# 2

# Early Evolutionary Ideas and Darwin's Insight



◀ Some of the Galápagos finch species that so fascinated Darwin on his voyage aboard HMS *Beagle.* These museum specimens are arrayed on a copy of Darwin's research journal.

Long before the science of evolutionary biology was born, people contemplated both the origin of life and why it was that organisms often seem so well suited for the environments in which they live. More than two millennia ago, the Greek philosopher Empedocles (ca. 492–432 B.C.E.) proposed that body parts arose independently from the ground, describing organisms

> where many heads grew up without necks, and arms were wandering about naked, bereft of shoulders, and eyes roamed about alone with no foreheads. (Empedocles, Book II, 244, in Fairbanks 1898, p. 189)

These unattached parts, Empedocles continued, then wandered Earth before reassorting, sometimes into monstrous combinations such as creatures with two faces and animals with human heads, and sometimes into the well-proportioned forms that we observe in the animal world. When we read of such theories, we need to be careful not to fall into the trap of judging them based on what we know today. At the time, Empedocles was making a serious attempt to understand the origin of animals. He *might* have been correct, he just wasn't; but most ideas turn out to be wrong over the long run.

Empedocles' ideas did more than suggest how animal life originated: They also provided an explanation for why organisms seem to be so well adapted to their environments. Empedocles argued that if individuals were assembled from parts that were unable to function together to reproduce, they died off and their types became extinct. Without turning to supernatural intervention, Empedocles proposed a theory that explained not only why we observe an incredible diversity of living forms, but also why the component parts of each species tend to be well suited to one another and to the species' habitats (O'Brien 2012).

Empedocles and his ideas remind us that science has a rich and deep history. Sir Isaac Newton, the great physicist and mathematician, wrote in 1676 that if he had seen farther than others, it was only "by standing on the shoulders of giants." Therein lies the tremendous power of the scientific approach. On the one hand, scholars can build on decades, or even centuries, of previous work without needing to reinvent every step themselves. On the other hand, each of these previous discoveries or theories remains continually open to challenge, revision, and reinterpretation based on new evidence. Like all other great scientific ideas, Darwin's theory of evolution by natural selection did not arise in a vacuum. Instead, the idea of natural selection—as a process in which forms that are better suited to their environment increase in frequency in a population—emerged from a rich philosophical and scientific tradition that came before it.

Given that many theories from this pre-Darwinian tradition have since been discredited, why should a contemporary biologist study these ideas about evolution? Why pause in assessing the view from our time to look back at the figures that came before us?

We study the past to improve our work in the present. We hone our own scientific thinking by following the reasoning that led to both correct and incorrect conclusions, and we come to appreciate the intellectual risks that sparked the theories that we now take for granted. We learn from the work of those that came before us to be flexible in our current thinking. Exploring the debates underlying our assumptions reminds us to question our understanding and to approach contemporary problems from new angles.

And so, before investigating Darwin's theory and the developments in biology that have followed from it, we will examine the ideas about the nature of the biological world that preceded the publication of *On the Origin of Species* in 1859. The first part of this chapter will serve as an introduction to how ***pre-Darwinian thinkers*** tried to answer the big questions about life and biology, including these:

- What separates science from mythology?
- How should scientists reach conclusions about the natural world?
- How does the natural world change, and over what length of time?
- Why is the world filled with an astonishing diversity of living forms instead of a few basic types?
- Where do species come from?
- Why are organisms well suited to the environments in which they live?

Once we have tackled these questions, in the second part of the chapter we will introduce Darwin's ideas on the evolutionary process.

We will begin by briefly addressing what separates science from mythology, and we will discuss what sorts of explanations scientists can pursue.

## 2.1 The Nature of Science: Natural versus Supernatural Explanations

Throughout recorded history, every human culture has cultivated a set of creation myths that purport to explain—literally or metaphorically—how the world was created and how it came to be the way that it is. These mythologies address universal questions that stimulate the human imagination and gratify our need for explanations of our place in the world. Prior to the sixth or seventh century B.C.E., these creation myths provided the only answers that humankind had to the grand questions of our existence (Armstrong 2005). This approach to knowledge through mythmaking began to change with the early Greek philosophers.


**FIGURE 2.1 Anaximander (ca. 610–546 B.C.E.).** Anaximander proposed a mechanistic view of the Earth and heavens. The philosopher is illustrated in the 1493 history of the world, *The Nuremberg Chronicle*.

### Methodological Naturalism

The early Greeks, of course, had their own creation myths, but philosophers such as Anaximander (ca. 610–546 B.C.E.) (**Figure 2.1**) were among the first to develop a philosophy of a natural world in which physical laws replaced a supernatural world driven by divine action. They sought to explain the world around them according to fixed laws of nature, rather than by the operation of divine whim.

At a time when heavenly bodies were regarded as divine personages, Anaximander provided a mechanistic rather than divine conception of the Moon, Sun, and stars. He suggested that just like the earthly structures we experience with our senses, the celestial bodies were physical objects (**Figure 2.2**). Earth, he proposed, was a cylindrical disk. The Sun and the Moon rotated around it as if on wagon wheels. Beyond the Sun and the Moon, tiny holes in the firmament let through the light from a vast dome of fire; these pinpoints of light were the stars. Again, it is easy to look back on such ideas and laugh, but that would be a mistake. Anaximander got the details wrong, but given the state of scientific knowledge at the time, this is to be expected. The important thing here is that Anaximander and some of the Greek philosophers who followed him developed explanations based on natural, rather than supernatural, phenomena.

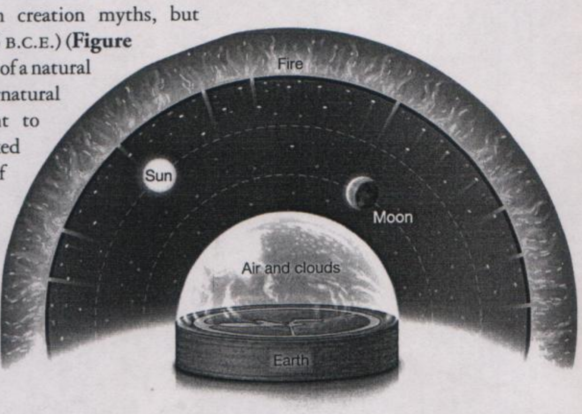


**FIGURE 2.2 Anaximander's cosmology.** In Anaximander's cosmology, Earth is a disk surrounded by vast wheels on which the Sun and Moon rotate and a dome of fire; stars were explained as light shining from the dome of fire through holes in a firmament.

The strategy of trying to explain the world based solely on natural phenomena is fundamental to the scientific method and is at the heart of modern evolutionary biology. It is sometimes called **methodological naturalism**. We call it *naturalism* because of the focus on the natural rather than the supernatural. We use the adjective *methodological* because this strategy provides a method or procedure for seeking scientific explanations of the world. Although philosophers began using methodological naturalism as early as 600 B.C.E., this approach would not be solidified or universally embraced until the eighteenth century (Barzun 2001).

## Hypothesis Testing and Logic

Although they were able to make the shift from supernatural to natural explanations, the early Greek philosophers failed to exploit one of the greatest advantages of methodological naturalism: hypothesis testing. If we propose an explanation of a phenomenon based on natural processes, that is, if we develop a **hypothesis**, we can then test this hypothesis because we can observe and often manipulate these processes. By contrast, we have no way to observe, let alone manipulate, the supernatural, and thus we cannot test supernatural explanations. However, the early Greeks formulated hypotheses without refining them through testing. This lack of verification for ideas would begin to change with the great philosopher Aristotle (ca. 384–322 B.C.E.) (**Figure 2.3**).


**FIGURE 2.3 Aristotle (ca. 384–322 B.C.E.).** The Greek philosopher Aristotle wrote, "We must not accept a general principle from logic only, but must prove its application to each fact; for it is in facts that we must seek general principles, and these must always accord with the facts."

### KEYCONCEPT QUESTION

**2.1** What does it mean for a hypothesis to be falsifiable?

Unlike those before him, Aristotle recognized the significance of testing one's hypotheses. In his *Natural History of Animals*, Aristotle was clear that "We must not accept a general principle from logic only, but must prove its application to each fact; for it is in facts that we must seek general principles, and these must always accord with the facts" (Aristotle, Book 1, p. 6, cited in Osborn 1894). In other words, principles must agree with the facts. If not, we need to rethink our principles and start over. This sort of approach is well accepted by modern evolutionary biologists, and for this we can thank Aristotle and those who followed in his footsteps. Of course, this approach did not take hold overnight, and even Aristotle did not always follow the practice he preached. In the very same volume where he advocated checking principles against the facts, Aristotle incorrectly asserted that men have more teeth than women. Philosopher Bertrand Russell famously remarked that "Aristotle maintained that women have fewer teeth than men; although he was twice married, it never occurred to him to verify this statement by examining his wives' mouths" (Russell 1952, p. 7).

After Aristotle, one advance in scientific methodology came through the use of logic. Application of logical and mathematical laws allowed thinkers to move carefully from facts to general principles. In modern evolutionary theory, not only must one gather physical evidence, but also one must formulate and test hypotheses based on such evidence.

Profound as they were, advances in methodological naturalism and logic alone would not prepare the intellectual framework necessary for eventual breakthroughs in evolutionary theory. People also needed to become accustomed to the idea of a world that was both *ancient* and *ever changing*. In the next section, we will examine historical conceptions of the nature of change, of the timescale for such changes, and of the sources of evidence for past changes.

## 2.2 Time and a Changing World

Darwin's theory of evolution by natural selection explains the form and diversity of living things as the consequence of gradual change over vast periods of time. As we will see in this section, Darwin was not the first to propose this idea, but the notion of change and huge expanses of time arrived late in the history of Western thought. This view was not the dominant one during most of Western history.

The view of the world as unchanging seems counterintuitive to anyone who has watched a storm roll in, a child grow up, or a candle burn. Yet, some Greek philosophers claimed that everything that exists has always existed and will always exist. The material world was permanent, unalterable, and unmoving. Even Aristotle, although he recognized change over small timescales, thought of the world as static and unchanging over longer periods of time. In contrast, Empedocles (**Figure 2.4**) proposed that historically, plant life preceded animal life, and Xenophanes (570–470 B.C.E.) studied fossils in sedimentary rocks in the mountains and concluded that at one time the rocks must have been underwater.

The ideas of both Empedocles and Xenophanes implied that important changes in the biological world had occurred. What sorts of changes had occurred, however, remained contentious for nearly 2000 years. Indeed, until the work of French natural historians Georges-Louis Leclerc, comte de Buffon (1707–1788), and Georges Cuvier (1769–1832) in the eighteenth century, the idea that species had gone extinct was thought of as an absurd challenge to the notion of a flawless Creator.

Even if philosophers accept and study the importance of change, a full theory of evolution by natural selection cannot exist without an understanding of the vast expanses of time over which some changes take place. That would not come for almost 2000 years after these early conjectures by the Greeks. Along the way, in the late Middle Ages, the written records of the Bible provided a starting place for estimating the age of Earth. Following similar endeavors by scholars before him, James Ussher (1581–1656), a seventeenth-century Anglican archbishop in Northern Ireland, performed complex calculations based on the Old Testament, and he concluded that the universe had been created on October 23, 4004 B.C.E. Though the precision of the date may sound ludicrous today, Ussher's attempt to date the creation of the world was part of a serious research tradition at the time


**FIGURE 2.4 Empedocles (ca. 492–432 B.C.E.).** Empedocles argued that plant life preceded animal life.

(Gould 1991). Famous scientific contemporaries of Ussher made similar attempts; for example, Isaac Newton dated creation at 3998 B.C.E.

At the same time that Archbishop Ussher was making his calculations, a radical shift was taking place in the way that other scholars viewed time and history. Inspired by the vastness of space made clear with the invention of the telescope and the discovery of countless stars beyond those visible to the naked eye, thinkers looked to an equally vast expanse of time.

