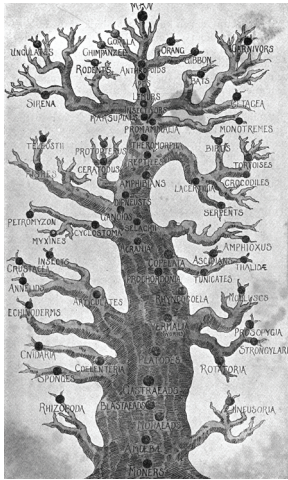


The evolutionary tree unifies biology.



2

Evolutionary Trees in the Ecological Garden

The history of life is magnificent in its depth and in its variety. There have been living things on this planet for almost 4 billion years. In the last billion years, multicellular plant and animal life has evolved. The historical details of that evolution were one of the main interests of biologists over the last century.

Here we present the ideas that biologists use to make sense of biological history. At the core of this group of ideas is the concept of the evolutionary tree. We introduce that concept in depth. Then we connect the evolutionary tree concept to some of the most important historical topics in biology: fossils, biogeography, and development. Finally, we show how to apply the tree concept to one of the

venerable tools of evolutionary biology, the comparative method. The evolutionary tree is one of the most unifying explanatory concepts in biology.

Determining a tree for a group of organisms may be the first step in understanding the evolution of the group. But Darwin's tree concept is also one of the best devices to understand some of the most important findings of biology.

Evolutionary trees do not grow in isolation. Their growth depends in part on the ecological conditions facing the evolving species. We refer to these conditions as the "ecological garden." As in Darwin's original theory of natural selection, which concerned the fate of individual organisms, the fate of species depends on their ecological circumstances. ❖

THE TREE CONCEPT

2.1 The history of life could have followed a variety of patterns, including an absence of evolution

The history of life did not have to grow like a tree. Other patterns might have arisen in the history of living things. We can call these possibilities “systems of life,” equivocating as to whether they have to be evolutionary. One system of life, for example, would be reincarnation, in which particular organisms, or even entire species, reappear at intervals. This circular system of life has been common in the thought of south Asian cultures. Before the advent of Christianity in Western civilization, there were various mythological systems of life in western Eurasia and northern Africa. Many specific systems of life were also developed by the aboriginal populations of the Americas and Africa, some very elaborate. But in Western thought, there have been four main systems of life: the traditional Judeo-Christian or Biblical system, the Lamarckian system, the pre-Darwinian system of Lyell, and the Darwinian system. We will look at each of these in turn, beginning with a brief consideration of the first two.

The Biblical or Creationist System of Life Over the last thousand years, most Western scholars accepted the Biblical scheme of creation as the definitive system of life. This system of life is based on the first book of the Bible, Genesis. Genesis describes the creation of life by an omnipotent deity, after that same deity has created the world in which these living things are to live. There is no mention of extinction in this system of life, except possibly at the time of the great flood of Noah, when it is conceivable that terrestrial forms of life might have drowned. On the other hand, Noah’s task was to preserve all forms of life that might otherwise have drowned in the great flood, which suggests that they should not have gone extinct.

To a first approximation, then, the Biblical system of life is one in which the original creations of God are supposed to survive indefinitely on Earth. This **creationist** system is shown in Figure 2.1A, in which the bottom of the figure represents the moment of creation, and the top of the figure represents

