Evolution vs. Creationism

An Introduction

Second Edition

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FOREWORD BY NILES ELDREDGE

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To my family, Charlie and Carrie

CHAPTER 2

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Evolution

EVOLUTION BROAD AND NARROW

It has been my experience as both a college professor and a longtime observer of the creationism/evolution controversy that most people define evolution rather differently than do scientists. To the question, What does evolution mean? most people will answer, "Man evolved from monkeys," or invoke a slogan like "molecules to man." Setting aside the sex-specific language (surely no one believes that only males evolved; reproduction is challenging enough without trying to do it using only one sex), both definitions are much too narrow. Evolution involves far more than just human beings and, for that matter, far more than just living things.

The broad definition of evolution is a cumulative change through time. Not just any change counts as evolution, however. The Earth changes in position around the sun, but this is not evolution; an insect changes from egg to larva to adult during metamorphosis, but this is not evolution. An individual person (or a star) is born, matures, and dies but does not evolve. Evolution in this broad sense refers to the cumulative, or additive, changes that take place in phenomena like galaxies, planets, or species of animals and plants. It refers to changes that take place in groups rather than in individuals and to changes that accumulate over time.

Think of evolution as a statement about history. If we were able to go back in time, we would find different galaxies and planets, and different forms of life on Earth. Galaxies, planets, and living things have changed through time. There is astronomical evolution, geological evolution, and biological evolution. Evolution, far from the mere "man evolved from monkeys," is thus integral to astronomy, geology, and biology. As we will see, it is relevant to physics and chemistry as well.

Evolution needs to be defined more narrowly within each scientific discipline because both the phenomena studied and the processes and mechanisms of cosmological, geological, and biological evolution are different. Astronomical evolution deals with cosmology: the origin of elements, stars, galaxies, and planets. Geological evolution is

concerned with the evolution of our own planet: its origin and its cumulative changes through time. Mechanisms of astronomical and geological evolution involve the laws and principles of physics and chemistry: thermodynamics, heat, cold, expansion, contraction, erosion, sedimentation, and the like. In biology, evolution is the inference that living things share common ancestors and have, in Darwin's words, "descended with modification" from these ancestors. The main—but not the only—mechanism of biological evolution is natural selection. Although biological evolution is the most contentious aspect of the teaching of evolution in public schools, some creationists raise objections to astronomical and geological evolution as well.

ASTRONOMICAL AND CHEMICAL EVOLUTION

Cosmologists conclude that the universe as we know it today originated from an explosion that erupted from an extremely dense mass, known as the Big Bang. Very soon thereafter, the universe inflated—it expanded at an inconceivably rapid rate. Within the first second after the Big Bang this rapid inflation had ceased, but the universe has continued expanding at a much slower pace ever since. Astronomers have found evidence that galaxies evolved from gravitational effects on swirling gases left over from the Big Bang. The total number of galaxies is estimated to be in the hundreds of billions. Stars formed within galaxies, and in the cores of the stars, helium and hydrogen fused into heavier elements. Additional elements are produced when stars explode. As stars die, many eject the heavy elements, enriching the gas and dust from which new generations of stars (and planets) will be born. Thus, the elements have evolved over the 13 billion years since the first galaxies began to form.

Cosmologists and geologists tell us that between 4 billion and 5 billion years ago the planet Earth formed from the accumulation of matter that was encircling the sun. In earliest times, Earth looked far different from what we see today: it was an inhospitable place scorched by radiation, bombarded by meteorites and comets, and belching noxious chemicals from volcanoes and massive cracks in the planet's crust. Yet it is hypothesized that Earth's atmosphere evolved from those gases emitted, and water might well have been brought to the planet's surface by those comets that were crashing into it.

Meteors and comets bombarded Earth until about 3.8 billion years ago. In such an environment, life could not have survived. After the bombardment ceased, however, primitive replicating structures evolved. Currently, there is not yet a consensus about how these first living things originated, and there are several directions of active research. Before there were living creatures, of course, there had to be organic (i.e., carbon-containing) molecules. Fortunately, such organic chemistry is common throughout space, so the raw material for life was probably abundant. Answering the question of chemical prebiotic evolution involves developing plausible scenarios for the emergence of organic molecules such as sugars, purines, and pyrimidines, as well as the building blocks of life, amino acids.

To explore this question, in the 1950s, scientists began experimenting to determine whether organic compounds could be formed from methane, ammonia, water vapor, and hydrogen—gases that were likely to have been present in Earth's early atmosphere. By introducing electrical sparks to combinations of gases, researchers were able to

produce most of the amino acids that occur in proteins—which are the same amino acids found in meteorites—as well as other organic molecules (Miller 1992: 19). Because the actual composition of Earth's early atmosphere is not known, investigators have tried introducing sparks to various combinations of gases other than the original hypothesized blend. These also produce amino acids (Rode 1999: 774). Apparently, organic molecules form spontaneously on Earth and elsewhere, which has led one investigator to conclude, "There appears to be a universal organic chemistry, one that is manifest in interstellar space, occurs in the atmospheres of the major planets of the solar system, and must also have occurred in the reducing atmosphere of the primitive Earth" (Miller 1992: 20).

For life to emerge, some organic molecules had to be formed and then combined into amino acids and proteins, while other organic molecules had to be combined into something that could replicate: a material that could pass information from generation to generation. Modern living things are composed of cells, which consist of a variety of functioning components that are enclosed by a membrane; membranes set cells off from their environments and make them recognizable entities. As a result, origin-of-life research focuses on explaining the origin of proteins, the origin of heredity material, and the formation of membranes.

Origin-of-life researchers joke about their models falling into two camps: heaven and hell. Hell theories point to the present-day existence of some of the simplest known forms of life in severe environments, both hot and cold. Some primitive forms of life live in hot deep-sea vents where sulfur compounds and heat provide the energy to carry on metabolism and reproduction. Could such an environment have been the breeding ground of the first primitive forms of life? Other scientists have discovered primitive bacteria in permanently or nearly permanently frozen environments in the Arctic and the Antarctic. Perhaps deep in ice or deep in the sea, protected from harmful ultraviolet radiation, organic molecules assembled into primitive replicating structures.

The heaven theories note that organic molecules occur spontaneously in dust clouds of space and that amino acids have been found in meteorites. Perhaps these rocky visitors from outer space brought these basic components of life, which combined in Earth's waters to form replicating structures.

ORIGIN OF LIFE

Whether the proponents of hell or heaven theories finally convince their rivals of the most plausible scenario for the origin of the first replicating structures, it is clear that the origin of life is not a simple issue. One problem is the definition of life itself. From the ancient Greeks up through the early nineteenth century, people from European cultures believed that living things possessed an élan vital, or vital spirit—a quality that sets them apart from dead things and nonliving things such as minerals or water. Organic molecules, in fact, were thought to differ from other molecules because of the presence of this spirit. This view was gradually abandoned in science when more detailed study on the structure and functioning of living things repeatedly failed to discover any evidence for such an élan vital, and when it was realized that organic molecules could be synthesized from inorganic chemicals. Vitalistic ways of thinking

persist in some East Asian philosophies, such as in the concept of chi, but they have been abandoned in Western science for lack of evidence and because they do not lead to a better understanding of nature.

How, then, can we define life? According to one commonly used scientific definition, if something is living, it is able to acquire and use energy, and to reproduce. The simplest living things today are primitive bacteria, enclosed by a membrane and not containing very many moving parts. But they can take in and use energy, and they can reproduce by division. Even this definition is fuzzy, though: what about viruses? Viruses, microscopic entities dwarfed by tiny bacteria, are hardly more than hereditary material in a packet—a protein shell. Are they alive? Well, they reproduce. They sort of use energy, in the sense that they take over a cell's machinery to duplicate their own hereditary material. But they can also form crystals, which no living thing can do, so biologists are divided over whether viruses are living or not. They tend to be treated as a separate special category.

If life itself is difficult to define, you can see why explaining its origin is also going to be difficult. Different researchers stress different components of the definition of life: some stress replication and others stress energy capture. Regardless, the first cell would have been more primitive than the most primitive bacterium known today, which itself is the end result of a long series of events: no scientist thinks that something like a modern bacterium popped into being with all its components present and functioning! Something simpler would have preceded it that would not have had all of its characteristics. A simple bacterium is alive: it takes in energy that enables it to function, and it reproduces (in particular, it duplicates itself through division). We recognize that a bacterium can do these things because the components that process the energy and allow the bacterium to divide are enclosed within a membrane; we can recognize a bacterium as an entity, as a cell that has several components that, in a sense, cooperate. But what if there were a single structure that was not enclosed by a membrane but that nonetheless could conduct a primitive metabolism? Would we consider it alive? It is beginning very much to look like the origin of life was not a sudden event, but a continuum of events producing structures that, early in the sequence, we would agree are not alive, and at the end of the sequence, we would agree are alive, with a lot of iffy stuff in the middle.