Scientists began to suggest that both the universe and Earth were much, much older than the thousands of years suggested by a literal interpretation of the Old Testament. In the latter part of the eighteenth century, Buffon used physical laws about the rate at which objects as large as Earth both heat up and cool down to calculate the age of Earth at between 75,000 and 2 to 3 million years (Buffon 1778; Roger 1997). Around the same time, James Hutton (1726–1797), a Scottish geologist, naturalist, and chemist, argued that geological evidence—the way that rock strata were aligned, the processes of erosion and sedimentation, and the fossil data—suggested that the world was inconceivably old (Hutton 1795; Repcheck 2003). Once the idea of a changing world and vast stretches of time became established, the question became this: How can we fully use the power of observation, experimentation, and hypothesis testing to understand change over immense periods of time? To do so, we require explanations that not only appeal to natural processes but also, more specifically, appeal to natural processes that are ongoing and observable or otherwise somehow accessible to us. Historically, the method to do this emerged first in the field of geology and from there migrated to the biological sciences. To see how, we need to examine the work of Scottish geologist Charles Lyell (1797–1875) (**Figure 2.5**).

Building on ideas first proposed by Hutton, Lyell aimed to explain Earth's geological features by appealing to the same geological processes currently observable. He argued that these same processes have operated over very long periods of time in a slow, gradual manner. From this, Lyell came up with the title of his famous book, *Principles of Geology, Being an Attempt to Explain the Former Changes of the Earth's Surface, by Reference to Causes Now in Operation* (Lyell 1830). As we will see shortly, this approach, known as **uniformitarianism**, had a strong influence on Charles Darwin.

Uniformitarianism explained the geological features of Earth in a radically different way than did **catastrophism**, the common theory of the time. According to catastrophism, Earth's major geological features arose through sudden cataclysmic, large-scale events, rather than through slow gradual change. Catastrophism also posited that these cataclysmic events often involve different forces than those that are currently operating.

The shift from catastrophism to uniformitarianism was an important development not only for geology, but also for science as a whole, because science attempts to relate natural processes to observable patterns. In the extreme catastrophic view, these processes are themselves neither observable nor subject to manipulative experiments, and they are not expected to occur again in the future, making it hard—but not impossible—to test hypotheses about how observed patterns have been generated. In the uniformitarian view, all of the processes that have generated the current geological patterns we see around us can themselves be

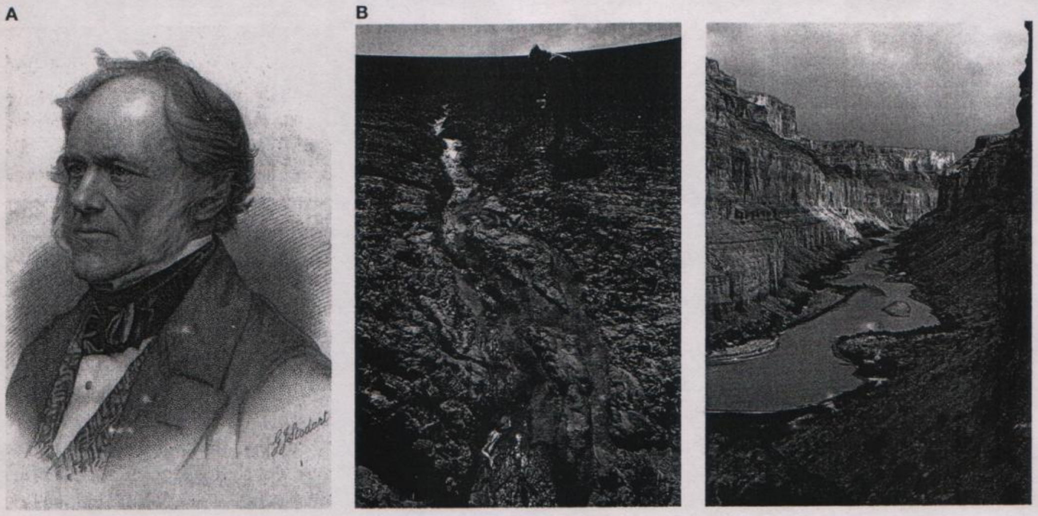

**FIGURE 2.5 Charles Lyell (1797–1875) and uniformitarianism.** (**A**) Lyell's theory of uniformitarianism helped pave the way for modern evolutionary thinking about the vast expanse of time. (**B**) Uniformitarianism posits that the slow process of erosion (left), when carried out over long stretches of time, can produce massive canyons (right).

observed in operation at present, providing scientists with much more power to test hypotheses.

While Lyell's work related directly to geology, his concept of change over time would also influence evolutionary biology. Darwin read Lyell's *Principles of Geology* while serving as captain's companion and ship's naturalist aboard HMS *Beagle*, and he was profoundly affected by Lyell's ideas (Recker 1990). Prior to publishing *On the Origin of Species*, Darwin wrote three books on geology, each of which drew heavily on Lyell's work on uniformitarian change. And, as we will see later in this chapter, in many ways Darwin's ideas on the gradual changes associated with evolution by natural selection are a sort of biological interpretation of Lyell's uniformitarianist ideas on geological processes. The diversity of life on Earth, Darwin proposed, can be explained by mechanisms that are in operation today, acting over very long periods of time.

By explaining the dramatic features of Earth's geography through uniformitarianism, Lyell conceived the world as changing across enormous expanses of time. As such, by the time Darwin began his work, the approach to scientific inquiry had changed from mythmaking and supernatural explanations to methodological naturalism—a method built on an increasingly sophisticated system of hypothesis testing and reason.

In the next section, when we explore theories of how new species come into existence, we will see that both uniformitarianism and the concept of deep time (vast periods of time) were essential in understanding the origins of the diversity of organisms on Earth.

## 2.3 The Origins and Diversity of Life

In addition to taking the first steps toward the scientific method and hypothesizing about events from the past, the Greek philosophers also developed a keen appreciation for the study of natural history. Again, Aristotle's contributions were exceptional. Aristotle's books *Physics* and *Natural History of Animals* marked the birth of the field of **natural history**, an enterprise that would be important for the development of any theory of the astonishing diversity of life, whether that theory was evolutionary or not (Schneider 1862).

Aristotle distinguished among 500 species of birds, mammals, and fish, and he wrote entire tracts on the anatomy and movement of animals. He also proposed a taxonomy of nature—a classification system of life—that led from polyps at the lowest level to humans at the pinnacle. This would later be called "the great chain of being," or *scala naturae*. According to this linear classification system, each species occupied a link in a chain of ever-increasing complexity. This concept influenced Western thinkers for more than 2000 years. While this view of nature contributed to the sense of the diversity of life, it was missing two critical concepts that were necessary for the development of evolutionary biology: shared degrees of complexity and the potential to change. On the *scala naturae*, every organism represented a specific and unique link in the chain, and each link represented a different level of complexity, which meant that different organisms could not share comparable degrees of complexity. Likewise, in this view, each specific link on the chain of being would remain forever fixed—precluding the possibility that organisms might change. Both of these misconceptions would have to be overcome before evolutionary biology could emerge as a science.

In addition to cataloging the details of natural history, the ancient Greeks also turned their attention to the problem of how life got started and how all of the diverse living forms around them arose. As we learned at the start of the chapter in our discussion of Empedocles, without the ability directly to observe life arising and diversity being generated, and without a broad conceptual framework for the diversity of the life they saw, the Greeks resorted to speculative accounts of how this process may have occurred. While these speculations represented progress in the sense that they involved natural rather than supernatural explanations, many of the specific mechanisms that the Greeks proposed seem bizarre today. The commonality among almost all of their suggestions is that they relied on **spontaneous generation**—the idea that complex life-forms arise repeatedly, without external stimuli, from nonliving matter, and *heterogenesis*—the idea that parents of one species could produce offspring of a different species.

Ideas on spontaneous generation existed before the Greeks and persisted for more than 2000 years after the Greeks. In Egypt, for example, people thought that frogs were created spontaneously from mud. This is because when the Nile River flooded every year, it transformed dry mudflats into wet mud, and simultaneously, hundreds of frogs appeared. Aristotle wrote extensively about spontaneous generation as a source of life and theorized that when parents thus generated went to reproduce, they formed new species by heterogenesis. Many medieval European farmers believed that mice were generated from moldy grain, and many urban residents believed that sewage created rats (McCartney 1920).

Finally, in 1668, in an early example of a controlled experiment, Francesco Redi (1626–1697), an Italian physician and naturalist, addressed the following question: Are flies spontaneously generated from meat carcasses? It seemed as if

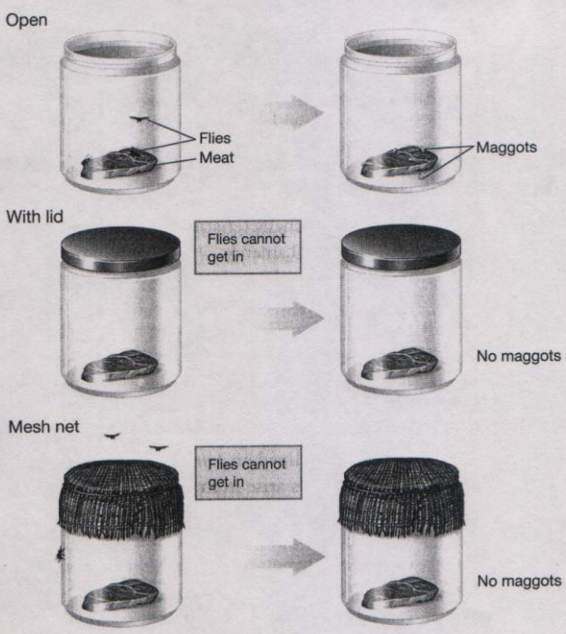


**FIGURE 2.6 Redi's experiment.** Redi's experiment demonstrated that maggots did not arise through spontaneous generation. Uncovered jars with meat have fly eggs and maggots. When the jars are covered, and flies cannot enter and lay eggs on the meat, no eggs or maggots are found.

they were, because when meat rotted, flies appeared. So, Redi placed raw meat in a series of jars. Covering some jars (for a control group) and leaving other jars uncovered or partially uncovered, Redi determined that flies only arise from the maggot offspring of other flies, and that maggots cannot spontaneously generate from meat (**Figure 2.6**). Redi's experiment prompted his contemporaries to question whether any organism could appear from a nonliving substance. In spite of this experiment, spontaneous generation persisted as a theory, in part because the new technology of the microscope showed organisms such as bacteria and fungi appearing on substances such as spoiled broth without any clear parental source.

The late eighteenth and early nineteenth centuries brought new theories to explain the origins of life and the diversity of species. Erasmus Darwin (1731–1802) (**Figure 2.7**), an English physician, philosopher, and the grandfather of Charles Darwin, was one of the first to propose the idea of evolutionary change in his book *Zoonomia* (Darwin 1796; King-Hele 1998).

**FIGURE 2.7 Erasmus Darwin (1731–1802).** Charles Darwin's grandfather proposed the idea of evolutionary change in his book *Zoonomia*.

Erasmus Darwin argued that all life evolved—although he did not use that word—from what he called a "single living filament" (Darwin 1796). For Erasmus Darwin, this living filament had been modified in endless ways, over millions of years, to produce the life that he saw around him. He also hypothesized that humans had initially walked on four limbs and, even more remarkably, that we had descended from another primate species. This was a radical idea at the time. In addition, Erasmus Darwin understood the **struggle for existence**—the notion that

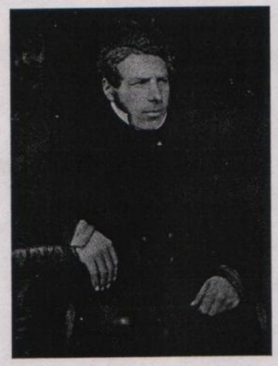

**FIGURE 2.8 Robert Chambers (1802–1871).** Chambers authored the book *Vestiges of the Natural History of Creation*.

organisms are in a constant struggle to obtain resources and to use these resources to produce more offspring than those around them. Despite Erasmus Darwin's insights, he did not develop a full-blown theory of evolution of new species by natural selection for at least two reasons: (1) with a few notable exceptions, he failed to connect the struggle for existence, which he described over and over again, to the evolutionary changes that such a struggle would produce (Krause 1879); and (2) he believed in the widely accepted, but largely incorrect, idea that new traits acquired *during the lifetime of an organism* could be passed down to progeny. We will return to this "inheritance of acquired characteristics" later in our discussion of its most famous proponent, Jean-Baptiste Lamarck.

