly all who have studied the evidence are led to the conclusion that evolutionary processes are the sole plausible explanation for the unity of life, at the molecular and cellular levels, as well as for the extraordinary diversity of the organisms now around us. There is little unanimity of thought as to the precise pathways of evolution. One authority is convinced that a certain group evolved from another, while other equally eminent authorities maintain that the exact reverse occurred. Part of the reason for such paradoxes is that the historical record is quite incomplete. Fossils represent a very small fraction of organisms that once existed. With incomplete evidence, scientists can deal only in probabilities, and it is inevitable that different interpretations result.

Summary

1. The theory of organic evolution received its greatest impetus from Charles Darwin's *On the Origin of Species.*
2. Before 1900, many biologists, notably Lamarck, believed that organic evolution occurred as a result of the inheritance of acquired characteristics. This theory was discredited experimentally.
3. Evidence in support of organic evolution is drawn from fossils and from the form, ecology, geographical distributions, and relationships of living organisms, homologies, molecular structures, and analogies such as succulent form in deserts.
4. Darwin's natural selection theory is based on four principles: (1) overproduction; (2) struggle for existence; (3) variation and inheritance; and (4) survival and reproduction of the fittest.
5. The primary mechanisms of organic evolution include natural selection, mutations, migration, and genetic drift.
6. Darwin believed that evolution through natural selection was a gradual process over great periods of time. Some contemporary biologists believe that organic evolution has taken place in spurts between long periods of little change, based on evidence from the fossil record. Interpretation of the fossil record, however, can be controversial and will be debated indefinitely.
7. If new genes are produced in a freely interbreeding population, they will gradually be spread throughout the population, and the nature of the whole population will change in time. If a population is divided by a barrier, genes occurring in the one population will not spread throughout the isolated population as before. In time, because of the isolation, each new population may develop into separate species incapable of breeding with one another.
8. Reproductive isolation and hybridization play major roles in the evolution of species, especially in plants.
9. Mechanisms of organic evolution include mutations in chromosomes or genes, hybridization, introgression, polyploidy, apomixis, and reproductive isolation.
10. Opinions and convictions on origins vary, but few can deny the major impact that theories of evolution have had on modern peoples and on their concepts of life.
11. Biologists generally feel evolution is the only plausible explanation for the unity of life at the molecular and cellular level and the great diversity of life, but there is little agreement among them as to the precise pathways of evolution in the past.

Review Questions

1. How does organic evolution differ from other forms of evolution?
2. How did Darwin's theory of evolution differ from Lamarck's?
3. What basic modifications have been made in evolutionary theory since Darwin's time?
4. What is meant by a mechanism of evolution?
5. What evidence is there to support modern concepts of evolution? Are there any problems with the evidence?

Discussion Questions

1. One of Darwin's principles was that there is a struggle for existence among living organisms. Do plants struggle with one another to survive? If so, how do they do it?
2. Some populations change noticeably in form within a hundred years. If only one gene in every 200,000 mutates and if most mutations are harmful, how is such change possible?
3. Do you think there might be scientifically supportable alternatives to organic evolutionary theory to account for the diversity of life around us? Explain.

Additional Reading

Arnold, M. L. 1997. *Natural hybridization and evolution.* Fair Lawn, NY: Oxford University Press.

Avers, C. J. 1989. *Process and pattern in evolution.* Fair Lawn, NY: Oxford University Press.

Baltscheffsky, H., et al. (Eds.). 1996. *Origin and evolution of biological energy conversion.* Fair Lawn, NY: Oxford University Press.

Darwin, C. 1999. *The origin of species* (facsimile ed.) Westminster, MD: Bantam Books.

Eldredge, N. 2000. *The pattern of evolution.* San Francisco: W. H. Freeman.

Hancock, J. F. 2003. *Plant evolution and the origin of crop species.* Cambridge, MA: CAB International.

Henry, R. J. 2005. *Plant diversity and evolution: Genotypic and phenotypic variation in higher plants.* Cambridge, MA: CAB International.

Margulis, L. 2000. *Microcosmos, vol. 2: Evolution and diversity.* Sudbury, MA: Jones & Bartlett.

Willis, K. J., and J. C. McElwain. 2002. *Evolution of plants.* Fair Lawn, NY: Oxford University Press.

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Kahili ginger (*Hedychium gardnerianum*) and Hawaiian tree ferns (*Cibotium* sp.).

Figure 15.1 Lamarck and his contemporaries believed that the long neck of a giraffe developed over time as the animals stretched to reach higher leaves and that the little length increases were inherited and became cumulative. This theory of inheritance of acquired characteristics was experimentally disproved.

Figure 15.2 Charles Darwin. *(Courtesy National Library of Medicine)*

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1. Our understanding of the term *species* has been modified and refined since Darwin's time, but, as discussed in Chapter 16, most biologists today think of a species in general terms of a *population of individuals of similar form and structure with a common ancestry, capable of interbreeding freely with one another in nature but not generally interbreeding with individuals of other dissimilar populations.* A shorter definition is simply to refer to a species as *a group of organisms with a common gene pool.* Note that species is like the word *sheep* in that it is spelled and pronounced the same in either singular or plural usage. There is no such thing as a plant or animal "specie."

Figure 15.3 Convergent evolution. Plants of different ancestry that adapt to similar habitats may evolve similar life forms. The barrel cactus on the left (*Jasminocereus howellii*) and the barrel spurge on the right (*Euphorbia obesa*) are completely unrelated but have evolved similar forms in adaptation to arid habitats.

Figure 15.4 A fossil fern.

Figure 15.5 Some types of chromosomal changes that can occur. *A.* **Deletion.** Part of a chromosome breaks off and is lost. *B.* **Translocation.** Part of one chromosome becomes attached to another. *C.* **Inversion.** Part of a chromosome breaks off, becomes inverted from its original position, and then is reattached.

A.
B.
Figure 15.6 Two species of redbud, both native to North America. *A.* Eastern redbud (*Cercis canadensis*). *B.* Western redbud (*Cercis occidentalis*).

A.
B.
Figure 15.7 *A.* Dutchman's breeches plant (*Dicentra cucullaria*). *B.* Squirrel corn (*Dicentra canadensis*).

Figure 15.8 A pair of *pollinia* (sacs of pollen) produced by members of the Orchid Family (Orchidaceae). The pollinia become attached to the bodies of visiting insects, which transport them to other orchid flowers. ×10.

Figure 15.9 *Catasetum* orchids.

Figure 15.10 Fireweed (*Epilobium angustifolium*)—a polyploid found primarily in North American mountainous areas below 3,050 meters (10,000 feet). One subspecies has four sets of chromosomes, with a chromosome number of $2n = 36$. A second subspecies has 8 sets of chromosomes, with a chromosome number of $2n = 72$.

Figure 15.11 A common dandelion. In addition to reproducing by ordinary vegetative and sexual means, dandelions reproduce apomictically. Apomixis is a form of sexual reproduction through which seeds are produced without fertilization.

Because environment is a driver of natural selection, ecology is central to understanding this key evolutionary process. Darwin's theory of natural selection proposed that limiting factors in the environment produce differences in the rate of reproduction of individuals within populations. He reasoned that those individuals best adapted to the environment have the best chance for survival and reproduction and that the characteristics of these better-adapted individuals will increase in frequency within the population. Speciation, the origination of new species, is often influenced by ecological factors, and closely related species, derived from a common ancestor, often have different environmental requirements. In addition, biological diversity, a central concern of ecology, depends ultimately on a balance between rates of speciation and extinction.