PART ONE

INTRODUCTION TO DARWINIAN BIOLOGY

Have you ever looked through the two ends of a kaleidoscope? Depending on which end you look through, you get a very different impression of the contents of the device. But the actual contents do not change. Only your perspective changes. The different views of the inside of one toy are like the different views that two scientific disciplines can have of the world.

There is nothing unusual about two scientific fields studying the same things. The life sciences come in two parts, like the physical sciences. In the physical sciences, these two parts are known as physics and chemistry. They are usually taught by different departments in universities. They even have different Nobel Prizes. To speak of physicists and chemists as different kinds of scientists is normal in the sciences. They both deal with the nonliving world, but from different perspectives. Physicists talk about the theory of relativity, gravity, and the makeup of the sun. Chemists work on problems like the synthesis of compounds containing carbon, or the properties of plastics. There is some overlap in their interests, especially the physics of chemical bonds. But the two fields are thought of as separate.

The same division exists in the life sciences. Some biologists are primarily interested in topics like the makeup of the cell membrane, the replication of nucleic acids like DNA, and the chemistry of metabolism. Other biologists study mass extinctions of species, the ecology of competition, and the evolution of sex ratios. There is little overlap between these two areas—except for some topics in genetics, such as the evolution of DNA repair. These two areas of life science have no more to do with each other than physics and chemistry do, perhaps less. But we have no names that signify the two as clearly as physics and chemistry do.

Biologists who study the biochemical foundations of cellular life are often referred to as *molecular biologists*, *cell biologists*, and *biochemists*. About 30 years ago, these were very different disciplines. Now it is hard to find dividing lines between them. Perhaps the most common name for these specialists is *molecular biologist*, which has the advantage of indicating that they are usually extremely interested in particular molecules, be they DNA, a protein, whatever. The name does not do justice to the great concern that these scientists have for the functioning of molecules within cells. But titles that might do this, like *cell-molecular biologist*, are too cumbersome. So molecular biologist tends to be the label of convenience.

The other type of biology is even harder to label. Thirty years ago, *population biology* was a common term. But since then, this end of biology has incorporated many theories and findings about organisms, cells, and molecules. This kind of biology is based on a general perspective that incorporates ideas about inheritance, selection, ecology, and evolution. It is a perspective that can be historically associated with one preeminent person: Charles Darwin (1809–1882). Darwin brought all of these elements together to form a new approach to biology. First published in his *Origin of Species* (1859), Darwin's approach to biology has never been lost. To this day, many thousands of biologists are happy to acknowledge their intellectual debt to him. For that reason, here we will speak of this part of biology as *Darwinian biology*.

As the twentieth century gives way to the twenty-first, molecular biology is perhaps the most successful scientific discipline. Its most important competitor for prestige and money has been physics. But physics has been increasingly limited by the expense and difficulty of generating the extreme conditions in which smaller and smaller particles can be observed. Although molecular biology is expensive, its experiments cost thousands of dollars, not the millions or billions of dollars required by those of big-time physics. Thus molecular biologists have been able to acquire substantial funding from governments and corporations.

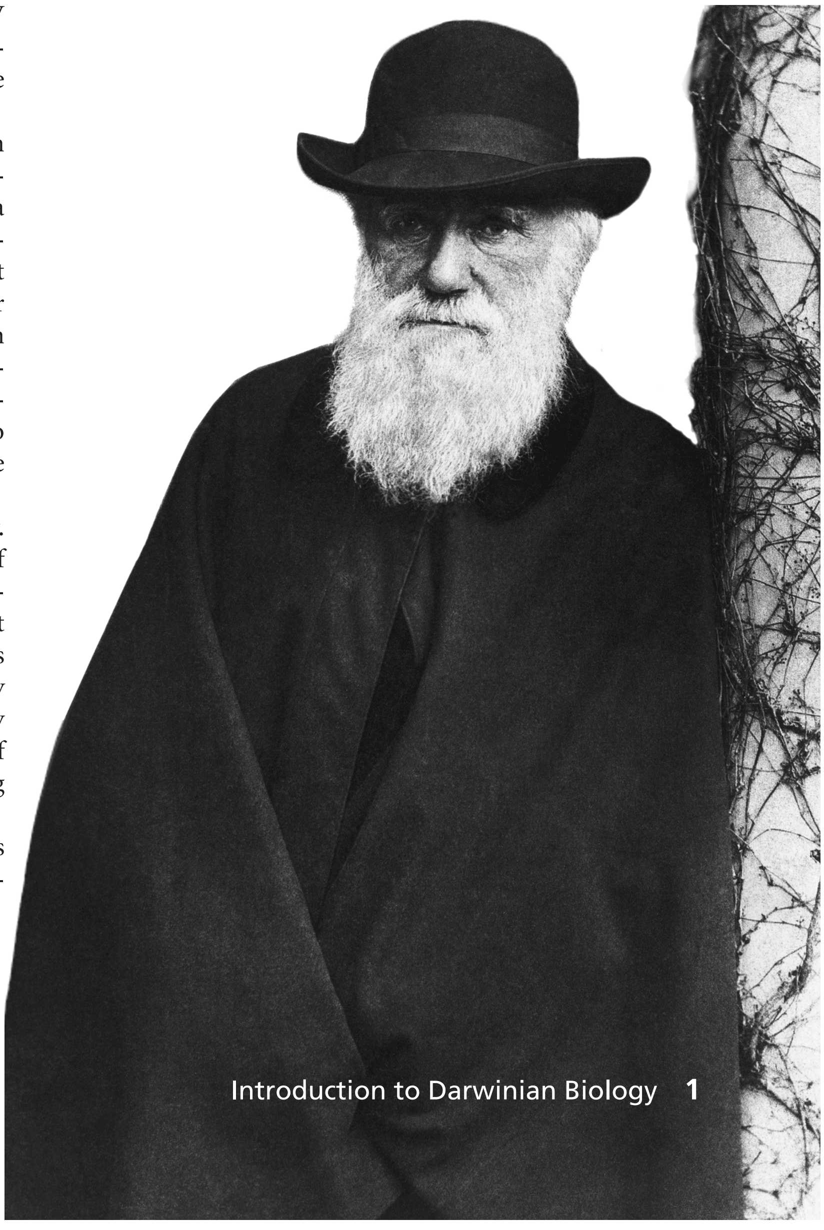
Molecular biology has also been very successful at attracting funding based on practical concerns. With the end of the Cold War, physicists were no longer as important militarily; powerful thermonuclear weapons became effectively obsolete. But molecular biologists can continue to play to concerns about cancer and other health problems, problems that they have promised to alleviate. Rapid progress in the development of anti-HIV drugs has perhaps been the most dramatic fulfillment of these promises. Medicine would have had grave difficulty even identifying, much less treating, HIV infection without modern molecular biology. Molecular biology is on the march, and it will contribute a great deal to the welfare of our species.

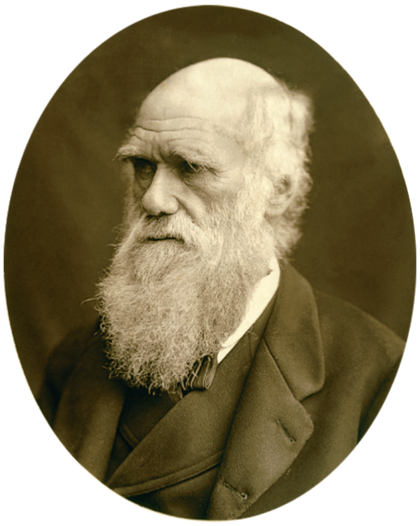
So what is the status of Darwinian biology, at this time in history? Darwinian biology has never truly dominated biology, not even during Darwin's lifetime. It may have been at a peak of influence from 1930 to 1970. By 1930, Darwinian biology was well-developed theoretically, and the subsequent 40 years were to see its ideas applied to most of the major problems of biology, a phenomenon known as "the modern synthesis." But since the 1960s, there have been tendencies toward counterproductive specialization and vacuous intellectual fights. As one century turns into another, there is no question that molecular biology is the dominant force in the life sciences.

But Darwinian biology is showing signs of recovery. One of the most important of these is the breaking down of boundaries between specializations within Darwinian biology. Another sign of recovery is that the life sciences that have been discarded by molecular biology are joining forces with Darwinian biology. A further symptom of health may be the reduced importance of heavily mathematical theory and an increased emphasis on experiments. At the level of research and graduate study, Darwinian biology is enjoying a renaissance.

This book introduces Darwinian biology to new students of biology. There are many advanced treatises of Darwinian biology, books that are read carefully by dozens of people worldwide. We have written some of these books ourselves. This book is not like them. This book is for the new visitor to Darwinian biology, not the settled inhabitant. It is focused on developing the ability to think in a Darwinian way. Many matters of fact were entirely unknown to Charles Darwin, including information crucial to Darwinian biology. But it is certain that he could have readily understood them, if he had traveled to our time, because he had a mental framework on which he could hang each particular fact. If you learn to think this way, as a Darwinian, you will have a mental framework that will always be of value when you are faced with a new piece of biology.

There are two basic ways to begin the study of any scientific field. One is historically, so that the actual development of ideas can be understood. One advantage of understanding science historically is that arguments and ideas that may seem utterly bizarre on their own will fall into place, into sequence. Chapter 1 is this kind of historical introduction to Darwinian biology. Another way to begin learning about a new field is to study its most elementary concepts and theories, in the abstract. That way, these concepts can be absorbed without any distractions. Chapter 2 takes this approach. Studying these two chapters, together, provides a more complete introduction to Darwinian biology than studying either of them separately.





1 Darwin, Ecology, and Evolution

The greatest watershed in the history of biology was not the invention of the electron microscope, or even DNA cloning. It was the career of Charles Darwin. Before Darwin, biology was an offshoot of theology, like most sciences before 1800. Darwin made biology part of natural science.

Who was this scientific revolutionary? As a man, Charles Darwin (1809–1882) was full of contradictions. Son of a very wealthy doctor, he abandoned the study of medicine because of squeamishness. Unlike his college chums, he had radical opinions on social issues, such as the abolition of slavery. He was almost painfully shy and never publicly defended his theory of evolution. Yet he was willing to publish books that were widely denounced from church pulpits and university lecterns. Perhaps the most intuitive biological theorist of all time, he was hopelessly confused about how inheritance operates. Reviled by some who were pillars of polite society, he is a controversial figure to this day. Yet his body lies in Westminster Abbey, where English royalty are entombed, not far from the resting place of Sir Isaac Newton (1642–1726), the principal creator of physics.

Darwin is the starting point for the fields of evolution, ecology, and organismal biology—but not because he was the first to put forward ideas or findings in these fields. He was not the first. He had forerunners from the Enlightenment, such as Jean-Baptiste Lamarck (1744–1829) and even his own grandfather, Erasmus Darwin (1731–1802). But Charles Darwin's thought departed radically from these earlier evolutionists. Instead of explaining evolution in terms of spiritual forces, he supplied materialistic explanations for evolution that transformed biology from natural theology to natural science. And he supplied two of the most important ideas that underlie biology: evolutionary descent with modification and the direction of evolution by natural selection. We will explain these later.

Here we introduce first Darwin and after that his thinking. We then show how Darwin's thought led to the type of biology that is the subject of this book. In some ways, it is good to have the foundations of the field so perfectly embodied in the career of one man, one humble Prometheus.

Darwin's Life

1.1 There are many Darwin myths, perhaps because Darwin had an impact on the general culture

Charles Darwin is probably the most famous biologist of all time. Though the Greek philosopher **Aristotle** (384–322 B.C.) was essentially the founder of academic biology, most people, even most academics, do not think of him primarily as a biologist. Although the Austro-Hungarian monk Gregor Mendel (1822–1884) also made a huge contribution to the development of biology by discovering the foundations of genetics, Mendel is not a name that most people recognize. As for Darwin, his name appears on metal plates attached to cars, and people wear T-shirts with his image.

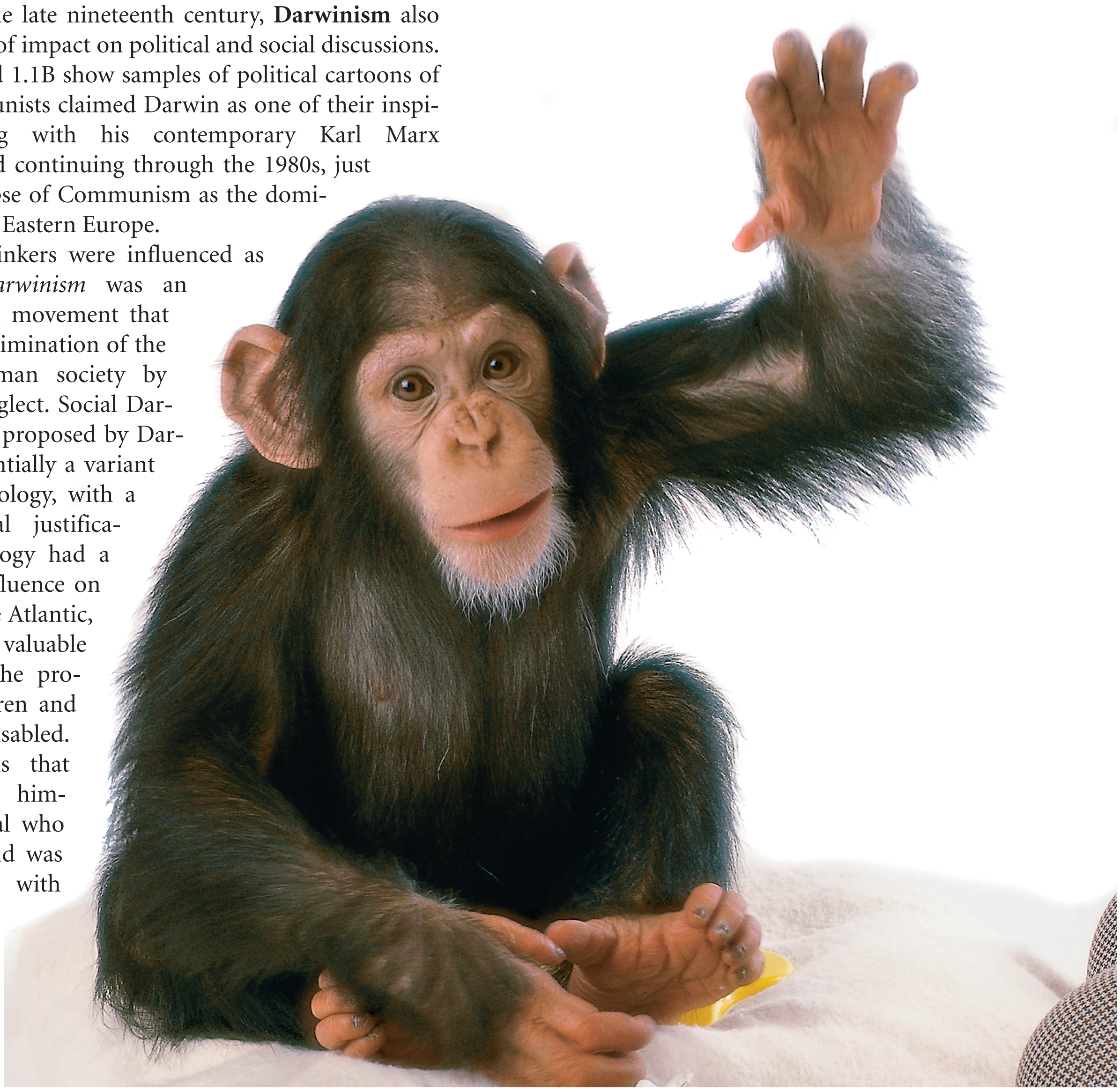
Broadly speaking, Darwin is a controversial figure among Christian and Muslim denominations. Some denominations accept his work, and some do not. The amazing thing is that so many religious authorities feel a need to state their opinion about Darwinism.

Starting in the late nineteenth century, **Darwinism** also had a great deal of impact on political and social discussions. Figures 1.1A and 1.1B show samples of political cartoons of Darwin. Communists claimed Darwin as one of their inspirations, starting with his contemporary Karl Marx (1818–1883) and continuing through the 1980s, just before the collapse of Communism as the dominant ideology of Eastern Europe.

But other thinkers were influenced as well. *Social Darwinism* was an Anglo-American movement that argued for the elimination of the unfit from human society by starvation or neglect. Social Darwinism was not proposed by Darwin. It was essentially a variant of capitalist ideology, with a vague biological justification. This ideology had a great deal of influence on both sides of the Atlantic, blocking much valuable legislation for the protection of children and the care of the disabled.

The irony is that Charles Darwin himself was a liberal who hated slavery and was very concerned with the suffering of the unfortunate. He was no Communist revolutionary, but no Social Darwinist either.

The problem of Darwinism was that Darwin's ideas were much bigger than his public persona. They have also remained influential long after his death. As a result, his ideas have been appropriated by many different ideologies and personalities, and denounced by still more. Yet most of these commentaries were developed with very little understanding of Darwin's actual views, whether political or scientific.



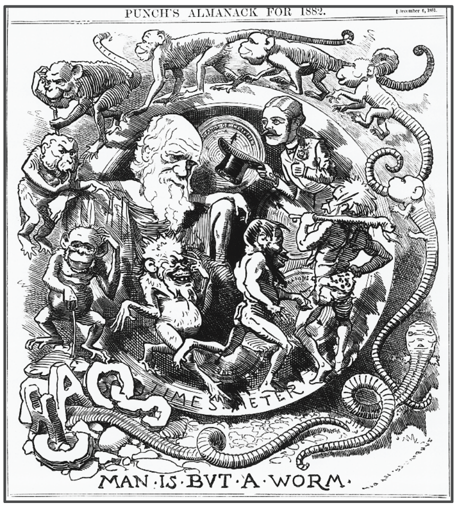


FIGURE 1.1A **Victorian-Era Caricature Satirizing Darwin**

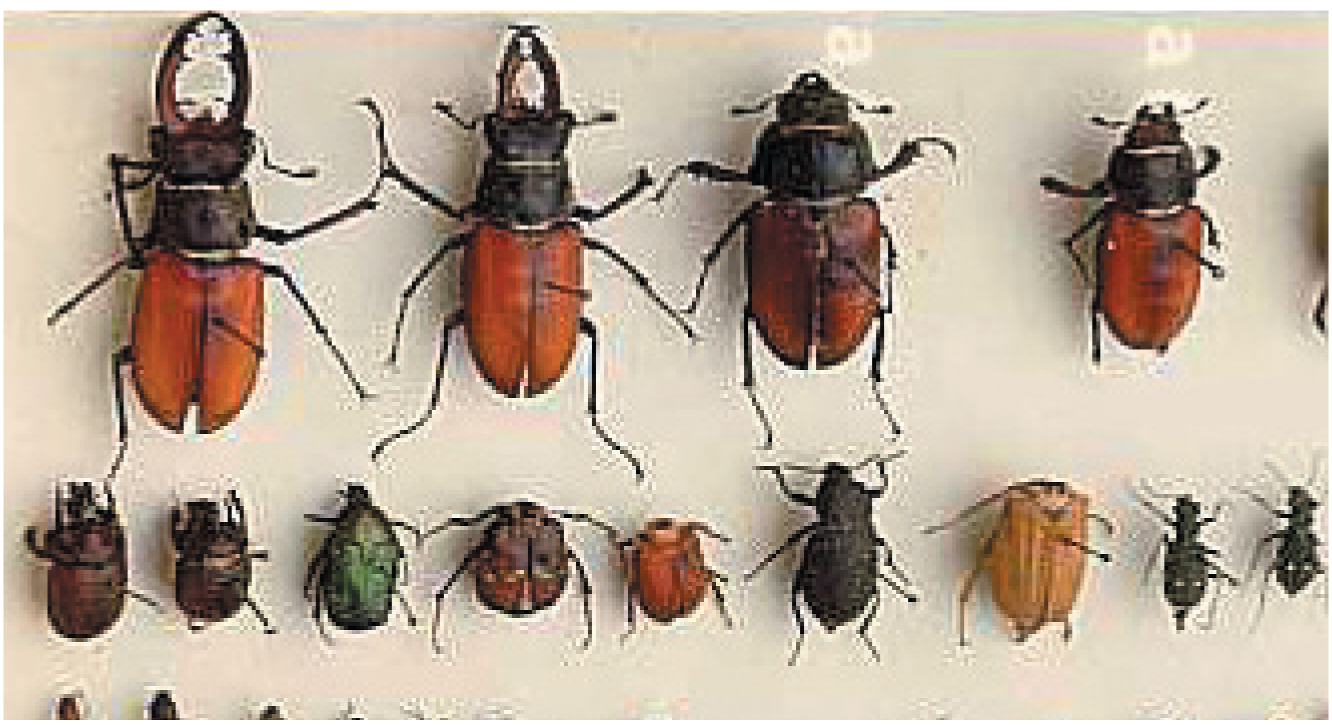
FIGURE 1.1B **Victorian-Era Cartoon Satirizing Darwin**

Darwin Myths

Many people think they know about Darwin. One version of his life is that he was a determined atheist who developed a perverse theory of life evolving in order to destroy Christianity. This myth supposes that Darwin was primarily a political radical who used biology to make mischief.

A competing myth is that while Darwin may have been a nasty radical in his youth and in his middle age, deep study of science left him convinced of the existence of a Creator. This myth is also embroidered with the story that Darwin took Communion or confessed on his deathbed, expressing regret about his theories. There is no documented evidence that such events ever took place.

Still, distortion and misappropriation are probably as much forms of flattery as imitation is. Such dubious accounts of Darwin's life reveal the fact that he has obsessed, impressed, and frustrated people for some time.



1.2 Darwin grew up an intellectually curious, but unemployed, member of the English landed gentry

Amazingly, Charles Darwin was not the first evolutionist in the Darwin family. That distinction belonged to his paternal grandfather, **Erasmus Darwin** [shown in Figure 1.2A, part(i)]. Erasmus was a much-published physician who was interested in chemistry and biology as hobbies. He published what were then "popular science" books and had a wide influence. Mary Shelley cited him as an inspiration in the preface to her novel *Frankenstein*. This inspiration came from Erasmus's support for the view that species evolve into one another. However, Erasmus was not a well-trained biologist, and his biological ideas were generally sketchy or ill formed. His chemistry, by contrast, was first-rate.