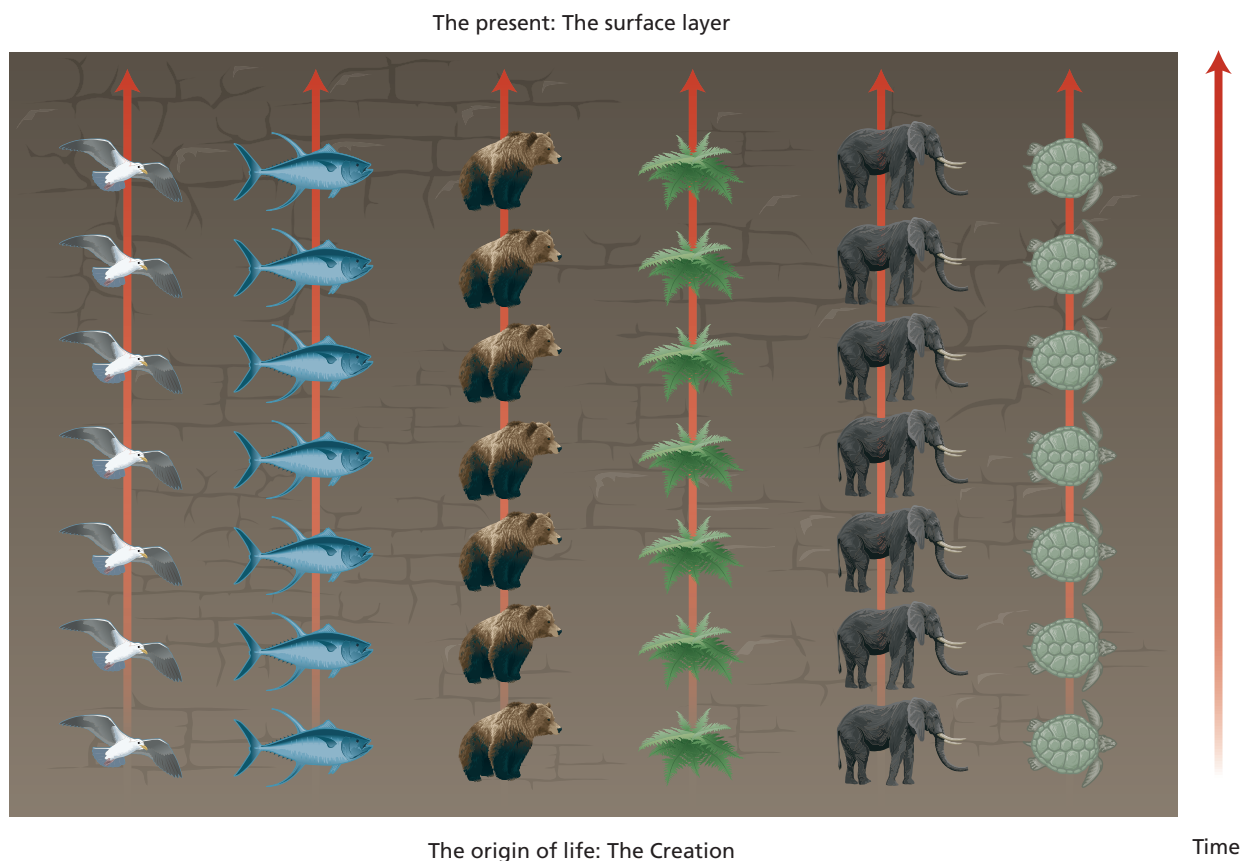


FIGURE 2.1A The Creationist System of Life

the present. After the initial creation, no new life-forms arise, and none of the original forms go extinct.

The scientific problems facing this scheme are immense. Much fossil evidence seems to contradict it. Why are there no fossil vertebrates from more than 600 million years ago? Why are there so many more multicellular fossils in rocks less than 500 million years old, compared with the billion years before that? What happened to the dinosaurs? What happened to the trilobites? Mammoths? Saber-toothed tigers? Extremely few professional biologists still accept the Biblical system of life.

The Lamarckian System of Life As European scientists found more and more fossils of life-forms that they had never seen before, crude schemes of evolution were proposed in the eighteenth century. The first evolutionary scheme to have much influence was that of Jean-Baptiste Lamarck, introduced in Chapter 1.

Lamarck was not entirely consistent. For one thing, he had several proto-Darwinian ideas that were not formally

incorporated in his thinking. But the essential model for the Lamarckian system of evolution can be roughly summarized. It is shown in Figure 2.1B.

The basic Lamarckian concept was “linear” progressive evolution. Lamarck thought that life was frequently produced by spontaneous generation from inanimate precursors. Once a particular lineage came to life, Lamarck thought that it then tended to evolve toward more and more complex forms. New species were not supposed to be created by the splitting of lineages. Interestingly, Lamarck also did not suppose that species went extinct. They were supposed to evolve into new life-forms instead.