After Erasmus Darwin, Robert Chambers (1802–1871), a Scottish geologist, writer, and publisher (**Figure 2.8**), presented a more formally developed and widely influential theory on how new species originate in his 1845 book, *Vestiges of the Natural History of Creation* (Chambers 1845).

In the section of his book on what today we would call evolution, Chambers highlighted two critical points: (1) the composition of species has changed over time, and (2) this change was slow, gradual, and unlinked to catastrophes (Mayr 1982). From these ideas, Chambers outlined his *principle of progressive development*, in which he hypothesized that new species arise from old species: "The simplest and most primitive type . . . gave birth to the type next above it . . . and so on to the very highest, the stages of advance being in all cases very small—namely, from one species only to another; so that the phenomenon has always been of a simple and modest character" (Chambers 1845, p. 222).

One aspect of *Vestiges* that often goes unnoticed is that Chambers thought not in terms of individuals so much as **populations**—groups of individuals of the same species that are found within a defined area and, if they are a sexual species, interbreed with one another. Chambers was perhaps the first to recognize that, in the parlance of modern evolutionary biology, populations evolve; individuals do not.

Robert Chambers and his *Vestiges* profoundly influenced a broad range of readers. The book was widely read by scientists and laypeople alike, including a young Abraham Lincoln, who quickly became "a warm advocate of the doctrine" (Herndon and Weik 1893). *Vestiges* would eventually sell an astonishing 100,000 copies (Secord 2000). For all its success, the greatest deficit in Chambers' book was the lack of a theory to explain *why* new species come into being. That is, there was nothing akin to the theory of natural selection that Darwin would propose some 15 years later.

## 2.4 Organisms Are Well-Suited to Their Environments

While *Vestiges* presented the idea of new species gradually arising from existing species, the book did not explicitly consider the enormous influence of the environment on these slow changes. Any observer of nature will notice the remarkable degree of fit between the structures of organisms and their environments. The mammals of cold climates have thick coats and layers of insulating fat; swimming animals have shapes that allow them to move efficiently through the water; desert plants have thick waxy cuticles and low surface area that help them avoid water loss. How do we explain this seemingly marvelous fit? Prior to Darwin's work, philosophers and scientists entertained a diverse array of answers to this question.

## Paley's Natural Theology

**FIGURE 2.9 William Paley (1743–1805).** Paley discussed the exquisite fit of organism to environment by using an analogy in which, just as a watch requires a watchmaker, so too living organisms require a conscious designer.

For the English naturalist and theologian William Paley (1743–1805), the fit of diverse species to their environments resulted from the planning of some supernatural deity. In his textbook, *Natural Theology*, Paley discussed the famous metaphor of God as watchmaker (Paley 1802) (**Figure 2.9**). If a single part of the clockwork within a watch were shaped differently or placed elsewhere, he observed, the watch would fail to function. Because living creatures are even more complex than watches, they could not have come to fit their habitats perfectly through chance, Paley argued, just as it is virtually impossible for a fully working watch to come into being simply by chance arrangement of clockwork parts. Organisms, then, must have been intentionally designed by a benevolent deity in order to thrive in their environments.

Years later, Darwin would read and admire Paley's work, particularly his arguments on how the structures of organisms fit the functions they need to serve in order for individuals to survive. As we will see in greater detail in a moment, however, Darwin would disagree with Paley's explanation of the source of these adaptations. Darwin sought to explain adaptation by purely natural, rather than supernatural, causes.

## Jean-Baptiste Lamarck and the Inheritance of Acquired Characteristics

With Jean-Baptiste Lamarck (1744–1829), we return fully to methodological naturalism as the explanation for species fitting their environments (**Figure 2.10**). Originally trained as a botanist at the French Jardin du Roi as a student of Buffon, Lamarck eventually became an animal systematist specializing in the study of invertebrates. His long-term studies of such organisms as mussels, which he compared to less complex fossil mussels, no doubt led him to think in terms of increasing complexity occurring in a group of organisms over time.

**FIGURE 2.10 Jean-Baptiste Lamarck (1744–1829).** Lamarck developed a "transformation" theory for evolutionary change in his *Zoological Philosophy*.

In his 1809 book, *Zoological Philosophy*, Lamarck rejected the idea that new species suddenly appeared after large-scale extinctions resulting from catastrophic events. Instead he proposed that new, more complex species—humans being the most complex—had descended, gradually, from older, less complex species. Because of this, Lamarck is often credited with developing the first truly evolutionary theory for how organisms adapt to their different environments over evolutionary time. Actually, Lamarck outlined two mechanisms for evolutionary change, but here we will focus on his more famous one—the **inheritance of acquired characteristics**.

The idea behind the inheritance of acquired characteristics is that *during the lifetime of an organism*, the habits of the organism bring about changes in its structure, and such structural changes are passed down across generations (Lamarck 1809). Consider Lamarck's description of this process in birds (**Figure 2.11**):

> One may perceive that the bird of the shore, which does not at all like to swim, and which however needs to draw near to the water to find its prey, will be continually exposed to sinking in the mud. Desiring to avoid immersing its body in the liquid [the bird] acquires the habit of stretching and elongating its legs. The result of this for the generations of these birds that continue to live in this manner is that the individuals will find themselves elevated as on stilts, on naked long legs. (Lamarck 1801, cited in Burkhardt 1995, p. 172)

**FIGURE 2.11 Lamarck, acquired characteristics, and shorebirds.** Lamarck argued that the long legs of shorebirds such as this black-necked stilt (*Himantopus mexicanus*) are the result of birds stretching their legs as far as possible to avoid sinking in the mud. This stretching itself, Lamarck postulated, lengthened the legs of individuals doing the stretching, and their new trait of "longer legs" was then also passed down to offspring.

Lamarck observed that we find long-legged birds in environments in which long legs are beneficial. Rather than crediting a watchmaker deity for this perfect fit, he hypothesized a process of adaptation over time. Lamarck's hypothesis that traits acquired *during* the lifetime of an individual are passed on to its progeny was interesting, reasonable, and based on an idea that was universally accepted by scientists and nonscientists alike. After all, we are all aware of how our habits of life lead to changes in physiology; lifting weights, for example, leads to the development of increased muscle mass and lifting power. In the absence of evidence to the contrary, it is only a short leap from there to suppose that such changes could also be passed on to one's offspring. Today, however, we have plenty of evidence to the contrary. We know that acquired characteristics are not ordinarily inherited, and we now ground our ideas of how traits are passed from generation to generation in the laws of genetics, which were formulated about 100 years after Lamarck (Chapter 6).

Lamarck's legacy, however, is not that he postulated the wrong processes for evolutionary change, but that he proposed a process in the first place, and that he connected it to environmental fit. As we will see, although Darwin did not completely reject the inheritance of acquired characteristics, his ideas on how and why evolutionary changes occur were quite different from those of Lamarck.

**KEYCONCEPT** QUESTION

**2.2** A blacksmith's muscles get larger the more he pounds his metals into shape. Suppose, as is likely the case, that the sons of blacksmiths are on average more muscular than other males their age. Why might this mistakenly lead someone to think that muscle size here is an example of the inheritance of an acquired characteristic? How else could we explain this observation?

## Patrick Matthew and Natural Selection

In the history of biology, we hear little about the developments in evolutionary thinking in the 50 years between Lamarck's *Zoological Philosophy* (1809) and Charles Darwin's *On the Origin of Species*. Yet, it was during this period that Patrick Matthew (1790–1874), a Scottish landowner and writer, proposed his own theory of evolution by natural selection, predating the ideas laid out in *On the Origin of Species* by more than a quarter of a century (Matthew 1831; Mayr 1982; Dempster 1996). In an obscure 1831 work entitled *On Naval Timber and Arboriculture*, Matthew proposed a theory very similar to Darwin's on the interaction between environment and evolutionary change. In the notes at the end of *On Naval Timber and Arboriculture*, in a section only tangentially related to the rest of the book, Matthew outlined his ideas on both evolution and natural selection. He understood the idea that individuals best suited to their environments would be selected over others. The difference between this idea and Lamarck's theory is that Matthew relied on what Darwin would one day call natural selection rather than the inheritance of acquired traits.

Matthew's discussion of environmental fit and natural selection—what he dubbed "the circumstance-adaptive law"—is remarkably similar to what Darwin would discuss almost 30 years later. Matthew, for example, noted,

> The self regulating adaptive disposition of organized life may, in part, be traced to the extreme fecundity of Nature, who . . . has in all the varieties of her offspring, a prolific power much beyond (in many cases a thousandfold) what is necessary to fill up the vacancies caused by senile decay. As the field of existence is limited and pre-occupied, it is only the hardier, more robust, better suited to circumstance, individuals who are able to struggle forward to maturity . . . from the strict ordeal by which Nature tests their adaptation to her standard of perfection and fitness to continue their kind by reproduction, . . . the breed gradually acquiring the very best possible adaptation. (Matthew 1831, pp. 384–385)

Matthew outlines three important evolutionary ideas here: (1) resources are limited, and only so many offspring can survive to the age of reproduction; (2) individuals will differ in terms of traits that allow them to garner such resources; and (3) over time, this will lead to organisms that are well adapted to their environments.

Matthew's name is not readily associated with the theory of evolution by natural selection—despite the fact that on page 22 of the preface to the sixth edition of *The Origin of Species*, Darwin noted that Matthew presented "precisely the same view on the origin of species as that propounded by . . . myself . . . in the present volume." There are many reasons for Matthew's relative obscurity. His ideas were published in a book that no one interested in biological diversity would have been likely to read, and even there his ideas were hidden in his notes and appendix section rather than presented as a unified theory. Moreover, Darwin discussed both natural selection and common descent, while Matthew mentioned only the former. Perhaps most important, Matthew presented scant evidence in support of his ideas. Darwin, in contrast, spent 20 years gathering evidence for evolution by natural selection before publishing *On the Origin of Species*. All of that said, Matthew's work merits more attention than it has garnered.

If we stop and take stock for a moment, what we have seen in this chapter so far is that five major developments preceded and facilitated Darwin's *On the Origin of Species*. These changes involved moving (1) from supernatural explanations to methodological naturalism, (2) from catastrophism to uniformitarianism, (3) from logic and pure reason to observation, testing, and refutation, (4) from an unchanging world to a world in flux, and (5) away from the idea of spontaneous generation to the idea that species come from other closely related species.

## 2.5 Darwin's Theory

We will begin our exploration of Darwin's contributions with a brief overview of the major ideas that he presented in *On the Origin of Species*. Darwin had two fundamental insights that he referred to as "two great laws" about the process of evolution.

### Darwin's Two Fundamental Insights

The first of Darwin's fundamental insights deals with the conditions of existence and the process of natural selection. Here, Darwin hypothesized that the environment—what we might think of in the abstract sense as "nature"—selects on variation in the traits of individual organisms, because some variants are more successful than others at increasing the probability of survival and reproduction.

With this hypothesis, Darwin offered a mechanistic explanation both for how the characteristics of organisms change over time and for why organisms are well suited to their environments. That explanation was, of course, the process that Darwin dubbed ***natural selection***. The effect that a given variant of a trait has on survival and ultimately reproductive success depends on the environment in which an organism finds itself. As Darwin noted, once the "conditions of existence" are determined, "natural selection acts by either now adapting the varying parts of each being to its organic and inorganic conditions of life; or by having adapted them during past periods of time" (Darwin 1859, p. 206). Here, when Darwin writes of the conditions of existence, he is referring to the living (biotic) and nonliving environment that sets the stage on which natural selection operates.