We know that virtually all life on Earth today is based on DNA, or deoxyribonucleic acid. This is a chainlike molecule that directs the construction of proteins and enzymes, which in turn direct the assembly of creatures composed of one cell or of trillions. A DNA molecule instructs cellular structures to link amino acids in a particular order to form a particular protein or enzyme. It also is the material of heredity, as it is passed from generation to generation. The structure of DNA is rather simple, considering all it does. A DNA molecule that codes for amino acids uses a "language" of four letters— A (adenine), T (thymine), C (cytosine), and G (guanine)—which, combined three at a time, determine the amino-acid order of a particular protein. For example, CCA codes for the amino acid proline and AGU for the amino acid serine. The exception to the generalization that all life is based on DNA is viruses, which can be composed of strands of RNA, another chainlike molecule that is quite similar to DNA. Like DNA, RNA is based on A, C, and G, but it uses uracil (U) rather than thymine.

The origin of DNA and proteins is thus of considerable interest to origin-of-life researchers, and many researchers approach the origin of life from the position that

the replication function of life came first. How did the components of RNA and DNA assemble into these structures? One theory is that clay or calcium carbonate—both latticelike structures—could have provided a foundation upon which primitive chainlike molecules formed (Hazen, Filley, and Goodfriend 2001). Because RNA has one strand rather than two strands like DNA, some scientists are building theory around the possibility of a simpler RNA-based organic world that preceded our current DNA world (Joyce 1991; Lewis 1997), and very recently there has been speculation that an even simpler but related chainlike molecule, peptide nucleic acid (PNA), preceded the evolution of RNA (Nelson, Levy, and Miller 2000). Where did RNA or PNA come from? In a series of experiments combining chemicals available on early Earth, scientists have been able to synthesize purines and pyrimidines, which form the backbones of DNA and RNA (Miller 1992), but synthesizing complete RNA or DNA is extraordinarily difficult.

After a replicating structure evolved (whether it started out as PNA or RNA or DNA or something else), the structure had to acquire other bits of machinery to process energy and perform other tasks. Some researchers, the so-called metabolism-first investigators (Shapiro 2007), are looking at the generation of energy as the key element in the origin of life. In this scenario, replication is secondary to the ability to acquire energy.

Finally, this replicating and energy-using structure had to be enclosed in a membrane, and the origin of membranes is another area of research into the origin of life. A major component of membranes are lipids, which are arranged in layers. Precursors of lipids, layered structures themselves, apparently form spontaneously, and models are being developed to link some of these primitive compounds to simple membranes capable of enclosing the metabolizing and reproducing structures that characterize a cell (Deamer, Dworkin, Sandford, Bernstein, and Allamandola 2002). The origin of life is a complex but active research area with many interesting avenues of investigation, though there is not yet consensus among researchers on the sequence of events that led to the emergence of living things. But at some point in Earth's early history, perhaps as early as 3.8 billion years ago but definitely by 3.5 billion years ago, life in the form of simple single-celled organisms appeared. Once life originated, biological evolution became possible.

This is a point worth elaborating on. Although some people confuse the origin of life with evolution, the two are conceptually separate. Biological evolution is defined as the descent of living things from ancestors from which they differ. Evolution kicks in after there is something, like a replicating structure, to evolve. So the origin of life preceded evolution, and is conceptually distinct from it. Regardless of how the first replicating molecule appeared, we see in the subsequent historical record the gradual appearance of more complex living things, and many variations on the many themes of life. Predictably, we know much more about biological evolution than about the origin of life.

BIOLOGICAL EVOLUTION

Biological evolution is a subset of the general idea that the universe has changed through time. In the nineteenth century, Charles Darwin spoke of "descent with modification," and that phrase still nicely communicates the essence of biological

evolution. *Descent* connotes heredity, and indeed, members of species pass genes from generation to generation. *Modification* connotes change, and indeed, the composition of species may change through time. Descent with modification refers to a genealogical relationship of species through time. Just as an individual's genealogy can be traced back through time, so too can the genealogy of a species. And just as an individual's genealogy has missing links—ancestors whose names or other details are uncertain—so too the history of a species is understandably incomplete. Evolutionary biologists are concerned both with the history of life—the tracing of life's genealogy—and with the processes and mechanisms that produced the tree of life. This distinction between the patterns of evolution and the processes of evolution is relevant to the evaluation of some of the criticisms of evolution that will emerge later in this book. First, let's look briefly at the history of life.

The History of Life

Deep Time. The story of life unfurls against a backdrop of time, of deep time: the length of time the universe has existed, the length of time that Earth has been a planet, the length of time that life has been on Earth. We are better at understanding things that we can have some experience of, but it is impossible to experience deep time. Most of us can relate to a period of one hundred years; a person in his fifties might reflect that one hundred years ago, his grandmother was a young woman. A person in her twenties might be able to imagine what life was like for a great-grandparent one hundred years ago. Thinking back to the time of Jesus, two thousand years ago, is more difficult; although we have written descriptions of people's houses, clothes, and how they made their living in those times, there is much we do not know of official as well as everyday life. The ancient Egyptians were building pyramids five thousand years ago, and their way of life is known in only the sketchiest outlines.

And yet the biological world of five thousand years ago was virtually identical to ours today. The geological world five thousand years ago would be quite recognizable: the continents would be in the same places, the Appalachian and Rocky mountains would look pretty much as they do today, and major features of coastlines would be identifiable. Except for some minor remodeling of Earth's surface due to volcanoes and earthquakes, the filling in of some deltas due to the deposition of sediments by rivers, and some other small changes, little has changed geologically. But our planet and life on it are far, far older than five thousand years. We need to measure the age of Earth and the time spans important to the history of life in billions of years, a number that we can grasp only in the abstract.

One second is a short period of time. Sixty seconds make up a minute, and sixty minutes make up an hour. There are therefore 3,600 seconds in an hour, 86,400 in a day, 604,800 in a week, and 31,536,000 in a year. But to count to 1 billion seconds at the rate of one per second, you would have to count night and day for approximately thirty-one years and eight months. The age of Earth is 4.5 billion years, not seconds. That is an enormous amount of time. As Stephen Jay Gould remarked, "An abstract, intellectual understanding of deep time comes easily enough—I know how many zeros to place after the 10 when I mean billions. Getting it into the gut is quite another

matter. Deep time is so alien that we can really only comprehend it as metaphor" (Gould 1987: 3).
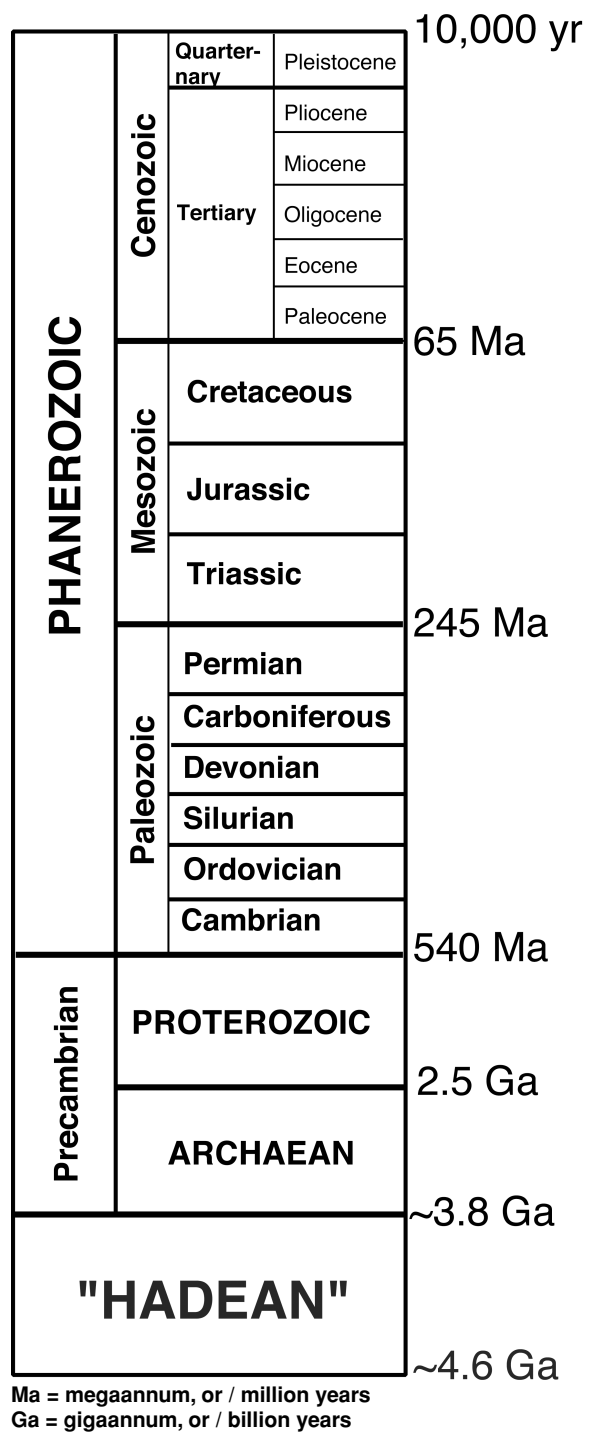
Figure 2.1 presents divisions of geological time used to understand geological and biological evolution. The solar system formed approximately 4.6 billion years ago; Earth formed about 4.5 billion years ago. The emergence of life was probably impeded by the bombardment of the Earth and moon by comets and meteorites until about 3.8 billion years ago, because only after the bombardment stopped do we find the first evidence of life. As discussed in the section "Astronomical and Chemical Evolution," there was a period of hundreds of millions of years of chemical evolution before the first structures that we might consider alive appeared on Earth: primitive one-celled organisms, less complex than any known bacterium.