But Charles never knew his grandfather, who died in 1802, seven years before Charles was born. Charles also hardly knew his mother, Sukey, who died when he was a child, probably of acute peritonitis. He was left to be brought up by older sisters. He had an older brother named Erasmus. Though Charles was spoiled as a young child, his physician father, Robert, sent him to a boarding school to enjoy the regimen of abuse and deprivation that was then the hallmark of an upper-class education. Father Robert amassed an ample fortune, which would pay for the education of Charles and his brother Erasmus, as well as all of their later adventures and labors. Neither had paid employment for a single day of their lives.

At the age of 16, Charles followed his brother to Edinburgh University, where he was supposed to study medicine. But cadavers disgusted Charles, and he turned his attention to biology. Leaving Edinburgh, he went to Cambridge University to study for service as a minister of the Church of England. At that time, he was absolutely conventional in his religious beliefs. His main interest was to live at a country parsonage where he could collect insects, especially beetles, one of his great passions as a young man.

Charles Darwin was mostly a gentleman student during his years in Cambridge. Hunting and horses were major concerns, and Charles never faced stringent exams or other challenges. But he did collect a great many beetles. He had a passion for collecting things, or shooting them, that would oddly prove central to his later life. Charles also "walked" with his professors a great deal, taking promenades beside them while they propounded their views on the academic questions of the day. From this experience, Charles Darwin apparently learned how to reason scientifically, his greatest single asset. Figure 1.2B shows Charles Darwin at various ages.

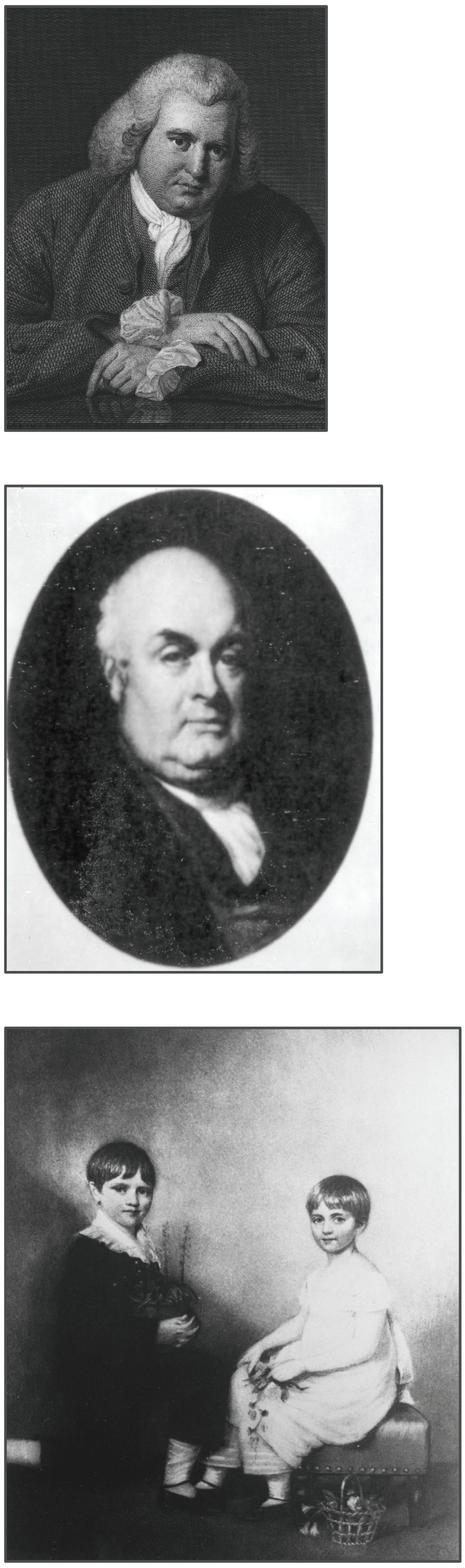


FIGURE 1.2A Paintings of (i) Erasmus Darwin (grandfather of Charles), (ii) Robert Darwin (father of Charles), and (iii) the young Charles Darwin (with his sister Catherine).

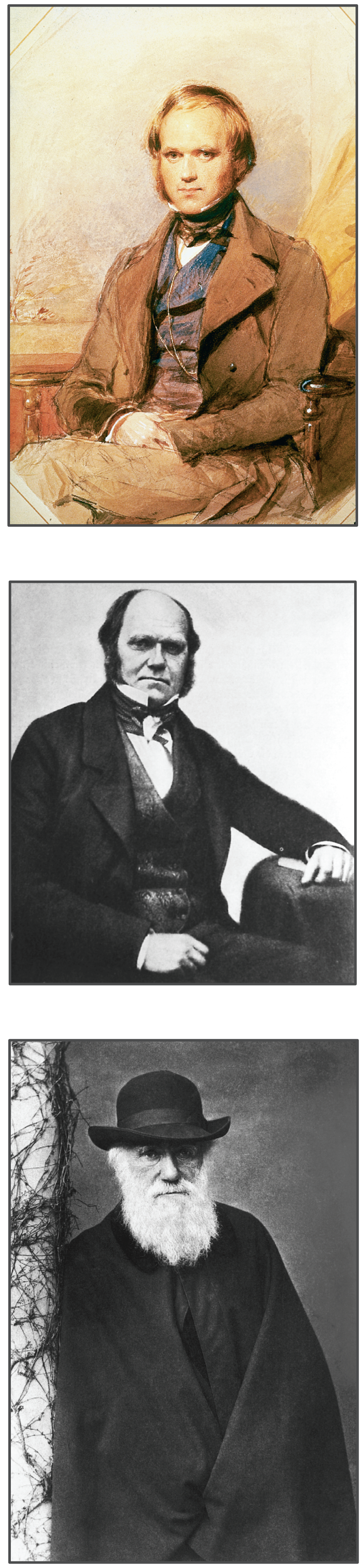


FIGURE 1.2B **Darwin at Different Ages** As a young man (top), a middle-aged man (center), and an old man (bottom).

1.3 On the voyage of the *Beagle*, Darwin learned a lot of biology, but he did not discover evolution

Darwin did not become an Anglican minister, because he was offered a chance to go on a trip that was his fondest aspiration. This was the voyage of the *Beagle*. The ***Beagle*** was a British Royal Navy ship, commissioned to survey the biology and geology of South America. The ship is shown in Figure 1.3A. This commission reflected the global reach of the Royal Navy, which the British Empire used as its principal instrument of military domination. South America had broken free of Spain in the nineteenth century, and the British wanted to make sure that they knew enough about the geography of the continent so that the Royal Navy would face no unpleasant surprises as it sailed in South American waters.

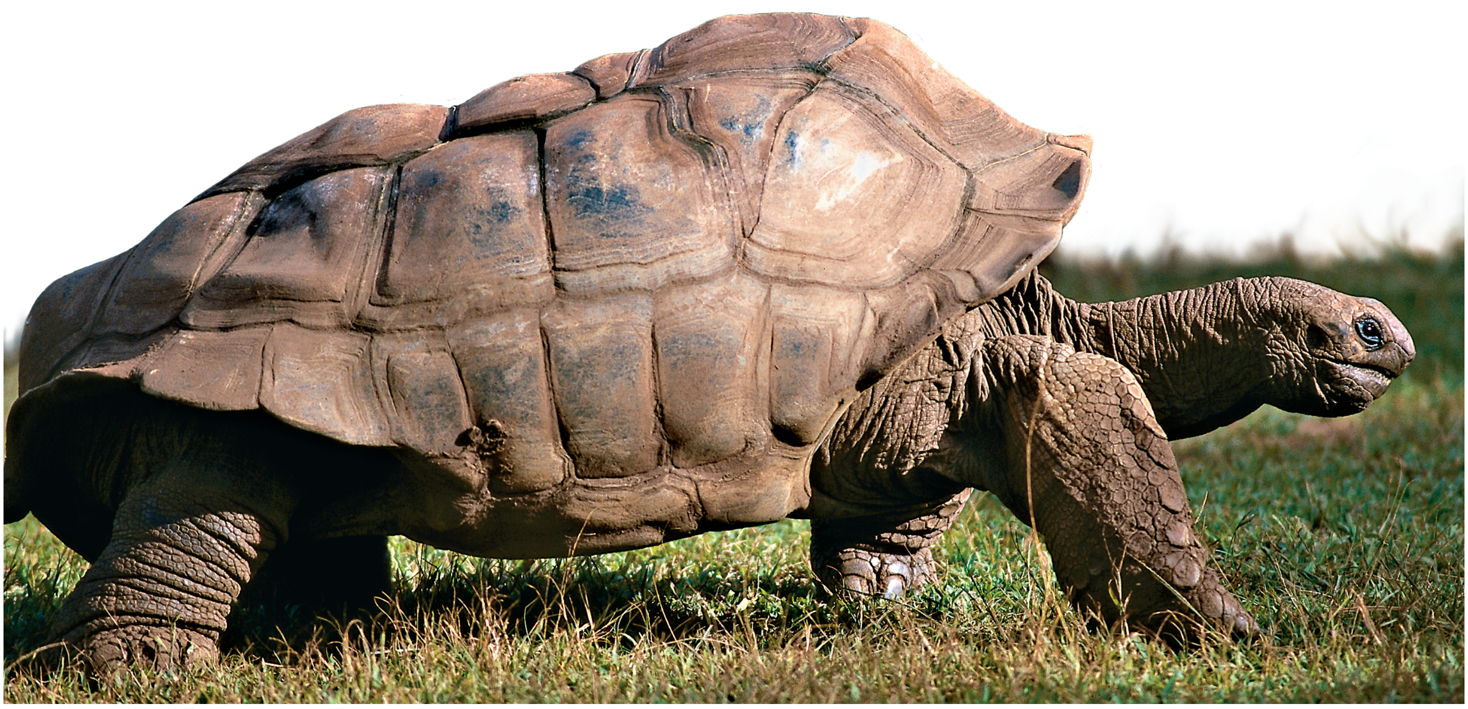
FIGURE 1.3A The HMS *Beagle*

The Captain of the *Beagle* was **Robert FitzRoy**. FitzRoy was truculent and obsessed with social rank. It was imperative for him that the ship's naturalist, the single most important person on board after the captain, be of the right social class. A middle-class, scholarly type would not do. Thus Darwin, who was no professional biologist or geologist, got the job. He knew some biology. He knew how to collect scientific specimens. But most important for FitzRoy, Darwin was upper class.

It is a famous story that Darwin sailed around the world with the crew of the *Beagle*, which set sail late in 1831 and returned in 1836—a voyage of almost five years (Figure 1.3B). It is less generally known that Darwin collected a vast number of geological and biological specimens on this trip, enough to fill warehouses back in London. This feat was possible because the *Beagle* frequently met other Royal Navy ships, which transshipped Darwin's specimens back to London.

It is commonly thought that Darwin developed the theory of **evolution** on the rocky islands of the Galápagos Archipelago, right on the equator. This is not true. He developed his theory of evolution only after coming home to England. On first returning to London in 1836, Darwin was as much in the dark about the deep questions of biology as he had been at the time of his departure.

What Darwin did learn from his trip was the astonishing diversity of living forms, and their frequent occurrence as fossils located in rocks. Furthermore, some of these fossils were of forms that apparently no longer lived. Though Darwin remained an essentially **creationist** biologist during the voyage of the *Beagle*, the staggering heterogeneity among the plants and animals that he collected showed him the difficulty of understanding life. Darwin saw with his own eyes, as few biologists had up to that time, the range of living things on the planet Earth. It was an experience that was to color the rest of his life.



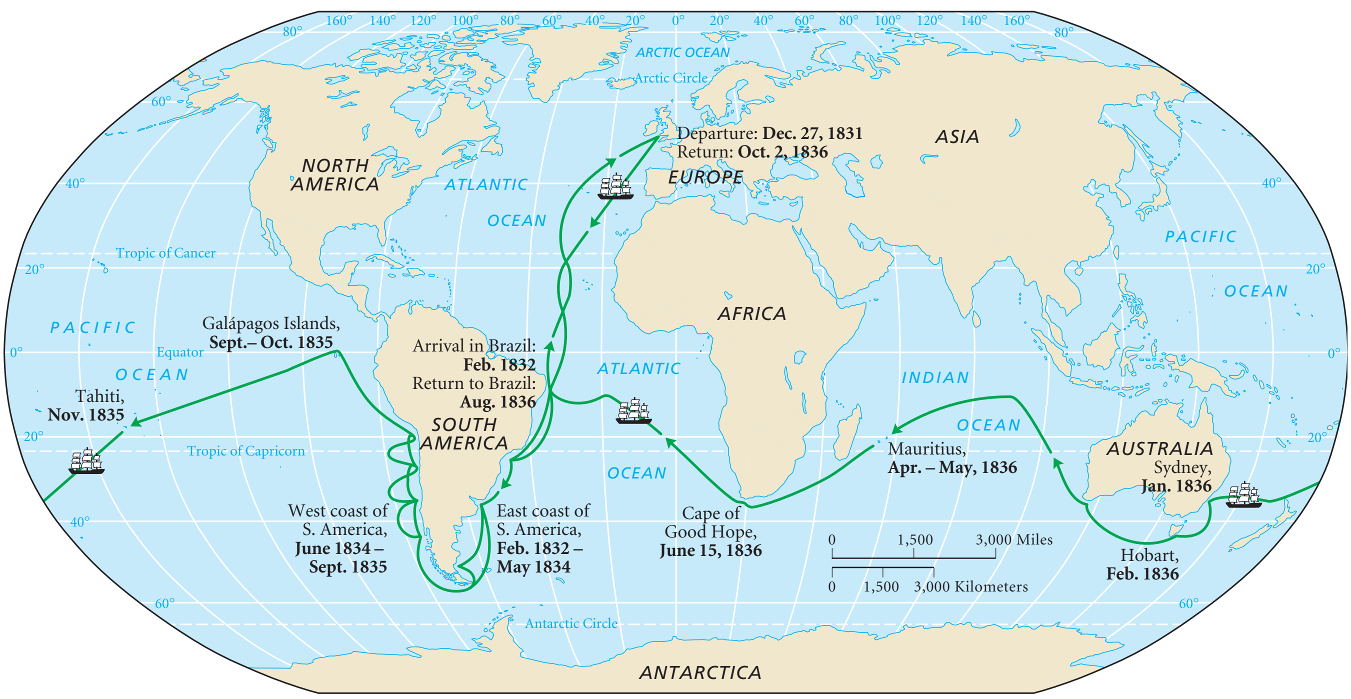


FIGURE 1.3B **The Voyage of the HMS *Beagle***

1.4 Darwin intuited evolution from the differences between birds from the Galápagos Islands

The key moment in the history of biology came while Darwin was supervising the unpacking of his collections back in London. Darwin and the other members of the *Beagle*'s crew had collected a number of finches and mockingbirds from the Galápagos Islands, usually recording the specific island from which each bird came. Darwin had thought that these birds were so similar to each other that they were no more than different breeds within a common species of finch or mockingbird.

But the mockingbird specimens were examined more carefully by an ornithologist, John Gould. In March 1837, Gould sent Darwin a note in which he argued that the mockingbirds of the various Galápagos Islands were in fact distinct species. There was not enough overlap in their anatomy to indicate they were merely varieties of a common species. Moreover, the Galápagos finches and mockingbirds appeared to be very similar to species living on the mainland of South America, not far from the Galápagos. In principle, the islands could have been colonized by the mainland forms and then somehow changed, it seemed to Darwin. Darwin at first called this process of change from one form into another **transmutation**. Initially, Darwin's thinking about transmutation was little improved over the ideas of **Jean-Baptisk Lamarck** or grandfather Erasmus Darwin. But Charles's thinking progressed rapidly.

Figures 1.4A to 1.4D summarize Darwin's idea of transmutation applied to the birds of the Galápagos. Species originally only on the mainland colonize the Galápagos Islands, more accurately mapped in Figure 1.4E. This might have happened if a flock of birds were swept out to sea and then flew away from the mainland, perhaps because of an unusual storm.

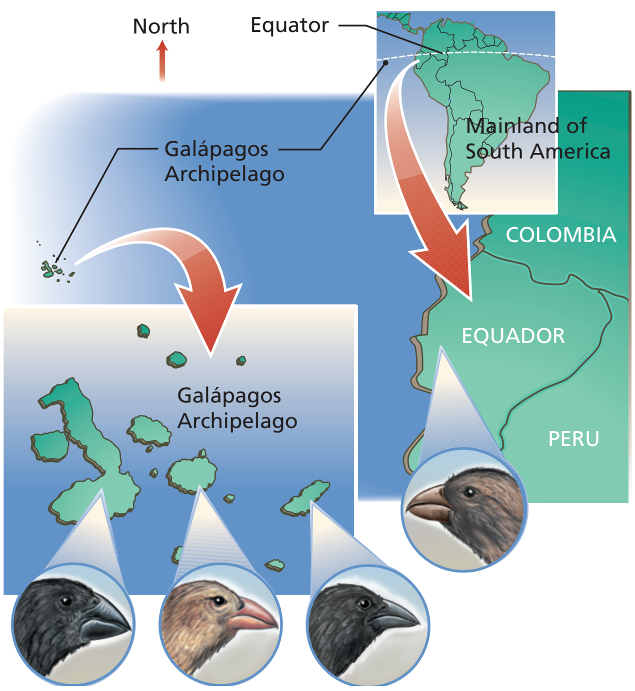


FIGURE 1.4A Darwin's *Beagle* Collections Different bird species were found on the islands of the Galápagos and on the mainland of South America.

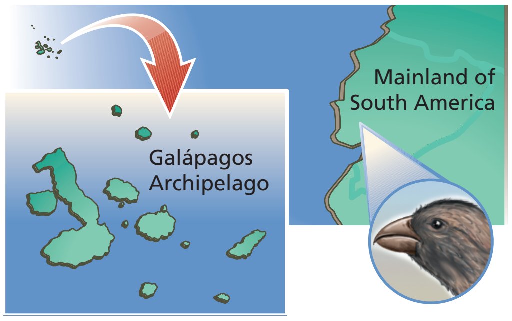


FIGURE 1.4B Darwin's Evolutionary Scenario The scenario starts with just one bird species found only on the mainland.

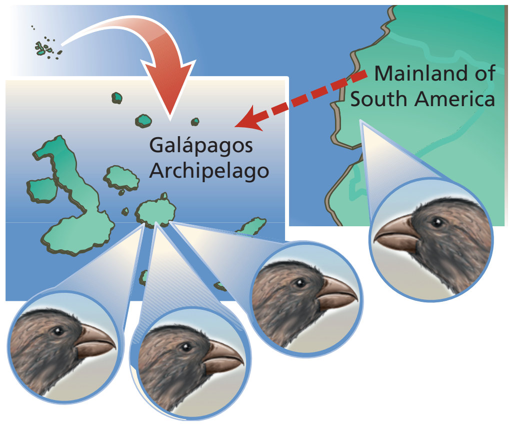


FIGURE 1.4C Darwin's Evolutionary Scenario Step two is the accidental migration of a flock from mainland to the Galápagos.

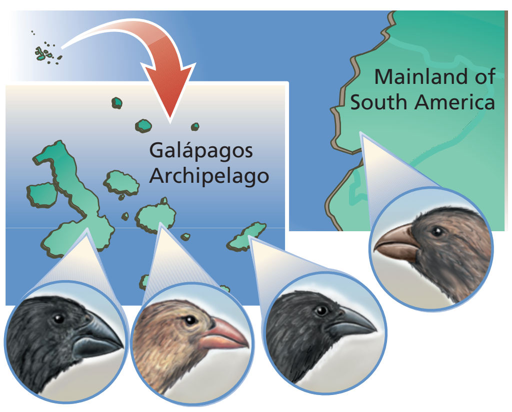
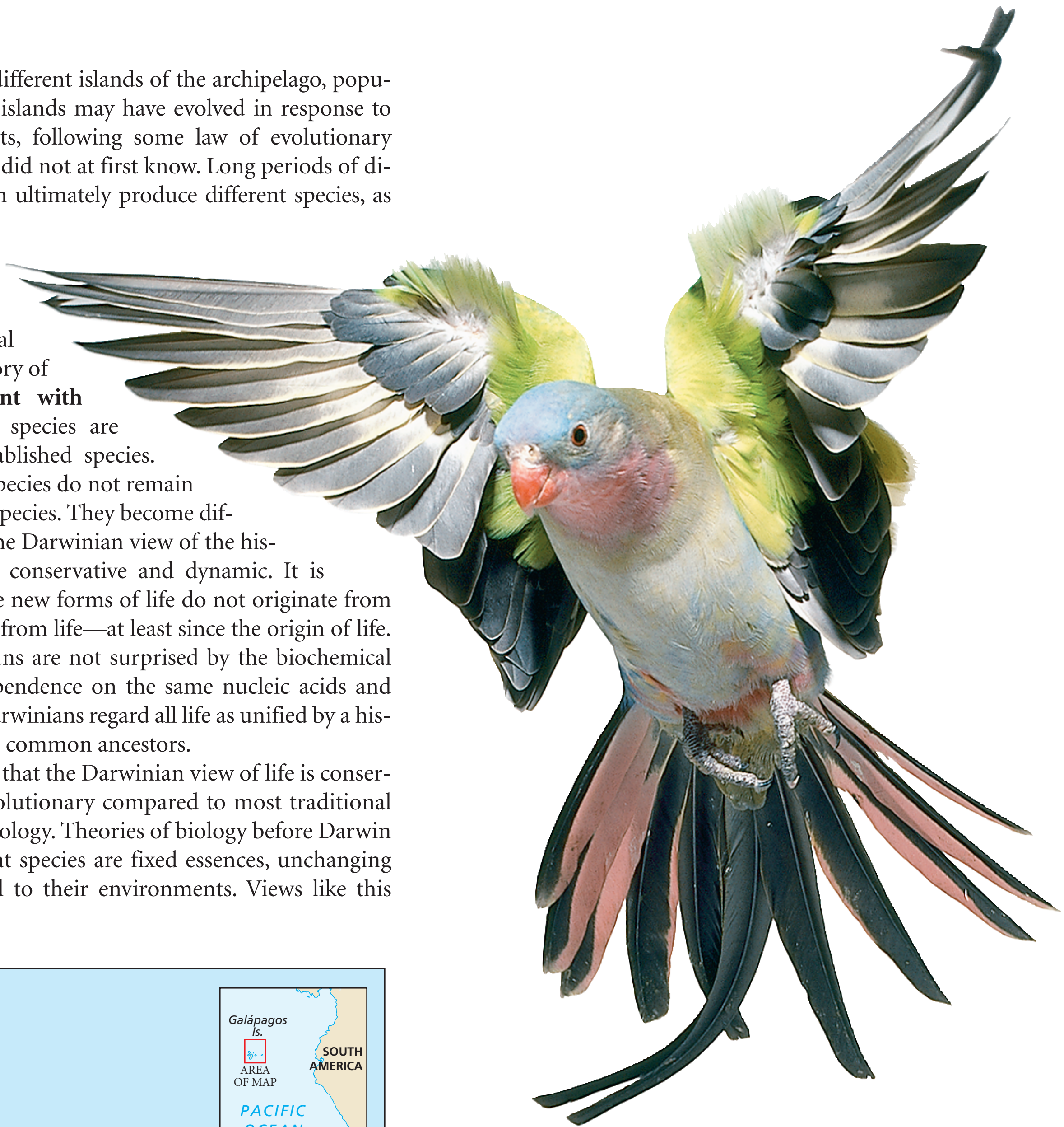


FIGURE 1.4D Darwin's Evolutionary Scenario Slow evolutionary diversification of birds on the Galápagos.