The second of Darwin's insights centers on the common ancestry of all living things. Darwin hypothesized that all species have descended from one or a few common ancestors; species that share a recent common ancestor tend to resemble one another in many respects for the very reason that they share recent common ancestry. In short, Darwin hypothesized that new species do not arise through independent acts of creation or spontaneous generation, but rather from preexisting species. This process generates a branching pattern of ancestry relating all life.

These two insights are major themes not only within this chapter, but throughout the textbook, and we will go into much more detail about them in other chapters. For now, we will look at how Darwin arrived at these ideas, at how he collected evidence to support them, and at how he chose to present his challenging conclusions to his nineteenth-century contemporaries.

### Publication of *On the Origin of Species*

Darwin begins *On the Origin of Species* as follows: "When on board H.M.S. '*Beagle*,' as naturalist, I was much struck with certain facts in the distribution of the inhabitants of South America, and in the geological relations of the present to the past inhabitants of that continent. These facts . . . seemed to throw some light on the origin of species—that mystery of mysteries" (Darwin 1859, p. 1) (**Figure 2.12**).

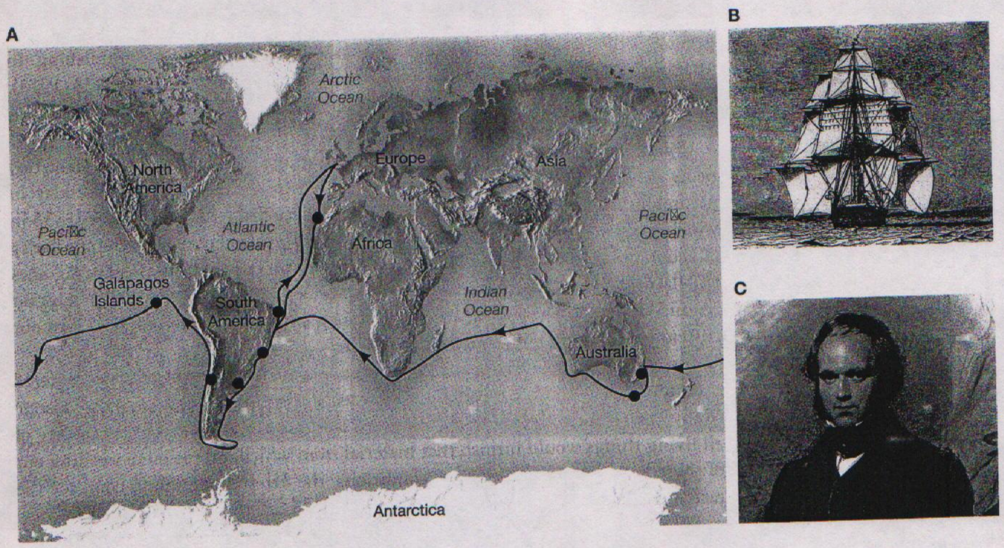


**FIGURE 2.12 The voyage of the *Beagle*.** **(A)** Map of the voyage of HMS *Beagle*, which began in England. **(B)** HMS *Beagle* was a 10-gun brig of the Royal Navy. **(C)** Portrait of a young Charles Darwin, shortly after returning from his journey aboard the *Beagle*.

As we have seen, some of Darwin's predecessors talked of evolutionary change and even of processes similar to natural selection. Darwin's *On the Origin of Species*, however, was the first to present a *complete theory* of evolution by natural selection and to support that theory with an enormous body of evidence: evidence that included, but was not limited to, his observations of finches, tortoises, coral reefs, and so much more in the Galápagos Islands (**Figure 2.13**).

Twenty-three years separated Darwin's return from his time on HMS *Beagle* and the publication of *On the Origin of Species*. Darwin postponed releasing his work, in part because he knew that his ideas were revolutionary, and he wanted to have the

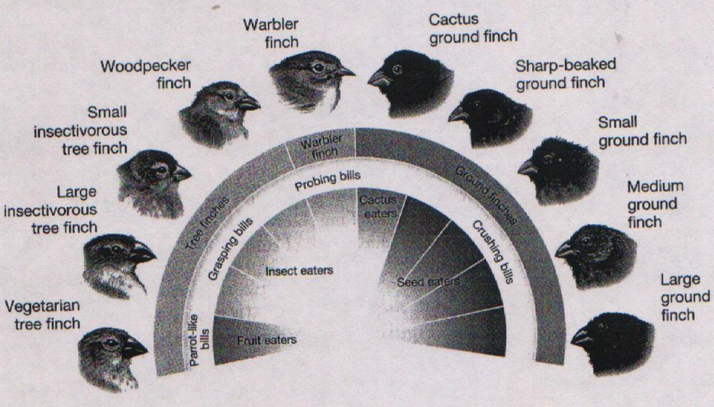


**FIGURE 2.13**
**Darwin's finches.** Darwin observed substantial variation in the beak morphologies of the finches across the Galápagos Islands. These observations, along with many others, led Darwin to formalize his ideas on the process of natural selection. Over the years, evolutionary biologists have studied how this variation in morphology maps to differences in food sources and feeding strategies.

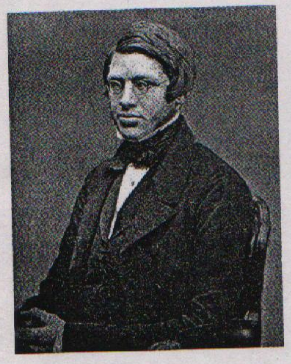

**FIGURE 2.14 Alfred Russel Wallace (1823–1913).** Wallace independently developed a theory of evolution by natural selection very similar to that of Darwin.

strongest possible case before unveiling them to both the scientific world and the general public. But in the end, competition pressured Darwin into publishing. In 1858, as part of an ongoing correspondence with Alfred Russel Wallace (1823–1913), Darwin received a manuscript in which Wallace proposed a theory very similar to his own (**Figure 2.14**).

Wallace was a brilliant natural historian, geographer, and collector; he identified many new species of birds and insects, and his collections can be seen today in natural history museums around the world. Wallace had written a paper in 1855 in which he speculated on the origin of species; there he concluded from the similarity of geographically nearby species that new species must arise from preexisting ones (Wallace 1855). Wallace's concept of how species are formed led him to suggest the hierarchical branching relationship among species that is fundamental to our current understanding of the diversity of life.

It was during a bout with malaria on the Spice Islands, however, as he suffered from fever, that Wallace figured out the mechanism that drives species to change (Raby 2001). As he recollected, "I at once saw that the ever present variability of all living things would furnish that material from which, by the mere weeding out of those less adapted to the actual conditions, the fittest alone would continue the race" (Wallace 1905, pp. 191–192). Darwin would call this process *natural selection*.

When Wallace wrote to Darwin outlining these ideas on evolution, Darwin yielded to pressure from friends and colleagues and publicized his own theories, first in a joint Darwin–Wallace paper that was read to the Linnaean Society in 1858 (with neither Darwin nor Wallace present), and later in longer form as *On the Origin of Species*. Wallace still holds a place in the pantheon of great evolutionary thinkers, but history primarily associates Darwin's name with the theory of evolution by natural selection. In large part this is due to Wallace's professional generosity. While his theory closely resembled Darwin's, Wallace graciously agreed that Darwin deserved the credit. Darwin had worked for decades on developing the theory and had amassed huge amounts of data from many sources to provide evidence for his theory of evolution by natural selection.

In 1859, when Darwin finally published *On the Origin of Species*, he laid out his evidence and his argument carefully, cognizant of the criticism his ideas would draw. But before he could describe either his data or the process involved in generating a new species, Darwin first needed to prepare his reader for what was to come. He did so cautiously, but in a strategically brilliant fashion.

## Means of Modification and Pigeon Breeding

The opening chapter of *On the Origin of Species* may strike the modern reader as odd, with Darwin writing:

> It is, therefore, of the highest importance to gain a clear insight into the means of modification. . . . At the commencement of my observations it seemed to me probable that a careful study of domesticated animals and of cultivated plants would offer the best chance of making out this obscure problem. (Darwin 1859, p. 4)

Indeed, Darwin writes about numerous domestication programs, with an emphasis on pigeon breeding (**Figure 2.15**). What most biologists consider the most important book ever written opens not with his grand theory explaining diversity of life on earth, but rather with an extended discussion of how to breed

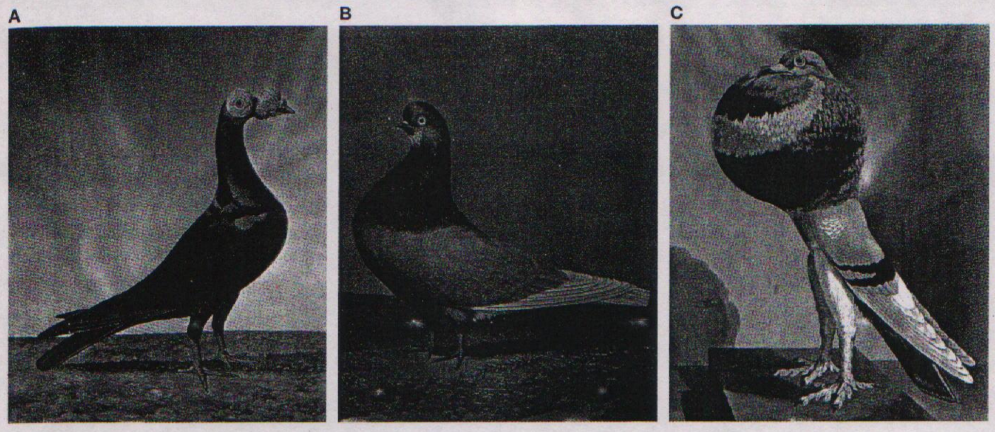


**FIGURE 2.15 Pigeon varieties.** Darwin used pigeon breeding to explain artificial selection to the readers of *On the Origin of Species*. Here we see three domesticated pigeon varieties: **(A)** the carrier pigeon, **(B)** the beard pigeon, and **(C)** the pouter pigeon.

for bizarre, if beautiful, pigeons. But there was a reason Darwin chose to do this. While this choice of subject matter appears unusual today, pigeon breeding was a popular pastime in Victorian England and would have been comfortingly familiar to Darwin's audience. With this example, Darwin set up an analogy that would help his readers of 1859 relate to the novel ideas in the rest of the book.

Darwin hoped to introduce readers to natural selection by first convincing them that the breeding programs that pigeon fanciers had developed—programs that had led to a wide range of extraordinary variation in pigeon color, flying habits, behavior, and so on—resembled the processes that led to differences within and between species in nature. Here, Darwin aimed first to illustrate the processes by which he thought species changed over time and second to help his readers get beyond their preconceptions of species as eternal and immutable. We address these two aims in turn.

## Artificial Selection

In artificial selection, humans systematically breed certain varieties of an organism over others. For thousands of years, humans have been shaping animals and plants by this process. Ever since our ancestors *selected* some varieties of wheat, corn, and rice over others, and systematically planted such seeds, we have engaged in artificial selection. The same process describes our systematic breeding of certain types of dogs and our domesticated livestock. The process that pigeon breeders developed is an example of *artificial selection*, whereas the process leading to the wide variety of traits we see in nature is *natural selection*.

Following Darwin, let us examine how artificial selection works in the context of pigeon breeding. Suppose that like pigeon breeders in Victorian days, we want to produce a variety of pigeon with snow-white plumage. We would begin our artificial selection process by systematically allowing only those individuals in our population with the whitest plumage to breed. We would then continue this process generation after generation, in each generation sorting the birds based on plumage coloration, and allowing the whitest—those that are closest to the type we want to produce—to breed. *If* offspring resembled their parents in terms of plumage coloration, each generation of offspring would have whiter and whiter feathers. Eventually, we would exhaust all genetic variation for plumage coloration, and, so far as possible, we would have achieved our goal of a snow-white pigeon (**Figure 2.16**).

