18 Introduction to Darwinian Evolution

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Charles Darwin. This portrait was made shortly after Darwin returned to England from his voyage around the world.

KEY CONCEPTS

18.1 Evolution is the accumulation of inherited changes within populations over time.

18.2 Ideas about evolution originated long before Darwin's time.

18.3 Darwin's scientific theory of evolution, natural selection, explained how natural forces in the environment could cause evolution. Natural selection occurs because individuals with traits that make them better adapted to local conditions are more likely to survive and produce offspring than are individuals that are not as well adapted. The modern synthesis combines Darwin's theory with genetics.

18.4 The evidence that evolution has taken place and is still occurring is overwhelming. This evidence includes fossils, biogeography, comparative anatomy, molecular biology, developmental biology, and evolutionary experiments with living organisms.

A great deal of evidence suggests that the biological diversity represented by the millions of species currently living on our planet evolved from a single ancestor during Earth's long history. Thus, organisms that are radically different from one another are in fact distantly related, linked through numerous intermediate ancestors to a single, common ancestor. The British naturalist Charles Darwin (1809–1882) developed a simple, scientifically testable mechanism to explain the relationship among Earth's diversity of organisms. He argued persuasively that all the species that exist today, as well as the countless extinct species that existed in the past, arose from earlier ones by a process of gradual *divergence* (splitting into separate evolutionary pathways), or *evolution*.

The concept of evolution is the cornerstone of biology because it links all fields of the life sciences into a unified body of knowledge. As stated by U.S. geneticist Theodosius Dobzhansky, "Nothing in biology makes sense except in the light of evolution."[1] Biologists seek to understand both the remarkable variety and the fundamental similarities of organisms within the context of evolution. The science of evolution allows biologists to

[1] *American Biology Teacher,* Vol. 35, No. 125 (1973).

compare common threads among organisms as seemingly different as bacteria, whales, lilies, slime molds, and tapeworms. Animal behavior, developmental biology, genetics, evolutionary ecology, systematics, and molecular evolution are examples of some of the biological disciplines that are grounded in evolution.

This chapter discusses Charles Darwin and the development of his evolutionary theory by natural selection. It also presents evidence that supports evolution, including fossils, biogeography, comparative anatomy, molecular biology, developmental biology, and experimental studies of ongoing evolutionary change in both the laboratory and nature.

18.1 WHAT IS EVOLUTION?

LEARNING OBJECTIVE

1 Define *evolution.*

In beginning our study of evolution, we define **evolution** as the accumulation of genetic changes within populations over time. A **population** is a group of individuals of one species that live in the same geographic area at the same time. Just as the definition of a *gene* changed as you studied genetics, you will find that the definition of *evolution* will become more precise in later chapters.

The term *evolution* does not refer to changes that occur in an individual within its lifetime. Instead, it refers to changes in the characteristics of populations over the course of generations. These changes may be so small that they are difficult to detect or so great that the population differs markedly from its ancestral population.

Eventually, two populations may diverge to such a degree that we refer to them as different species. The concept of species is developed extensively in Chapter 20. For now, a simple working definition is that a **species** is a group of organisms, with similar structure, function, and behavior, that are capable of interbreeding with one another.

Evolution has two main perspectives—the minor evolutionary changes of populations usually viewed over a few generations (*microevolution,* discussed in Chapter 19) and the major evolutionary events usually viewed over a long period, such as formation of different species from common ancestors (*macroevolution,* discussed in Chapter 20).

Evolution has important practical applications. Agriculture must deal with the evolution of pesticide resistance in insects and other pests. Likewise, medicine must respond to the rapid evolutionary potential of disease-causing organisms such as bacteria and viruses (**FIG. 18-1**). (Significant evolutionary change occurs in a very short time period in insects, bacteria, and other organisms with short lifespans.) Medical researchers use evolutionary principles to predict which flu strains are evolving more quickly, information that scientists need to make the next year's flu vaccine. Also, researchers developing effective treatment strategies for the human immunodeficiency virus (HIV) must understand its evolution, both within and among hosts.