Once living on the different islands of the archipelago, populations on different islands may have evolved in response to the different habitats, following some law of evolutionary change that Darwin did not at first know. Long periods of divergence would then ultimately produce different species, as shown in Figure 1.4D.

Darwin's first great contribution to biological thought was his theory of evolutionary **descent with modification**: New species are produced from established species. Furthermore, new species do not remain the same as the old species. They become different. In this way, the Darwinian view of the history of life is both conservative and dynamic. It is conservative because new forms of life do not originate from nothing. Life comes from life—at least since the origin of life. Therefore, Darwinians are not surprised by the biochemical unity of life, its dependence on the same nucleic acids and proteins, because Darwinians regard all life as unified by a history of descent from common ancestors.

At the same time that the Darwinian view of life is conservative, it is also revolutionary compared to most traditional interpretations of biology. Theories of biology before Darwin usually assumed that species are fixed essences, unchanging and perfectly suited to their environments. Views like this may be found in the writings of **Plato**, Aristotle, and much Christian theology. Darwin's simple idea that one type of bird may be a "transmutation" of another type of bird breaks from the assumption that species are fixed. Instead of species being created by a deity, or being present unchanged for all eternity, in the Darwinian view species are contingent creations of an historical process: evolution. Species do not have a special status in Darwin's theory. Their coming into being and their extinction may take more time than the creation or destruction of other things, such as individual organisms. But they still arise and disappear, slower than most familiar things, quicker than mountain ranges. The Darwinian view of life constrains life to evolve from life, except at its origin; but at the same time, it frees our view of life from static theories in which change is not possible. ❖

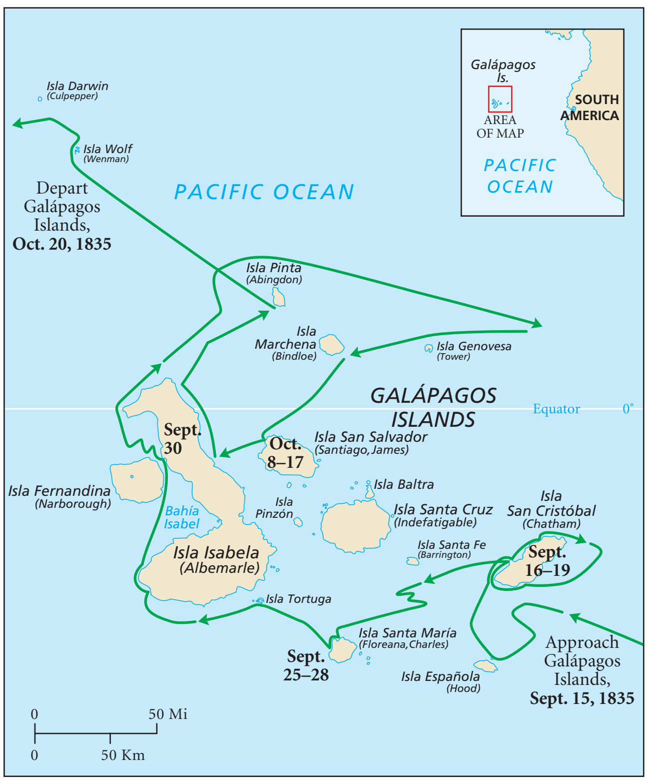


FIGURE 1.4E Map of the Galápagos Islands

1.5 Darwin developed the concept of natural selection to explain the direction of evolutionary change

With his theory of evolution as descent with modification, Darwin solved many of the long-standing problems in biology: the underlying similarities of organisms, the superficial diversity of organisms, and the pattern of the fossil record, among other issues. But the mere plausibility of his evolutionary theory was not enough for Darwin. He wanted a well-behaved process to explain how evolution takes place. Such a well-defined process would be a scientific *mechanism* for evolution.

This need to go another step came from Darwin's training in geology, especially the writings of **Charles Lyell** (1797–1875), whose *Principles of Geology* was one of the few books that Darwin took with him on the voyage of the *Beagle*. Lyell argued that scientific explanations should use the cumulative effects of well-known processes. The alternative was to invoke catastrophes and miracles. This was not a merely hypothetical alternative in the nineteenth century. At that time, almost all scientists were devout Christians, if not religious ministers. It was natural to them to explain unusual fossil patterns in relation to Noah's Flood or some other biblical event. But Lyell explicitly rejected that kind of scientific explanation. For him, scientific explanations had to be based on processes that could be observed in the present, not on unknowable cataclysms from the distant past. Darwin adopted this stricture as his own, even though it made his intellectual struggles much harder.

> *Living a life of bachelor study in London in his late twenties, Darwin searched for more than a year for an explanation of evolution, without success.*

Darwin was ashamed of his evolutionary theory, because he had found no mechanism that could drive the evolutionary process—at least not at first. Living a life of bachelor study in London in his late twenties, Darwin searched for more than a year for an explanation of evolution, without success. Then one day in 1838 he read Malthus's essay on human population growth. **Thomas Robert Malthus** (1766–1834) was concerned that the European population would inevitably outgrow its ability to produce food, resulting in mass starvation, plague, and so on. Darwin read Malthus and thought instead of animals and plants living in nature. If they developed very large population sizes, then they too would be subject to very bad, very competitive conditions in which there would be too few resources for all to survive. This scenario, Darwin reasoned, would tend to favor those individuals who were better equipped to compete with their rivals, individuals with a greater ability to survive and prosper under bad conditions. These were the individuals most likely to reproduce. Darwin's reasoning to this point seems indubitable. A diagram of his logic is shown in Figure 1.5A.

The bold step came next. Don't offspring tend to resemble their parents? If it was primarily the more robust who survived and reproduced under difficult conditions, wouldn't their offspring tend to be better equipped for these conditions

How Darwin Used Malthusian Reasoning

Darwin was impressed with the antagonism between excessive reproduction and later mortality due to ecological processes. The later mortality opened up the possibility for natural selection to do its work.

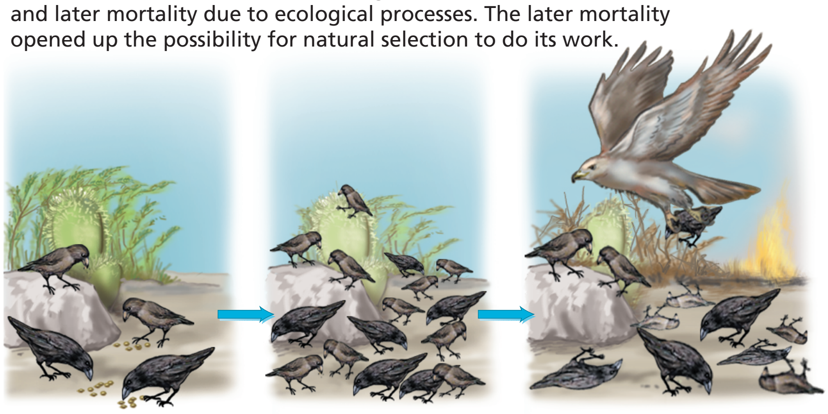
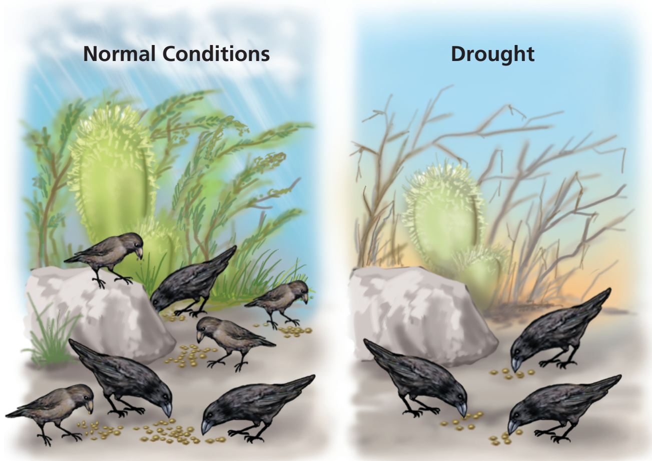


FIGURE 1.5A From Malthus to Darwin—the Malthusian Problem of Limited Resources and Ecological Disaster

as well? Thus stressful environments should produce selective reproduction, or "natural selection," to use Darwin's term. Generally, **natural selection** can be defined as the net reproductive advantage of individuals with favored characteristics. Darwin immediately saw that natural selection might, under some conditions, produce sustained evolutionary change. Thus natural selection is a mechanism that might produce the evolutionary patterns of descent with modification that Darwin had already discerned. Natural selection could meet Lyell's stipulation about scientific explanation, because the process by which superior organisms prosper and inferior ones die was there to be seen in the everyday lives of plants and animals.

An example of natural selection from the Galápagos Islands is described in Figure 1.5B. In this example, drought conditions create selection in favor of those birds that can crack the seeds that remain available during drought. ❖

The Galápagos Islands are relatively barren and dry. In some years rainfall is rare. During these years, the plants produce fewer seeds. The seeds that are more common during drought are large, with thick husks. Only birds with large powerful bills can open and eat these seeds.

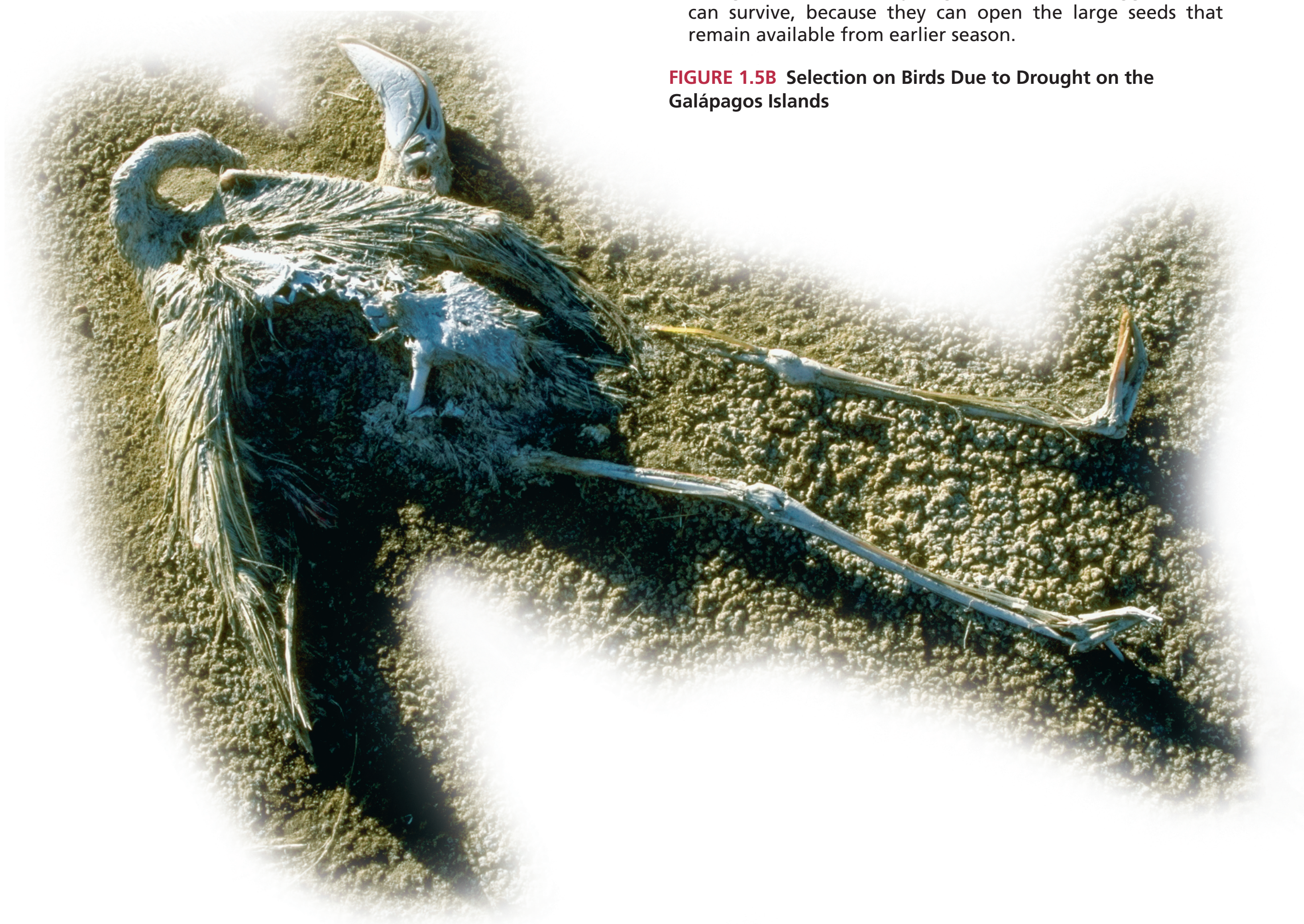


Large and small seeds available for large and small finches

Only large seeds, left over from earlier season

Under normal conditions, finches that are larger and smaller can survive on the Galápagos Islands. Under drought conditions, only larger finches, with bigger beaks, can survive, because they can open the large seeds that remain available from earlier season.

FIGURE 1.5B Selection on Birds Due to Drought on the Galápagos Islands



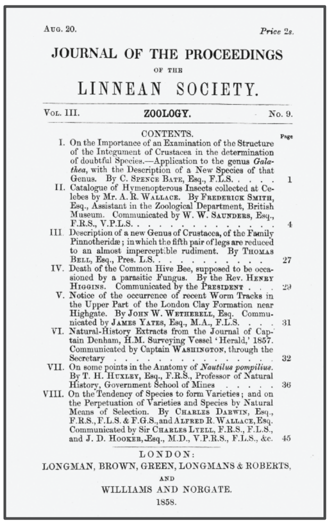
1.6 Despite publishing the *Origin of Species*, Darwin was a much-honored scientist during his life

Despite having developed in detail two of the greatest concepts in biology—evolution and natural selection—Darwin was afraid to publish. In the middle of the nineteenth century, most academic biologists were still creationists who believed either in the exact words of the Bible or something closely related to them. After Darwin had become a closet evolutionist, **Robert Chambers** (1802–1871) anonymously published the evolutionist book *Vestiges* in 1844. It contained a number of arguments in favor of evolutionary change, conceived crudely. Some of these arguments were remarkably weak. The book was greeted with a storm of protest, particularly from biologists. Darwin was mightily intimidated, because some of his own friends and colleagues joined in the savaging of the book. Instead of publishing his own evolutionary theories, he turned to harmless pursuits, including a monumental study of barnacles. He received the Royal Medal of London's Royal Society for his work on barnacles and coral reefs.

So Darwin remained silent for twenty years. It is not clear that he would ever have published his ideas in his lifetime. He was a well-respected member of the Royal Society with considerable wealth. His will directed his colleagues to publish his draft essays on evolution in the event that he died. But posthumous publication was not the outcome of Darwin's story.

In 1858 Darwin received a letter from a young English naturalist, **Alfred Russell Wallace** (1823–1913), who was traveling in the South Seas, off southeast Asia. Wallace had independently discovered the theory of evolution by natural selection, and he wanted Darwin's comments and his help getting it published, if he thought it worthy. This event turned Darwin from fear of public hostility to an even greater fear of being scooped. But being an English gentleman, he could not tear up Wallace's letter and go ahead with publishing his own theory. Instead, it was arranged that Wallace's letter would be presented and published along with one of Darwin's unpublished essays. The table of contents of the journal involved is shown in Figure 1.6A. For the record, the two men were given codiscoverer status at the time.

But the initial publication of the theory of evolution by natural selection received little reaction from the scientific community. Some scientists were stunned. Others did not



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LINNEAN SOCIETY.

Vol. III. ZOOLOGY. No. 9.

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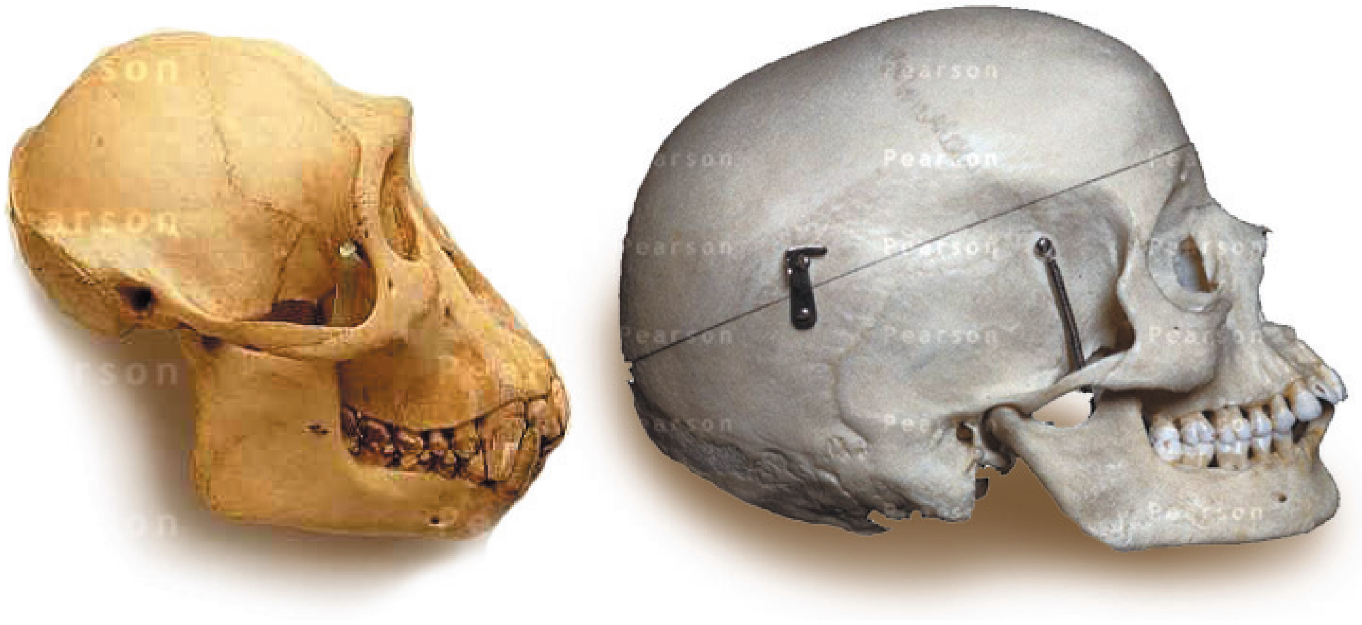
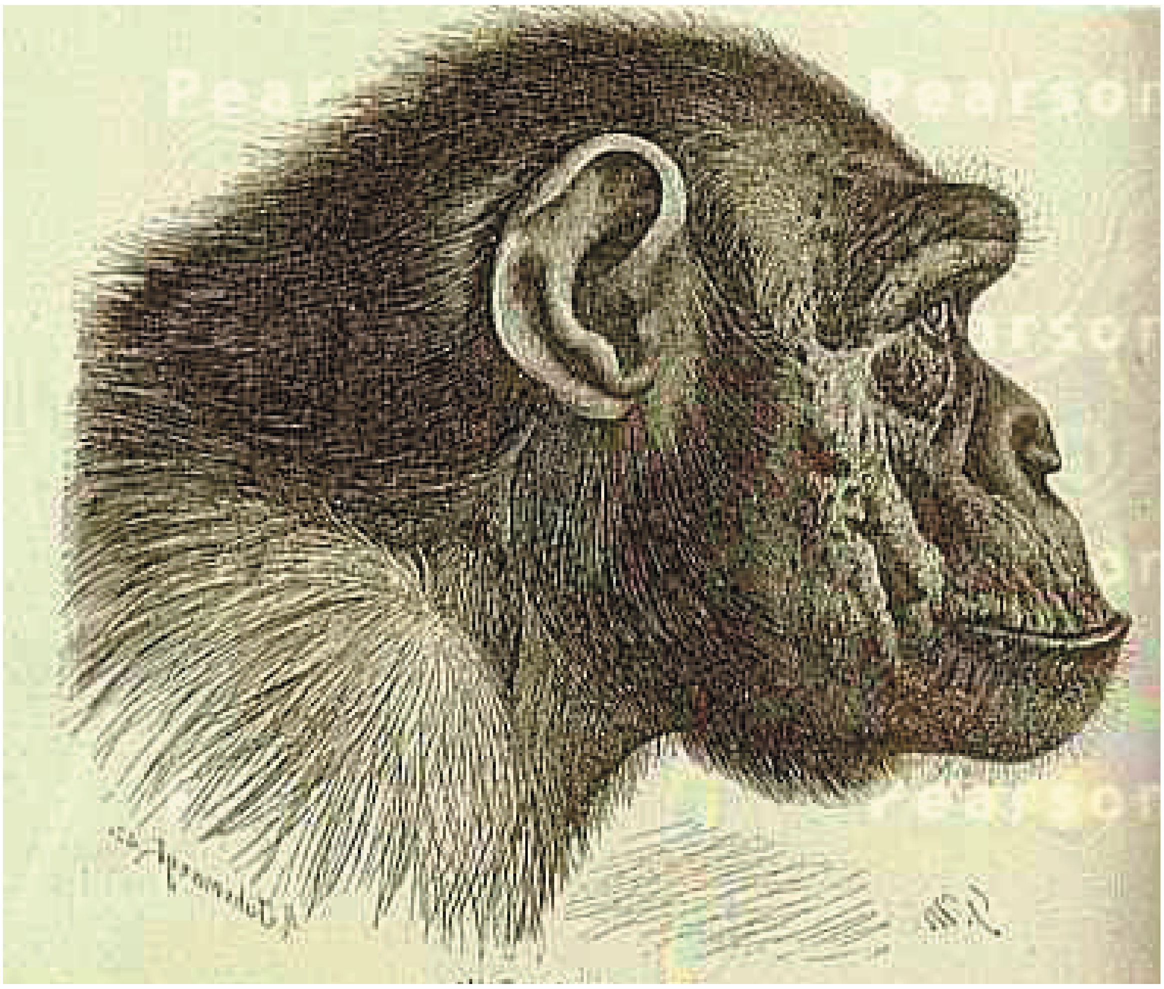
LONDON:
LONGMAN, BROWN, GREEN, LONGMANS & ROBERTS,
AND
WILLIAMS AND NORGATE.
1858.