With these assumptions, the diversity of species present at any one time was explained by the particular ensemble of lineages evolving in parallel. The features of any one species were explained by Lamarck in terms of its progress toward complexity and its immediate adaptation to the environment in which it lived, as we saw in Chapter 1. This process of adaptation was based on use and disuse, not selection. ❖

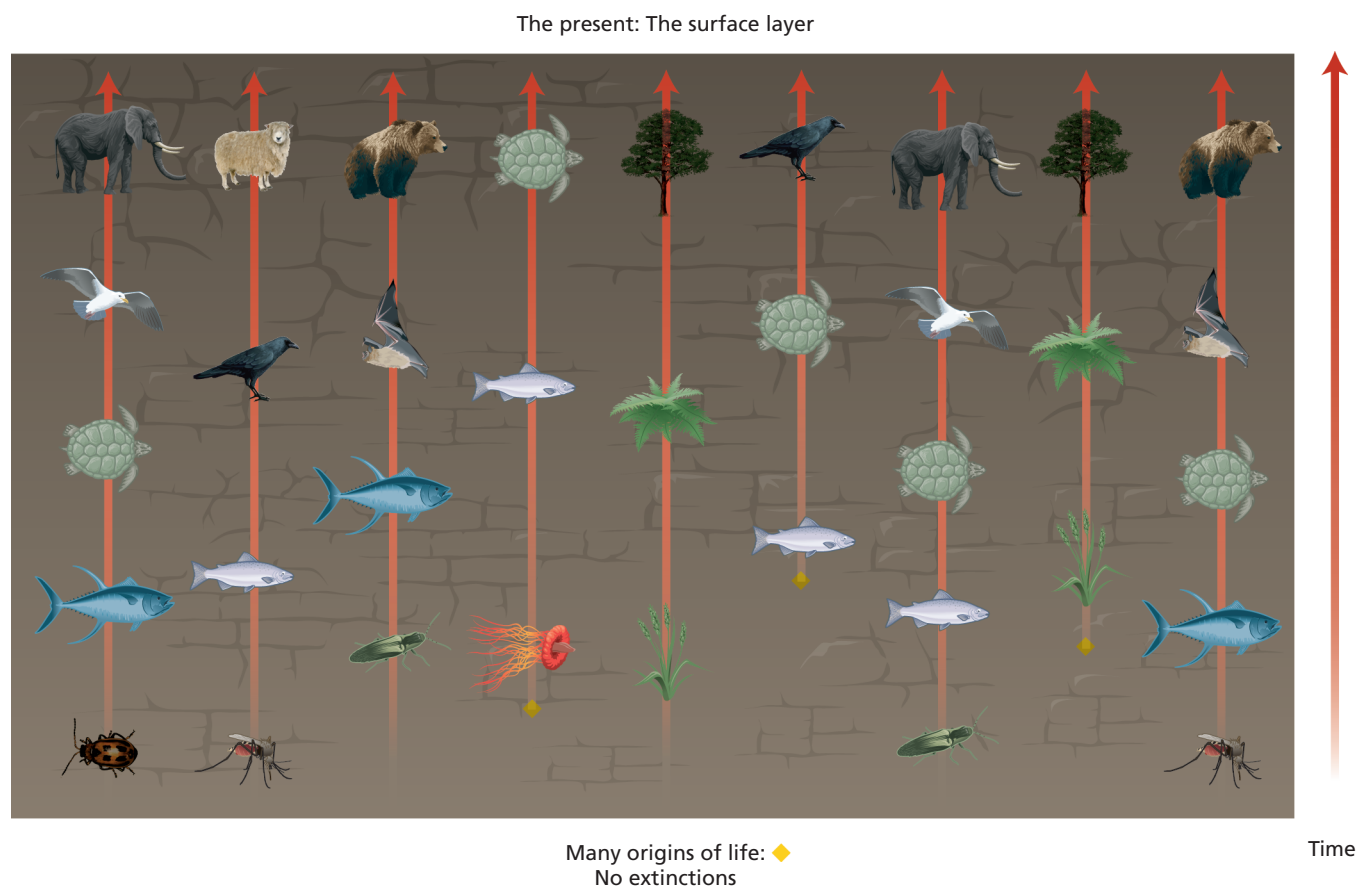


FIGURE 2.1B The Lamarckian System of Life

2.2 Lyell's system of life allowed many origins of species and many extinctions, but no evolution

By the nineteenth century, biologists were aware of enough of the fossil history of life to find the Biblical scheme untenable. At the same time, the beneficial contrivances of living things, from their physiology to their anatomy, left many scientists convinced that some type of beneficent creation was required to explain life.

Most students of the fossil record, such as the geologist Charles Lyell, accepted the principle that extinction had occurred. Yet, if extinction occurred, then new species must originate, because there was little evidence that the Earth was progressively losing species. Therefore a consensus developed that the Creator allowed some species to go extinct, with new species being created to take their place, in some way. This Lyellian system of life is shown in Figure 2.2A. This system of life, however, was not an evolutionary

scheme. It was not necessarily supposed that species change, once they have been created. An important feature of this system of life was that it faced no difficulties in explaining the premise that species went extinct, because falling numbers of organisms can arise from everyday ecological processes, like exhaustion of food supplies. So the extinction process was not a mystery. It fits the pattern of good gradualist science. It was the origin of new species that was the abiding mystery.