After these first living things appeared between 3.5 billion and 4 billion years ago, life continued to remain outwardly simple for more than 2 billion years. Single-celled living things bumped around in water, absorbed energy, and divided—if some other organism didn't absorb them first. Reproduction was asexual: when a cell divided, the result was almost always two identical cells. Very slow changes occur with asexual reproduction, and this is probably an important reason that the evolution of life moved so slowly during life's first few billion years. Yet some very important evolutionary changes were taking place on the inside of these simple cells: the earliest living things gave rise to organisms that developed a variety of basic metabolic systems and various forms of photosynthesis.

Nucleated Cells. The first cells on Earth got along fine without a nucleus or a membrane around their DNA; in fact, bacteria today generate energy, carry out other cell functions, and reproduce new daughter bacteria without having nucleated DNA. Nucleated (eukaryotic) cells didn't evolve until about 1.5 billion years ago. Around 2 billion years ago, great changes in Earth's surface were taking place: continents were moving, and the amount of oxygen had increased in the atmosphere. Where did this oxygen come from? Oxygen is a by-product of photosynthesis, and indeed, oxygen produced by photosynthesizing bacteria built up in the atmosphere over hundreds of millions of years. This would explain the appearance of large red-colored geological deposits dating from this time: dissolved iron oxidized in the presence of free oxygen. In the words of researcher William Schopf, "The Earth's oceans had been swept free of dissolved iron; lowly cyanobacteria—pond scum—had rusted the world!" (Schopf 1992: 48). The increase of oxygen in the atmosphere resulted in a severe change in the environment: many organisms could not live in the new "poisonous" oxygenated environment. Others managed to survive and adapt.

The surface of Earth had been inhospitable for life: deadly radiation would have prevented life as we know it from existing at the planet's surface. The increase in oxygen as a result of photosynthesis resulted in the establishment of an ozone layer in the stratosphere. Oxygen is O_2; when ultraviolet radiation in the stratosphere strikes oxygen, ozone, which is O_3, is formed. The ozone shield protects living things from ultraviolet radiation, which permitted the evolution of life at the surface of the planet and eventually of the evolution of organisms composed of more than one cell (multicellular organisms, or metazoans).

Figure 2.1
Timescale of Earth's history. Courtesy of Alan Gishlick.

PHANEROZOIC	Cenozoic	Quarter-nary	Pleistocene	10,000 yr
		Tertiary	Pliocene	
			Miocene	
			Oligocene	
			Eocene	
			Paleocene	
	Mesozoic	Cretaceous		65 Ma
		Jurassic		
		Triassic		
	Paleozoic	Permian		245 Ma
		Carboniferous		
		Devonian		
		Silurian		
		Ordovician		
		Cambrian		540 Ma
Precambrian		PROTEROZOIC		
				2.5 Ga
		ARCHAEAN		
				~3.8 Ga
		"HADEAN"		
				~4.6 Ga

Ma = megaannum, or / million years
Ga = gigaannum, or / billion years

Eukaryotic cells may have evolved from unnucleated cells that were able to enclose their DNA in an interior membrane (forming the nucleus), and that incorporated other cells within their cell membranes. Nucleated cells have structures called organelles within their cytoplasm that perform a variety of functions having to do with energy capture and use, cell division, predation, and other activities. Some of these structures, such as mitochondria and chloroplasts, have their own DNA. Similarities between the DNA of such organelles and that of some simple bacteria have supported the theory that, early in evolution, the ancestors of eukaryotes absorbed certain bacteria and formed a cooperative, or symbiotic, relationship with them, whereby the newcomers functioned to enhance performance of metabolism, cell division, or some other task (Margulis 1993). The nucleus itself may have been acquired in a similar fashion, from "recycled" parts obtained after the absorption of other bacteria. Evidence for these theories comes, of course, not from the fossil record but from inferences based on biochemical comparisons of living forms.

Once nucleated cells developed, sexual reproduction was not far behind. Sexual reproduction has the advantage of combining genetic information from more than one individual, thus providing more variation to the population. Having more variation allows both the individual organism and the population of organisms to adjust to environmental change or challenge. Some researchers theorize that geological and atmospheric changes, together with the evolution of sexual reproduction, stimulated a burst of evolutionary activity during the late Precambrian period, about 900 million years ago, when the first metazoans (organisms composed of many cells) appear in the fossil record.

The Precambrian and the Cambrian Explosion. The first evidence we have of multicelled organisms comes from the Precambrian period, about 900 million years ago, and consists of fossils of sponges and jellyfish. Sponges are hardly more than agglomerations of individual cells; jellyfish are composed of two layers of cells that form tissues. Jellyfish, then, have a more consistent shape from organism to organism than do sponges, yet they lack a head and digestive, respiratory, circulatory, or other organs. Early echinoderms, represented today by starfish, sea urchins, and sea cucumbers, also occur in the Precambrian. Like the other Precambrian groups, early echinoderms have a rather simple body plan, but they do have a mouth and an anus, three tissue layers, and organs for digestion.

In the Cambrian, about 500 million years ago, there was rapid divergent evolution of invertebrate groups. New body plans appeared: "inventions" like body segmentation and segmented appendages characterized new forms of animal life, some of which died out but many of which continue to the present day. These new body plans appear over a geologically sudden—if not biologically sudden—period of about 10 million to 20 million years. Crustaceans, brachiopods, mollusks, and annelid worms, as well as representatives of other groups, appear during the Cambrian.

Evolutionary biologists are studying how these groups are related to one another and investigating whether they indeed have roots in the Precambrian period. In evolutionary biology, as in the other sciences, theory building depends on cross-checking ideas against different types of data. There are three basic types of data used to investigate the evolutionary relationships among the invertebrate groups: size and

shape (morphological) comparisons among modern representatives of these groups, biochemical comparisons among the groups' modern descendants, and the fossil record. Largely because of problems in the preservation of key fossils at key times—and the fact that the evolution of these basic body plans might have taken "only" tens of millions of years, an eye blink from the perspective of deep time—the fossil evidence currently does not illuminate links among most of the basic invertebrate groups. Nonetheless, much nonfossil research is being conducted to understand similarities and differences of living members of these groups, from which we may infer evolutionary relationships.

One particularly active area of research has to do with understanding the evolution and developmental biology (embryology) of organisms, a new field referred to as "evo-devo."

Evo-Devo. Advances in molecular biology have permitted developmental biologists to study the genetics behind the early stages of embryological development in many groups of animals. What they are discovering is astounding. It is apparent that very small changes in genes affecting early, basic structural development can cause major changes in body plans. For example, there is a group of genes operating very early in animal development that is responsible for determining the basic front-to-back, top-to-bottom, and side-to-side orientations of the body. Other early-acting genes control such bodily components as segments and their number, and the production of structures such as legs, antennae, and wings. Major changes in body plan can come about through rather small changes in these early acting genes. What is perhaps the most intriguing result of this research is the discovery of identical or virtually identical early genes in groups as different as insects, worms, and vertebrates. Could some of the body plan differences of invertebrate groups be the result of changes in genes that act early in embryological development?

Probable evolutionary relationships among the invertebrate groups are being established through anatomy, molecular biology, and genetics, even if they have not been established through the fossil record. One tantalizing connection is between chordates, the group to which vertebrates belong (see the subsequent section), and echinoderms, the group to which starfish and sea cucumbers belong. On the basis of embryology, RNA, and morphology, it appears that the group to which humans and other vertebrates belong shared a common ancestor with these primitive invertebrates hundreds of millions of years ago. Although adult echinoderms don't look anything like chordates, their larval forms are intriguingly similar to primitive chordates. There are also biochemical similarities in the way they use phosphates—but read on to find out more about chordates!

Vertebrate Evolution. Our species belongs to the vertebrates, creatures with a bony structure encircling the nerve cord that runs along the back. Vertebrates are included in a larger set of organisms called chordates. Although all vertebrates are chordates, not all chordates are vertebrates. The most primitive chordates look like stiff worms. Characteristically, chordates have a notochord, or rod, running along the back of the organism with a nerve cord running above it. At some time in a chordate's life, it also has slits in the neck region (which become gills in many forms) and a tail. An example of a living chordate is a marine filter-feeding creature an inch or so long called

Figure 2.2
Amphioxus shows the basic body plan of chordates in having a mouth, an anus, a tail, a notochord, and a dorsal nerve chord. Courtesy of Janet Dreyer.
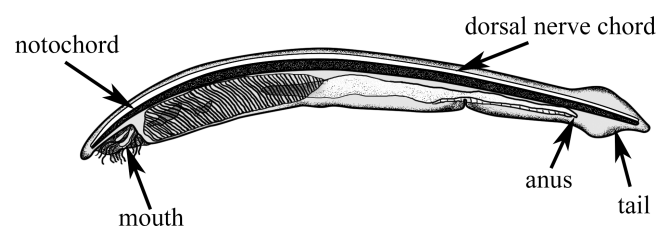
amphioxus. To look at it, you wouldn't think it was very closely related to vertebrates, but it is. Amphioxus lacks vertebrae, but like vertebrates, it has a notochord, a dorsal nerve cord, a mouth, an anus, and a tail. Like vertebrates, it is the same on the right side of the body as it is on the left (i.e., it is bilaterally symmetrical), and it has some other similarities in the circulatory system and muscle system that are structurally similar to vertebrates. It is probably fairly similar to an early chordate, but because it has been around the planet for a long time, it has evolved as well. Still, it preserves the diagnostic features of chordates in a relatively simple form (Figure 2.2).