FIGURE 1.6A The Table of Contents of the Journal Which Published the Papers by Darwin and Wallace, Published in 1858



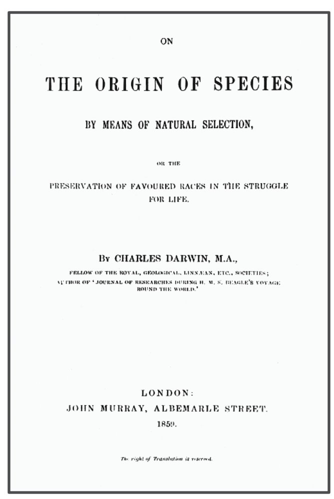


understand. Darwin set about writing a short book, which he liked to call an "abstract," describing his theory. This book was *On the Origin of Species by Means of Natural Selection,* published by John Murray of London in 1859. Part of the title page is shown in Figure 1.6B.

The book caused a furor. It quickly acquired supporters and detractors. There were scientists for and against, clerics for and against, novelists for and against, journalists for and against. Few seemed to be neutral. It was a true intellectual sensation. Ever since, and more than any other single scientific theory, Darwin's theory of evolution has been in the public eye.

But Darwin went back to being a staid country scientist. He wrote books on inheritance, facial expressions, and earthworms. He did some elegant experiments in plant breeding. He very much wanted to figure out how heredity worked, but he never did. He refused to defend his theory of evolution before a public audience, though he wrote numerous letters in defense of it. Wallace and others—such as "Darwin's bulldog," T. H. Huxley (1825–1895)—played a more visible role than Darwin did.

When Darwin died in the spring of 1882, there was some controversy about how to honor him. His friends in the scientific establishment prevailed upon the authorities to have him buried in Westminster Abbey, near **Isaac Newton**. Darwin's burial slab there is large and dark. The only words are his name, Charles Robert Darwin, and the dates he lived—February 12, 1809, to April 19, 1882. Never knighted, he has nonetheless been widely regarded as the second greatest English scientist, after Newton.



ON

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

OR THE

PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.

By CHARLES DARWIN, M.A.,

FELLOW OF THE ROYAL, GEOLOGICAL, LINNÆAN, ETC., SOCIETIES;
AUTHOR OF 'JOURNAL OF RESEARCHES DURING H. M. S. BEAGLE'S VOYAGE ROUND THE WORLD.'

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1859.

The right of Translation is reserved.

FIGURE 1.6B Title Page of the First Edition of Darwin's *Origin of Species*

DARWIN'S ECOLOGY AND EVOLUTION

1.7 Darwin used ecology to create evolutionary biology

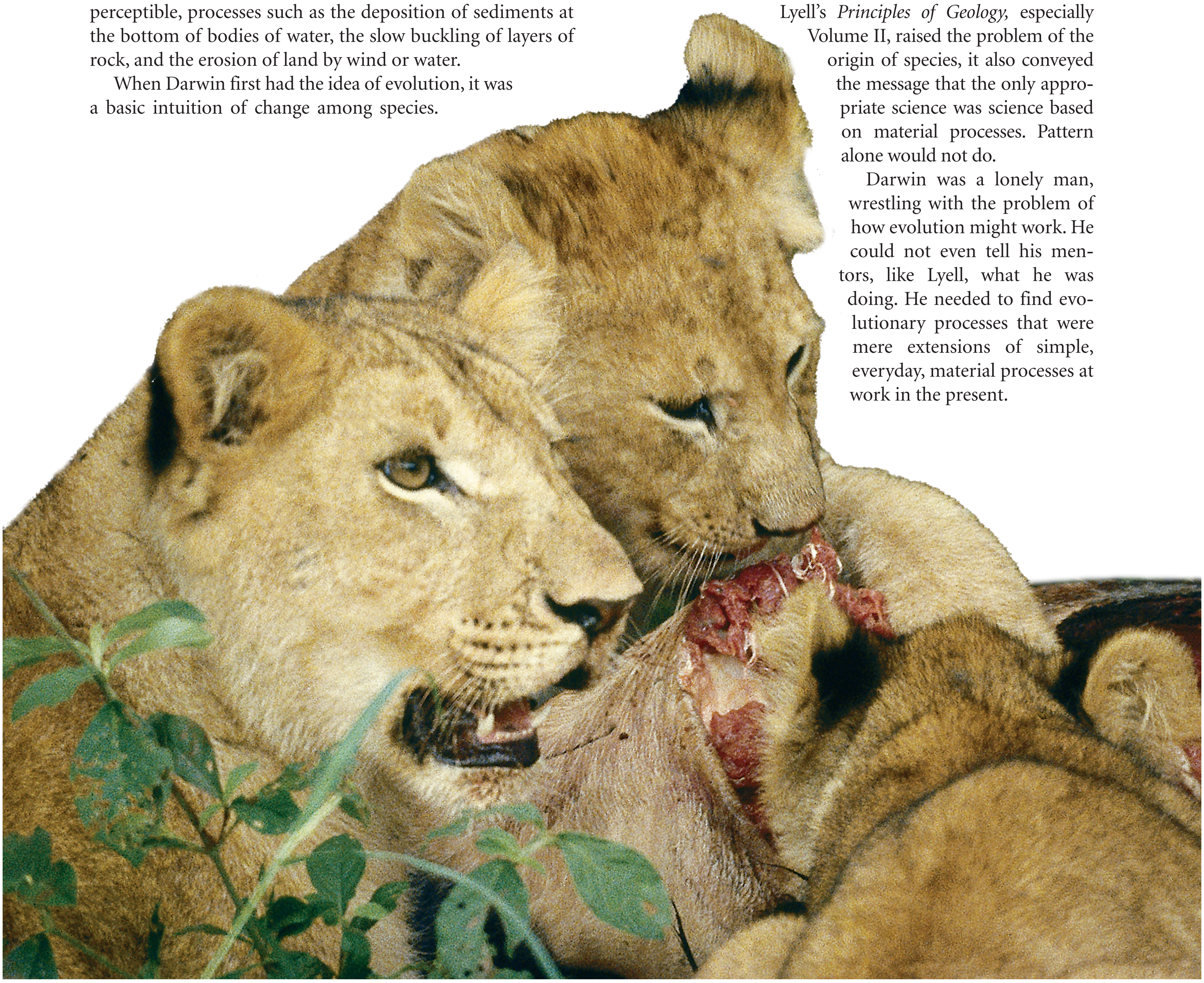
The moment when Darwin made the connection between Malthus's ideas and evolution is one of the single most important episodes in the history of science. The consequences of that moment are still with us. But the intellectual core of Darwin's insight is worthy of a much closer look, because that core contains the essence of Darwinian biology, from molecular evolution to behavioral ecology.

The key to understanding this moment is the role of simple material processes in geology. Geologists deal with such striking things as mountains, rivers, and oceans. But they explain the existence of these objects by mundane, usually imperceptible, processes such as the deposition of sediments at the bottom of bodies of water, the slow buckling of layers of rock, and the erosion of land by wind or water.

When Darwin first had the idea of evolution, it was a basic intuition of change among species. He thought that evolutionary change was the most appropriate way to explain the evolution of the birds of the Galápagos Islands. He even drew pictures of evolutionary trees in his notebooks. But he had no idea of *how* evolution occurred. His thinking was just pattern, without process.

As already mentioned, he was practically embarrassed about having a pattern without a process. His professional affiliation at that time was with geology. He was the Secretary of the Geological Society of London, in fact. And not just any kind of geologist. He was a self-conscious disciple of Charles Lyell, the leading gradualist of the day. Although Lyell's *Principles of Geology,* especially Volume II, raised the problem of the origin of species, it also conveyed the message that the only appropriate science was science based on material processes. Pattern alone would not do.

Darwin was a lonely man, wrestling with the problem of how evolution might work. He could not even tell his mentors, like Lyell, what he was doing. He needed to find evolutionary processes that were mere extensions of simple, everyday, material processes at work in the present.



This was where Malthus and his *Essay on the Principle of Population,* published in 1798, came in. In his essay, Malthus constructed a history-making argument about the problem of human **overpopulation**. Malthus was by no means the first to write about overpopulation. The philosopher **David Hume** (1711–1776) and the economist **Adam Smith** (1723–1790) had broached the subject of overpopulation earlier, but their writings were fairly superficial. Malthus took on the subject in detail. Malthus's main thesis was not that important to Darwin; he was not trying to solve the problem of human overpopulation. The important thing was that Malthus supplied a semiquantitative ecological model. Malthus argued that the human population size was increasing geometrically while food production increased only linearly. This model was not correct, because food production has increased geometrically—not linearly—since the early 1800s. But his reasoning was like that of geologists in that Malthus wrote about everyday ecological processes: reproduction, death, disease, farming, and so forth.

All Darwin had to do was apply this ecological reasoning to the lives of animals and plants. Like humans, animals and plants have a great capacity to reproduce. But normally their population sizes do not explode. Therefore, there must be checks to animal or plant population growth. These checks must take the form of deadly misfortunes. Nature must then select in some way. The better must be sorted out from the lesser. In realizing this, Darwin would start on a journey of discovery that would last him the rest of his life, as his understanding of evolution by natural selection progressively deepened.

Figure 1.7A shows graphically the parallel between Malthus's thinking about population growth and Darwin's basic ideas about natural selection. Darwin did not proceed by any kind of formal logic. Once Malthus had supplied him with the elements of ecological thinking, Darwin appropriated them wholesale to solve his problem of how evolution worked. Biology would never be the same again.

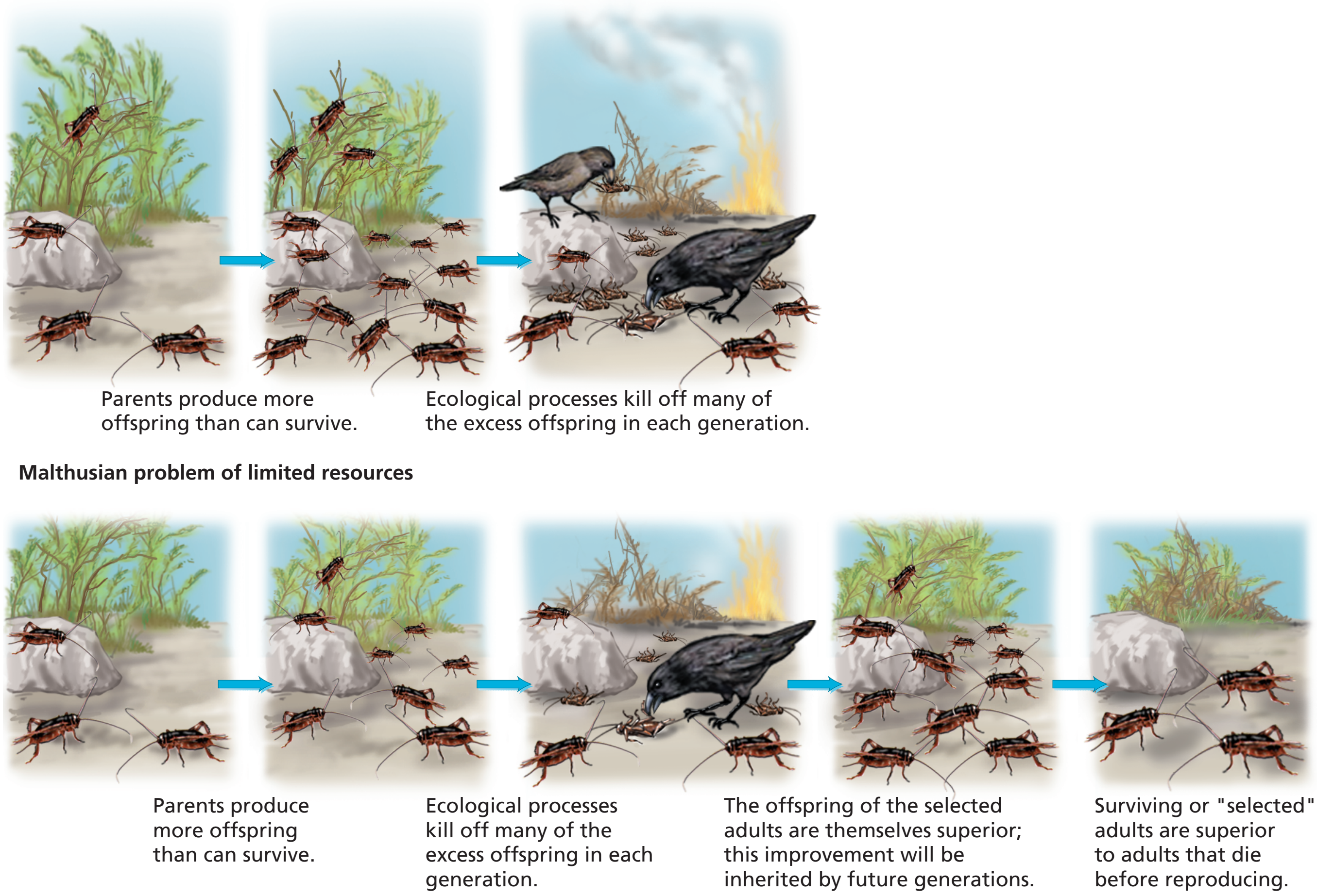


FIGURE 1.7A Darwin's Extrapolation from Ecology to Evolution

1.8 Malthus's essay led Darwin to apply ecology to other problems of evolutionary biology

As we have seen, Darwin got the idea of connecting ecology to evolution from reading T.R. Malthus. The essential Malthusian argument was that people reproduce faster than agriculture can be developed. In his words, "Population, when unchecked, increases in a geometrical ratio. Subsistence increases only in an arithmetical ratio." From this, Malthus concluded that the tendency for people to reproduce will necessarily be checked. It could be checked by famine, pestilence, war, and other disasters. Or it could be checked by social policies that prevent marriage and the birth of children out of wedlock. Malthus argued strongly for measures that would prevent poor people from marrying young and having children. He also advocated "moral restraint," which meant sexual restraint. The analysis of Malthus played an important role in nineteenth-century politics, often being used in arguments against supplying welfare.

But for Darwin, the ecological reasoning was more important. He was captivated by the idea that in nature, many more offspring are produced than can possibly survive. As shown in the box, "The Malthusian Moment", Darwin accepted Malthus's argument wholesale, where overpopulation was concerned.

Why was this essay such a revelation for Darwin? Darwin needed simple, observable machinery to drive evolution. He wanted a process like erosion to shape species, so that they would evolve materialistically. Malthus supplied the ecological machinery of reproduction, famine, and disease to get Darwin's evolution working, as Darwin himself explained in the quotation shown in the first box.

The Malthusian argument concerning overpopulation is an example of the effects of population growth on ecology, a major concern of Chapter 10. But Darwin used other ecological principles as well. For example, he considers the interaction between extreme environments and ecological competition in the passage quoted in the second box "Darwin Reasoning Ecologically," taken from the end of his chapter on the *struggle for existence,* his term for ecology. Here we see Darwin stretching beyond the ideas of Malthus. He was opening up the ideas of ecology, and generalizing them, to make evolution work. ❖

The Malthusian Moment

A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms; for in this case there can be no artificial increase of food, and no prudential restraint from marriage. . . .

There is no exception to the rule that every organic being naturally increases at so high a rate, that, if not destroyed the earth would soon be covered by the progeny of a single pair. . . . the geometrical tendency to increase must be checked by destruction at some period of life. . . . Lighten any check, mitigate the destruction ever so little, and the number of the species will almost instantaneously increase to any amount. . . . The amount of food for each species of course gives the extreme limit to which each can increase; but very frequently it is not the obtaining food, but the serving as prey to other animals, which determines the average numbers of a species."

—Charles Darwin, 1859, *Origin of Species* (Chapter III, "Struggle for Existence")

Darwin Reasoning Ecologically

Look at a plant in the midst of its range, why does it not double or quadruple its numbers? We know that it can perfectly well withstand a little more heat or cold, dampness or dryness, for elsewhere it ranges into slightly hotter or colder, damper or drier districts. In this case we can clearly see that if we wish in imagination to give the plant the power of increasing in number, we should have to give it some advantage over its competitors, or over the animals which prey on it. On the confines of its geographical range, a change of constitution with respect to climate would clearly be an advantage to our plant; but we have reason to believe that only a few plants or animals range so far, that they are destroyed exclusively by the rigour of the climate. Not until we reach the extreme confines of life, in the Arctic regions or on the borders of an utter desert will competition cease. The land may be extremely cold or dry, yet there will be competition between some few species, or between the individuals of the same species, for the warmest or dampest spots.

—Charles Darwin, 1859, *Origin of Species* (Chapter III, "Struggle for Existence")

1.9 Artificial selection allowed Darwin to develop the concept of evolution by natural selection further

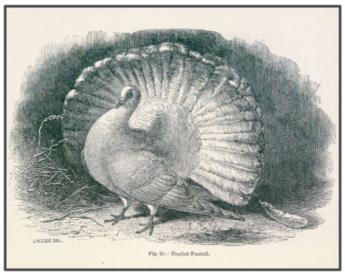
It would have been ideal if Darwin had performed experimental studies of evolution. That way he could have seen how natural selection and inheritance work together, and he might have developed his theory accordingly. But in the years between Darwin's discovery of the theory of evolution by natural selection and the publication of the *Origin of Species*, no one had any notion of how to perform experimental evolution.

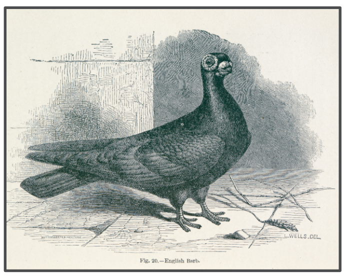
Instead, Darwin took advantage of the literature on breeding plants and animals. By Victorian times, enough was known of breeding to make this literature extremely useful for Darwin. The breeds of animal and varieties of plant could be treated as analogous to animal and plant species in Darwin's theory.

In the *Origin* and his other writings, Darwin made some critical points about breeding. His most important point of emphasis was that a wide diversity of breeds and varieties could be derived from a single ancestral species. With respect to pigeon breeds, some people held that they were derived from several wild species. Darwin argued against this theory on several grounds. First, crosses of pigeon breeds were always fertile. If the original species were separate from each other, then they should not be able to interbreed. If that were so, then why should breeds derived from different wild species be able to interbreed? Second, the dozens of pigeon breeds were thought to derive from rock pigeons, but there are only a handful of rock pigeon species. Third, the original wild species of rock pigeons do not resemble some of the domesticated breeds more than any other. That is, it is difficult to associate one particular wild species with particular domesticated breeds and another wild species with other domesticated breeds. Indeed, the general pattern is that all pigeon breeds seem to be related to *Columba livia*. (See the box, "Darwin and the Pigeons," for a quotation and Figure 1.9A for some examples of pigeon breeds.) Darwin's point in this argument is that breeding is capable of producing extensive variety, as embodied in living breeds.

Darwin also observed that domesticated breeds and varieties are not usually mere variants, established in a single step from a wild species. Rather, the diversity of breeds is to be explained by "man's power of accumulative selection; nature gives successive variations; man adds them up in certain directions useful to him" (*Origin,* chap. I). The point here is evolutionary **gradualism**. Like artificial selection, Darwin argued, evolution by natural selection cumulatively adds small modifications.

Finally, Darwin argued that artificial selection could powerfully modify breeds and varieies. "The great power of this principle of selection is not hypothetical" (*Origin,* chap. I). And since artificial selection can be demonstrably powerful, so can natural selection. ❖





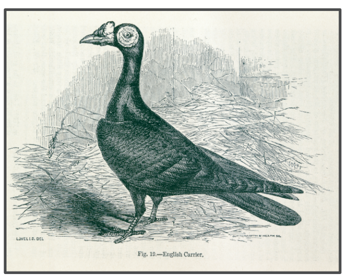


FIGURE 1.9A Breeds of the Common Pigeon, *Columbia livia*

Darwin and the Pigeons

Though Darwin accumulated a large collection of notes, letters, manuscripts, and published articles on animal breeds and plant varieties, he actually bred pigeons himself. He even joined two London pigeon clubs.

The following is an excerpt from Chapter I of the *Origin of Species*, which shows Darwin's obsession with pigeons:

> The diversity of the [pigeon] breeds is something astonishing. Compare the English carrier and the short-faced tumbler, and see the wonderful difference in their beaks, entailing corresponding differences in their skulls. The carrier, more especially the male bird, is also remarkable from the wonderful development of the carunculated skin about the head, and this is accompanied by greatly elongated eyelids, very large external orifices to the nostrils, and a wide gape of mouth. The short-faced tumbler has a beak in outline almost like that of a finch; and the common tumbler has the singular and strictly inherited habit of flying at a great height in a compact flock, and tumbling in the air head over heels.