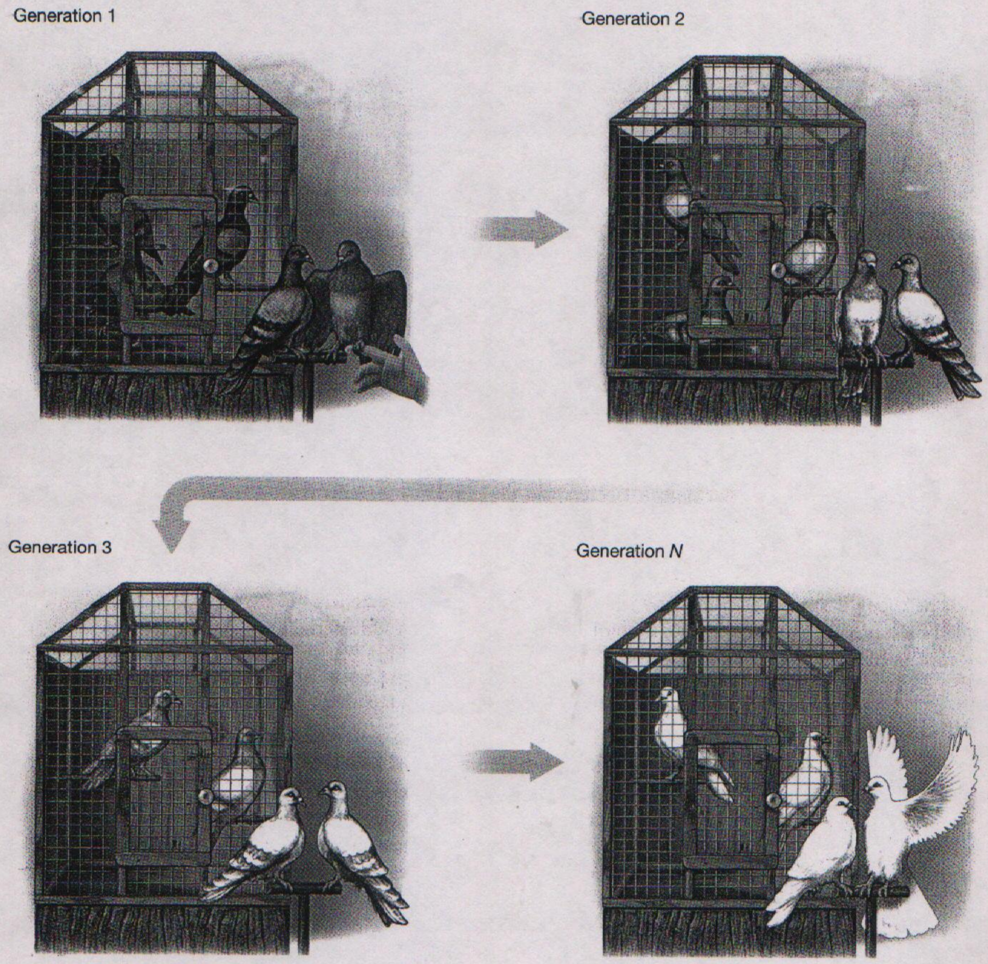


**FIGURE 2.16 Artificial selection for white plumage in pigeons.** Each generation, a breeder selects the pigeons with the whitest plumage and allows them to breed. Many generations later (generation *N*), at the end of the process, the breeder has a pigeon variety with much whiter plumage than that of the original stock.

**KEYCONCEPT** QUESTION

**2.3** Choose another example of artificial selection and describe a breeding program that would produce the desired aim of the breeder.

### Changing Species

While many of Darwin's contemporaries would have accepted the explanation of artificial selection as the mechanism producing new *varieties* of pigeons—pigeons with new colors, new morphological traits, new behaviors, and so on—the claim that this process could generate new *species* was much more controversial, as it implied that it would lead to original and new life-forms, an idea that was still widely unaccepted at the time. Darwin knew this all too well and in Chapter 2 of *On the Origin of Species*, he seems almost obsessed with the definition of a variety versus a species and with the problems in distinguishing between these two categories.

Darwin presents example after example in which one naturalist calls a group of organisms "species 1," while another classifies the same group as a "variety of species 2." In Darwin's eyes, the line between a variety and a species was arbitrary. He conceptualized species as merely "strongly marked and permanent varieties." Conversely, when he saw varieties, he viewed them as "leading to subspecies and then to species," and he often spoke of varieties as "incipient species"—species in the making.

Challenging the distinction between species and varieties was essential to Darwin's overarching argument. Pointing to examples in plant and animal breeding, Darwin could provide extensive evidence that new *varieties* often arise from a single stock through a branching mechanism of descent. Having established that varieties are similar to species, Darwin could then claim that they probably both respond to similar processes, most notably, some process of selection (artificial or natural). As such, he could argue that, like varieties, species change over time, and that new species arise from other species.

To explain how varieties were on the path to becoming new species, Darwin introduced the concept of descent with modification. For example, he hypothesized that if we want to understand how species 2 got to be what it is today, we need to recognize that it *descended* from another species—let's call it species 1—and that over evolutionary time, numerous *modifications* occurred. Darwin argued that these modifications resulted largely from the process he dubbed natural selection, a process analogous to the familiar technique of artificial selection that had been used by breeders for thousands of years.

Once Darwin had walked the reader of *On the Origin of Species* through the process of artificial selection and the concept of species as changing entities similar to varieties, he could move on to the details of the process of natural selection.

## 2.6 Darwin on Natural Selection

Darwin argued, over and over, that the process of natural selection resembles that of artificial selection. The two important differences between the processes are the *selective agent* and the *traits* being selected. With artificial selection, the selective agent is the human breeder who chooses which traits to modify and attempts to modify them in a way that is beneficial to the breeder. In the case of natural selection, we can think of nature as the selective agent, though nature is not, in any sense, a conscious agent in the way that humans are.

With respect to what traits are selected, Darwin noted,

> Man can act only on external and visible characters; nature cares nothing for appearances, except in so far as they may be useful to any being. She can act on every internal organ, on every shade of constitutional difference, on the whole machinery of life. (Darwin 1859, p. 83)

That is, the process of natural selection favors any variant of a trait that increases the survival and reproductive success of an individual, even if the difference is not easily detected by a human observer or if the increase in reproductive success is small.

## Darwin, Variation, and Examples of Natural Selection

In part by taking Lyell's ideas on uniformitarianism and applying them to biology, Darwin hypothesized that evolution by natural selection is a gradual but powerful process. He argued that the process of natural selection acts on small differences between individuals. If one variety of a trait leads to even a small reproductive advantage compared to other varieties, it will be favored by natural selection. These small differences can translate into much larger changes as they accumulate over evolutionary time.

For example, Darwin asked his reader to imagine the wolf that "preys on various animals, securing some by craft, some by strength, and some by fleetness" (Darwin 1859, p. 90). When prey animals are scarce—and prey are almost always scarce—natural selection acts strongly in such wolf populations. Wolves that possess the traits that best suit them for hunting (speed, stealth, and so on) tend to survive longer and produce more offspring. These offspring in turn are likely to possess the traits that benefited their parents in the first place. The repetition of this process for generation after generation produces wolves that are very efficient hunters. "Slow though the process of selection may be," noted Darwin, the eventual outcome is a more effective wolf predator.

Darwin applied similar arguments to many other examples in nature. Among these, he discussed the process of natural selection on plants that rely on insects as their pollinators. Darwin saw this case as more complicated than the case of the wolves, because insects often eat most of the plant's pollen. He argued that natural selection might nonetheless favor plant traits that foster more efficient insect pollination, because only a small amount of pollen is needed by the plant for fertilization (**Figure 2.17**). Darwin explained:

> . . . as pollen is formed for the sole object of fertilisation, its destruction appears a simple loss to the plant; yet if a little pollen were carried . . . by the pollen-devouring insects from flower to flower, and a cross thus effected, although nine-tenths of the pollen were destroyed, it might still be a great gain to the plant; and those individuals which produced more and more pollen, and had larger and larger anthers, would be selected. (Darwin 1859, p. 92)

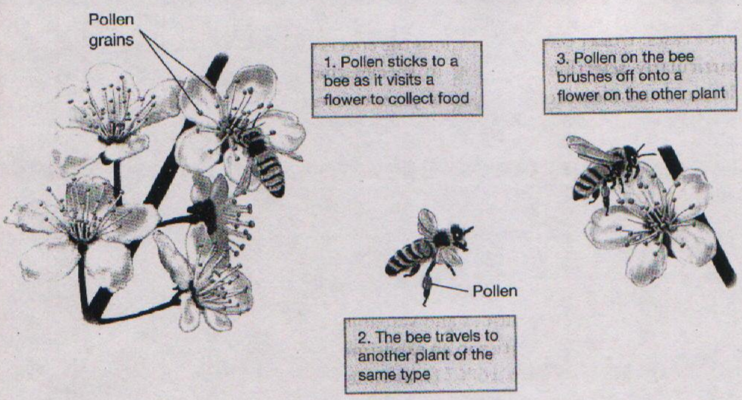


**FIGURE 2.17 Plants and their pollinators.** Darwin discussed the relationship between plants and the insects that cross-fertilized them as an example of how natural selection operates. Insects, such as the bee seen here, may eat some of the pollen produced by a plant, but if they move enough pollen from plant to plant, their actions may be in the plant's reproductive interests as well.

Once we see traits in terms of their effect on overall *reproductive success*—as Darwin did for wolves, insect-pollinated plants, and myriad other examples—the concept of natural selection becomes a powerful tool for understanding the world around us.

## The Power of Natural Selection

Darwin's own writings demonstrate that he attributed enormous power to the process of natural selection. He ends the introductory chapter of *On the Origin of Species* by claiming, "I am convinced that natural selection has been the most important, but not the exclusive, means of modification" (Darwin 1859, p. 6). Darwin lays out his position in even more detail for the reader in a later passage:

> It may be said that natural selection is daily and hourly scrutinising, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages. (Darwin 1859, p. 84)

This is a very powerful statement. For Darwin, the process of natural selection operated 24 hours a day, every day, everywhere, over vast periods of time. Only a process of such magnitude could have shaped all the life that we see around us and, for that matter, all life that has ever lived. As long as offspring resemble their parents with respect to a given trait, any differences in reproductive success associated with varieties of a given trait will be acted on by natural selection. This includes differences so slight that even the most thorough and patient human investigator might struggle to detect them.

An analogy might help here: The process of natural selection acts as an editor, removing what is not as well suited to its environment by increasing the frequency of what is better suited. Changes take place constantly, but usually they will not manifest in measurable differences until the passing of eons. In later chapters, we

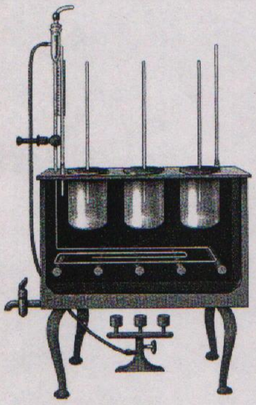

**FIGURE 2.18 Experimental evolution, circa 1880.** The device that William Dallinger used to examine evolutionary change in temperature tolerance in protozoa over the course of his 7-year experiment. Adapted from Dallinger (1887).

will see that Darwin underestimated the potential rate of evolutionary change in some cases. Under certain conditions the effects of the process of natural selection—particularly selection operating in species that reproduce very quickly—can be detected and measured in a span of years or even less.

Even in Darwin's day, researchers found that they could observe evolutionary change on human timescales. From 1880 through 1886, clergyman, microscopist, and Royal Society member William Dallinger conducted a 7-year **experimental evolution** study in which he tracked changes in temperature tolerance in communities of three protozoan species in which cells reproduced on average every 4 minutes (Dallinger 1887; Haas 2000).

Dallinger, encouraged by Darwin, who wrote to Dallinger that his work will "no doubt . . . be extremely curious and valuable," began by placing large populations of his protozoan communities in an experimental device he built (**Figure 2.18**) and setting the temperature at 16°C. Over time, he gradually raised the temperature. Each time he did so, many cells died, unable to survive at the higher temperature. But some cells, those with the highest thermal tolerance, survived. After the experiment had been going on for 7 years, the cells in Dallinger's experimental device survived at temperatures in excess of 66°C. This adaptation to high temperatures came at a cost—cells that could survive at 66°C died when exposed to the 16°C in which their ancestors flourished.