Amphioxus is iconic in biological circles. There aren't very many evolution songs (there are far more antievolution songs!), but one that many biologists learn is sung to the tune of "It's a Long Way to Tipperary":

The Amphioxus Song
by Philip H. Pope

A fish-like thing appeared among the annelids one day.
It hadn't any parapods nor setae to display.
It hadn't any eyes nor jaws, nor ventral nervous cord,
But it had a lot of gill slits and it had a notochord.

    Chorus:
    It's a long way from Amphioxus. It's a long way to us.
    It's a long way from Amphioxus to the meanest human cuss.
    Well, it's goodbye to fins and gill slits, and it's welcome lungs and hair!
    It's a long, long way from Amphioxus, but we all came from there.

It wasn't much to look at and it scarce knew how to swim,
And Nereis was very sure it hadn't come from him.
The mollusks wouldn't own it and the arthropods got sore,
So the poor thing had to burrow in the sand along the shore.

He burrowed in the sand before a crab could nip his tail,
And he said "Gill slits and myotomes are all to no avail.
I've grown some metapleural folds and sport an oral hood,
But all these fine new characters don't do me any good.

(chorus)

It sulked awhile down in the sand without a bit of pep,
Then he stiffened up his notochord and said, "I'll beat 'em yet!
Let 'em laugh and show their ignorance. I don't mind their jeers.
Just wait until they see me in a hundred million years.

My notochord shall turn into a chain of vertebrae
And as fins my metapleural folds will agitate the sea.
My tiny dorsal nervous cord will be a mighty brain
And the vertebrates shall dominate the animal domain.

(chorus)

Now that you have some idea of what a primitive chordate was like, let's return to my earlier comment that larval forms of echinoderms have similarities to primitive chordates. Unlike adult echinoderms, which are radially symmetrical (think of a starfish, where body parts radiate around a central axis), echinoderm larval forms are bilaterally symmetrical like chordates. In terms of embryology, echinoderms and chordates have a number of developmental similarities that set them apart from other bilaterally symmetrical animals. One hypothesis for chordate origins is that the larval form of an early echinoderm may have become sexually mature without growing up—that is, without going through the full metamorphosis to an adult. This phenomenon is uncommon, but it is not unknown. It occurs in salamanders such as the axolotl, for example.

In the Middle Cambrian is a small fossil called *Pikaia*, which is thought to be a primitive chordate because it looks rather like amphioxus (Figure 2.3). A new marine fossil discovered in the Late Cambrian Chengjiang beds of China might even be a primitive vertebrate. Although *Haikouella* swam, it certainly didn't look much like a fish as we think of fish today; it more resembled a glorified amphioxus (Figure 2.4). From such primitive aquatic chordates as these eventually arose primitive jawless

Figure 2.3
***Pikaia,* a Middle Cambrian fossil, shows some characteristics of primitive chordates. Courtesy of Janet Dreyer.**
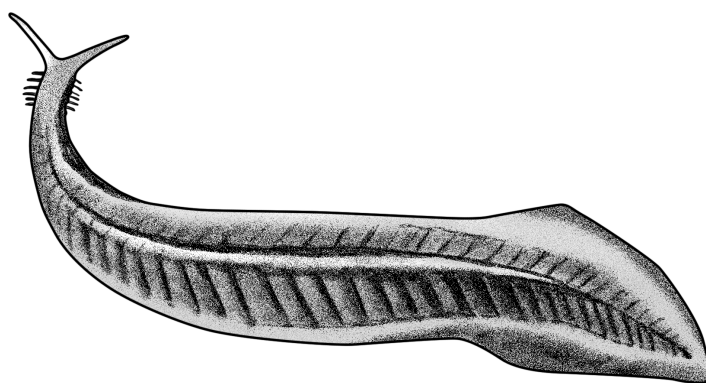
Figure 2.4
Haikouella, a Late Cambrian marine fossil, may be a primitive vertebrate. Courtesy of
Janet Dreyer.
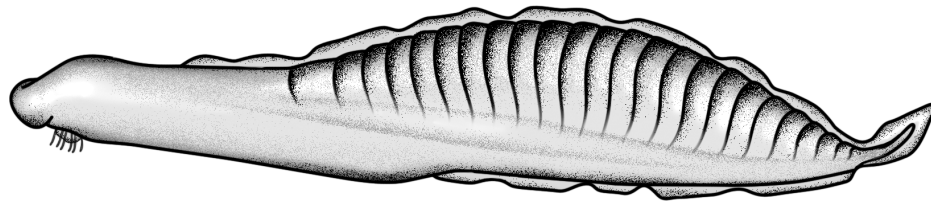
fish, then sharks and modern fish, and eventually the first land vertebrates: tetrapods
(which means "four footed"). These in turn became the ancestors of the other great
groups of land animals, reptiles and mammals. Later, more detail will be provided
about the evolution of many of these groups. But it is worthwhile to first present four
basic principles of biological evolution to keep in mind as you read the rest of the
book: natural selection, adaptation, adaptive radiation, and speciation.

MAJOR PRINCIPLES OF BIOLOGICAL EVOLUTION

Natural Selection and Adaptation

Natural selection is the term Charles Darwin gave to what he considered the most
powerful force of evolutionary change, and virtually all modern evolutionary biolo-
gists agree. In fact, the thesis that evolution is primarily driven by natural selection
is sometimes called Darwinism. Unfortunately, many people misapply the term to
refer to the concept of descent with modification itself, which is erroneous. Natural
selection is not the same as evolution. As discussed in chapter 1, there is a concep-
tual difference between a phenomenon and the mechanisms or processes that bring it
about.

When Darwin's friend T. H. Huxley learned of the concept of natural selection,
he said, "How extremely stupid not to have thought of that!" (Huxley 1888), so
obvious did the principle seem to him—after it was formulated. And indeed, it is a
very basic, very powerful idea. The philosopher Daniel Dennett has called natural
selection "the single best idea anyone has ever had" (Dennett 1995: 21). Because of
its generality, natural selection is widely found not only in nature but also increasingly
in engineering, computer programming, the design of new drugs, and other applica-
tions.

The principle is simple: generate a variety of possible solutions, and then pick the
one that works best for the problem at hand. The first solution is not necessarily the
best one—in fact, natural selection rarely results in even a good solution to a problem
in one pass. But repeated iterations of randomly generated solutions combined with
selection of the characteristics that meet (or come close to meeting) the necessary
criteria result in a series of solutions that more closely approximate a good solution.
Engineers attempting to design new airplane wings have used natural selection ap-
proaches; molecular biologists trying to develop new drugs have also used the approach

(Felton 2000). In living things, the problem at hand, most broadly conceived, is survival and reproduction—passing on genes to the next generation. More narrowly, the problem at hand might be withstanding a parasite, finding a nesting site, being able to attract a mate, or being able to eat bigger seeds than usual when a drought reduces the number of small seeds. What is selected for depends on what, in the organism's particular circumstances, will be conducive to its survival and reproduction. The variety of possible solutions consists of genetically based variations that allow the organism to solve the problem.

Variation among members of a species is essential to natural selection, and it is common in sexually reproducing organisms. Some of these variations are obvious to us, such as differences in size, shape, or color. Other variations are invisible, such as genetically based biochemical and molecular differences that may be related to disease or parasite resistance, or the ability to digest certain foods. If the environment of a group of plants or animals presents a challenge—say, heat, aridity, a shortage of hiding places, or a new predator—the individuals that just happen to have the genetic characteristics allowing them to survive longer and reproduce in that environment are the ones most likely to pass on their genes to the next generation. The genes of these individuals increase in proportion to those of other individuals as the population reproduces itself generation after generation. The environment naturally selects those individuals with the characteristics that provide for a higher probability of survival, and thus those characteristics tend to increase in the population over time.

So, the essence of natural selection is genetic variation within a population, an environmental condition that favors some of these variations more than others, and differential reproduction (some have more offspring than others) of the individuals that happen to have the favored variations.

A classic example of natural selection followed the introduction of rabbits into Australia—an island continent where rabbits were not native. In 1859, an English immigrant, Thomas Austin, released twelve pairs of rabbits so that he could go rabbit hunting. Unfortunately, except for the wedge-tailed eagle, a few large hawks, and dingoes (wild dogs)—and human hunters—rabbits have no natural enemies in Australia, and they reproduced like, well, rabbits. Within a few years, the rabbit population had expanded to such a large number that rabbits became a major pest, competing for grass with cattle, other domestic animals, and native Australian wildlife. Regions of the Australian outback that were infested with rabbits became virtual dust bowls as the little herbivores nibbled down anything that was green. How could rabbit numbers be controlled?