The conservation management of rare and endangered species makes use of the evolutionary principles of population genetics. The rapid evolution of bacteria and fungi in polluted soils is used in the field of **bioremediation,** in which microorganisms are employed to clean up hazardous-waste sites. Evolution even has applications beyond biology. For example, certain computer applications make use of algorithms that mimic natural selection in biological systems.

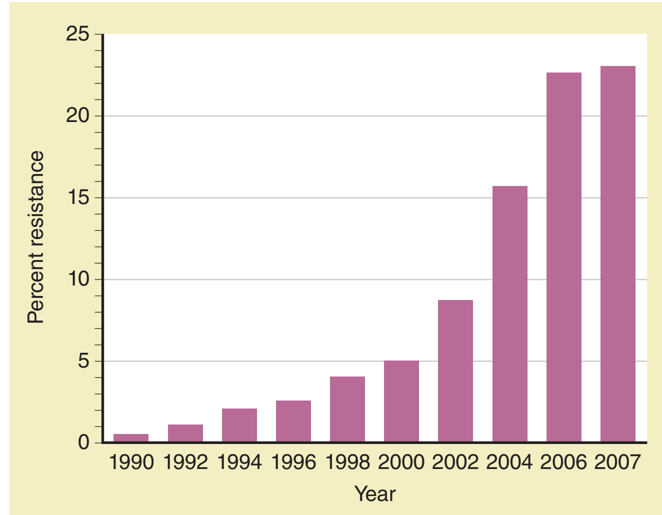

FIGURE 18-1 Evolution of antibiotic resistance to ciprofloxacin in *E. coli*

These data show an increasing resistance to *E. coli* in patients with blood and cerebrospinal infections in England, Wales, and Northern Ireland, 1990 to 2007. (Source: Livermore, D. "Zietgeist of Resistance." *The Journal of Antimicrobial Chemotherapy,* Vol. 60, i59–i61, 2007. By permission of Oxford University Press.)

Review

- What is evolution?
- Do individuals evolve? Explain your answer.

18.2 PRE-DARWINIAN IDEAS ABOUT EVOLUTION

LEARNING OBJECTIVE

2 Discuss the historical development of evolutionary theory.

Although Darwin is universally associated with evolution, ideas of evolution predate Darwin by centuries. Aristotle (384–322 BCE) saw much evidence of natural affinities among organisms. This led him to arrange all the organisms he knew in a "scale of nature" that extended from the exceedingly simple to the most complex. Aristotle visualized organisms as being imperfect but "moving toward a more perfect state." Some scientific historians have interpreted this idea as the forerunner of evolutionary theory, but Aristotle was vague on the nature of this "movement toward perfection" and certainly did not propose that natural processes drove the process of evolution. Furthermore, modern evolutionary theory now recognizes that evolution does not move toward more "perfect" states or even necessarily toward greater complexity.

Long before Darwin's time, fossils had been discovered embedded in rocks. Some of these corresponded to parts of familognized his own theory and realized Wallace had independently arrived at the same conclusion—that evolution occurs by natural selection. Darwin's colleagues persuaded him to present Wallace's manuscript along with an abstract of his own work, which he had prepared and circulated to a few friends several years earlier. Both papers were presented in July 1858 at a London meeting of the Linnaean Society. Darwin's monumental book, *On the Origin of Species by Natural Selection; or, The Preservation of Favored Races in the Struggle for Life,* was published in 1859. In 1870, Wallace's book, *Contributions to the Theory of Natural Selection,* was published, 8 years after he returned from the Malay Archipelago.

Darwin proposed that evolution occurs by natural selection

Darwin's mechanism of evolution by natural selection consists of observations on four aspects of the natural world: variation; overproduction; limits on population growth, or a struggle for existence; and differential reproductive success.

1. *Variation.* The individuals in a population exhibit variation (**FIG. 18-4**). Each individual has a unique combination of traits, such as size, color, ability to tolerate harsh environmental conditions, and resistance to certain parasites or infections. Some traits improve an individual's chances of survival and reproductive success, whereas others do not. Remember that the variation necessary for evolution by natural selection must be inherited. Although Darwin recognized the importance to evolution of inherited variation, he did not know the mechanism of inheritance.
2. *Overproduction.* The reproductive ability of each species has the potential to cause its population to geometrically increase over time. A female frog lays about 10,000 eggs, and a female cod produces perhaps 40 million eggs! In each case, however, only about two offspring survive to reproduce. Thus, in every generation each species has the capacity to produce more offspring than can survive.