The mystery concerning the origin of new species was Darwin's particular interest. It led him to the fourth major Western system of life. As we saw in Chapter 1, the Darwinian system is a simple materialistic scheme by which life evolves from life without either a cosmic drive to perfection or an intervening deity. ♦

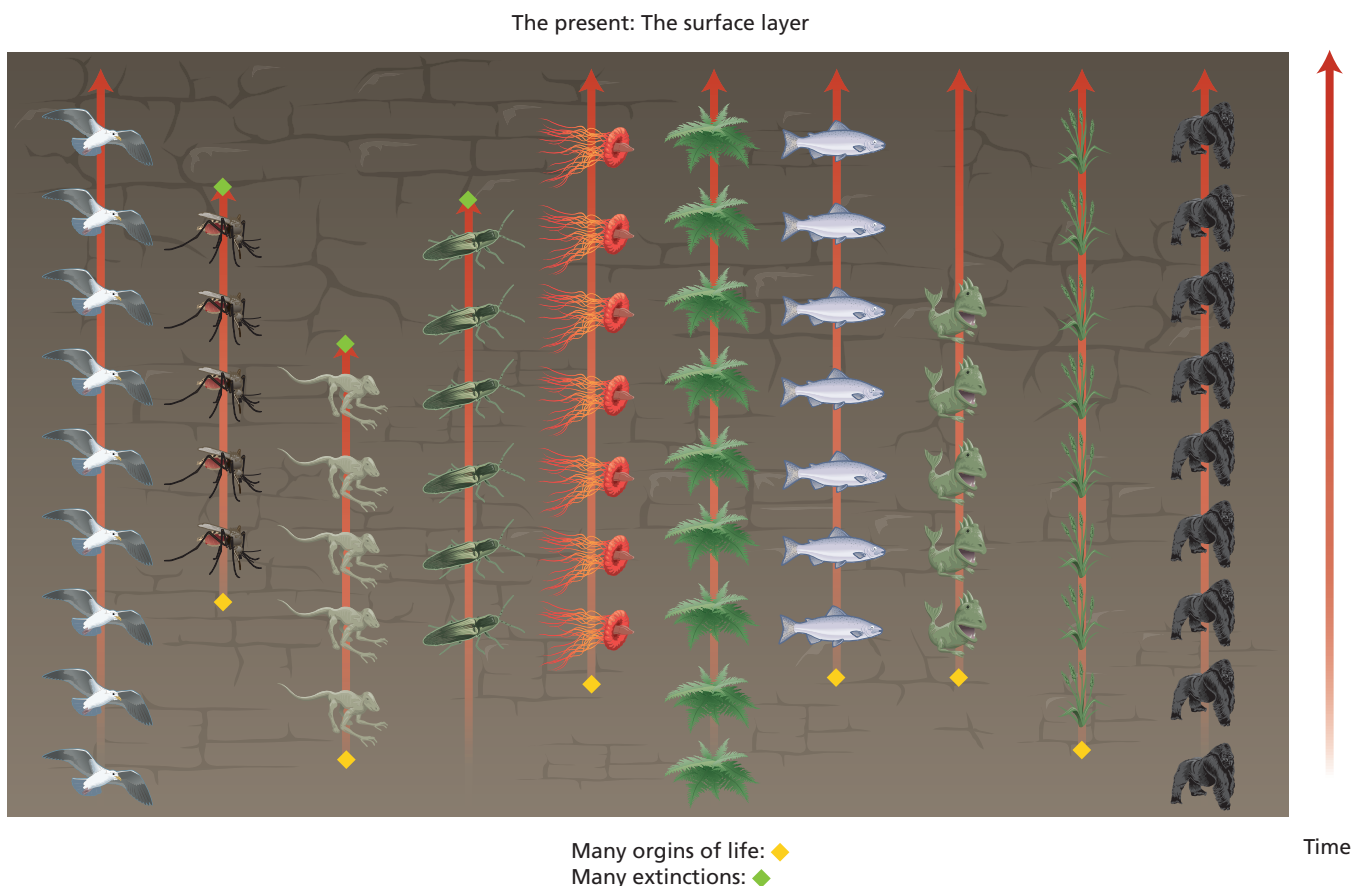


FIGURE 2.2A The Lyellian System of Life

The only figure in the *Origin of Species* was an evolutionary tree 2.3

We now know that Darwin's first step toward developing his system of life was the concept of an **evolutionary tree**, a representation of the history of life as a treelike pattern of diversification. Despite this, he began the *Origin* with the problem of natural selection. This beginning probably reflected the influence of Lyell, who argued for the preeminence of slow, cumulative change as the foundation of natural processes, geological and biological.