Officials in Australia decided to import a virus from Great Britain that was fatal to rabbits but that was not known to be hazardous to native Australian mammals. The virus produced myxomatosis, or rabbit fever, which causes death fairly rapidly. It is spread from rabbit to rabbit by fleas or other blood-sucking insects. The virus first was applied to a test population of rabbits in 1950. Results were extremely gratifying: in some areas the count of rabbits decreased from five thousand to fifty within six weeks. However, not all the rabbits were killed; some survived to reproduce. When the rabbit population rebounded, myxomatosis virus was reintroduced, but the positive effects of the first application were not repeated: many rabbits were killed, of course, but a larger percentage survived this time than had survived the first treatment. Eventually,

myxomatosis virus no longer proved effective in reducing the rabbit population. Subsequently, Australians have resorted to putting up thousands of miles of rabbit-proof fencing to try to keep the rabbits out of at least some parts of the country.

How is this an example of natural selection? Consider how the three requirements outlined for natural selection were met:

1. Variation: The Australian rabbit population consisted of individuals that varied genetically in their ability to withstand the virus causing myxomatosis.
2. Environmental condition: Myxomatosis virus was introduced into the environment, making some of the variations naturally present in the population of rabbits more valuable than others.
3. Differential reproduction: Rabbits that happened to have variations allowing them to survive this viral disease reproduced more than others, leaving more copies of their genes in future generations. Eventually the population of Australian rabbits consisted of individuals that were more likely to have the beneficial variation. When myxomatosis virus again was introduced into the environment, fewer rabbits were killed.

Natural selection involves adaptation: having characteristics that allow an organism to survive and reproduce in its environment. Which characteristics increase or decrease in the population through time depends on the value of the characteristic, and that depends on the particular environment—adaptation is not one size fits all. Because environments can change, it is difficult to precisely predict which characteristics will increase or decrease, though general predictions can be made. (No evolutionary biologist would predict that natural selection would produce naked mole rats in the Arctic, for example.) As a result, natural selection is sometimes defined as adaptive differential reproduction. It is differential reproduction because some individuals reproduce more or less than others. It is adaptive because the reason for the differential in reproduction has to do with a value that a trait or set of traits has in a particular environment.

Natural Selection and Chance. The myxomatosis example illustrates two important aspects of natural selection: it is dependent on the genetic variation present in the population and on the value of some of the genes in the population. Some individual rabbits just happened to have the genetically based resistance to myxomatosis virus even before the virus was introduced; the ability to tolerate the virus wasn't generated by the need to survive under tough circumstances. It is a matter of chance which particular rabbits were lucky enough to have the set of genes conferring resistance. So, is it correct to say that natural selection is a chance process?

Quite the contrary. Natural selection is the opposite of chance. It is adaptive differential reproduction: the individuals that survive to pass on their genes do so because they have genes that are helpful (or at least not negative) in a particular environment. Indeed, there are chance aspects to the production of genetic variability in a population: Mendel's laws of genetic recombination are, after all, based on probability. However, the chance elements are restricted to affecting the genetic variation on which natural selection works, not natural selection itself. If indeed evolution is driven primarily by natural selection, then evolution is not the result of chance.

Now, during the course of a species' evolution, unusual things may happen that are outside anything genetics or adaptation can affect, such as a mass extinction caused by an asteroid that strikes Earth, but such events—though they may be dramatic—are exceedingly rare. Such contingencies do not make evolution a chance phenomenon any more than your life is governed by chance because there is a 1 in 2.8 million chance that you will be struck by lightning.

Natural Selection and Perfection of Adaptation. The first batch of Australian rabbits to be exposed to myxomatosis virus died in droves, though some survived to reproduce. Why weren't the offspring of these surviving rabbits completely resistant to the disease? A lot of them died, too, though a smaller proportion than that of the parent's generation. This is because natural selection usually does not result in perfectly adapted structures or individuals. There are several reasons for this, and one has to do with the genetic basis of heredity.

Genes are the elements that control the traits of an organism. They are located on chromosomes, in the cells of organisms. Because chromosomes are paired, genes also come in pairs, and for some traits, the two genes are identical. For mammals, genes that contribute to building a four-chambered heart do not vary—or at least if there are any variants, the organisms that have them don't survive. But many genetic features do vary from individual to individual. Variation can be produced when the two genes of a pair differ, as they do for many traits. Some traits (perhaps most) are influenced by more than one gene, and similarly, one gene may have more than one effect. The nature of the genetic material and how it behaves is a major source of variation in each generation.

The rabbits that survived the first application of myxomatosis bred with one another, and because of genetic recombination, some offspring were produced that had myxomatosis resistance, and others were produced that lacked the adaptation. The latter were the ones that died in the second round when exposed to the virus. Back in Darwin's day, a contemporary of his invented a sound bite for natural selection: he called it "survival of the fittest," with *fit* meaning best adapted—not necessarily the biggest and strongest. Correctly understood, though, natural selection is survival of the fit enough. It is not, in fact, only the individuals who are most perfectly suited to the environment that survive; reproduction, after all, is a matter of degree, with some rabbits (or humans or spiders or oak trees) reproducing at higher than the average rate and some at lower than the average rate. As long as an individual reproduces at all, though, it is fit, even if some are fitter than others.

Furthermore, just as there is selection within the rabbit population for resistance to the virus, so there is selection among the viruses that cause myxomatosis. The only way that viruses can reproduce is in the body of a live rabbit. If the infected rabbit dies too quickly, the virus doesn't have a chance to spread. Viruses that are too virulent tend to be selected against, just as the rabbits that are too susceptible will also be selected against. The result is an evolutionary contest between host and pathogen, which reduces the probability that the rabbit species will ever be fully free of the virus but also reduces the likelihood that the virus will wipe out the rabbit species.

Another reason natural selection doesn't result in perfection of adaptation is that once there has been any evolution at all (and there has been considerable animal evolution since the appearance of the first metazoan), there are constraints on the direction in which evolution can go. As discussed elsewhere, if a vertebrate's forelimb is shaped for running, it would not be expected to become a wing at a later time; that is one kind of constraint. Another constraint is that natural selection has to work with structures and variations that are available, regardless of what sort of architecture could best do the job. If you need a guitar but all you have is a toilet seat, you could make a sort of guitar by running strings across the opening, but it wouldn't be a perfect design. The process of natural selection works more like a tinkerer than an engineer (Monod 1971), and these two specialists work quite differently.

Evolution and Tinkering. Some builders are engineers and some are tinkerers, and the way they go about constructing something differs quite a lot. An engineering approach to building a swing for little Charlie is to measure the distance from the tree branch to a few feet off the ground; to go to the hardware store to buy some chain, hardware, and a piece of wood for the bench; and to assemble the parts, using the appropriate tools: measuring devices, a drill, a screwdriver, screws, a saw, sandpaper, and paint. Charlie ends up with a really nice, sturdy swing that avoids the "down will come baby, cradle, and all" problem and that won't give him slivers in his little backside when he sits on it. A tinkerer, on the other hand, building a swing for little Mary, might look around the garage for a piece of rope, throw it over the branch to see if it is long enough, and tie it around an old tire. Little Mary has a swing, but it isn't quite the same as Charlie's. It gets the job done, but it certainly isn't an optimal design: the rope may suspend little Mary too far off the ground for her to be able to use the swing without someone to help her get into it; the rope may be frayed and break; the swing may be suspended too close to the trunk so Mary careens into it—you get the idea. The tinkering situation, in which a structural problem is solved by taking something extant that can be bent, cut, hammered, twisted, or manipulated into something that more or less works, however crudely, mirrors the process of evolution much more than do the precise procedures of an engineer. Nature is full of structures that work quite well—but it also is full of structures that just barely work, or that, if one were to imagine designing from scratch, one would certainly not have chosen the particular modification that natural selection did.

Several articles by Stephen Jay Gould have discussed the seemingly peculiar ways some organisms get some particular job done. An anglerfish has a clever "lure" resembling a wormlike creature that it waves at smaller fish to attract them close enough to eat. The lure, actually a modified dorsal fin spine, springs from its forehead (Gould 1980a). During embryological development, the panda's wrist bone is converted into a sixth digit, which forms a grasping hand out of the normal five fingers of a bear paw plus a "thumb" that is jury-rigged out of a modifiable bone (Gould 1980b). Like a tinkerer's project, it gets the job done, even if it isn't a great design. After all, natural selection is really about survival of the fit enough.

Natural selection is usually viewed as a mechanism that works on a population or sometimes on a species to produce adaptations. Natural selection can also bring about adaptation on a very large scale through adaptive radiation.

Adaptive Radiation

To be fruitful and multiply, all living things have to acquire energy (through photosynthesis or by consuming other living things), avoid predation and illness, and reproduce. As is clear from the study of natural history, there are many different ways that organisms manage to perform these tasks, which reflects both the variety of environments on Earth and the variety of living things. Any environment—marine, terrestrial, arboreal, aerial, subterranean—contains many ecological niches that provide means that living things use to make a living. The principle of adaptive radiation helps to explain how niches get filled.

The geological record reveals many examples of the opening of a new environment and its subsequent occupation by living things. Island environments such as the Hawaiian Islands, the Galápagos Islands, Madagascar, and Australia show this especially well. The Hawaiian archipelago was formed as lava erupted from undersea volcanoes, and what we see as islands actually are the tips of volcanic mountains. Erosion produced soils and land plants—their seeds or spores blown or washed in— subsequently colonized the islands. Eventually land animals reached the islands as well. Birds, insects, and a species of bat were blown to Hawaii or rafted there from other Pacific islands on chunks of land torn off by huge storms.