1.10 To support his theory Darwin used the fossil record, but regarded it as highly imperfect

As a geologist, Darwin was well qualified to use information from the record of fossils. In this respect, as in so many others, the logic of his case for evolution was more or less devastating. Note, however, that Darwin did not regard the fossil record as a perfect record of evolution. As explained in the box "Darwin against the Fossil Record," he was a strong critic of the quality of fossils as documentation for evolution. His strategy, as a theorist, was to predict and describe the general features of the fossil record in relation to evolution.

His strategy, as a theorist, was to predict and describe the general features of the fossil record in relation to evolution.

Because Darwin's theory of evolution was based on local patterns of selection and inheritance, he predicted that fossils would not suggest global patterns of change. Instead, "species of different classes do not necessarily change together, or at the same rate, or in the same degree" (this and all subsequent quotations in this module are taken from *Origin,* chap. X). Likewise, "Groups of species increase in numbers slowly, and endure for unequal periods of time." Because there is no coordinated driving force to evolution, when groups of species are successful, it is because of many individual instances of evolutionary good fortune. This makes evolutionary patterns slow to develop and haphazard in form.

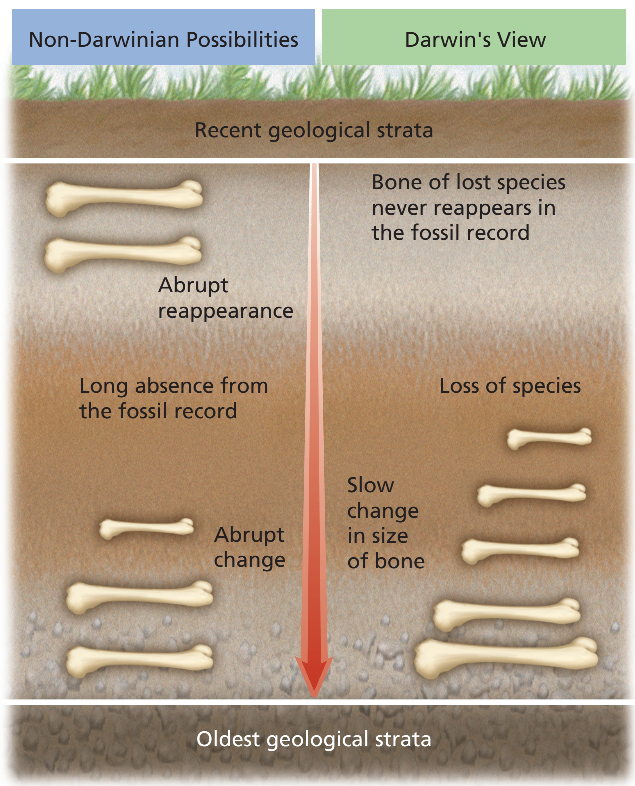


FIGURE 1.10A Alternative Views of the Fossil Record, Illustrated by a Single Fossil Bone

When a species disappears from the fossil record, it never reappears. Evolution is too historical to allow exact repetitions. Even though pterodactyls resemble large birds of prey, flying birds have never approached the size of pterodactyls, which were related to the terrestrial dinosaurs. Similarly, once an entire group has disappeared, like the dinosaurs, it does not reappear except in Steven Spielberg films.

Extinction is a slow process, in Darwin's opinion, especially in groups of species: "The utter extinction of a whole group of species may often be a very slow process, from the survival of a few descendants, lingering in protected and isolated situations." Again, because Darwin's tree of life lets each species grow or die off independently, in evolutionary terms, there is little likelihood that extinctions will be coordinated across large groups. (This, as it turns out, is not true every 30 or 50 million years, as already mentioned. We take up these rare exceptions in Chapter 6.)

Darwin also identified a universal pattern in the succession of fossils: "The more ancient a form is, the more it generally differs from those now living." And "the organic remains of closely consecutive formations are more closely allied to each other, than are those of remote formations." That is, the fossil record is like a story that begins at one point and continues on to other points without ever doubling back on itself. Indeed, Darwin regarded such repetition as deadly for his theory. We know of no such examples of repeated evolution in long-separated times. There are no vertebrate fossils from 1 billion years ago.

Figure 1.10A shows Darwin's predicted evolutionary patterns and the patterns that he asserted do not happen. In most respects, Darwin's expectations are those of modern-day evolutionists too.

Darwin Against the Fossil Record

Darwin regarded the fossil record as highly unreliable. Here are some of his reasons.

1. Only a small portion of the globe has been prospected for fossils.
2. Only some types of organisms fossilize well; examples of such organisms include vertebrates and shelled animals.
3. Far more species have lived than are preserved in all the museums of the world.
4. Because of the difficulty of fossilization, fossils will provide only a spotty record of evolution.
5. Species migrate from one location to another, preventing continuity of the local fossil record in most cases.

Darwin Needed Mendel

Evolution requires the inheritance of variation 1.11

In most respects, Darwin's reasoning about evolution was impeccable. This probably reflected his background as a geologist, especially a Lyellian geologist. Lyell set high standards for scientific reasoning.

But there was a hole in Darwin's fabric of argumentation: inheritance. If there is variation for characteristics that determine survival or reproduction, then the organisms with the greatest tendency to survive and reproduce will have more reproduction. For this reason, Darwin continually emphasized **variation**. The word appears repeatedly in the chapter headings of the *Origin* and throughout the text of the book. Darwin also published a book devoted to the phenomenon of variation: *The Variation of Animals and Plants under Domestication.* In his words, "individual differences are highly important for us, as they afford materials for natural selection" (*Origin,* chap. II). But the transmission of these materials to the next generation is not explained in the *Origin*.

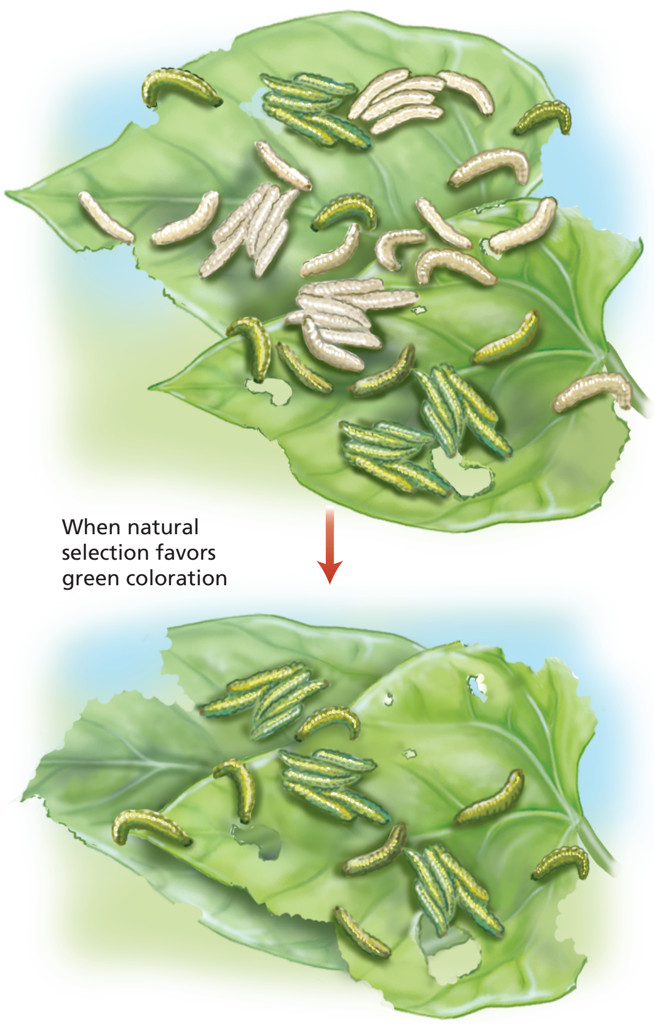


FIGURE 1.11A **Darwin's Concept of Variation as the Raw Material for Selection**

Everything Darwin writes about a struggle in nature leading to differences in the success of particular kinds of organisms would count for nothing if there was no way for differences to be inherited. Otherwise, the selection of particular types has no lasting impact on the population. Selection absolutely requires variation, as shown in Figure 1.11A.

The problem was that the pattern and nature of inheritance was an unsolved problem when Darwin wrote *Origin of Species* in the late 1850s. This lack of information led Darwin to speak vaguely about inheritance (see box). He also tried to sort out unrelated phenomena that, in the minds of biologists at that time, were connected with the problem of inheritance. For example, he had to argue against the view that only unimportant biological characters vary significantly. On the other hand, he found that some characters, such as the flowers of the genus *Rosa,* were extensively variable in a trivial fashion. This variation he considered of "no service or disservice to the species," and therefore unrelated to the action of natural selection.

But things became still murkier when Darwin turned to consider variation between individuals, between varieties, and between species. One of Darwin's characteristic points in the *Origin* is that species are little more than strongly differentiated varieties. He is fond of citing examples of varieties that had been regarded as species, and examples of species that had been regarded as varieties.

Darwin's Thoughts on Variation and Inheritance in the *Origin of Species*

The effects of variability are modified by various degrees of inheritance of reversion. Variability is governed by many unknown laws, more especially by that of correlation of growth. Something may be attributed to the direct action of the conditions of life. Something must be attributed to use and disuse. The final result is thus rendered infinitely complex. (chap. I)

I am convinced that the most experienced naturalist would be surprised at the number of the cases of variability, even in important parts of structure, which he could collect on good authority, as I have collected, during a course of years. (chap. II)

1.12 Darwin tried to explain the mechanism of inheritance using his theory of pangenesis, but failed

Darwin struggled mightily to sort out the problem of inheritance. In the process, he accumulated as much, or more, information on the subject as anyone in the nineteenth century. Part of his problem may have been that he was willing to accept data that were not scientifically valid. This is not surprising, because nineteenth-century biology was grossly deficient as an experimental science. Most biologists just documented natural history; they did not do critical experiments.

The final result was that Darwin developed a hugely complex theory of inheritance to accommodate the varied and often shoddy information that he was given. He called this theory *pangenesis*. It is important to understand that pangenesis is not a theory of genetics. At the core of this theory are things that Darwin called gemmules. He thought that gemmules normally reside in all the tissues of life, shaping organs and processes (Figure 1.12A). In addition, he felt that the conditions of life in each organ or limb would shape the gemmules.

When reproduction occurs, according to Darwin's theory of pangenesis, gemmules migrate from the parts of the body to the gonads. Gametes are then made from mixtures of gemmules. Particular characters can be influenced by many gemmules. The quantitative balance of gemmules of a particular type determines the pattern of inheritance. For example, many gemmules specifying great height are needed to make offspring tall.

With all these gemmules moving about the body, it is reasonable to expect that gemmules should be found in the blood of mammals. Darwin and his cousin, Francis Galton, tested for gemmules in rabbits. They reasoned that rabbits with dark coloration should have gemmules for dark fur circulating in their bodies. So they gave white rabbits blood from dark rabbits and observed the offspring of these white rabbits (Figure 1.12B). If Darwin was right about the circulation of gemmules, the white rabbits that received blood from dark rabbits should have had offspring with some dark coloration, perhaps just a few flecks of dark. The dark color should have been there, but it was not. Darwin expressed the possibility that gemmules might circulate by some means other than blood, but it was a faint hope. His gemmules have never been found. Darwin never sorted out the mechanism of inheritance.

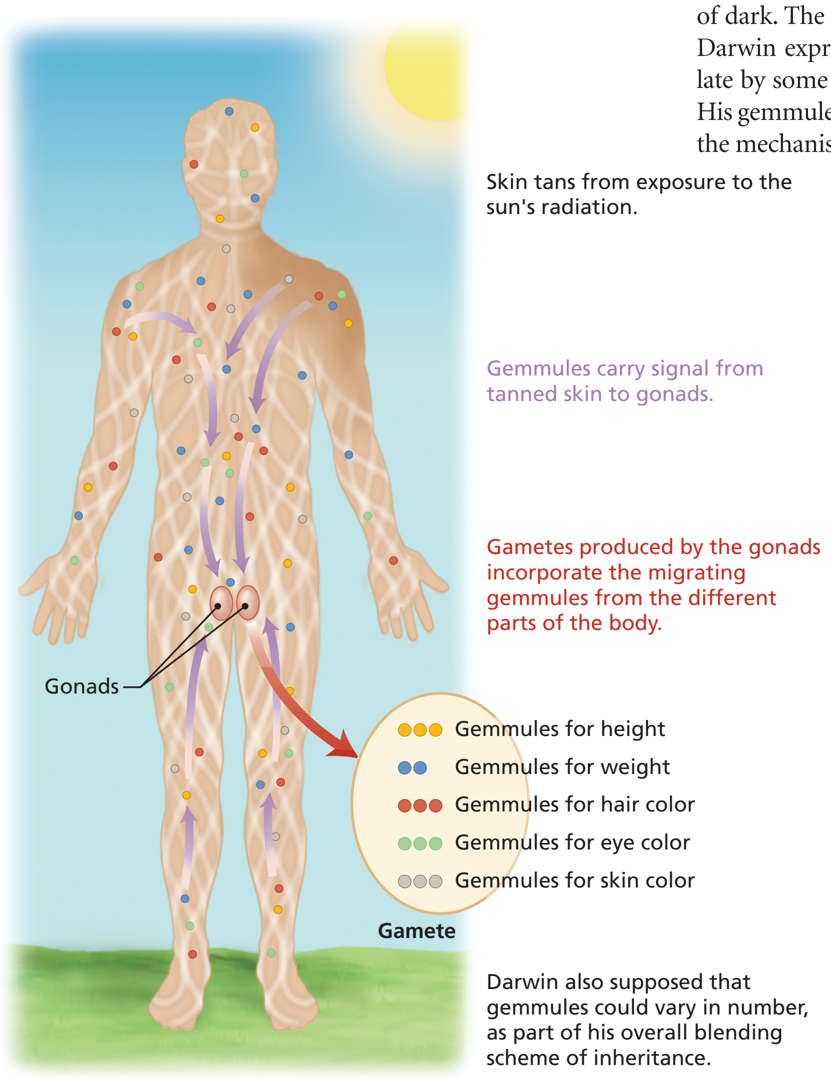


FIGURE 1.12A Darwin's Gemmules Moving About the Body

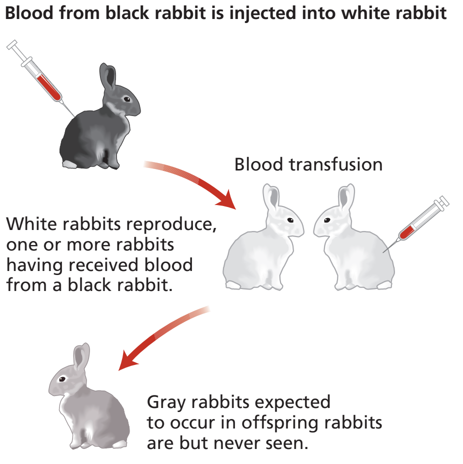


FIGURE 1.12B Blood transfusion experiments with rabbits did not reveal gemmules.

1.13 Mendel solved the problem of inheritance, but it took time for Mendel's genetics to join with Darwinism

It is one of the great ironies in the history of science that in the same period when Darwin was struggling with the problem of inheritance, **Gregor Mendel** (1822–1884), an obscure monk in the Austro-Hungarian Empire, was solving it. The solution that Mendel found is now known as genetics. Mendel himself is described in the following box.

With the concepts of genetics, it would eventually prove possible to sort out the foundations of evolution. But it took a long time for that to happen. The first problem was that Mendel's genetic experiments were published in a journal that few scientists read. The second problem was that Mendel's main connection to the larger scientific community, a botanist called Karl Nägeli, was horrified by Mendel's experimental findings. He did little to communicate Mendel's findings. Indeed, he might have "spiked" them, trying to suppress genetics instead of spreading it.

Even though Darwin was still alive when Mendel's work appeared, he never read it or heard of it, so far as we know. Mendel himself died in middle age of an acute kidney infection, without ever receiving substantial scientific recognition. This is one of the most unfortunate failures of communication in the history of science.

But science has a way of finding the truth, even when it has been neglected or suppressed. Around 1900, several scientists independently rediscovered Mendel's work. They appreciated its immense significance immediately. However, there was still some confusion because Darwin had explicitly rejected theories like Mendel's, and Darwin's followers had continued in his footsteps. This gave rise to the entirely erroneous notion that genetics and Darwin's evolution were incompatible. As a result, evolutionists and geneticists fought with each other for a few decades.

Finally, biologists calmed down and saw that genetics and evolution worked perfectly well together. This reconciliation of Darwinism and **Mendelism**, together with systematics and other parts of biology, came to be known as the **modern synthesis**.

The Strange Career of Gregor Mendel

The key person in the genetic revolution was the monk Gregor Mendel—one of the most obscure of all the great scientists, if not *the* most obscure. He died unnoticed in 1884. Born Johann Mendel in 1822, he became Gregor on taking orders in 1843. Mendel was rather bad at exams. Though he taught natural science at a high school, he never passed the examination for a teacher's license. Deep within the Austro-Hungarian Empire (in the town of Brno, now part of the Czech Republic), Mendel toiled away in the gardens of the monastery where he was first monk and then abbot.

An important part of Mendel's education was his study at the University of Vienna, where he learned an obscure branch of mathematics called *combinatorics*. Combinatorics is the mathematics of combining things by chance. For example, you do combinatoric experiments every time you shuffle a deck of cards and deal out four hands of five-card stud poker. Combinatorics lets you calculate the odds that you will get four aces and a king in your hand.

What was the significance of Mendel learning combinatorics? This knowledge made him better qualified than any other biologist then living to calculate the probability of particular outcomes from breeding experiments. Darwin, for example, who probably knew the literature of plant breeding better than Mendel, was unable to calculate mathematical odds with Mendel's precision.

The Birth of Modern Ecology

1.14 Predator-prey cycles and the origins of theoretical ecology

In the early part of the twentieth century, ecology remained a largely descriptive science. This would change as scientists from the physical and mathematical sciences, especially Alfred Lotka and Vito Volterra (Figure 1.14A), became interested in ecology. Lotka and Volterra brought with them an interest in developing general theoretical principles that would apply to many organisms. Perhaps because of their mathematical backgrounds, they were willing to ignore many complications that can characterize natural populations.

William Robin Thompson was an entomologist motivated by practical problems. Working in a biological laboratory in Paris, his goal was to control the corn borer insect using their naturally occurring parasites. Scientists in both the United States and France had independently noted that many host and parasite species appear to fluctuate in concert. Thompson took this to mean there should be some mathematical representation for that regularity. He explored these host-parasite relationships in his own work with simple equations. Many of Thompson's colleagues were apprehensive about developing theory that relied on parameters that had not been estimated for real populations. But Thompson's work influenced others, including Alfred Lotka.

Raymond Pearl, an established scientist in 1920, admired Alfred Lotka's work and invited him to give a series of lectures at Johns Hopkins University. These lectures then fostered a professional respect between Pearl and Lotka. Pearl would later help Lotka secure an unsalaried position at Johns Hopkins. Pearl also encouraged Lotka to develop a book of his theoretical work in ecology. This book, *Elements of Physical Biology*, was eventually published in 1925.

Lotka did not consider himself an ecologist, although his work was of great interest among ecologists. Lotka's grand vision was to found a field of physical biology that would accomplish the same goals as physical chemistry had for its discipline. Lotka's *Elements of Physical Biology* considers food webs, nutrient cycles, and the transfer of energy between organisms. However, Lotka is best known for a small part of his book that treats the dynamics of predator-prey systems. Lotka's grand scheme of establishing the field of physical biology was never realized.

About a year after Lotka's book came out, Vito Volterra published a nearly identical predator-prey model. Volterra was already an accomplished mathematician by 1925. His daughter was an ecologist who happened to be engaged to Umberto D'Ancona, a marine biologist. D'Ancona was responsible for getting Volterra interested in ecology after describing how he had noted a increase in predatory fish in the Adriatic Sea during World War I, when fishing had all but ceased. Volterra determined, as had Lotka, that interacting predator and prey species could give rise to oscillations in population size.

FIGURE 1.14A Vito Volterra (1860–1940) Held the chair of mathematical physics in Rome. Prior to his work on predator-prey models, Volterra was known for his work on elasticity and differential equations. He became interested in biological problems through his daughter's fiancé, who worked in ecology and marine biology.

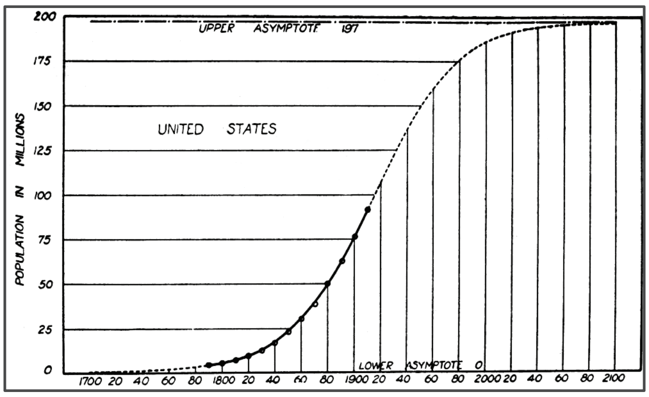


FIGURE 1.14B Logistic Curve Fitted to U.S. Census Data (solid lines) The dashed lines show the predicted population sizes from this fit. This graph is from Pearl's 1925 book, *The Biology of Population Growth*.

In the 1920s Raymond Pearl was driven to show that the logistic equation was an important law in ecology that described the growth of nearly all populations, including humans (Figure 1.14B). To that end, Pearl solicited Lotka's approval. Lotka found the logistic equation a useful starting point for describing population growth, but he did not give it the same status that Pearl did. Pearl argued for the utility of the logistic equation because it fit population growth curves from humans and fruit flies (see Figure 1.14B). These arguments were not universally accepted, even at that time.