Nonetheless, the centrality of the evolutionary tree is revealed by the fact that the only figure in the *Origin* is an abstract evolutionary tree in Chapter IV, "Natural Selection." This figure is reproduced here as Figure 2.3A. Darwin's explanation of how evolution worked is somewhat disingenuous. He consistently commingles the ideas of natural selection and evolution. Yet he knew very well that evolution is a pattern of change that results from underlying processes, with natural selection one of those processes.

For now, we are going to focus specifically on the pattern of evolution, separately from its mechanism. The bare hypothesis of evolution is enough of a revolution in our understanding of the history of life. We will take up natural selection

in detail in Chapter 4, although some general features of its role in evolution are discussed in this chapter.

A sample of Darwin's own explanation of his figure is given in the accompanying box. An important feature of the figure is the species lineages that go extinct. Darwin used no particular notation to indicate extinction, just the termination of a branch of the evolutionary tree. When a new lineage originates, Darwin gave it its own letter of the alphabet; but he indicated successive forms within evolutionary lineages by a superscript only. Note that Darwin did not suppose that all lineages have to diverge into multiple descendant lineages. His "F" lineage never undergoes speciation, but survives over many thousands of generations.

In the following modules, we will unpack the evolutionary tree concept in its modern form and then apply it to some of the central problems of biology.

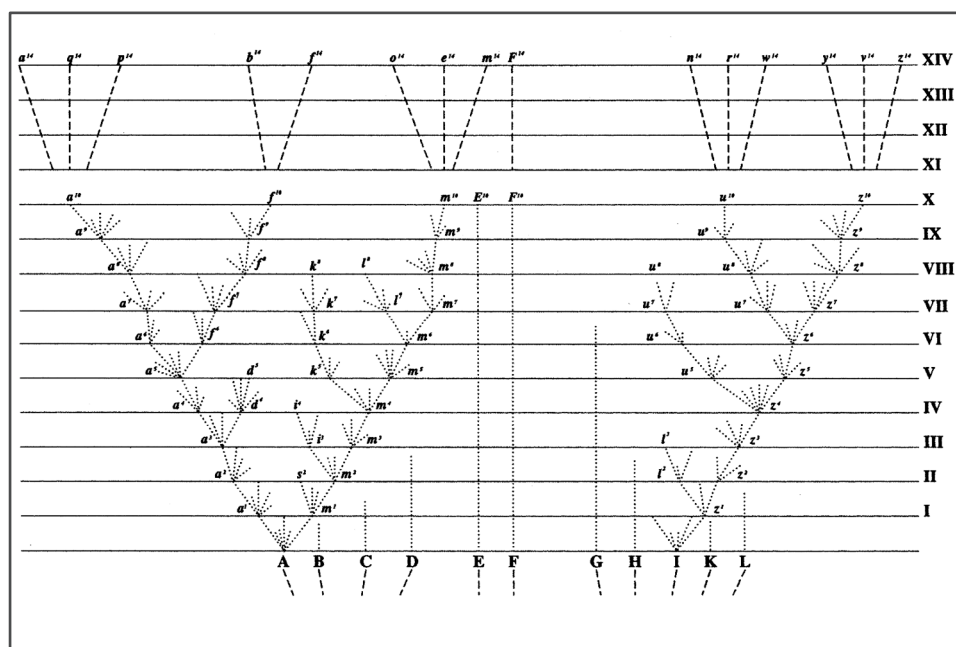


FIGURE 2.3A Darwin's Evolutionary Tree from *Origin of Species*

Darwin's Introduction of the Evolutionary Tree Concept

The accompanying diagram will aid us in understanding this rather perplexing subject. Let A to L represent the species of a genus large in its own country; these species are supposed to resemble each other in unequal degrees, as is so generally the case in nature, and as is represented in the diagram by the letters standing at unequal distances. . . . Let (A) be a common, widely-diffused, and varying species. . . . The little fan of diverging dotted lines of unequal lengths proceeding from (A), may repre-

sent its varying offspring. . . . After a thousand generations, species (A) is supposed to have produced two fairly well-marked varieties, namely a^1 and m^1 the diagram illustrates the steps by which the small differences distinguishing varieties are increased into the larger differences distinguishing species.