The Hawaiian honeycreepers are a group of approximately twenty-three species of brightly colored birds that range from four to eight inches long. Ornithologists have studied them extensively and have shown them to be very closely related. Even though they are closely related, honeycreeper species vary quite a bit from one another and occupy many different ecological niches. Some are insectivorous, some suck nectar from flowers, others are adapted to eating different kinds of seeds—one variety has even evolved to exploit a woodpecker-like niche. The best explanation for the similarity of honeycreepers in Hawaii is that they are all descended from a common ancestor. The best explanation for the diversity of these birds is that the descendants of this common ancestor diverged into many subgroups over time as they became adapted to new, open ecological niches. Honeycreepers are, in fact, a good example of the principle of adaptive radiation, by which one or a few individual animals arrive in a new environment that has empty ecological niches, and their descendants are selected to quickly evolve the characteristics needed to exploit these niches. Lemurs on Madagascar, finches on the Galápagos Islands, and the variety of marsupial mammals in Australia and prehistoric South America are other examples of adaptive radiation.

A major adaptive radiation occurred in the Ordovician period (about 430 million years ago), when plants developed protections against drying out and against ultraviolet radiation, vascular tissue to support erect stems, and other adaptations allowing for life out of water (Richardson 1992). It was then that plants could colonize the dry land. The number of free niches enabled plants to radiate into a huge number of ways of life. The movement of plants from aquatic environments onto land was truly an Earth-changing event. Another major adaptive radiation occurred about 400 million years ago in the Devonian, when vertebrates evolved adaptations (lungs and legs) that permitted their movement onto land. One branch of these early tetrapods radiated into the various amphibians and another branch into reptiles and mammals. A major difference between the reptile and mammal branch and amphibians was the amniotic

egg: an adaptation that allowed reproduction to take place independent of a watery environment.

During the late Cretaceous and early Cenozoic, about 65 million years ago, mammals began adaptively radiating after the demise of the dinosaurs opened up new ecological niches for them. Mammals moved into gnawing niches (rodents), a variety of grazing and browsing niches (hoofed quadrupeds, the artiodactyls and perissodactyls), insect-eating niches (insectivores and primates), and meat-eating niches (carnivores). Over time, subniches were occupied: some carnivores stalk their prey (lions, saber-toothed cats), and others run it down (cheetahs, wolves); some (lions, wolves, hyenas) hunt large-bodied prey, and some (foxes, bobcats) hunt small prey.

If a particular adaptive shift requires extensive changes, such as greatly increasing or reducing the size or number of parts of the body, the tendency is for that change to occur early in the evolution of the lineage rather than later. Although not a hard-and-fast rule, it follows logically from natural selection that the greatest potential for evolutionary change will occur before specializations of size or shape take place. Early in evolutionary history, the morphology of a major group tends to be more generalized, but as adaptive radiation takes place, structures are selected to enable the organisms to adapt better to their environments. In most cases, these adaptations constrain, or limit, future evolution in some ways. The forelimbs of perch are committed to propelling them through the water and are specialized for this purpose; they will not become grasping hands.

We and all other land vertebrates have four limbs. Why? We tend to think of four limbs as being "normal," yet there are other ways to move bodies around on land. Insects have six legs and spiders have eight, and these groups of animals have been very successful in diversifying into many varieties and are represented in great numbers all over the world. So, there is nothing especially superior about having four limbs, although apparently, because no organism has evolved wheels for locomotion, two or more limbs apparently work better. But all land vertebrates have four limbs rather than six or eight because reptiles, birds, and mammals are descended from early four-legged creatures. These first land vertebrates had four legs because the swimming vertebrates that gave rise to them had two fins in front and two in back. The number of legs in land vertebrates was constrained because of the number of legs of their aquatic ancestors. Imagine what life on Earth would have looked like if the first aquatic vertebrates had had six fins! Might there have been more ecological niches for land creatures to move into? It certainly would have made sports more interesting if human beings had four feet to kick balls with—or four hands to swing bats or rackets.

We see many examples of constraints on evolution; mammalian evolution provides another example. After the demise of the dinosaurs, mammals began to radiate into niches that had previously been occupied by the varieties of dinosaurs. As suggested by the shape of their teeth, mammals of the late Cretaceous and early Paleocene were small, mostly undifferentiated creatures that occupied a variety of insectivorous, gnawing, and seed-eating niches that dinosaurs were not exploiting. As new niches became available, these stem mammals quickly diverged into basic mammalian body plans: the two kinds of hoofed mammals, the carnivores, bats, insectivores, primates, rodents, sloths, and so on. Once a lineage developed (for example, carnivores), it radiated within the basic pattern to produce a variety of different forms (for example,

Figure 2.5
Vertebrate forelimbs all contain the same bones, although these bones have evolved over time for different locomotor purposes, such as running, swimming, flying, and grasping. Courtesy of Janet Dreyer.
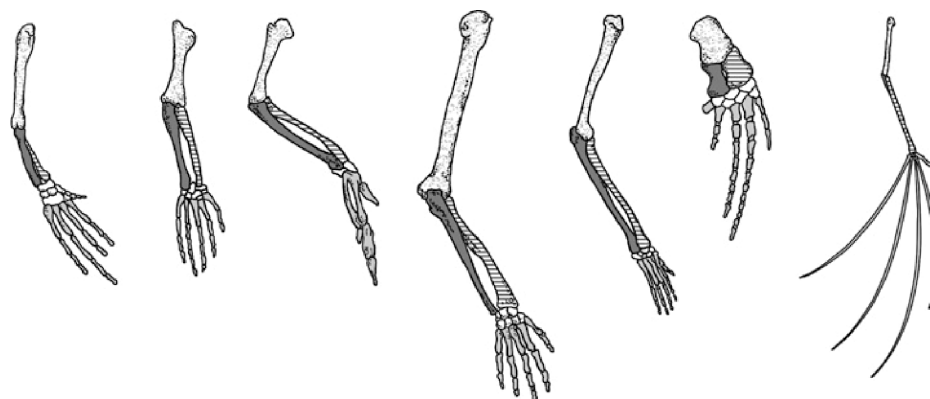
cats, dogs, bears, raccoons) in many sizes and shapes, all of which inherited basic dental and skeletal traits from the early carnivore ancestor. Once a lineage is "committed" to a basic way of life, it is rare indeed for a major adaptive shift of the same degree to take place. Although both horses and bats are descended from generalized quadrupedal early mammalian ancestors, the bones in a horse's forelimbs have been modified for swift running: some bones have been greatly elongated, others have been lost completely, and others have been reshaped. A bat has the same basic bones in its forelimb, but they have been greatly modified in other ways: some bones have been elongated, others have been lost, and yet others have been reshaped for flight (Figure 2.5).

Humans belong in the primate group of mammals, and primates are characterized by relatively fewer skeletal changes than have occurred in other mammal lineages. A primate doesn't have the extensive remodeling of the forelimb and hand that resulted in a bat's wing or a horse's hoof. We primates have a relatively basic "four on the floor" quadruped limb pattern of one bone close to the body (the femur in the leg and the humerus in the arm), two bones next to that one (the tibia and fibula in the leg and the radius and ulna in the arm), a group of small bones after this (tarsal or ankle bones in the leg and carpal or wrist bones in the arm), and a fanlike spray of small bones at the end of the limb (metatarsals and toe bones in the leg and metacarpals and finger bones in the arm) (Figure 2.5). Most primates locomote using four limbs; we human primates have taken this quadrupedal pattern and tipped it back so that our hind limbs bear all our weight (and not too successfully, as witnessed by hernias and the knee and lower-back problems that plague our species). Being bipedal, though, meant that we did not have to use our hands for locomotion, and they were thus freed for other purposes, like carrying things and making tools. Fortunately for human beings, dependent on tools and brains to survive, our early primate ancestors did not evolve to have specialized appendages like those of horses or bats.

Which is better, to be generalized or to be specialized? It's impossible to say without knowing more about the environment or niche in which a species lives. Specialized

organisms may do very well by being better able to exploit a resource than are their possible competitors, yet generalized organisms may have an advantage in being able to adjust to a new environmental challenge.

Speciation

A species includes all the individuals that are capable of exchanging genes with one another. Some species are composed of very few individuals located in a restricted area, and others have millions of members spread out over large areas of the world. Some plant species are restricted to small areas of rain-forest habitat, while rats and humans live on literally every continent. It is more likely that an individual will mate with another individual that lives close by than farther away, and as a result, most species can be divided into smaller populations. Sometimes geographical factors, such as rivers or mountains or temperature gradients in different depths of water, naturally carve species into populations.

Because of geographical differences among populations, natural selection tends to result in populations varying from one another. A typical widespread species may be divided into many different populations. As long as they exchange genes at least at intervals, populations are likely to remain part of the same species. But how do new species form? New species form when members of a population or subdivision of a species no longer are able to exchange genes with the rest of the species. This is more likely to happen at the edges of the species range than in the center. We can say that speciation has occurred when a population becomes reproductively isolated from the rest of the species.