1.15 The idea of competitive exclusion and the start of experimental ecology

The Russian scientist, Vladimir Alpatov, had interests in the geographical distribution of invertebrates. In 1927 he secured a fellowship from the Rockefeller Foundation to study in the United States with Raymond Pearl for two years. During his stay, Alpatov worked on experimental research with fruit flies. In addition to his research accomplishments in the United States, Alpatov developed a very high respect for Pearl. Alpatov also encouraged his young student in the Soviet Union, Georgii Gause, to secure funding to work with Pearl in the United States. Gause was unsuccessful on the first attempt to secure a fellowship; the major reason given was Gause's young age—21. Pearl and Gause agreed that if Gause were to publish a book, it might elevate his scientific stature in the United States and thus help win a fellowship. Although Gause did not receive the fellowship, publication of his book *The Struggle for Existence* (from Darwin's original phrase) established Gause's scientific legacy.

Gause had initially started his experimental work with fruit flies that Alpatov had brought back with him from the United States. But Gause then switched to protozoans and yeast because they were easier to handle. In studying competition between species, Gause made small modifications in the logistic equation to account for the effects of a second species. By keeping two species of protozoans on the same resource, he was able to show that extinction of one species was the ultimate outcome, as predicted by the competition equations (Figure 1.15A). Gause was also able show that when competing paramecia were given two food sources, the levels of competition could be reduced and the species could coexist. It would have been easy to discount Gause's experimental results as overly simplistic. Gause, however, tried to tie his work to the larger picture of ecology and thus make his work appeal to a large audience.

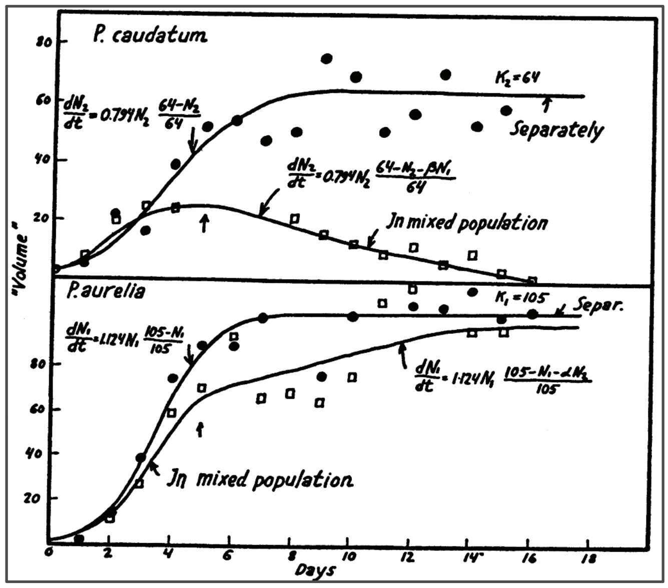
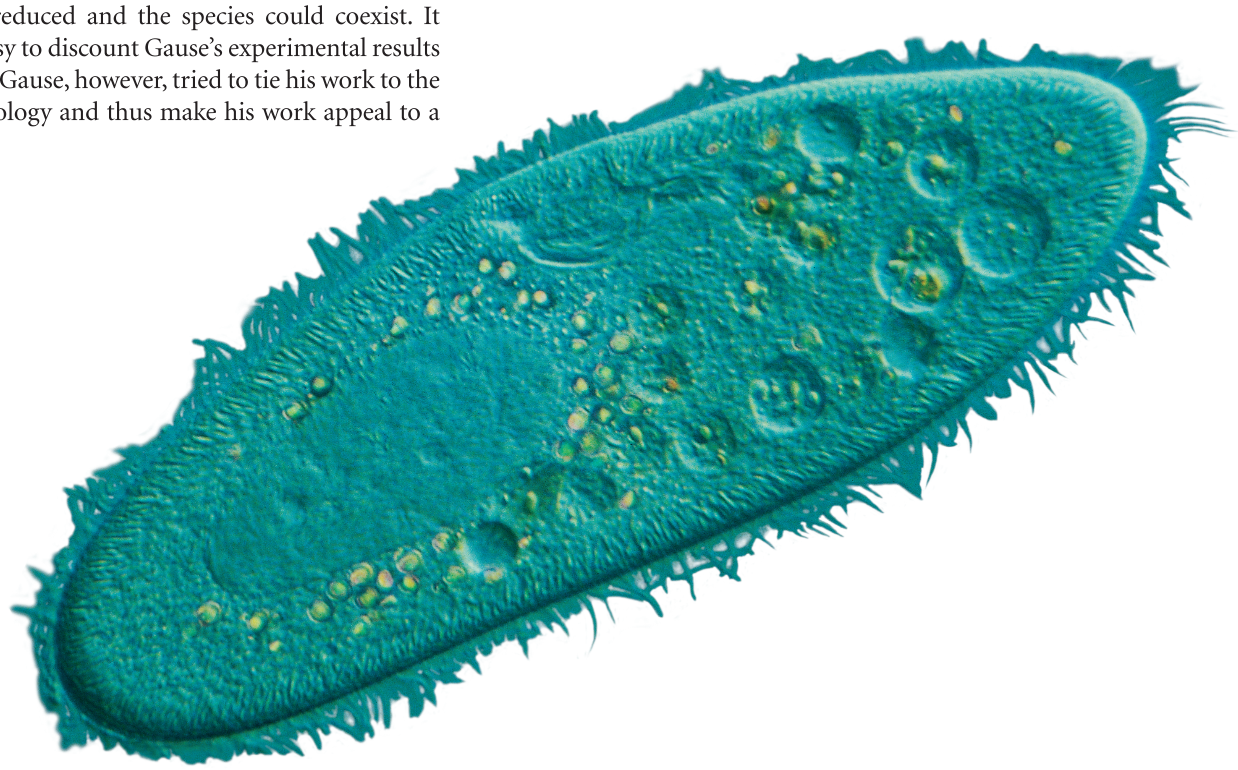


FIGURE 1.15A **One of Gause's Original Figures from *The Struggle for Existence*** This particular figure shows the change in the numbers of the two species of *Paramecium* when raised alone and when raised together. In this experiment *P. caudatum* is driven to extinction by *P. aurelia*.



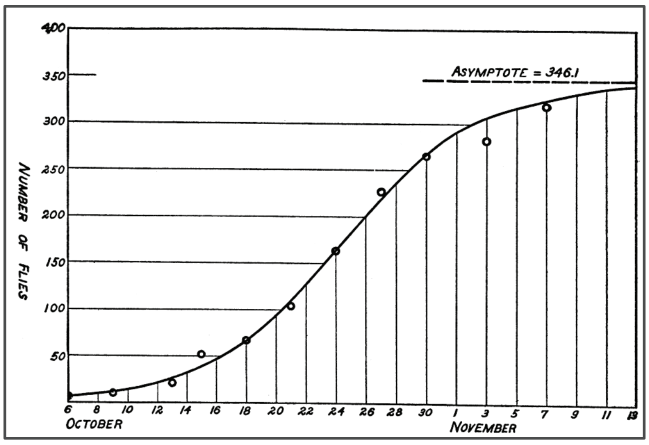


FIGURE 1.15B A Growth Curve from Pearl's Experimental Work, First Published in 1925 The y-axis shows the total numbers of *Drosophila* adults in a single culture over a period of about 1 month. The solid curve is a logistic equation fit to these data, which predict an equilibrium size of 346.

Gause is probably best known for the competitive exclusion principle, which suggests that no two species can occupy exactly the same niche, because one will be driven to extinction. Several others had in fact suggested this idea. In 1874 Karl Nägeli described the displacement of plant forms by competitors. Joseph Grinnell in 1917 suggested that "no two species regularly established in single fauna have precisely the same niche relationships." J.B.S. Haldane, the noted theoretical population geneticist, also stated the competitive exclusion principle in 1924. However, the clear experimental demonstration of this principle by Gause is almost certainly why he continues to get credit for this idea.

Experimental ecology also flourished under Raymond Pearl. Much of his experimental work on population growth and aging focused on fruit flies. That Pearl was working with fruit flies was in part accidental. In 1919 he had actually started a mouse research colony. However, a fire in the laboratory destroyed the colony. Before beginning a new colony, Pearl talked to T. H. Morgan, who convinced him to work with *Drosophila*. Much of Pearl's experimental research with *Drosophila* was aimed at showing the utility of the logistic equation (Figure 1.15B). Pearl and his colleagues carried out an extensive program of experimental research with *Drosophila*. These studies included investigating the effects of nutrition and density on a variety of life-history traits. Pearl also looked at the effects of density on age-specific survival; this work established *Drosophila* as an important organism for experimental ecology. At the same time, *Drosophila* was also establishing itself as one of the most important model organisms for genetic studies.

1.16 The controversy between density-dependent and density-independent population regulation

One of the greatest debates in ecology during the twentieth century concerned the role of density-dependent factors in population regulation. The debate lingered longer than necessary, partly because of the extreme positions taken by some of the protagonists. Curiously, the major protagonists in this debate were all from Australia. H.G. Andrewartha and L.C. Birch felt that environmental conditions were the major factors determining ultimate population numbers. In particular, they believed that favorable periods when populations might grow exponentially were short lived and to some extent unpredictable. The net result would be limited population increase from one season to the next.

Alexander Nicholson argued for the preeminence of competitive interactions between species. These interactions might be between members of the same species, or between the predators that feed on those animals. For Nicholson these competitive interactions, or governing reactions as he called them, determined the equilibrium that a population would reach.

Andrewartha and Birch were influenced by a series of studies on a small insect called a thrip (Figure 1.16A). These insects undergo large fluctuations in numbers in natural populations, but apparently they never completely deplete their food resources. Davidson and Andrewartha used a statistical regression model to predict these fluctuations in thrip numbers (Figure 1.16B). This statistical model was based on environmental measurements of temperature and rainfall and appeared to be able to account for most of the variation in thrip population size. Davidson and Andrewartha took this result to mean that environmental factors alone were responsible for the regulation of population size, and therefore there was no need to invoke competition as a regulating factor. As statistical methodologies and sophistication improved in ecology, later studies of the same thrip data were able to demonstrate that future population sizes were in fact influenced by density.

Nicholson, on the other hand, had a long career devoted to the study of blowflies in carefully controlled laboratory settings. Under these conditions, the blowflies were allowed to increase in number until the levels of food supplied by the experimenters could no longer support continued growth of population size. Given these conditions, it is not surprising that the competition for food is crucial to understanding some of the complex dynamics of blowfly populations.

Today there can be no doubt that competition and density-dependent regulation are important in many natural populations. However, some populations are regulated by other factors, like predation, to a much greater extent than by competition. There is no single ecological explanation for the size of natural populations.

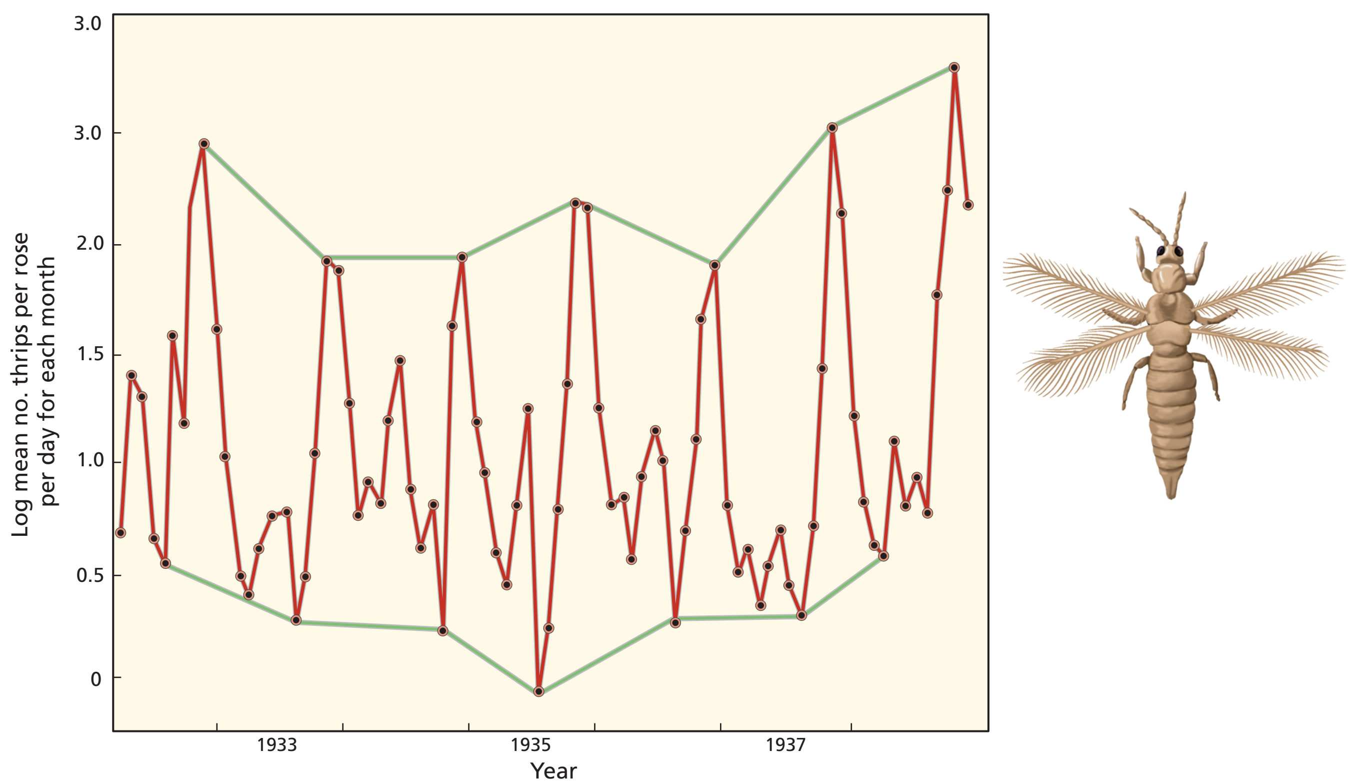


FIGURE 1.16A Fluctuations in the Numbers of Apple Blossom Thrips in Southern Australia Thrips are small insects, about 1 mm long, found in flowers of roses, fruit bushes, and other garden plants in Southern Australia. This figure, which is on a log scale, illustrates the large variation in numbers that are typical of this insect.

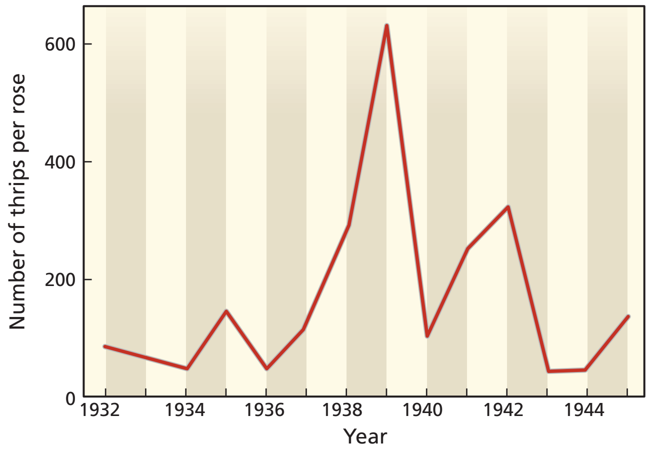


FIGURE 1.16B Population Density of Thrips over Many Years Davidson and Andrewartha used a model that incorporated the current and previous years' temperatures and the current year's rainfall to predict the numbers of thrips. Based on the ability of these abiotic factors to accurately model the thrip populations, Davidson and Andrewartha concluded that competitive interactions were not very important factors in the regulation of thrip numbers.

DARWIN'S VIEW OF LIFE

1.17 Darwin's theories broke with prevailing biological doctrines, which were theological and vitalist in their foundations

It is hard to imagine what biology was like before Darwin. Many people know that the European Middle Ages were dominated by the authority of the Bible. Bitter controversies arose over access to it. The Bible stood at the center of Christian theology and defined the ultimate limits of knowledge for a millenium.

Less widely known is a medieval doctrine of great importance for the development of science in Europe. This doctrine held that God revealed Himself to people by two devices—the Bible and His Creation. Thus God could also be understood by studying His works in the world, in addition to studying His Word. In a sense, this view made European science fundamentally theological before Darwin.

Indeed, there was a long tradition of theologically informed European science. Isaac Newton was an intensely mystical Christian who hated atheism with a passion. The Polish astronomer Nicolas Copernicus (1473–1543) advocated a sun-centered solar system within a religious, if not mystical, framework. Darwin's science professors at Cambridge University were often clergymen, many of whom saw their study of science as a devout occupation. When Darwin was a young man, his career fantasy was to preach to a small country congregation while collecting insects during his spare time. Science and Christianity were intertwined well into the nineteenth century.

At the time of the Renaissance, about A.D. 1400–1600, European thought acquired numerous ideas from the classical world of 1000 B.C. to A.D. 400. It is commonly believed that classical thinking led to a great improvement in European thinking, but this view is not altogether correct. A particular problem for biology was that classical theories were based on spiritual forces investing simple biological processes, and those forces were used to explain everything from growth to aging to physical processes. If there were distinct vital spirits that explained each biological process, how could a scientist make sense of biology?

Such thinking was so difficult to reconcile with traditional European science that Darwin and other nineteenth-century leaders of Western science recoiled from it. They preferred watered-down Christian science to the ancient scientific thinking, which they found repugnantly mystical. The rejection of such classical ideas was part of a general scientific movement that was started primarily by the physicist and astronomer Galileo. This movement is now known to us as **materialism**. In science, materialism is the doctrine that observations are to be explained in relation to the action of simple, observable processes—not spiritual forces such as angels or demons. The triumph of materialism played a large part in the acceptance of Darwin's ideas, because he did not invoke gods, spirits, or other magical agents in living processes.

Geology supplied one of the important proving grounds for materialism. There were two main doctrines in geology to explain the formation of mountain ranges, lakes, and other features of the Earth. The **catastrophists** followed the Bible and supposed that such events as Noah's Flood and other biblical upheavals could explain the creation of geological features. The **uniformitarians**, or **gradualists**, argued instead that the slow, cumulative action of everyday processes like sedimentation and erosion was a sufficient explanation of geology. In particular, uniformitarians assumed that the geological processes at work in the present were the same as those at work in the past. The tension between these two main points of view hinged on materialism. The uniformitarians were committed to a materialistic view of the world. The catastrophists were closer to a biblical view, in which God could arbitrarily achieve anything.

Darwin began his scientific career as a geologist siding with Charles Lyell, the great gradualist geologist (see box). One way to describe Darwin's career is to say that he extended Lyell's gradualist beliefs to the realm of biology.

Sir Charles Lyell, 1797–1875, the Founder of Modern Geology

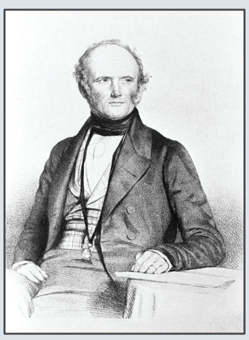


FIGURE 1.17A
Sir Charles Lyell

Trained as a lawyer, Charles Lyell (1797–1875; shown in Figure 1.17A) was a gentleman English scientist who found teaching at King's College, London, too much of a distraction from research. He was central to the success of England's Geological Society, the world's first. Starting in 1830, his *Principles of Geology* created the foundations of modern geology. Later in life, he was a key scientific colleague of Charles Darwin's, though he mostly sat on the fence where the doctrines of the *Origin of Species* were concerned.

1.18 Darwin's evolution was materialistic, unlike other evolutionary theories

There have been many theories of evolution other than Charles Darwin's. But most of these other theories of evolution have not been materialistic. The significance of Darwin's materialism requires some explanation.

First, let's consider the role of materialism in scientific theories generally. Some elaboration of the general concept of materialism is provided in the box "Materialism." As noted earlier, there is a strong connection between materialism and ideas like gradualism. On the other hand, catastrophism and related doctrines of dramatic coordinated change fit best with theistic and other supernatural doctrines. After all, an all-powerful supernatural being should be able to change trivial details like the nature or number of the species living on a small planet orbiting a mediocre star. How dramatic changes in life-forms could be produced by material causes alone was not clear in Darwin's lifetime. (We now know how this might happen, as discussed in Chapter 6 on speciation and extinction.) So catastrophism and materialism did not tend to combine well in theories of biological evolution until recent times. Materialistic doctrines in science instead have the same general properties as Lyell's gradualism: Ordinary things happen in ordinary ways, step by step, without large discontinuities.

Second, there are the nonmaterialistic theories of evolution. Many theories of evolution are based on vague or mystical assumptions. Some of these theories assume cosmic progress, a tendency for the universe to improve. Much of ancient Greek thought made this assumption, reflecting the then prevalent Greek assumption that the cosmos as a whole was benign. Even in the twentieth century, intellectuals often assumed some kind of mystical direction to evolution, a way of thinking that ranged from the writings of the German Oswald Spengler (1880–1936) to those of the French philosopher Henri Bergson (1859–1941). Jean-Baptiste Lamarck was the preeminent biologist who thought along these lines. Lamarck's scheme is diagrammed in Figure 1.18A. But it can be regarded fairly simply as the biological manifestation of a general tendency to upward progress in response to environmental challenge.

Third, Darwin and his closest colleagues reacted to **Lamarckism**—Lamarckian thinking—with revulsion, almost disgust. Darwin's intellectual forbears were men like Adam Smith and Sir Charles Lyell, who argued in concrete terms, who favored mechanical examples and analogies. People like Smith and Lyell were materialists who disliked cosmic ideas and speculations. Darwin's work on evolution was resolutely driven by a need to conform to the same intellectual standards as Smith and Lyell did, and Darwin utterly forswore any kind of mystical drive to evolution. There is nothing mystical about Darwin's thinking; everywhere he found such a hole in his reasoning, he worked very hard to patch it with a materialistic argument or explanation. Darwin's goal was to propose a materialistic theory of evolution, or he wasn't going to put forward a theory of evolution at all. ❖

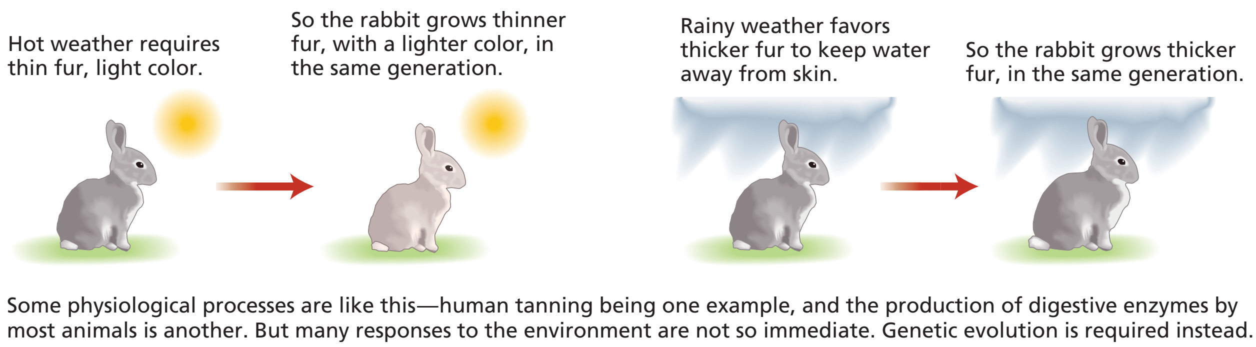


FIGURE 1.18A Lamarck's Theory of Evolution Jean-Baptiste Lamarck proposed a theory of change among living things some time before Darwin, in the eighteenth century. His theory of evolution also starts from the effects of the environment. But Lamarck supposed that organisms respond directly to the effects of the environment. There is no natural selection in Lamarck's scheme, only direct physiological response to the environment.