—Charles Darwin, 1859, *Origin of Species*
(Chapter IV, "Natural Selection")

2.4 Modern evolutionary trees represent species as growing, splitting, and truncated branches

Modern-day evolutionary biologists use much of Darwin's original reasoning, but they do so following somewhat different conventions and meanings. From this point on, we will focus on modern usage, rather than Darwin's.

Figure 2.4A presents some of the typical graphical conventions built into evolutionary trees. Time flows from the past, at the bottom of a tree, toward the more recent past—even the present, which is located higher up on the diagram. Branches that grow from the bottom of the tree to the top without splitting or truncating, as shown in Figure 2.4B, represent the evolution of individual species. These species may

change morphologically, because evolutionary change does not require the evolution of new species. Or they may remain unchanged. Such unchanging species are sometimes called “fossil species.”

When new species evolve from existing or *extant* species, the evolutionary event is called **speciation**. Speciation is graphically represented as a fork in a branch, where two or more branches grow out of one branch.

When species go extinct, their branch is truncated. Proceeding from the bottom of Figure 2.4A to the top, the branches representing species that go extinct do not grow to

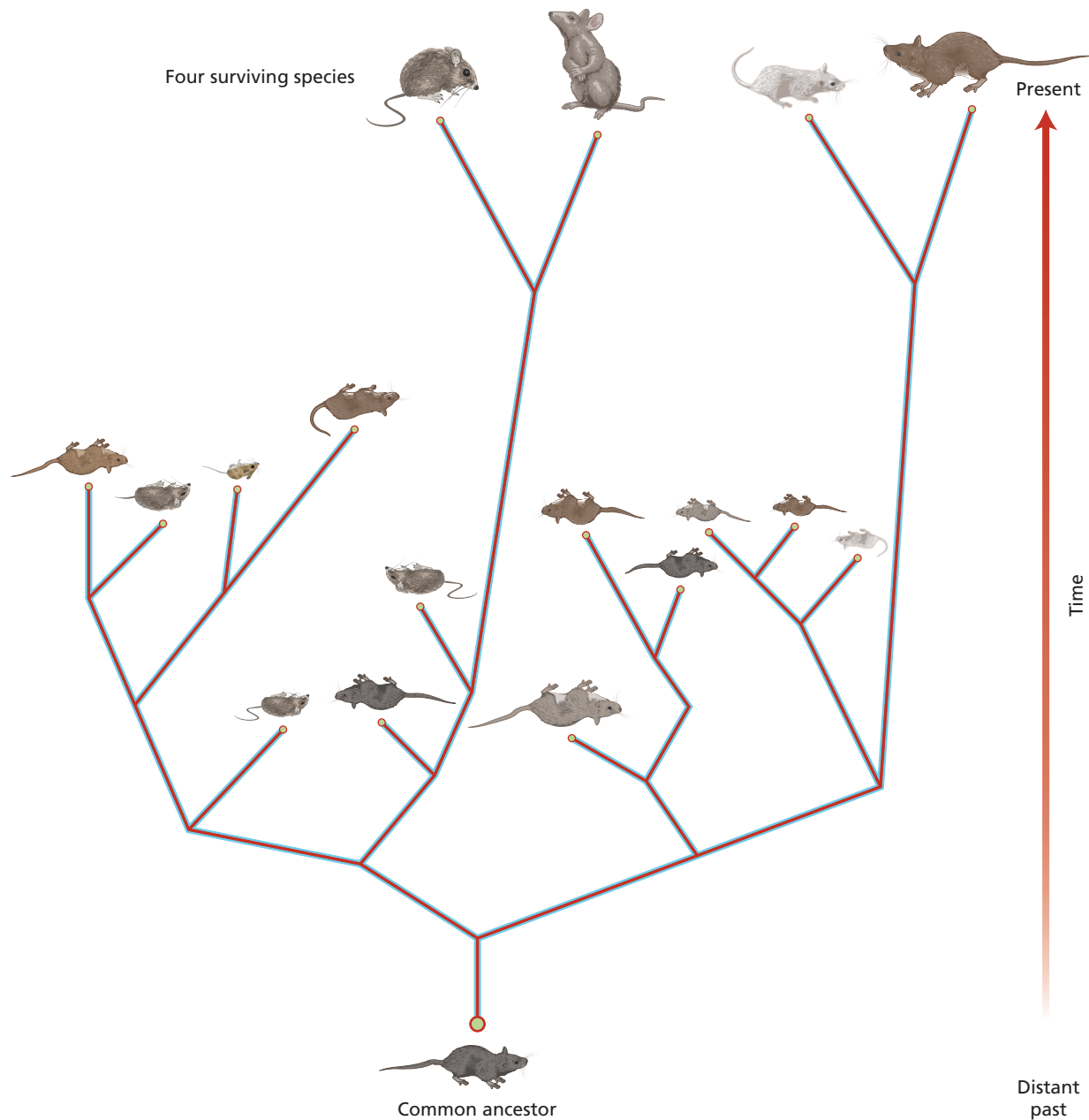


FIGURE 2.4A An Evolutionary Tree

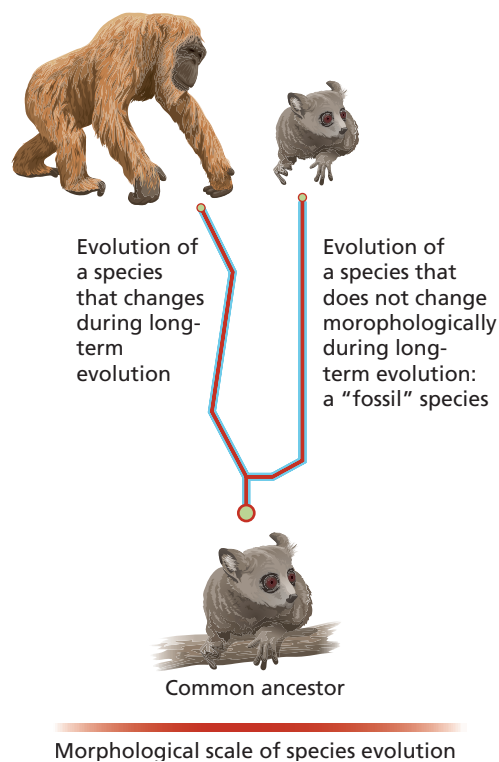


FIGURE 2.4B Evolution of Long-Lasting Species

the top of the figure. Extinction “prunes” branches from the evolutionary tree.

Several points should be borne in mind about evolutionary trees. The most important is that trees represent normal ecological and evolutionary process. Extinction still happens