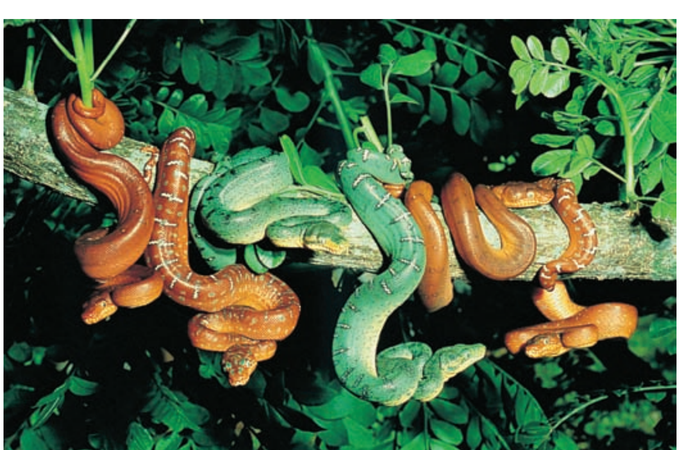

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FIGURE 18-4 Genetic variation in emerald tree boas
These snakes, all of the same species (*Corallus caninus*), were caught in a small section of forest in French Guiana. Many snake species exhibit considerable variation in their coloration and patterns.

3. *Limits on population growth, or a struggle for existence.* There is only so much food, water, light, growing space, and other resources available to a population, so organisms compete with one another for these limited resources. Because there are more individuals than the environment can support, not all survive to reproduce. Other limits on population growth include predators, disease organisms, and unfavorable weather conditions.
4. *Differential reproductive success.* Those individuals that have the most favorable combination of characteristics (those that make individuals better adapted to their environment) are more likely to survive and reproduce. Offspring tend to resemble their parents because the next generation inherits the parents' genetically based traits. Successful reproduction is the key to natural selection: the best-adapted individuals produce the most offspring, whereas individuals that are less well adapted die prematurely or produce fewer or inferior offspring.

Over time, enough changes may accumulate in geographically separated populations (often with slightly different environments) to produce new species. Darwin noted that the Galápagos finches appeared to have evolved in this way. The 14 species are closely related. All descended from a common ancestor—a single species that found its way from the South American mainland 2 million to 3 million years ago. (The closest genetic relatives of the Galápagos finches are small seed-eating birds known as grassquits that live in western South America.)

During this 2-million to 3-million year period, the number of islands increased, the climate changed, and the plant life and food supply changed. The different islands of the Galápagos kept the finches isolated from one another, thereby allowing them to diverge into separate species in response to varying conditions (**FIG. 18-5**).

Peter Grant, Rosemary Grant, and colleagues have documented natural selection in the Galápagos finches in their natural environment since the early 1970s. As an example of the evolutionary process in action, consider the sharp-beaked ground finch (*Geospiza difficilis*). This species lives on several different islands, and each population has evolved different beak shapes and sizes depending on the diet available on the island where it lives.

We revisit the Galápagos finches in later chapters. Some long-term research by Peter Grant, Rosemary Grant, and colleagues on the microevolution of Galápagos finches when droughts affect the food supply is described in Chapter 19; these studies have demonstrated that environmental change can drive natural selection. *Character displacement,* an aspect of evolutionary ecology, is described in Galápagos finches in Chapter 54.

The modern synthesis combines Darwin's theory with genetics

One of the premises on which Darwin based his scientific theory of evolution by natural selection is that individuals transmit traits to the next generation. However, Darwin was unable to explain *how* this occurs or *why* individuals vary within a population. As discussed in Chapter 11, Gregor Mendel elucidated the basic patterns of inheritance. Darwin, who was a contemporary of Mendel, was apparently not acquainted with Mendel's work. Indeed, the scientific community did not recognize Mendel's work until the early part of the 20th century.