If a population at the end of the geographic range of a species is cut off from the rest of the species, through time it may become different from other populations. Perhaps natural selection is operating differently in its environment than it is in the rest of the species range, or perhaps the population has a somewhat different set of genes than other populations of the species. Just by the rules of probability, a small population at one end of the range of a species is not likely to have all the variants of genes that are present in the whole species, which might result in its future evolution taking a different turn.

No longer exchanging genes with other populations of the species, and diverging genetically through time from them, members of a peripheral, isolated population might reach the stage at which, were they to have the opportunity to mate with a member of the parent species, they would not be able to produce offspring. Isolating mechanisms, most of which are genetic but some of which are behavioral, can arise to prevent reproduction between organisms from different populations. Some isolating mechanisms prevent two individuals from mating; in some insects, for example, the sexual parts of males and females of related species are so different in shape or size that copulation cannot take place. Other isolating mechanisms come into effect when sperm and egg cannot fuse for biochemical or structural reasons. An isolating mechanism could take the form of the prevention of implantation of the egg or of disruption of the growth of the embryo after a few divisions. Or the isolating mechanism could kick in later: mules, which result from crossing horses and donkeys, are healthy but sterile. Donkey genes thus are inhibited from entering into the horse species,

and vice versa. When members of two groups are not able to share genes because of isolating mechanisms, we can say that speciation between them has occurred. (Outside of the laboratory, it may be difficult to determine whether two species that no longer live in the same environment are reproductively isolated.)

The new species would of course be very similar to the old one—in fact, it might not be possible to tell them apart. Over time, though, if the new species manages successfully to adapt to its environment, it might also expand and bud off new species, which would be yet more different from the parent—now grandparent—species. This branching and splitting has, through time, given us the variety of species that we see today.

We can see this process of speciation operating today. Speciation in the wild usually takes place too slowly to be observed during the lifetime of any single individual, but there have been demonstrations of speciation under laboratory conditions. The geneticist Dobzhansky and his colleagues isolated a strain of Venezuelan fruit fly and bred it for several years. This strain of flies eventually reached a point of differentiation where it was no longer able to reproduce with other Venezuelan strains with which it had formerly been fertile. Speciation had occurred (Dobzhansky and Pavlovsky 1971).

Although not observed directly, good inferential evidence for speciation can be obtained from environments that we know were colonized only recently. The Hawaiian and Galápagos islands have been formed within the last few million years from undersea volcanoes and acquired their plants and animals from elsewhere. The Galápagos flora and fauna derive from South America, whereas the native Hawaiian flora and fauna are more similar to those of the Pacific islands, which in turn derive mostly from Asia. But Hawaiian species are reproductively isolated from their mainland counterparts.

One of the most dramatic examples of speciation took place among cichlid fish in the East African great lakes: Lake Victoria, Lake Malawi, and Lake Tanganyika. Geological evidence indicates that about twenty-five thousand years ago, Lake Tanganyika underwent a drying spell that divided the lake into three separate basins. Perhaps as a result of this and similar episodes, the cichlid fish that had entered the lake from adjacent rivers and streams underwent explosive adaptive radiation. There are at least 175 species of cichlid fish found in Lake Tanganyika and nowhere else. Similar speciation events took place in Lake Victoria and Lake Malawi—only over shorter periods of time (Goldschmidt 1996). Large lakes like these can be watery versions of an island: interesting biological things can go on.

Occasionally speciation can take place very quickly. The London subway, known as "the Tube," was built during the 1880s. At that time, some mosquitoes found their way into the miles of tunnels, and they successfully bred in the warm air and intermittent puddles—probably several times per year. Because they were isolated from surface mosquitoes, differences that cropped up among them would not have been shared with their relatives above, and vice versa. In the late 1990s, it was discovered that the Tube mosquitoes were a different species from the surface species. One major, if unfortunate, difference is that the surface mosquitoes, *Culex pipiens*, bite birds, whereas the related Tube species, *Culex molestus*, has shifted its predation to people. What is surprising about this discovery is that it shows that at least among rapidly breeding insects like mosquitoes, speciation does not require thousands of years but can occur

within a century (Bryne and Nichols 1999). Natural selection, adaptation, adaptive radiation, and speciation—these are the major principles that help us explain the pattern and understand the process of evolution. These principles have resulted in an immense proliferation of living things over time that occupy a mind-boggling array of ecological niches.

A famous anecdote: asked by a member of the clergy what his study of nature had revealed to him about the mind of God, the biologist J. B. S. Haldane is supposed to have answered, "An inordinate fondness for beetles." And in fact one-fifth of the known animal species are species of beetles. Because there are so many different kinds of organisms, and not just beetles, human beings have always sought to make some sense of them by grouping them in various ways. All human cultures attempt to group plants and animals according to various schemes, which often have to do with how they can be used. In the Bible, the dietary laws of the Jews divided animals into clean and unclean, the latter being unsuitable for eating. Plants might be grouped according to whether they are for human consumption, for animal consumption, used for making dyes, or for some other purpose. Students of nature, naturalists, of the 1700s and 1800s sought to group animals and plants according to similarities and differences independent of their utility. The science of systematics, the study of the relationship among organisms, dates to a Swedish scientist known by his Latinized name, Carolus Linnaeus.

ORGANIZING THOSE BEETLES

Linnaeus classified a huge number of plants and animals during his lifetime. His rationale was overall similarity: the more similar organisms were, the more closely together they were placed in the ranked (hierarchical) system familiar to anyone who has taken middle school or high school biology. The highest Linnaean ranking is kingdom, followed by phylum, class, order, family, genus, and species. (There are a variety of mnemonics to remember their order, such as Kings Play Chess On Fine Golden Sets, or Kids Playing Chicken On Freeways Get Smashed.) Any plant or animal can be assigned a series of labels reflecting its membership in a group from each of these categories. Species was the smallest category, consisting of organisms that have the greatest similarity. But all members of the genus—a group of species—have certain characteristics in common as well, and the same can be said for family, and for every other category all the way up to kingdom. Here are the Linnaean classifications for house cats, chimpanzees, and human beings:

	House cats	Chimpanzees	Human beings
Kingdom:	Animalia	Animalia	Animalia
Phylum:	Chordata	Chordata	Chordata
Class:	Mammalia	Mammalia	Mammalia
Order:	Carnivora	Primates	Primates
Family:	Felidae	Pongidae	Hominidae
Genus:	Felis	Pan	Homo
Species:	cattus	troglodytes	sapiens

House cats, chimpanzees, and humans all belong to the same kingdom, phylum, and class; they have very many characteristics in common, and their Linnaean classification

reflects this. Among other characteristics, they lack chlorophyll, so they are animals; they have a notochord, so they are chordates; and they have a single bone in the lower jaw, so they are all mammals. But chimpanzees and humans have more characteristics in common than either one has with cats, and Linnaeus grouped chimps and humans into the same order and cats into a different order. Humans and chimps were separated at the level of family, indicating that they were quite similar to one another.

Linnaeus's classification is useful, but classifying organisms on the basis of their similarities alone does not truly get at the underlying reality of nature. Why is it that all mammals have a single bone in the lower jaw? Why is it that humans and chimps are able to swing their arms over their heads but horses cannot? Organisms often have the same traits because they share genes. You and your brother or sister are more similar to each other than you are to your cousins because you and your siblings share more of your gene sequences with one another than you share with your cousins. Genes have a lot to do with important traits that an organism exhibits: they are why insects have six legs and spiders have eight, and why you walk on two legs and a monkey on four.

You and your siblings and cousins are similar in some traits (perhaps hair color, or stature, or blood type) because you share genes, and you share genes because you have a genealogical relationship to one another. You have descended with modification from common ancestors: parents in the case of your siblings and grandparents in the case of your first cousins. Similarly, all species are kin to one another in varying degrees because of common descent. The history of life is a branching and splitting genealogy of species changing through time. The Linnaean system, based on similarity and differences, provides an overall shape of this huge family tree of life, but it is not based on the underlying genealogical relationship of species—and thus does not always reflect the true relationship of organisms.

Ideally, a classification scheme would reflect genealogical relationships of organisms rather than just similarity, because similarity can be relatively superficial. Consider dolphins and tuna: both have an overall streamlined shape because that shape is very useful for getting around at high speeds in an open, watery environment. Yet there are many interior differences between dolphins and tuna: the skeletal systems, the circulatory systems, nervous systems, digestive systems, and so on. So, just because creatures are similar in overall shape does not mean that they are very closely related.

A late-twentieth-century classification method that has largely replaced the Linnaean system among biologists today is cladistics. *Clade* is a Greek word for "branch," and cladistics focuses on the branching of lineages through time. Both cladistics and the classical Linnaean system look at similarities among organisms to establish their relationships, but cladistics seeks in addition to reflect the actual results of evolution. In cladistics, the only groups of organisms that are considered natural are monophyletic, that is, groups comprising a single common ancestral species and all of its descendants. In terms of the tree of life, monophyletic groups correspond to whole branches that can be separated from the tree with a single cut. In contrast, the class of reptiles in the Linnaean system is not monophyletic because it excludes birds, which are descended from reptiles (as I discuss later). Similarly, a group consisting of warm-blooded animals (e.g., birds and mammals) also would not be monophyletic because all warm-blooded animals do not share a recent common ancestor.