## Malthus and the Scope of Selection

Before his readers could accept the potency of evolutionary change, Darwin needed them to reconsider their beliefs about survival in the natural world. To do this, Darwin used an analogy. Just as selective breeders must discard numerous individuals bearing undesirable traits in order for artificial selection to work, "nature" must "discard" numerous individuals in order for natural selection to be effective. While it may seem obvious to us, in Darwin's time this concept ran against the prevailing notion of an orderly, efficient, and harmonious operation of nature.

To persuade his readers that his mechanism of natural selection could shape the natural world, Darwin first had to prove to them that nature was sufficiently "wasteful" for selection to operate. That is, he needed to demonstrate to his readers that many individuals did not survive to the age of reproduction, and of those that did, only a fraction actually reproduced. To do this, Darwin drew on the ideas of Thomas Robert Malthus (1766–1834), an English political economist and demographer.

Malthus noticed that human population, unless kept in check by war, famine, disease, or other causes, grows geometrically in time (Malthus 1798). He contrasted the geometric growth of unconstrained human populations with the growth of food production, which he believed could increase at best arithmetically (**Figure 2.19**). As a result, Malthus argued that humans would inevitably outstrip the available resources necessary to sustain themselves, and that population growth would inevitably be checked by famine, war, disease, or other forces.

Darwin recognized that Malthus' argument applies to animal and plant populations as well as to human populations. For animal and plant populations in nature, food supply is usually not increasing at all, yet the power of reproduction would lead to a geometric increase in population size if growth were not checked by a struggle for existence. The difference between the potential growth and the maximum size allowed by the food supply denotes the number of individuals lost in the struggle

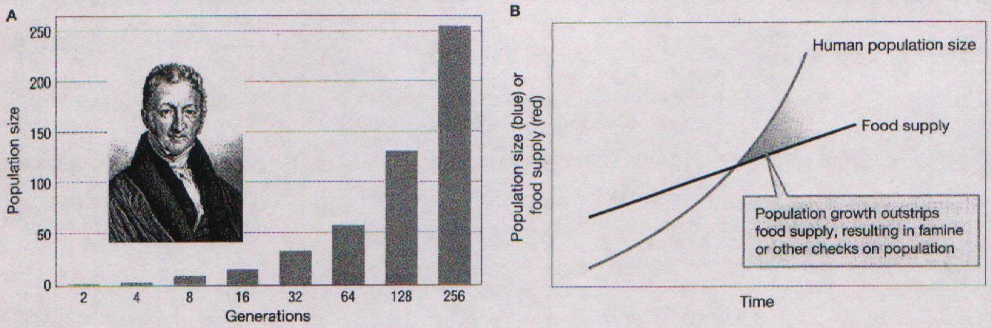


**FIGURE 2.19 Malthus and population growth.** Thomas Malthus argued that humans would outstrip the available resources necessary to sustain themselves, leading to population growth that would be checked by famine, war, and disease. Malthus' writings were influential in helping Darwin develop his ideas on natural selection. **(A)** Geometric population growth is shown in this graph. If each mother produces two replacements for herself, a single mother at time 0 gives rise to 2 additional mothers after a single generation. There will then be 4 mothers after 2 generations, 8 after 3 generations, 16 after 4 generations, and so forth. **(B)** Malthus argued that the human population was geometrically increasing (blue curve) and thus would inevitably outstrip its food supply (red curve), which he believed to be arithmetically increasing.

for existence, and thus it represents the opportunity that natural selection has to sort based on even the smallest differences in form (**Figure 2.20**). Darwin neatly summarized this as follows:

> As many more individuals of each species are born than can possibly survive; and as, consequently, there is a frequently recurring struggle for existence, it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be *naturally selected*. (Darwin 1859, p. 5)

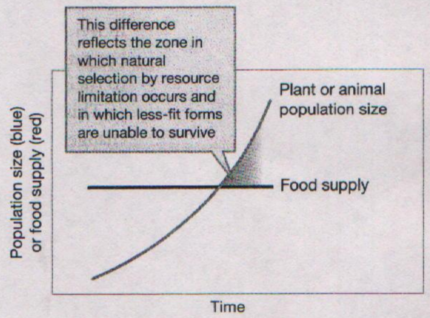


**FIGURE 2.20 Darwin, Malthus, and natural selection.** Darwin adapted Malthus' argument to natural populations of plants and animals. The food supply curve (red) is flatter here than in Figure 2.19. In that figure, the food supply curve also increased as a result of human innovations in food production.

## Transformational and Variational Processes of Evolution

Darwin's mechanism of evolutionary change differed radically from previous concepts of evolution. Before Darwin, scientists had envisioned change as a **transformational process**, in which the properties of an ensemble change because every member of the ensemble itself changes. For example, a mountain range becomes less rugged and more rounded over geological timescales because *each* individual peak itself becomes more rounded.

Lamarck's theory of evolution was a transformational theory. According to Lamarck, the properties of a lineage of organisms shift over time because of changes that each member undergoes during its lifetime and then passes along to its descendants. By contrast, Darwin's theory of evolutionary change was a variational one. In a **variational process** of evolution, the properties of an ensemble change, not because the individual elements change, but rather because of the action of some process *sorting* on preexisting variation within the ensemble (Levins and Lewontin 1987). For Darwin's theory, that sorting process was the process of natural selection.

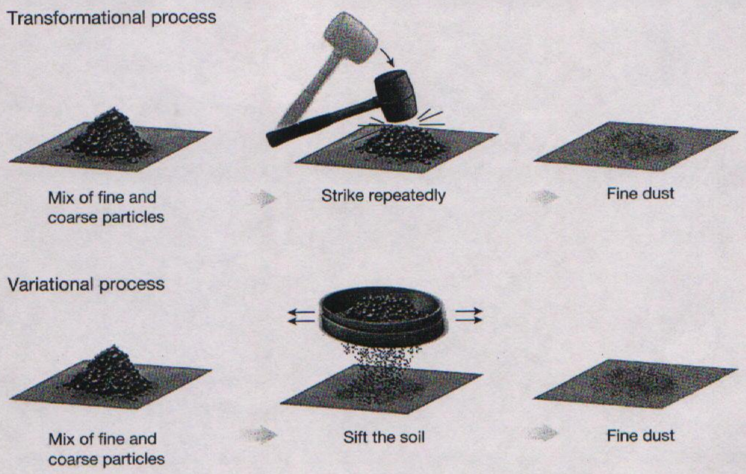


**FIGURE 2.21 Different processes of change.** In a transformational process, the ensemble changes because each individual member changes. In a variational process, the ensemble changes because something sorts among the variants in the original ensemble. In this example, crushing the soil particles is a transformational process—the ensemble shifts toward smaller particles because the individual particles are reduced in size. Sifting the soil is a variational process—the ensemble shifts toward smaller particles because the larger particles are sorted out.

To see how such a sorting process operates, imagine sifting a bucket of soil with particles ranging in size from fine sand to small pebbles. After sifting, the soil particles remaining in the sifter will be considerably larger on average than those in the original soil mixture. This is not because of any change on the part of individual particles—no transformation in the size of soil particles has occurred—but rather it is because the sifter has sorted the members of the ensemble according to their characteristics (**Figure 2.21**).

This kind of sorting process is what takes place when we use artificial selection to change the characteristics of a breed of animals or plants. And just as a pigeon breeder sorts on variation when selecting breeding pairs so as to produce a snow-white pigeon, the conditions of existence sort on variation within the members of species. Natural selection favors those variants that survive and outreproduce other variants, while passing on their characteristics to their offspring.

To arrive at his theory of evolution by natural selection, Darwin needed not only to establish that the process of natural selection involves "wasteful" deaths within populations but also to dispel the belief in an eternally unchanging world, as discussed earlier in this chapter. To arrive at a specifically *variational* theory of evolution, Darwin also had to reject the existing conception of nature that viewed any variation as aberrant and unimportant, and instead place variation itself in the forefront, as an absolute necessity for a sorting process without which variational evolutionary change cannot occur.

## **KEYCONCEPT** QUESTION

**2.4** Robert bought a small iPod that held a small fraction of his full CD collection. It seemed like too much trouble to select his favorite CDs, so he simply picked 50 of his discs at random and put them on the iPod. Each month, he deleted any of the albums that he didn't listen to over the past month; he added new ones, again selected randomly, in their place. At first, Robert thought the music on his iPod was so-so, but after a year, he thought the music it contained was really great. Is this a transformational or variational process of evolution? Explain.

## 2.7 Darwin on Common Ancestry

Thus far in the chapter, we have concentrated on the details of Darwin's first insight, the process of natural selection. We now turn to the second of Darwin's revolutionary insights, his answer to the question: Where do species come from? Darwin correctly recognized that all living creatures derive from one or a few common ancestors, and that new species are formed when populations of a preexisting species diverge from one another.

### The Tree of Life

In *On the Origin of Species*, Darwin explained that just as artificial selection can create multiple new varieties from a single domesticated variety, natural selection can, over time, generate multiple new species from a single ancestral species. Indeed, Darwin conjectured that the vast diversity of species that we see throughout the world has arisen from precisely this process.

Darwin's explanation suggests that all living things are linked by a pattern of descent dramatically different from that implied by either special creation—the idea that each species was created in its current form by a supernatural deity—or Lamarck's theory of evolution (**Figure 2.22**). While these latter explanations envision species as a set of independent organisms, Darwin's theory links species according to their historical pattern of descent.

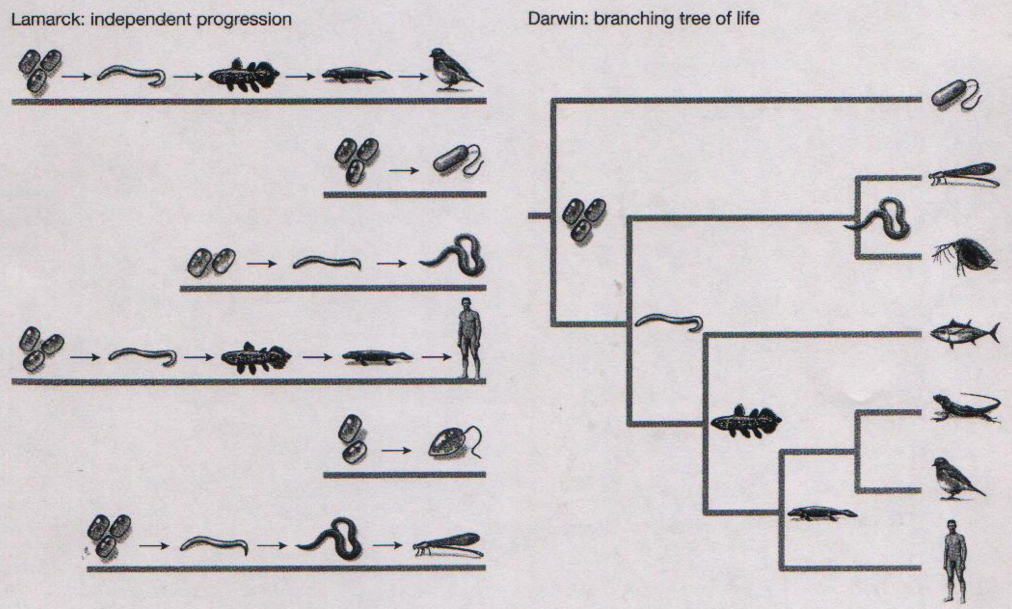


**FIGURE 2.22 Darwin's theory versus Lamarck's theory.** In Lamarck's theory, species evolve independently and in parallel; in Darwin's theory, species are descended one from another to form a branching tree of life.

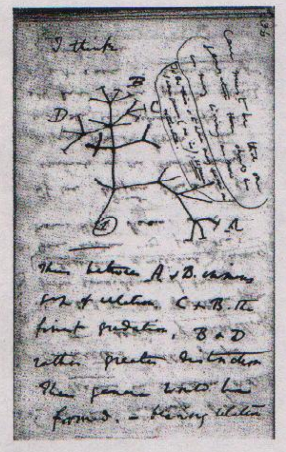


**FIGURE 2.23 An early phylogenetic tree from Darwin.** One of Darwin's first sketches of the branching relationships among species.