Materialism

Put simply, materialism is the doctrine that everything is made of matter. But the matter-energy interchangeability revealed by modern physics undermines any such simple theory of materialism. Matter just isn't what it used to be. A more subtle view is that matter is whatever stuff science can study, and therefore energy is also materialistic, even though it isn't matter.

A secondary meaning of materialism is the de-emphasis of mental and other nonmaterial states in causal explanations. To a materialist, you didn't eat the apple because "you felt hungry." Instead, you ate the apple because nerves in your stomach signaled to your brain that your stomach was empty, and thereafter your behavior was modified by the actions of further cerebral neurons. Materialistic explanation has as its hallmark the use of simple physical processes to explain more complex events.

1.19 Natural selection supplies direction to Darwin's evolution, but is not itself directed

In Darwin's theory, natural selection supplies a direction to each process of evolution. Darwin ruled out cosmic directing forces like God, or urges to perfection. Indeed, a shorthand way of understanding natural selection is that it is the ultimate supervisor of the living world, scrutinizing and guiding life on Earth. Much of Darwin's language implies as much.

The unusual thing about Darwin's theory of evolution by natural selection was that the natural selection that was supposed to drive the process was not a unified force, acting in parallel on all living things. Instead, natural selection acts within each species, separately, as sketched in Figure 1.19A. Darwin's entire theory rests on the evolutionary fates of individual species being separate from each other. This separation does not mean that Darwin saw no ecological interconnection between species. He certainly saw species as ecologically interconnected. But the evolutionary response of each species was, for Darwin, inherently its own. It did not share its selectively driven response to ecological circumstances with other species.

Furthermore, Darwin saw the individual members of each species as struggling with the other members of the species—for light (in the case of plants), for food (in the case of animals), and for mating opportunities (in the case of sexually reproducing organisms). Even within species, Darwinian evolution depends on the individual fates of organisms; see Figure 1.19B, in which the selective fates of the two birds are entirely separate. In this view, Darwin showed clear signs of his intellectual parentage in the laissez-faire capitalism of the eighteenth and nineteenth centuries. Darwin reasoned much like Adam Smith, the father of economics, with natural selection playing the role of Smith's economic competition in Darwin's discussion of biological evolution. Thus Darwin's theory of evolution was atomized. Species were distinct evolutionary units, with individual fates, and the organisms making up species also underwent selection as individuals.

Instead of some overarching force for evolutionary progress, Darwin supplied a natural selection acting separately within each species. And Darwin did not suppose that this action would be globally coordinated. Instead, each species was its own story—a story ecologically interacting with the stories of other species, but still its own story. The "direction" of Darwinian evolution is a meaningful concept only when applied to single species. Evolution as a whole has no direction, only the ensemble of directions unique to each species. And even the direction of natural selection within a species is changeable, rather than a fixed thing. For this reason, it is incorrect to think in terms of evolution on a grand scale. In fact, there are millions of distinct evolutionary processes, at least one for each species.

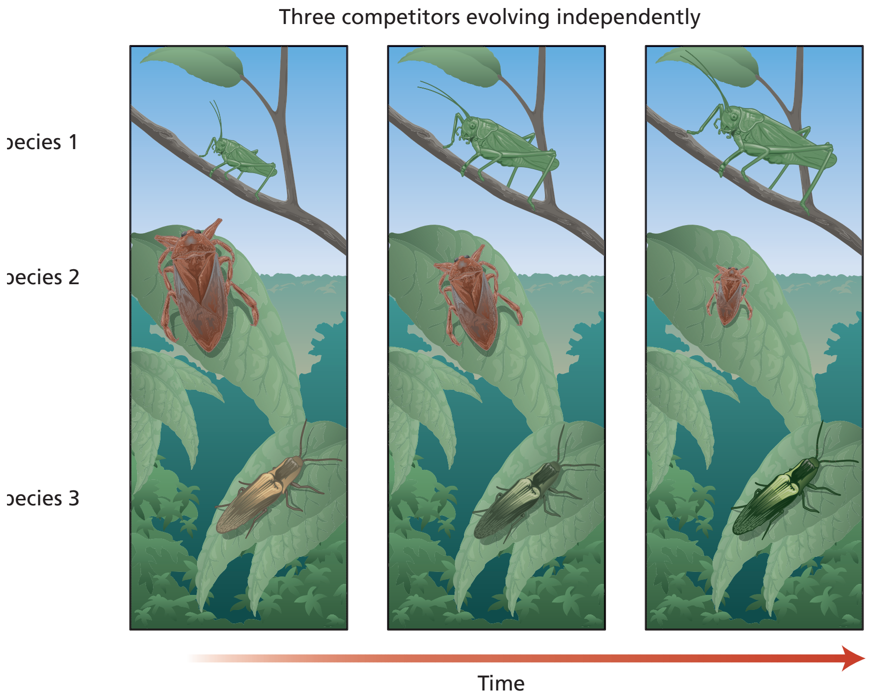


FIGURE 1.19A Darwin supposed that evolution occurred independently in separate species. We can think of each species as a discrete unit, possibly having effects on other species but remaining a separate entity during its evolution. An important scientific bonus of this is that we can study evolution one species at a time.

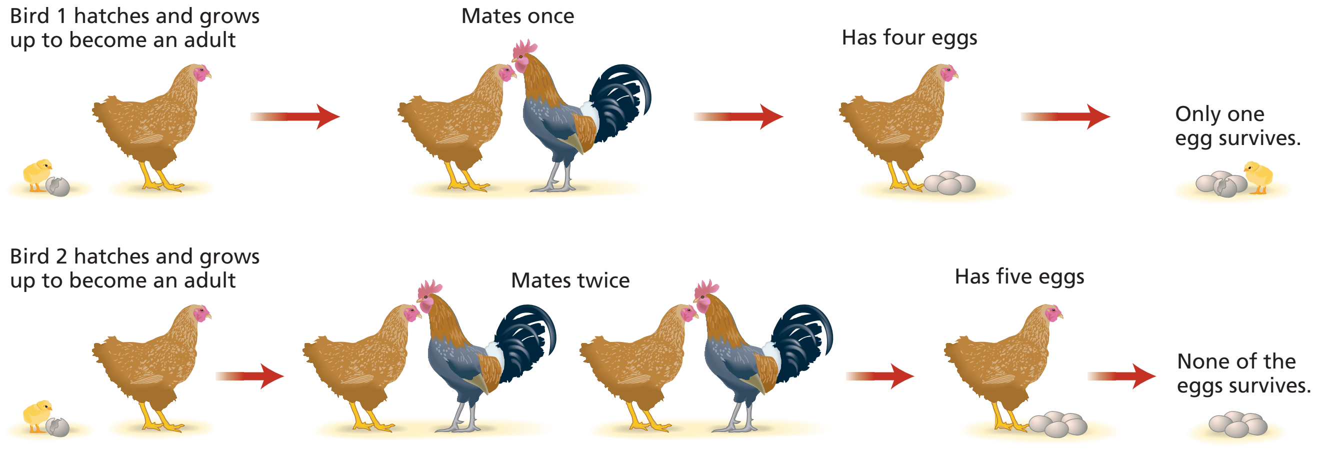


FIGURE 1.19B Darwin also supposed that natural selection acted separately on the individuals within populations; the process of differential survival and reproduction acts on individual organisms, killing them or their offspring, letting them mate independently.

In short, there cannot be "A Direction" to evolution, due to the splintering of the evolutionary process. Natural selection supplies "directions" to the evolutionary process, but these are always specific, not general. This feature of Darwin's theory of evolution by natural selection allied it firmly with modern, materialistic science, leaving behind the theologically based creationism of Darwin's own teachers.

1.20 Ecology and natural selection combine in Darwin's theory to produce inefficient and historical evolution

Because evolution by natural selection is not driven by a cosmic ordering principle, it has disorderly patterns. There is no Grand Conductor in Darwin's theory. Therefore, Darwin's view is that the extinction and origin of new species does not occur according to some overall imperative. This can be hard to understand, because the human mind naturally seeks coherent, simple stories.

Darwin *does* offer stories. The Galápagos finches are a story of migration, in which a specific finch population migrated from continental South America to a challenging new habitat. There the descendants of the original finch migrants overcame considerable difficulties, diversified into new species, and became one of the important life-forms of an important island group. But it could have been any of a variety of continental bird species that migrated and diversified on the Galápagos Archipelago. In fact, some other bird species did so. Mockingbirds (genus *Mimus*) are another group that migrated to the Galápagos, as shown in Figure 1.20A. They diversified too. There was no great historical necessity to the migration of a finch population; it was an historical accident.

The messiness of ecology led Darwin to another important conclusion: Evolution by natural selection does not produce perfection. "Natural selection will not produce absolute perfection, nor do we always meet, as far as we can judge, with this high standard under nature" (*Origin*, chap. VI). One example of this imperfection that Darwin brings forward is the mammalian eye, which does not have perfect optical properties. Another example is the flora and fauna of New Zealand. Darwin

FIGURE 1.20A **A Galápagos Mockingbird, *Mimus parvulus***

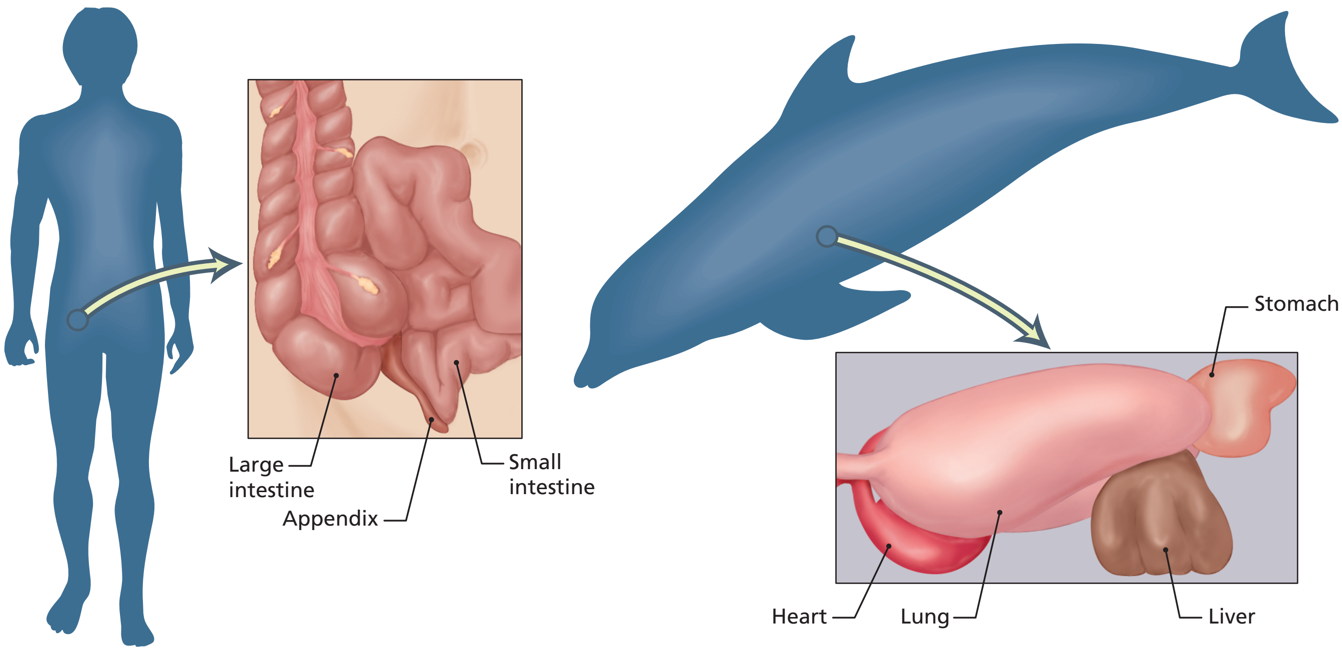


FIGURE 1.20B Two Examples of Imperfection among Living Things (i) The vermiform appendix in humans, which has no known function and can cause death when it ruptures; (ii) lungs in cetaceans, air-breathing aquatic mammals that are thereby forced to come to the surface to breathe, which can result in drowning.

argued that these species were essentially perfect relative to the other species of New Zealand, but still inferior to the invading species introduced by Europeans, which have been more successful than the endemic species in New Zealand. Darwin also considered the production of pollen by conifers, in which a few new seedlings result from the production of millions of pollen grains—highly inefficient. But in considering these examples, Darwin was complacent. He did not expect perfection. Indeed, he seems to have relished examples of imperfection, because they suited his view of life as a product of ecologically driven evolution, as opposed to a divine creation. If everything had been perfect in all living things, then a divine creation might still have been a credible theory compared with material evolution. Since Darwin's time, we have learned vastly more about the imperfections of life, even though living things still are remarkably efficient contrivances much of the time. Figure 1.20B shows several examples of imperfection among living things.

Though natural selection is a process that can theoretically change the morphology and behavior of a species with great speed, Darwin expected that it usually would not work quickly. Because it is not a directed process, because it has no inertia or intention, natural selection will act mindlessly and inconsistently. Only over a very long period are we likely to see natural selection produce a sustained change in an organism. Evolution by natural selection is neither efficient nor swift. Instead, it is usually inconsistent and unfocused, because it lacks the directed properties that make human actions deft and efficient. Natural selection is not to be thought of as a careful farmer of life. It is not that efficient, at least not in the short run.

1.21 Darwin argued that all order in the history of life was a result of evolution by natural selection

Even though Darwin did not view natural selection as all-powerful or consistent in direction, he still regarded evolution by natural selection as the sole and sufficient source of order in the living world. In particular, he held fast to some strikingly bold interpretations of life, all of them derived from his theory of evolution by natural selection. We list some of these here. They are all taken from the last chapter of the *Origin*, "Recapitulation and Conclusion."

1. *Complex organs* Darwin regarded complex organs—"organs of extreme perfection"—such as the human eye, as a challenge for his theory. But he held fast to his interpretation of them as products of gradual evolution:

   > Nothing at first can appear more difficult to believe than that the more complex organs and instincts have been perfected, not by means superior to, though analogous with, human reasons, but by the accumulation of innumerable slight variations, each good for the individual possessor. Nevertheless, this difficulty, though appearing to our imagination insuperably great, can not be considered real if we admit the following propositions, namely, that all parts of the organisation and instincts offer, at least individual differences—that there is a struggle for existence leading to the preservation of profitable deviations of structure or instinct—and, lastly, that graduations in the state of perfection of each organ may have existed, each good of its kind.

   This argument is illustrated by the example of the evolution of the vertebrate eye in Figure 1.21A.

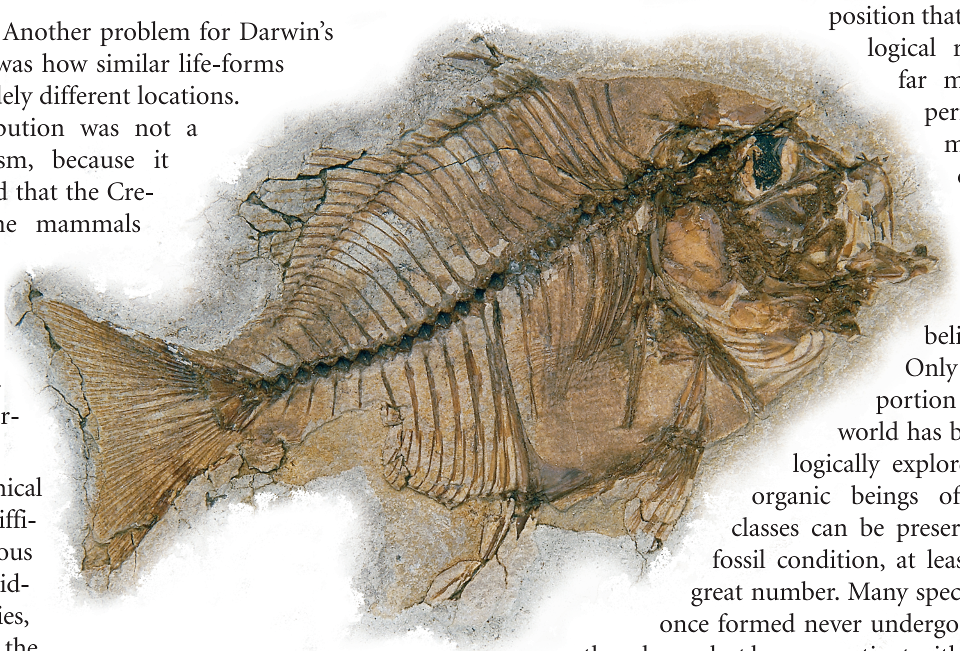
2. *Geographic distribution* Another problem for Darwin's non-creationist theory was how similar life-forms came to be found at widely different locations. This geographic distribution was not a problem for creationism, because it could easily be supposed that the Creator would want some mammals here, and some insects there, while creating the flora and fauna of the different continents. Again, despite this problem, Darwin was undeterred:

   > Turning to geographical distribution, the difficulties . . . are serious enough. All the individuals of the same species, and all the species of the same genus, or even higher group, are descended from common parents; and therefore, in however distant and isolated parts of the world they may now be found, they must in the course of successive generations have travelled from some one point to all the others. We are often wholly unable even to conjecture how this could have been effected. Yet, as we have reason to believe that some species have retained the same specific form for very long periods of time, immensely long as measured by years, too much stress ought not to be laid on the occasional wide diffusion of the same species; for during very long periods there will always have been a good chance for wide migration by many means. A broken or interrupted range may often be accounted for by the extinction of the species in the intermediate regions.

   Figure 1.21B illustrates this comment of Darwin's.

3. *Absence of intermediate fossil forms* Although Darwin was a geologist, one of the biggest problems facing his theory was the frequent absence of intermediate forms among known fossils. That is, the fossil record did not seem to follow the gradual pattern of change from one species to another assumed by Darwin. Here Darwin's geological expertise stood him in good stead:

   > Although geological research has undoubtedly revealed the former existence of many links, bringing numerous forms of life much closer together, it does not yield the infinitely many fine gradations between past and present species required on the theory . . . I can answer these questions and objections only on the supposition that the geological record is far more imperfect than most geologists believe. . . . Only a small portion of the world has been geologically explored. Only organic beings of certain classes can be preserved in a fossil condition, at least in any great number. Many species when once formed never undergo any further change but become extinct without leaving modified descendants.



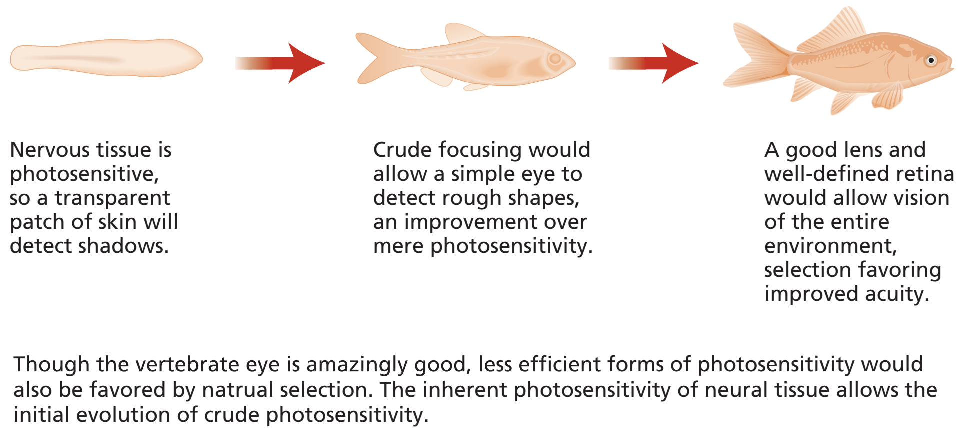


FIGURE 1.21A The eye illustrates the evolution of "organs of extreme perfection."