Table 2.1
Ancestral traits, derived traits

	Trait a Warm blood	Trait b Hair	Trait c Diversified dentition	Trait d Fingernails	Trait e Grasping hands	Trait f Flat chest	Trait g Shoulder mobility
Chimps	x	x	x	x	x	x	x
Humans	x	x	x	x	x	x	x
Monkeys	x	x	x	x			
Cats	x	x	x				

Letters indicate characteristics. Traits a–c are found in all mammals, traits d–e additionally are found in all primates, and traits f–g are found in chimps and humans. From the standpoint of humans and chimps, traits a–e are ancestral traits, inherited from earlier mammal and primate ancestors. From the standpoint of chimps and humans, traits f and g are shared derived traits, inherited from a more recent ancestor. Looking at traits as ancestral or derived can help us reconstruct the evolutionary relationships of groups.

Unlike the Linnaean system, cladistic taxonomy encourages naming and using only monophyletic groups. For that reason, cladistics focuses on a particular kind of trait (i.e., derived traits) as indicators of evolutionary (phylogenetic) relationships. A cladistic analysis divides traits into two kinds, ancestral and derived, and then constructs evolutionary trees based on the distribution of derived traits. Let me give an example of how that works.

Consider that humans, monkeys, cats, and chimps have many characteristics in common: they all have warm blood; hair; and incisor, canine, premolar, and molar teeth that come in different shapes (compared to, for example, a crocodile, whose teeth all have pretty much the same conical shape). These three traits (Table 2.1, traits a–c) cannot differentiate among these species because they are common to all, and being common to all, they must have been present in the common ancestor of all of these mammals; we call such traits ancestral traits. But note that monkeys, humans, and chimps have traits that cats lack: fingernails rather than claws and hands that can grasp rather than paws (Table 2.1, traits d–e). These traits are associated with the common descent of primates after they separated from other mammalian groups such as the cats and are therefore not shared with cats or other nonprimate mammals. Similarly, a broad, flat chest and the ability to move the arm in a circle at the shoulder (Table 2.1, traits f–g) are traits that chimps and humans share but monkeys lack, which provides evidence that chimps and humans form a separate branch from monkeys. These are derived traits.

Traits are ancestral or derived not in an absolute sense but relative to one group or another. Having fingernails is a derived trait of primates relative to mammals, but having fingernails—common to all primates—can be considered an ancestral trait and thus not useful when one is trying to determine the relationships among different primates, such as between monkeys and apes.

Being able to differentiate ancestral and derived traits makes it possible to reconstruct the evolutionary relationships among organisms. To do so, one must look at the

Figure 2.6
A Cladogram of Primates: A cladogram shows the evolution-ary relationship of organisms on the basis of their possession of shared and ancestral traits. Warm blood, hair, and diversi-fied dentition are found in all of the organisms in the diagram; they are ancestral traits. Flat chests and shoulder mobility are found only in the two groups above the mark: chimps and humans. These would be shared derived traits of chimps and humans. Courtesy of Alan Gishlick.
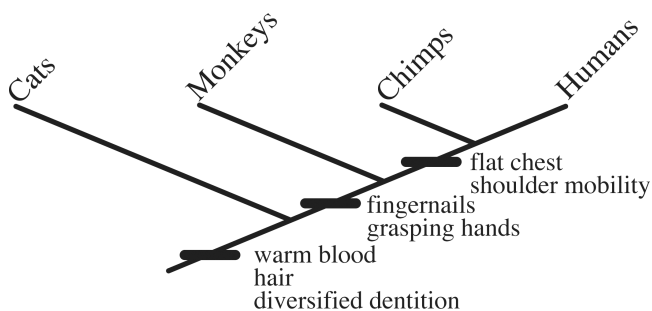
presence or absence of traits across a group of organisms, much as we did above with some traits of cats, monkeys, chimps, and humans. When enough traits are examined, certain traits emerge that indicate when a new lineage (a branch of the tree of life) appears—and these obviously are the most informative for reconstructing the tree of life. To determine the traits indicating a separate lineage, it is necessary to find an outgroup: a species or other group that is related to the group you are studying and that shows ancestral traits. To figure out the evolutionary relationships of monkeys, humans, and chimps, we can use cats as an outgroup: cats and primates both are mam-mals, and cats exhibit the mammalian ancestral traits. This allows us to set aside a very large number of traits that primates and cats share (like warm blood and diversified dentition) and focus on those derived traits that distinguish monkeys, humans, and apes from one another.

We can illustrate the relationships among these animals using a diagram called a cladogram, which indicates the characteristics that distinguish clades (Figure 2.6). Traits apply to all species to the right of where their labels appear, so mammalian characteristics such as warm blood and hair will occur in the animals named at the bottom of the diagonal line, because they are found in all of the organisms on the diagram: cats, monkeys, chimps, and humans. Cats lack fingernails and grasping hands, though, and because those characteristics set off primates from other mammals, they are shared derived traits of primates. Only humans and chimps have the flat chest and mobile shoulders that allow the arm-over-arm locomotion called brachiation, so these traits are shared derived traits for humans and chimps.

Mammals form a clade because they share a common ancestor, all of whose de-scendants are mammals; primates are a clade within the mammal clade because they share a common ancestor, all of whose descendants are primates, and humans and chimps form a clade within primates because they share a common ancestor, all of

whose descendants are hominids (the technical name for the animals descended from the last common ancestors of chimpanzees and humans). We often will lack the fossil evidence for an actual ancestor of a lineage, but by using cladistic reconstruction, we can reconstruct many of the traits this ancestor would have had. For example, the first member of the lineage leading to humans, separate from chimpanzees, would be a biped, because that is a derived trait of our lineage, as is the presence of relatively small canine teeth. Such reconstructive expectations also help us interpret fossil remains.

This is a very brief and necessarily incomplete introduction to cladistic taxonomy. I used anatomical characteristics, but one can also use biochemical similarities, genetic or chromosomal similarities, and even developmental (embryological) characteristics to form cladograms of evolutionary relationships. Most evolutionary biologists use the cladistic approach to classify organisms because it avoids grouping organisms together on the basis of characteristics that do not reflect evolutionary relationships. When I was in high school and college, the Linnaean system was used. Birds were considered a separate branch of vertebrate life at the same level (i.e., class) as mammals or reptiles, partly because they had warm blood. Yet cladistic analysis, which separates ancestral from derived traits, shows that birds have a large number of traits that they share with a group of dinosaurs, and evolutionarily are closer to them than to mammals. Indeed, because cladistic taxonomy produces nested monophyletic groups, birds *are* dinosaurs—think about that during your next Thanksgiving dinner! Warm blood turns out to be a trait that has evolved more than once in the lineage of tetrapods (the descendants of the fish that adopted a terrestrial lifestyle about 365 million years ago). So, warm blood is a derived trait of both the mammal lineage and the reptile lineage that gave rise to dinosaurs and birds. Warm blood is a trait birds and mammals share— but not a trait that indicates close relationship. The division of traits into ancestral and derived clears up the confusion. To classify birds as a separate class, parallel to mammals and amphibians, would not reflect what really happened in evolutionary history. If we want all of our clades to reflect monophyly, we need to include birds as a subgroup of reptiles.

So cladistics is preferred to traditional Linnaean taxonomy because, by forcing us to classify according to monophyletic relationships, it better reflects the true genealogical relationship of living things. It also focuses on clades, or branches of the tree of life, and especially on the traits that distinguish clades, rather than on difficult-to-obtain ancestors. Cladistics is also considered superior to the Linnaean system because it does not depend on hunches about relationships among species, but rather allows—and requires—rigorous testing of hypotheses of evolutionary relationships. If you are interested in cladistic analysis, a good place to begin is the Web site of the University of California Museum of Paleontology (http://www.ucmp.berkeley.edu/IB181/VPL/Phylo/PhyloTitle.html).

DID MAN EVOLVE FROM MONKEYS?

So, to end with the question we began with, Did man evolve from monkeys? No. The concept of biological evolution, that living things share common ancestry, implies that human beings did not descend from monkeys, but shared a common ancestor with them, and shared a common ancestor farther back in time with other mammals, and

farther back in time with tetrapods, and farther back in time with fish, and farther back in time with worms, and farther back in time with petunias. We are not descended from petunias, worms, fish, or monkeys, but we shared common ancestors with all of these creatures, and with some more recently than others. The inference of common ancestry helps us make sense of biological variation. We humans are more similar to monkeys than we are to dogs because we shared a common ancestor with monkeys more recently than we shared her a common ancestor with dogs. Humans, dogs, and monkeys are more similar to one another (they are all mammals) than they are to salamanders, because the species that provided the common ancestor of all mammals lived more recently than the species providing the common ancestors of salamanders and mammals. This historical branching relationship of species through time allows us to group species into categories such as primates, mammals, and vertebrates, which allows us to hypothesize about other relationships. Indeed, the theory of evolution, as one famous geneticist put it, is what "makes sense" of biology: "Seen in the light of evolution, biology is, perhaps, the most satisfying science. Without that light it becomes a pile of sundry facts, some of them more or less interesting, but making no comprehensible whole" (Dobzhansky 1973: 129). Evolution tells us why biology is like it is: living things had common ancestors, which makes a comprehensible whole of all those facts and details.

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