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(a) The cactus finch (*Geospiza scandens*), which feeds on the fleshy parts of cacti, such as their flowers, has a long, pointed beak.

(b) The large ground finch (*Geospiza magnirostris*) has an extremely heavy, nutcracker-type beak adapted for eating thick, hard-walled seeds.

(c) The warbler finch (*Certhidia olivacea*) has a slender beak for eating insects.

(d) The woodpecker finch (*Camarhynchus pallidus*) digs insects out of bark and crevices by using spines, twigs, or even dead leaves.

FIGURE 18-5 ***Animated*** **Galápagos finches**

Darwin inferred that these birds are derived from a common ancestral population of seed-eating birds from South America. Variation in their beaks is the result of adaptation to the availability of different kinds of food.

Beginning in the 1930s and 1940s, biologists experienced a conceptual breakthrough when they combined the principles of Mendelian inheritance with Darwin's theory of natural selection. The result was a unified explanation of evolution known as the **modern synthesis.** In this context, *synthesis* refers to combining parts of several theories to form a unified whole. Some of the founders of the modern synthesis were U.S. geneticist Theodosius Dobzhansky, British geneticist and statistician Ronald Fisher, British geneticist J. B. S. Haldane, British biologist Julian Huxley, U.S. biologist Ernst Mayr, U.S. paleontologist George Gaylord Simpson, U.S. botanist G. Ledyard Stebbins, and U.S. geneticist Sewell Wright.

Today, the modern synthesis incorporates our expanding knowledge in genetics, which on its own makes an irrefutable case for evolution, systematics, paleontology, developmental biology, behavior, and ecology. The modern synthesis explains Darwin's observation of variation among offspring in terms of **mutation,** or changes in DNA, such as nucleotide substitutions. Mutations provide the genetic variability on which natural selection acts during evolution. The modern synthesis, which emphasizes the genetics of populations as the central focus of evolution, has held up well since it was developed. It has dominated the thinking and research of biologists working in many areas and has resulted in an enormous accumulation of new discoveries that validate evolution by natural selection.

Most biologists not only accept the basic principles of the modern synthesis but also try to better understand the causal processes of evolution. For example, what is the role of chance in evolution? How rapidly do new species evolve? These and other questions have arisen in part from a re-evaluation of the fossil record and in part from new discoveries in molecular aspects of inheritance. Such critical analyses are an integral part of the scientific process because they stimulate additional observation and experimentation, along with re-examination of previous evidence. Science is an ongoing process, and information obtained in the future may require modifications to certain parts of the modern synthesis.

We now consider one of the many evolutionary questions currently being addressed by biologists: the relative effects of chance and natural selection on evolution.

Biologists study the effect of chance on evolution

Biologists have wondered whether we would get the same results if we were able to repeat evolution by starting with similar organisms exposed to similar environmental conditions. That is, would the same kinds of changes evolve, as a result of natural selection? Or would the organisms be quite different as a result of random events? Several recently reported examples of evolution in action suggest that chance may not be as important as natural selection, at least at the population level.

A fruit fly species (*Drosophila subobscura*) native to Europe inhabits areas from Denmark to Spain. Biologists noted that the northern flies have larger wings than southern flies (**FIG. 18-6**). The same fly species was accidentally introduced to North America in the late 1970s. Ten years after its introduction, biologists determined that no statistically significant changes in wing size had occurred in the different regions of North America. However, 20 years after its introduction, the fruit flies in North America exhibited the same type of north–south wing changes as in Europe. (It is not known why larger wings evolve in northern areas and smaller wings in southern climates.)

A study of the evolution of fishes known as *sticklebacks* in three coastal lakes of western Canada yielded intriguingly similar results to the fruit fly study. Molecular evidence indicates that when the lakes first formed several thousand years ago, they were populated with the same ancestral species. (Analysis of the mitochondrial DNA of sticklebacks in the three lakes supports the hypothesis of a common ancestor.) In each lake, the same two species have evolved from the common ancestral fish. One species is large and consumes invertebrates along the bottom of the lake, whereas the other species is smaller and consumes plankton at the lake's surface.