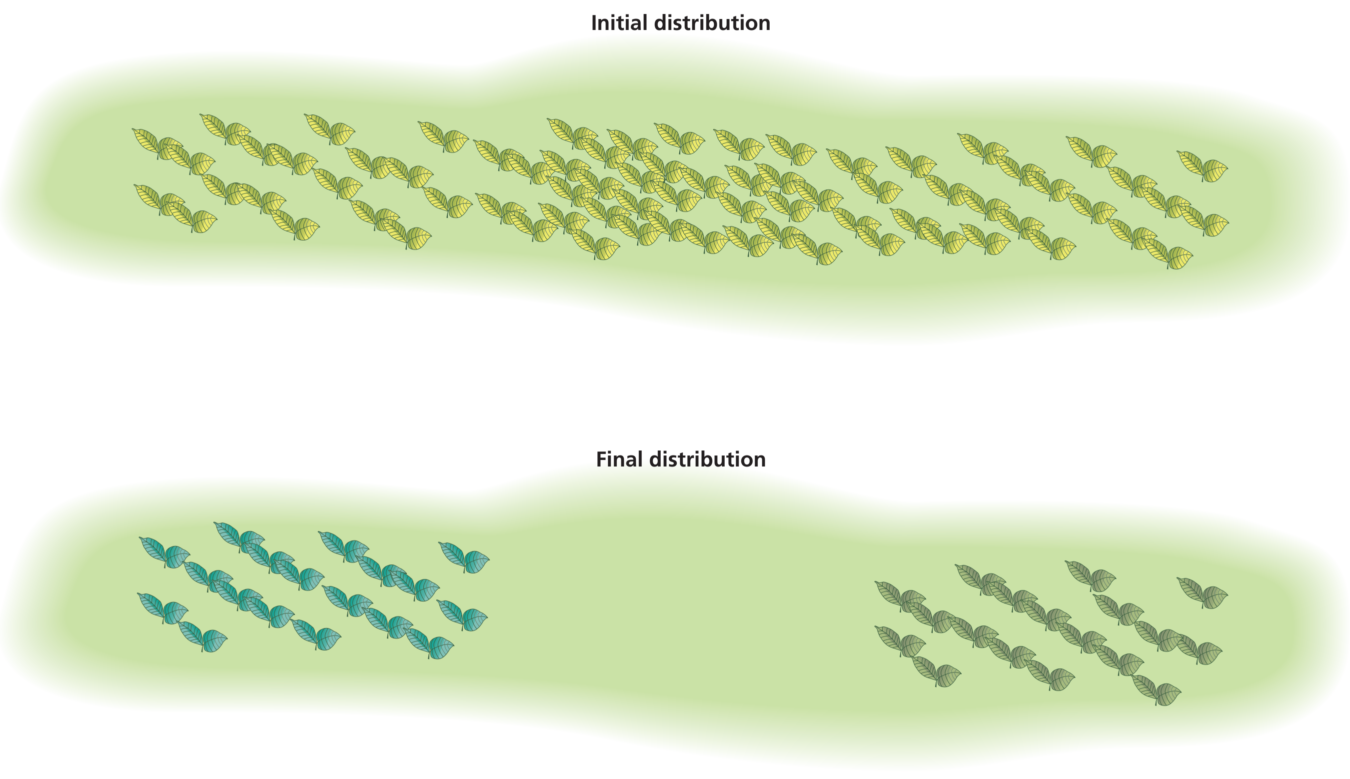


FIGURE 1.21B Species that are related to each other but widely dispersed can be explained by the loss of intermediate populations.

1.22 The Darwinian universe, and the organisms within it, undergoes materially important change

Corresponding to the Platonic notion of merely superficial variation is the idea of merely superficial change. If there is indeed nothing new under the sun, then understanding life on Earth is only a question of cataloging all the unchanging species, together with all their essential characteristics. With this model for science, apparent change in the universe is only the shuffling of unchanging objects in an essentially unchanging world, as shown in Figure 1.22A.

The Darwinian universe is radically different. Though there are constraints on the kind and degree of change allowed in Darwinian evolution, the principle of material change is fundamental. In the Darwinian universe, species are allowed to evolve. Small dog-sized herbivores can evolve into modern horses that are much larger and faster than their distant ancestors. Shrewlike mammals of 70 million years ago have descendants that are enormous whales, fleet bats, and humans that play chess. Entire groups of organisms, like dinosaurs, evolved and flourished over more than 100 million years, only to be wiped out in a few million years of cataclysm. This principle of material change is sketched in Figure 1.22B.

Though there are constraints on the kind and degree of change allowed in Darwinian evolution, the principle of material change is fundamental.

But it is not only the gross anatomy of living things that changes in the Darwinian universe. Fine morphology and molecular biology evolve too. A gill arch in the fishes of several hundred million years ago has evolved into the middle

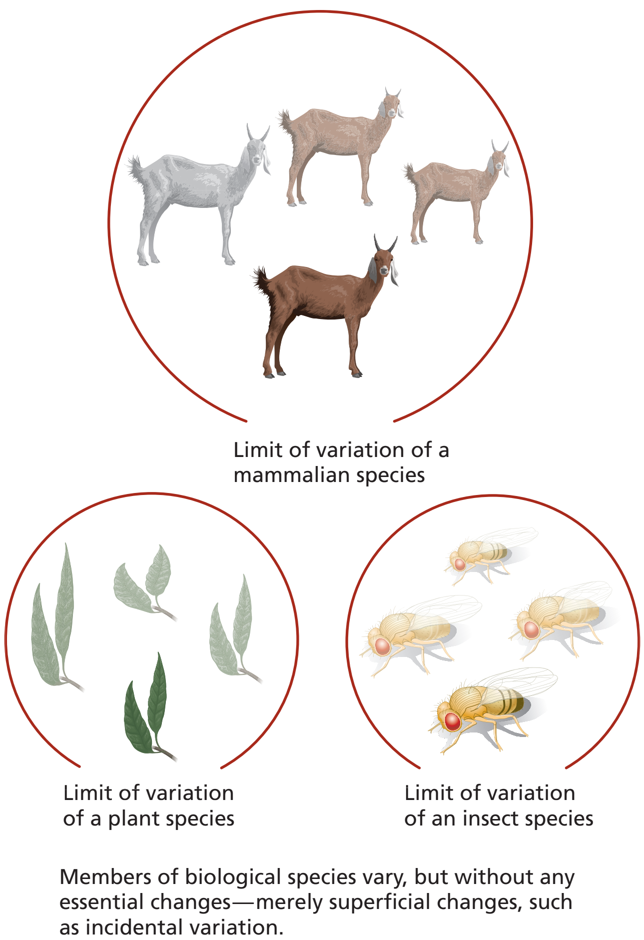


FIGURE 1.22A Western Idea of the Universe before Darwin Biological species never really change.

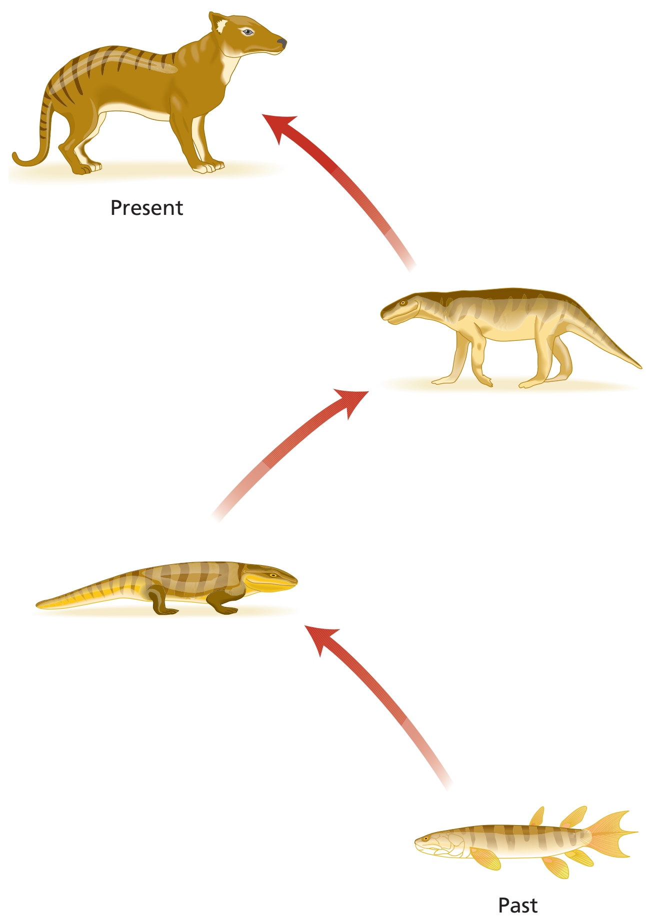
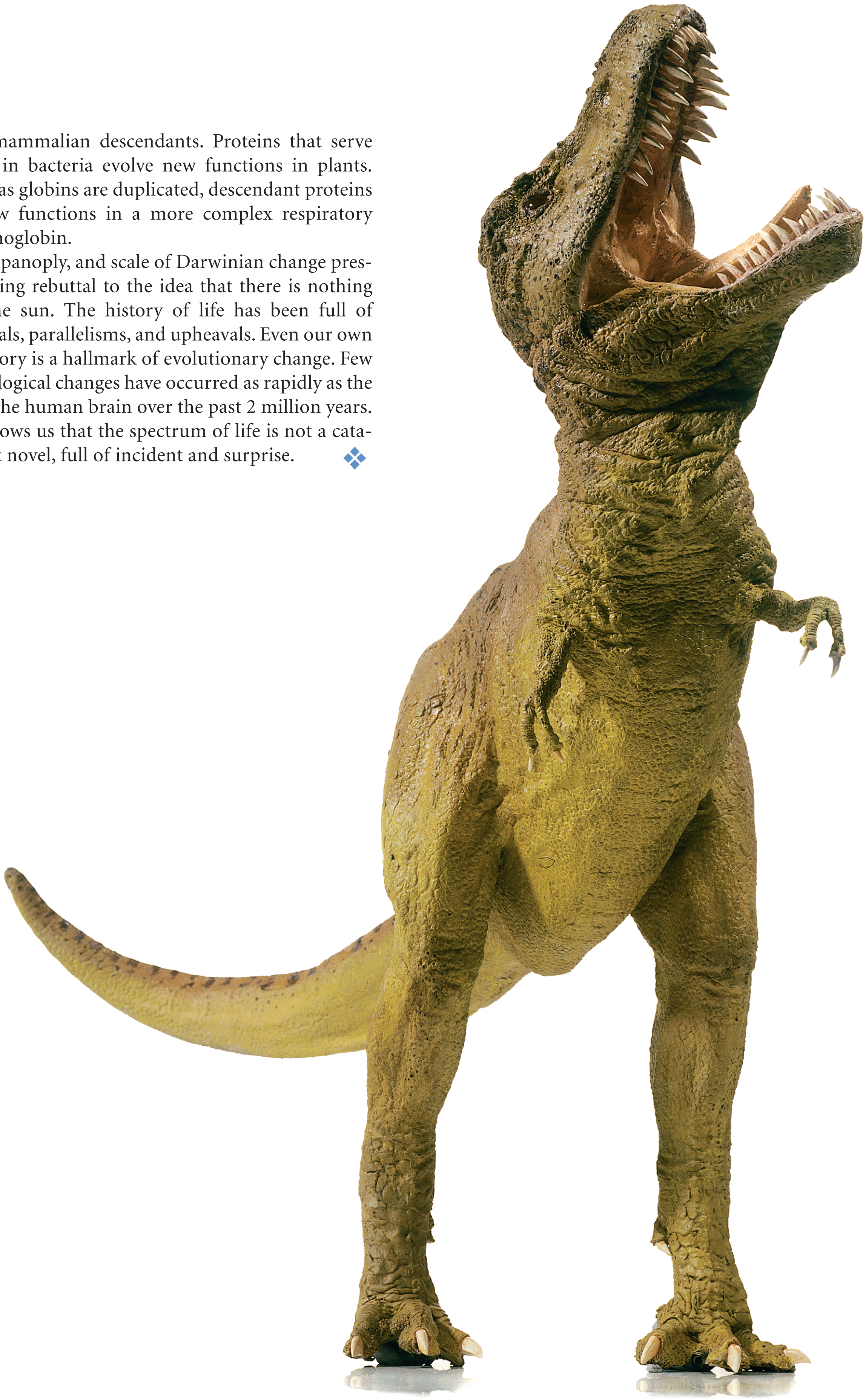


FIGURE 1.22B Western Universe after Darwin Biological species undergo important changes through evolution over long periods of time.

ear of their mammalian descendants. Proteins that serve one function in bacteria evolve new functions in plants. Proteins such as globins are duplicated, descendant proteins taking on new functions in a more complex respiratory molecule, hemoglobin.

The depth, panoply, and scale of Darwinian change present a devastating rebuttal to the idea that there is nothing new under the sun. The history of life has been full of change, reversals, parallelisms, and upheavals. Even our own biological history is a hallmark of evolutionary change. Few gross morphological changes have occurred as rapidly as the expansion of the human brain over the past 2 million years. Darwinism shows us that the spectrum of life is not a catalog but a giant novel, full of incident and surprise.



1.23 Despite great need, it took a long time for biology to be transformed by the Darwinian revolution

Before Darwin, the biological sciences had an abundance of minor theories and unreliable data. On the theoretical side, some Greeks of classical times used ideas about internal heat, drying, and coldness to explain growth, maturation, disease, and aging. In the late middle ages, the intellectual followers of Aristotle used elaborate theories of vital forces to explain all living processes, these theories being couched in terms of various types of "will" to be found in nature, in both animate and inanimate things. Gravity, for example, was explained as a will existing in many objects that made them want to return to the Earth. The quality of biological thought just before Darwin was not radically improved over that of Plato or Aristotle, even though the quantity of biological information was much greater.

Nor was the idea of an experimental method important to Darwin's breakthrough. Darwin did perform some experiments, particularly in plant breeding, but these came long after his theory of evolution was well developed. The young Darwin, the Darwin who developed evolutionary theory, was no more of an experimentalist than Aristotle was, perhaps less.

These points raise the question, why did biology have to wait so long for Charles Darwin to revolutionize the field? There are at least three possible reasons that the theory of evolution by natural selection took so long to arise. The first is that the basic ideas of species and adaptation needed to be developed. These ideas are present in classical Greek writings, but the work of European biologists after the Renaissance clarified them. In particular, the idea of an organism's suitedness to its natural habitat was central to European biology before Darwin.

A second possible reason the world had to wait for Darwin is that many of the ideas in his theory of evolution by natural selection were taken from eighteenth-century economics. Darwin transposed these ideas, both wittingly and unwittingly, to biology.

A third possible reason for the long wait may simply be luck. Darwin had several predecessors whose ideas were very close to his. For example, in 1831 Patrick Matthew published an obscure book on naval arboriculture that had an appendix on evolution by natural selection, but it was completely ignored. And there were others like him. Perhaps Darwin was just the first of a group of independent discoverers to develop evolutionary ideas enough to attract general attention. The very similar ideas of A. R. Wallace support this interpretation.

Whatever the source of Darwin's precedence, the Darwinian view of life transformed biology. Before Darwin, God was the most important explanatory principle of biology. Living things were manifestations of God's Book of Creation, testimonies to His Grace and Perfection.

After Darwin, biology was freed from theological components—or rather, it had the potential to be free of such components. To this day, some biologists are determined to interpret life based on a deity. However, these individuals are decreasing in number among the ranks of biologists. The burgeoning of Darwinian thinking is arrested only when powerful political regimes seek to impose particular religious or ideological views. Then, Darwinists are killed for their beliefs. This happened to population geneticists under Stalin's regime, even though Darwin was a hero in the Soviet Union. At that time, Stalin was interested in Lamarckian research, making him hostile to Darwinian materialism. Evolutionary biologists are likewise threatened in extremist Muslim regimes, where teaching evolutionary biology can be punishable with death. But in the developed countries of Europe, North America, Japan, and Australasia opposition to Darwinism is less extreme. Australia even has a town named Darwin.

To get some flavor of the worldwide view of Darwinism today, see the accompanying box. ❖

The 1982 Darwin Centennial around the World: From Academic Figure to Popular Hero

The world celebrated the centennial of Darwin's death in 1982, and the celebrations were various and surprising. Within the English-speaking world, Darwin's intellectual home, Darwin was feted as a great scientist by university professors and scientists in decorous symposia that were later published in thick hardcover books. This is the way American evolutionary biologists expected Darwin's centennial to proceed around the world.

But it didn't. Behind the then-Iron Curtain, in the Soviet Bloc countries, Darwin was celebrated as an official hero of communism. Because Karl Marx regarded Darwin's theories as the starting point for his "dialectical materialism," Darwin's vast scientific standing was exploited by the Soviets to bolster their ideological system only a few years before its collapse.

Perhaps even more amazing for biologists were the events in Italy and Spain. In Florence, for example, a conference on the Darwinian Heritage was organized by nonscientists. The Gramsci Institute, a political organization, organized civic celebrations in a variety of Italian cities. In Genoa alone, organizations ranging from the provincial government to an association of shipyard workers produced three lecture series, three roundtable discussions, six pamphlets, and five television broadcasts. The national weekly magazine *L'espresso* published a special supplement on the centennial in April 1982. In Spain, Barcelona held many events open to the public—a museum exhibit, a lecture series, a film series, and an exhibit of books. Comparable events occurred in other European countries.

Darwin has become a cultural hero, especially among those who reject priests and monarchs. Antiauthoritarians in many countries use Darwin as a buttress for their rejection of traditional Western religious and philosophical thought.

As a final note, Figure 1.23A shows some Darwin memorabilia, hisi scientific tools in particular.

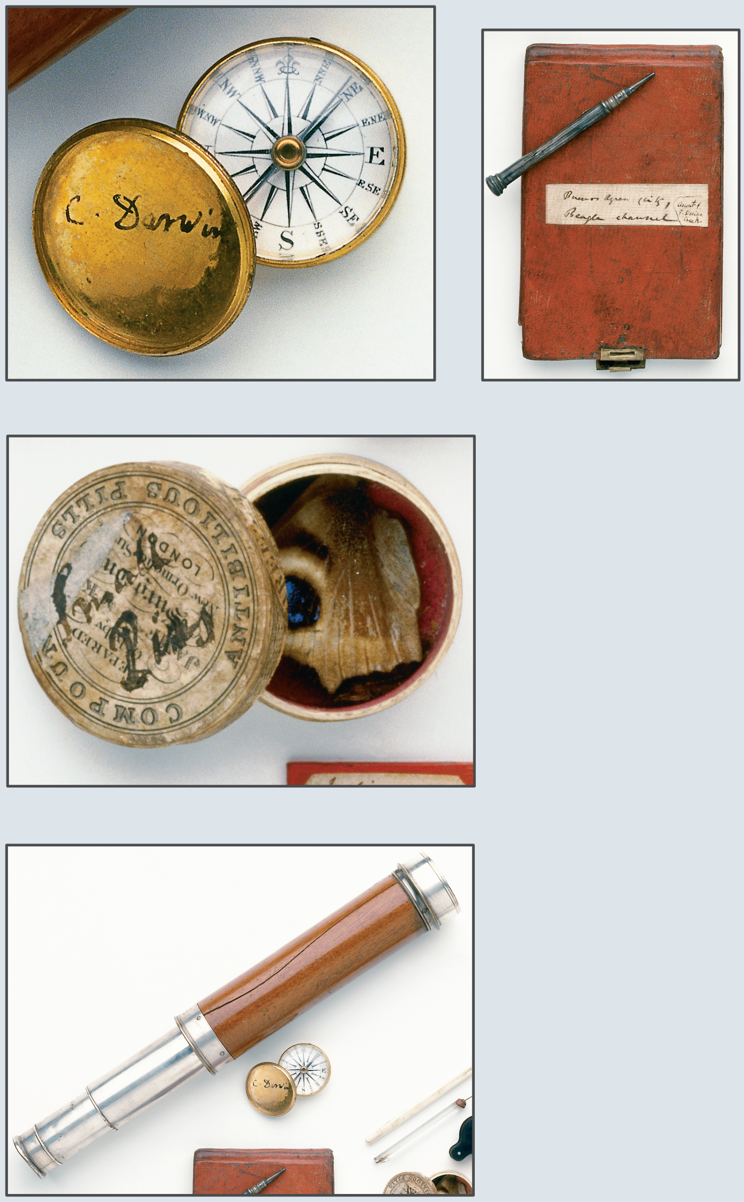


FIGURE 1.23A **Scientific Instruments and Other Darwin Memorabilia**

SUMMARY

1. Evolutionary biology, ecology, and organismal biology were founded largely by one man, Charles Darwin. Darwin came from the English landed gentry, and his father intended that Charles would study medicine. But Charles ended up as the naturalist aboard a ship that circumnavigated the world. On his return, Darwin stumbled on the idea of evolutionary change. Later he developed the concept of natural selection as a mechanistic explanation of evolution. These two concepts were Darwin's focus, and his legacy to all biologists.
2. The theory of natural selection is founded on ecological ideas that Darwin got from Thomas Robert Malthus, especially the tendency of all organisms to overpopulate. Darwin reasoned that there must always be a check to overpopulation, and this check will sometimes cause differential survival of those best suited to the environment, especially the hardy. This differential survival will change the composition of the parents of the next generation. Because offspring tend to resemble their parents, the offspring of the next generation will change, too. Thus evolutionary change can occur as a result of a natural selective process.
3. Darwin's theory of evolution by natural selection had a number of important features that would shape the future of biology. It was a materialistic theory that did not require the guiding hand of a deity or other higher intelligence. It was a gradualist theory. Abrupt change was not predicted. It was not a globally directed theory; individual species were expected to evolve independently, even when these species interacted with each other. Darwin's evolution was not a single process, affecting all species in a coordinated manner. At its root, it was an ecological theory, and the success of Darwinism made it possible for modern ecology to develop in the twentieth century.
4. At the core of Darwinism is the idea of variation. In Darwin's scheme, living things vary in ways that are materially important for survival and reproduction. This variation then supplies the raw material for the process of natural selection. Such true variation powers a process of true change, shaped by natural selection. In emphasizing variation and change, Darwinism broke with many elements of classical Greek thought.

REVIEW QUESTIONS

1. Why did Charles Darwin abandon the study of medicine?
2. What was Darwin's role on the *Beagle?*
3. Where on the Galápagos Islands did Darwin discover the theory of evolution by natural selection?
4. Did anyone else think of the theory of evolution besides Darwin?
5. Was *Origin of Species* a well-known book in Darwin's lifetime?
6. What views did Darwin share with the geologist Charles Lyell?
7. In Darwin's view of life, what is the general trend of evolution?
8. Why is ecology important for the theory of natural selection?
9. How did Darwin explain the evolution of complex structures like the vertebrate eye?
10. Why were materialism and gradualism important to the development of Darwin's theory of evolution by natural selection?

KEY TERMS

Aristotle
Beagle
catastrophism
Chambers, Robert
creationism
Darwin, Charles
Darwin, Erasmus
Darwinism
evolution
Fitzroy, Robert
Galápagos Islands
gradualism
Hume, David
Lamarck, Jean-Baptiste
Lamarckism
Lyell, Charles
Malthus, Thomas Robert
materialism
Mendel, Gregor
Mendelism
natural selection
Newton, Isaac
overpopulation
Plato
Smith, Adam
transmutation
uniformitarian
variation
Wallace, Alfred Russell

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