Darwin described the branching historical relationships among all living things using the metaphor of a tree of life (**Figure 2.23**). His eloquent depiction of the tree of life requires us to look at a lengthy quote, but this quotation is worth reproducing because of the profound implications of the tree of life metaphor:

> The affinities of all the beings of the same class have sometimes been represented by a great tree. I believe this simile largely speaks the truth. The green and budding twigs may represent existing species; and those produced during each former year may represent the long succession of extinct species. . . . The limbs divided into great branches, and these into lesser and lesser branches, were themselves once, when the tree was small, budding twigs. . . . Of the many twigs which flourished when the tree was a mere bush, only two or three, now grown into great branches, yet survive and bear all the other branches; so with the species which lived during long-past geological periods, very few now have living and modified descendants. From the first growth of the tree, many a limb and branch has decayed and dropped off; and these lost branches of various sizes may represent those whole orders, families, and genera which have now no living representatives, and which are known to us only from having been found in a fossil state. . . . As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications. (Darwin 1859, pp. 129–130)

Darwin recognized the enormous importance of the branching relationships among species in this tree of life as a model for both life's history and the patterns of life's diversity. He chose to include only a single figure in *On the Origin of Species*, and this figure serves to illustrate the branching historical relationships among all living things (**Figure 2.24**). Today, we refer to this type of figure as a phylogenetic tree.

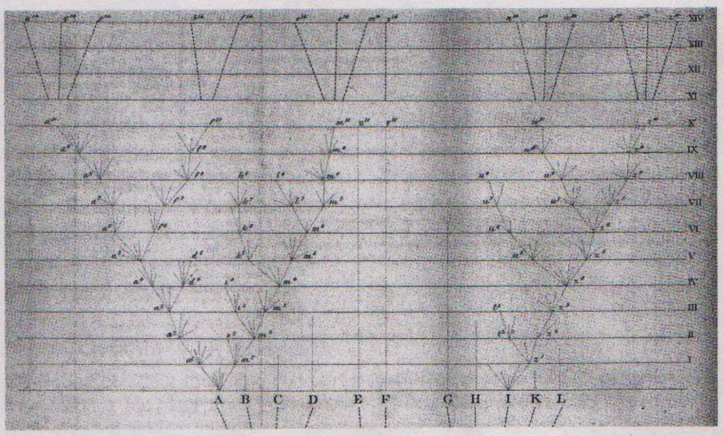


**FIGURE 2.24 A phylogenetic tree from *On the Origin of Species*.** Darwin included this diagram as the sole figure in *On the Origin of Species*. It illustrates the pattern of branching relationships among a number of initial populations (A–L) over vast periods of time (time moves forward as one moves up the vertical axis, from I to XIV).

## Groups within Groups

A major point supporting the hypothesis of common ancestry with branching descent is that it explains hierarchical patterns of similarity that are observed in nature. By hierarchical patterns of similarity, we mean something like this: Different species of squirrels resemble each other more than they resemble any species of deer. And different species of deer resemble each other more than they resemble any species of squirrel. That is, species of squirrels *cluster* together because of their similarity to one another, and species of deer *cluster* together. At a different hierarchical level, species of squirrels and deer are more similar to one another than either is to a species of frog. And so, at this hierarchical level, species of squirrels and deer cluster together (as mammals), and species of frogs, toads, and salamanders cluster together (as amphibians). Finally, squirrels, deer, frogs, and toads are all more similar to one another (as vertebrates) than they are to species of octopus or squid (invertebrates).

In *On the Origin of Species*, Darwin argues that branching descent explains this hierarchical patterning seen in nature, writing that "the forms of life throughout the universe become divided into groups subordinate to groups" (Darwin 1859, p. 59). Neither special creation nor a theory such as Lamarck's can explain these groupings and subgroupings of organisms. But a process of branches dividing and subdividing naturally gives rise to a hierarchical structure of relationships—varieties nested within species within genera (a *genus*, the singular of genera, is a taxonomic group, intermediate in scale between species and families), and so on up to kingdoms. Indeed, the modern field of **systematics**—the naming and classification of organisms—is based on the conceptual foundation of this hierarchical branching structure. As we will see in further detail in Chapter 4, evolutionary systematists aim to classify organisms into hierarchically arrayed groups, or *clades*, of organisms that have descended from a common ancestor (**Figure 2.25**).

Darwin's view of common descent provides an explanation not only for the hierarchy of organisms now studied by systematists but also for the clustering of species: "No naturalist pretends that all the species of a genus are equally distinct

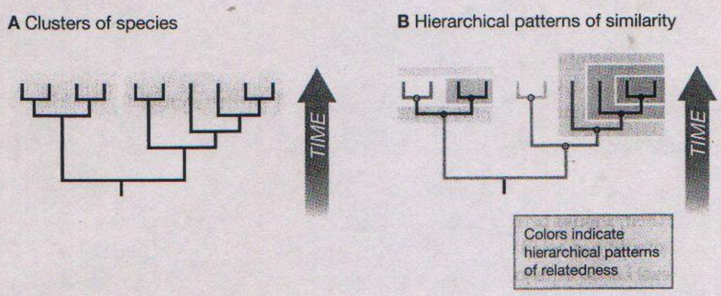


**FIGURE 2.25 Branching descent, clustering, and hierarchy.** Darwin's view of branching descent explains both the clustering of species in terms of similar form (**A**) and the hierarchical patterns of similarity (**B**) that we can discern when studying groups of species. In panel B, some of the different clades are shown in different colors, with the node representing the common ancestor of that entire clade in the clade's characteristic color.

from each other," Darwin told the reader of *On the Origin of Species* (Darwin 1859, p. 57). That is, we expect to see clusters at many levels, including that of the genus. Darwin reasoned that this clustering arose as a result of common ancestry. Groups of closely related species share common characteristics, in large part because they share a recent common ancestor.

## Common Descent and Biogeography

Both Wallace and Darwin traveled extensively across the globe, and in doing so, both were struck by the strong patterns that they observed in the geographic distribution of nature's diversity. In his 1855 paper that preceded Darwin's *On the Origin of Species* by 4 years, Wallace noted that living species tend to be similar to other species that are geographically nearby, and that species from the fossil record tend to be most similar to species that lived around the same time. In other words, species that closely resemble one another tend to be closely clustered in time and space, and from this observation Wallace proposed that "Every species has come into existence coincident both in space and time with a pre-existing closely allied species" (Wallace 1855, p. 186).

Wallace recognized that this pattern of descent—new species coming into existence from previous species—implies the branching system of phylogenetic relationships that we have described in detail earlier in this section. Like Darwin, Wallace proposed a tree metaphor in which groupings of species form a "complicated branching of the lines of affinity, as intricate as the twigs of a gnarled oak or the vascular system of the human body" (Wallace 1855, p. 187).

Darwin came to similar conclusions about the causes for groupings of species based on similar evidence. In *On the Origin of Species*, Darwin notes that similarities in "conditions of existence"—climate and physical conditions, for example—are insufficient to explain the geographic clustering of similar, closely related species. Instead, he thought that geographic features seemed to play an important role. He described the following pattern: Species separated by major geographic barriers to migration—mountain ranges, deserts, or large bodies of water—tend to be dissimilar even when the climate and physical conditions are similar on each side of the divide. Adjacent species that are not separated by geographic barriers tend to be similar to one another despite major differences in climate and habitat.

Darwin found some examples that seemed to violate the tenet that species separated by major geographic barriers to migration tended to be dissimilar, and he wanted to understand why. For example, while on the *Beagle* Darwin took note of how similar plants on mainland South America were to those on nearby islands. But the ocean separated the mainland and islands, and plants can't swim. The ocean, then, should be a major geographic barrier, and plants on the mainland and island should not be all that similar. The solution, Darwin posited, was that while the ocean *can be* a major geographic barrier to plant dispersal, *in this case* it was not, because seeds could survive in salt water and be transported by ocean currents to islands. Darwin even ran a series of experiments in which he tested whether seeds soaked in salt water survived to germinate, and found that they did (Darwin 1855a,b, 1857). Darwin also hypothesized that bivalves from the South American mainland might be transported to the islands when adhering to the mud-soaked feet of ducks, and evidence he had gathered from other friends suggested they might (Darwin 1882). Species separated by true geographic barriers to migration do tend to be dissimilar, but Darwin discovered that one must be very careful about what constitutes a true geographic barrier.

These geographic correlations supported Darwin's theory that each species arises only a single time in a single place, by descent with modification from a closely related species. Darwin then proposed the grandest uniformitarian extrapolation in the history of science. From these patterns he observed among groups of related species, Darwin hypothesized that in fact all living things have descended, with modification, from one or a few common ancestors. If so, all living things—plants, protozoa, humans, birds, insects, and every other life-form—share a common origin. In the next few chapters, we will explore the overwhelming weight of evidence that has since accumulated in support of Darwin's conclusion. But first, we will consider some of the problems with his theory of descent with modification that troubled Darwin in his lifetime.

## 2.8 Problems with Darwin's Theory

In science, no grand theory is without its problems, especially in its early stages. The important issue is whether scientists acknowledge such problems and generates new hypotheses or simply ignores any inconsistencies. In *On the Origin of Species*, Darwin was not afraid to discuss many of the problems associated with his theory of evolution by natural selection.

Here we briefly touch on three of the major challenges that Darwin faced, and we provide pointers to where we will discuss some of these problems in greater detail in later chapters. Although not all of these challenges were resolved within Darwin's lifetime, today we have a good understanding of how to account for each of them. In Chapters 6 and 7, we will also show how another challenge Darwin faced—understanding how inheritance operated—was finally resolved.

### Problem 1: Accounting for Complex Structures with Multiple Intricate Parts

Darwin generally portrayed natural selection as a slow process acting on very small differences between individuals. It is relatively straightforward to see how this process could lead to gradual adjustments in the thickness of an otter's fur or the length of a badger's forelimb. But how might natural selection operate as a genuinely creative process? How might it generate complex structures such as the eye, the mammary gland, or the instincts needed to construct the hexagonal cells of a honeycomb (**Figure 2.26**)?

Darwin's critics seized on this issue. If natural selection operates by gradual increments, they reasoned, the eye must be preceded by a quarter of an eye, then half of an eye, and so forth—and what good is half of an eye? These critics argued that

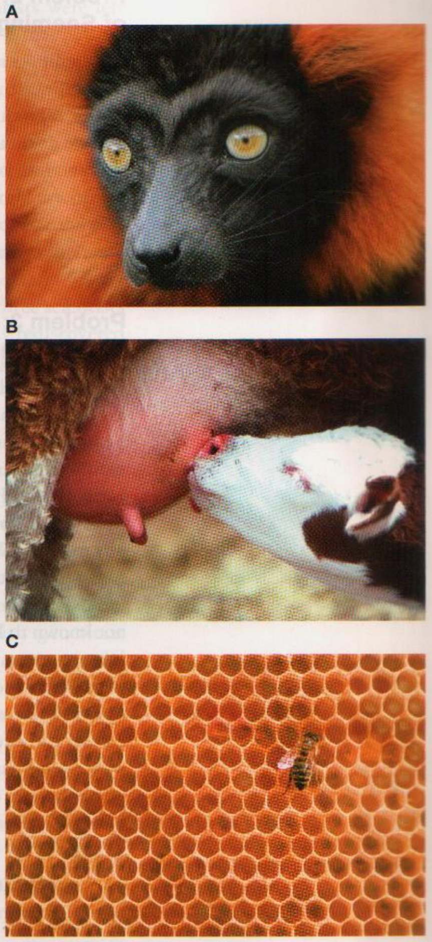


**FIGURE 2.26 Complex traits.** One of the challenges that Darwin faced was to explain how natural selection could create complex traits such as **(A)** the vertebrate eye, **(B)** the mammary gland, or **(C)** the ability to construct the hexagonal cells of a honeycomb.

complex traits would have no selective value until fully formed, and thus natural selection would not favor the intermediate steps necessary along the way. Darwin responded to this challenge with confidence; we will explore his explanation in depth in Chapter 3.

### Problem 2: Explaining Traits and Organs of Seemingly Little Importance

At the opposite extreme, Darwin wondered how his theory could explain traits that appear to lack any biological function. If a trait does not contribute to survival and/or reproductive success, it will not be favored by natural selection, and yet it seemed as though such traits existed. Snakes have "limb buds" that appear to have no function, ruminants have incisor teeth that never break through their gums, and so on. How can these things be explained? We explore the answers in Chapter 4 (where we treat vestigial traits) and Chapter 8 (where we consider the neutral theory of evolution).

### Problem 3: Why Does Variation Persist in the Face of Natural Selection?

As we saw earlier in this chapter, Darwin's theory relied on a variational process of evolution rather than a transformational one. This posed a problem: In order for natural selection to operate, it must have variation to sort on—but the action of natural selection itself reduces the amount of variation in a population as less-fit variants are eliminated from that population. Thus, the fire of natural selection threatens to consume the variation that fuels it. How can we explain the persistence of variation? Why doesn't evolution just come to a halt as variation is exhausted?

Adding to the scope of the problem, when Darwin wrote *On the Origin of Species*, biologists did not understand the basic principles of heredity. Mendel's laws were not known to Darwin; instead, like most of his contemporaries, Darwin envisioned inheritance as a blending of the hereditary elements from each parent. Such a blending process also consumes variation. In Chapters 6 and 7, we will explore the sources of new variation, and in Chapter 9, we will see how scientists in the early part of the twentieth century reconciled the process of inheritance with Darwin's ideas about natural selection.

## 2.9 The Reaction to Darwin and Early History of the Modern Synthesis

While various religious leaders challenged almost all of the major conclusions that Darwin presented in *On the Origin of Species*, the scientific community exhibited a more mixed reaction (Mayr 1982). Early on, for example, British scientists almost universally embraced Darwin's ideas on common ancestry, but many were unconvinced that the primary force generating evolutionary change was natural selection. That is, they accepted that evolutionary change, rather than special acts of creation, explained the world that we see around us, but they rejected the idea that the primary force generating evolutionary change was natural selection. A few British naturalists, including Alfred Russel Wallace, Henry

Walter Bates (1825–1892), and Joseph Dalton Hooker (1817–1911), thought that natural selection was important in driving evolutionary change, but many early evolutionary biologists disagreed (Glick 1974).

In the 1880s, experimental work—primarily that of German geneticist and evolutionary biologist August Weismann (1834–1914), who demonstrated that traits acquired during the lifetime of an organism could not be inherited—dealt a death blow to previous theories of Lamarckian inheritance. Scientists were left with only two possible mechanisms of evolution. The processes were either natural selection acting in a slow and methodological way on small genetic differences or **saltationism**; that is, "evolution via large, sudden changes from the existing norm" (Mayr 1982).

In his now-famous experiments of the 1850s and 1860s, Augustinian monk, plant breeder, and biologist Gregor Mendel (1822–1884) found that inherited factors that form the basis of traits come from both parents. His work on pea plants demonstrated that each parent plant has two copies of each gene, and that the two gene copies separate with equal probability into gametes (eggs, sperm, pollen, and so on). In Chapter 6, we will discuss Mendel's experiments in more detail.

Mendel's results remained virtually unnoticed until 1900, when three scientists (Hugo de Vries, Carl Correns, and Eric von Tschermak) independently rediscovered his work and made it available to the scientific world. Biologists began to explore how natural selection might operate when inherited material operated as Mendel suggested.

At that time, evolutionary biologists fell into one of two camps. On one side were the Mendelians, who viewed evolution as a saltational process. These scientists primarily worked in the lab, were trained more as physical than as biological scientists, and thought that the continuous variation in so many traits seen in nature was not primarily genetic in origin. This was because the Mendelian camp's original interpretation of Mendel's work allowed for discrete variation—for example, tall versus short—but not continuous variation in traits. In the other camp were the biometricians, including the English geneticist and statistician Karl Pearson (1857–1936). The biometricians were impressed by the amount of continuous variation—that is, extremely fine gradations of difference—that they saw all around them and thought natural selection was a slow, gradual process.

The differences between the Mendelians and the biometricians began to dissolve with experimental work in the 1930s and 1940s in what came to be called the **modern synthesis**, or the **evolutionary synthesis**. This synthesis included experimental work in genetics demonstrating that:

- Genes are passed on from parents to offspring in an intact form, even if they are not expressed in the offspring's phenotype. That is, genes are particulate: they don't "blend" with other genes.
- One source of genetic variation is mutation.
- Genetic variants that generate large and small phenotypic differences are not qualitatively different from one another—the effects of large differences may be more pronounced, but genetic variation is generated and inherited in similar ways in both cases.
- Not all genetic mutations are harmful, so positive changes can accrue over time—either slowly or in some cases more rapidly.

- Sexual reproduction is an important contributor to the production of massive amounts of genetic variation.
- Some traits are the result of the interaction of numerous genes, while some genes can affect more than one trait, helping to explain the evolution of complex traits without necessarily assuming some saltational (that is, large and sudden) change.
- Many (but not all) changes in the genotype affect the phenotype. Variation in the phenotype is the raw material for natural selection.

We discuss each of these points in more depth in later chapters, but for now, what we wish to emphasize is that this work demonstrated that there was no conflict between what was being found in the new, burgeoning field of genetics and Darwin's idea that evolutionary change was primarily a slow process, driven by natural selection. Another crucial ingredient of the modern synthesis was the work of mathematical population geneticists such as Sir Ronald A. Fisher (1890–1962), Sewall Wright (1889–1988), and J. B. S. Haldane (1892–1964), who developed mathematically sophisticated models of how evolutionary processes lead to changes in gene frequencies and how changes in gene frequencies map onto changes in the phenotypes of organisms (Chapters 7–9).

The modern synthesis represented the collected efforts of systematists, geneticists, paleontologists, population biologists, population geneticists, and naturalists. Although often associated with the publication of British biologist Julian Huxley's (1887–1975) book, *Evolution: The Modern Synthesis*, this synthesis was not so much an event per se, but the result of a gradual accumulation of information that melded together to shape biology at the time (Huxley 1942). In addition to the work listed earlier, this synthesis involved a combination of theoretical models and experimental manipulations, like that of German-American evolutionary biologist and ornithologist Ernst Mayr's (1904–2005) pathbreaking work on the process of speciation and its relationship to systematics (classifying organisms) (Mayr 1942). In essence, the evolutionary approach provided a framework for understanding both the fit of organisms to their environment and the diversity and history of life. We will discuss the major findings of the evolutionary synthesis in many subsequent chapters.

We have seen that midway into the nineteenth century, thinkers began to develop mechanistic, rather than supernatural, explanations for the world around them, and science as a whole began to center on experimentation, data gathering, and hypothesis testing. Theories in geology had created a sense of deep time and gradual, versus catastrophic, changes. Robert Chambers and others had suggested that new species might arise from existing species, Jean-Baptiste Lamarck had hypothesized that there were generational adaptations to environmental needs, and Patrick Matthew had presented a preliminary theory of natural selection. It was in this context that Charles Darwin developed his ideas. Having laid out both the basic elements of Darwin's theory and the problems facing that theory, we are now in a good position to examine the components of evolutionary change in subsequent chapters.

## SUMMARY

1. Critical changes that set the stage for Darwin and Wallace to come up with their ideas on evolutionary change and natural selection included the shift from supernatural to natural explanations, the move from catastrophism to uniformitarianism, the use of logic and pure reason, the acceptance that the world—both the biotic and abiotic worlds—was constantly changing, and the rejection of the idea that life formed by spontaneous generation.
2. Scientists sought mechanistic rather than supernatural explanations for the features of the physical world; they valued experimentation, data gathering, and hypothesis testing.
3. Lyell's ideas in geology created a sense of deep time, Robert Chambers and others proposed that new species arose from existing species, Jean-Baptiste Lamarck hypothesized generational adaptations to environmental needs, and Patrick Matthew presented a preliminary theory of natural selection.
4. Darwin prepared his readers for his revolutionary ideas on natural selection by introducing them to the artificial selection programs that breeders had long used.
5. Darwin's ideas on natural selection put variation at the forefront of evolutionary change. In this way, they differed dramatically from the transformational evolutionary changes that Lamarck had suggested at the start of the nineteenth century.
6. Darwin had two great insights: (1) natural selection occurs because populations are variable and because some individuals are more successful than others at surviving and reproducing in their environment, and (2) all species have descended from one or a few common ancestors; species that share a recent common ancestor tend to resemble one another in many respects for the very reason that they share recent common ancestry.

## KEY TERMS

catastrophism (p. 34)
evolutionary synthesis (p. 59)
experimental evolution (p. 50)
hypothesis (p. 32)
inheritance of acquired characteristics (p. 39)
methodological naturalism (p. 32)
modern synthesis (p. 59)
natural history (p. 36)
population (p. 38)
saltationism (p. 59)
spontaneous generation (p. 36)
struggle for existence (p. 37)
systematics (p. 55)
transformational process (p. 51)
uniformitarianism (p. 34)
variational process (p. 51)

## REVIEW QUESTIONS

1. What is methodological naturalism? Why is it an important foundation for science?
2. How did the discovery of fossils by the ancient Greeks help lead to the view that the world changes over time?
3. How did Lyell's uniformitarianism help set the stage for Darwin's ideas on evolution by natural selection?
4. In the Middle Ages, what did people believe about the age of Earth? What evidence led to this conclusion?

5. Define spontaneous generation. Why did early observations of bacteria and fungi using microscopes delay the abandonment of the idea of spontaneous generation?
6. What do evolutionary biologists mean by the inheritance of acquired characteristics?
7. What are Darwin's "two great laws"?
8. What are the two most important differences between artificial selection and natural selection?
9. What did Wallace conclude from the observation that "Every species has come into existence coincident in both space and time with a pre-existing closely allied species"?
10. Within the context of evolutionary biology, what is the difference between transformational and variational processes?
11. Explain why the linear hierarchy of Aristotle's *scala naturae* is incompatible with Darwin's phylogenetic view of biological diversity.

## KEY CONCEPT APPLICATION QUESTIONS

12. Why do you think the discovery that species go extinct was important for the development of evolutionary ideas?
13. Sarah bought herself a cheap turntable and a stack of her favorite records on vinyl. Unfortunately, each time she played a record, the poor-quality phonographic needle scratched and wore down the record, so that after a year, her music collection didn't sound nearly as good as when she first bought it. Is this a transformational or variational process of evolution? Explain.
14. It is well known that many lizard species have evolved the ability to detach their tails as a mechanism of escaping from the grasp of predators. In his *Natural History*, Pliny the Elder (23–79 C.E.) spins a similar tale about beavers (Healy 1991). He reports that beavers castrated themselves in order to escape hunters who pursued them for their testicles, which could be used to produce an analgesic medication (Book 8, Chapter 47). Borrowing from Pliny, the Roman author Claudius Aelianus (ca. 175–ca. 235 C.E.) describes this behavior in detail in his encyclopedic series *On the Nature of Animals* (Johnson 1997). When pursued by hunters, he writes, the beaver "puts down its head and with its teeth cuts off its testicles and throws them in their path, as a prudent man who, falling into the hands of robbers, sacrifices all that he is carrying, to save his life, and forfeits his possessions by way of ransom." Of course, beavers do not actually do anything of the sort. Explain why Darwin would have considered it reasonable that lizards should drop their tails, but implausible that beavers should self-castrate even to spare their own lives.
15. Many British readers in the 1850s were familiar with the sorts of breeding programs that were used to produce dog varieties, and Victorian Englishmen and Englishwomen were fascinated with pigeon breeding. Given this, why was it such a brilliant strategy for Darwin to open *On the Origin of Species* with a discussion of artificial selection?