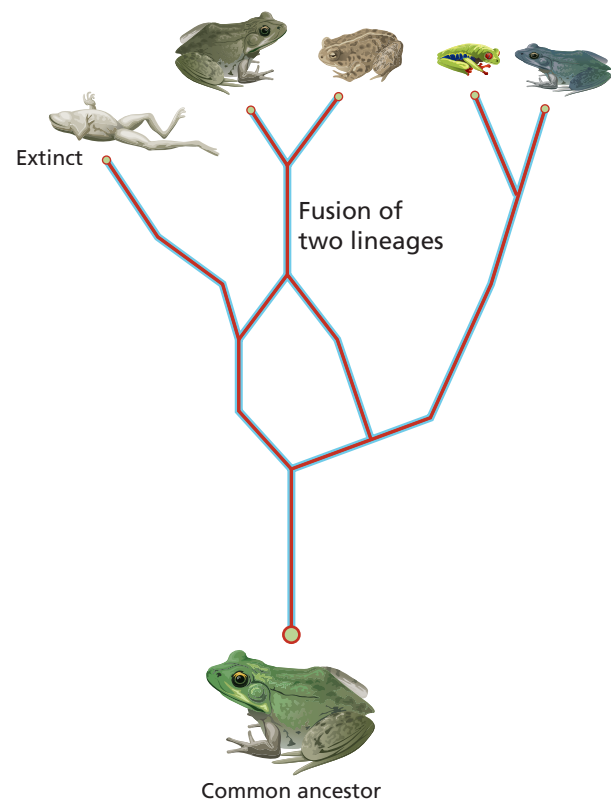
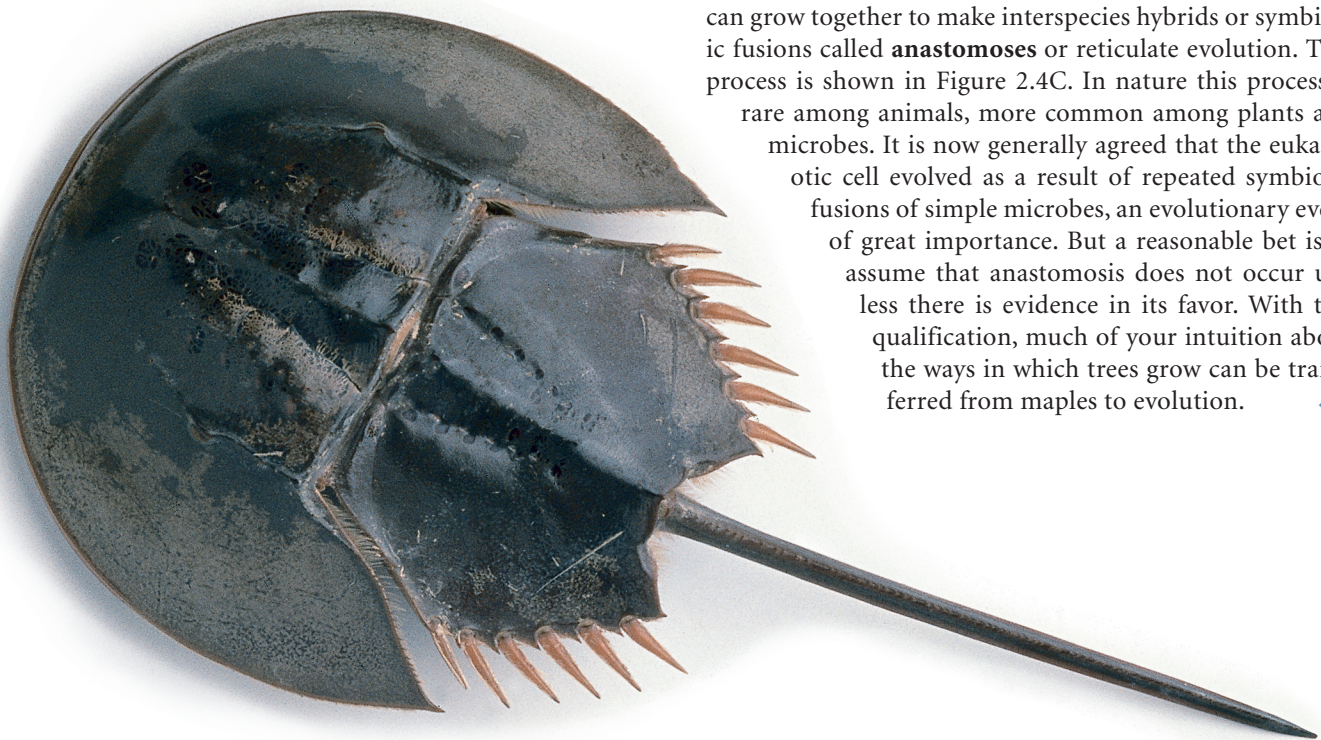


FIGURE 2.4C Evolutionary Anastomosis, also Known as Reticulate Evolution or Branch Fusion

due to failures of survival or reproduction among individual members of a species. Speciation depends on the reproductive biology of individual organisms. We will discuss speciation in Chapter 6. There is no general “forking principle” that explains speciation.

In both real trees and evolutionary trees, two branches can grow together to make interspecies hybrids or symbiotic fusions called **anastomoses** or reticulate evolution. This process is shown in Figure 2.4C. In nature this process is rare among animals, more common among plants and microbes. It is now generally agreed that the eukaryotic cell evolved as a result of repeated symbiotic fusions of simple microbes, an evolutionary event of great importance. But a reasonable bet is to assume that anastomosis does not occur unless there is evidence in its favor. With this qualification, much of your intuition about the ways in which trees grow can be transferred from maples to evolution. ♦



2.5 Evolutionary trees are often built using maximum parsimony

Evolution is often best understood using tree diagrams. How then do we get such diagrams? How do we infer the best evolutionary tree for horses? For insects? For flowering plants?

Often the best way to estimate which tree is best is to use the principle of **maximum parsimony**. This principle is the preference for a simple explanation over a complex one. The maximum parsimony principle is much like the ideas that

motivate the criminal justice system. Suppose you have two suspects. One of them fits an eyewitness description of a man fleeing from the crime scene, but he has an alibi. The other suspect does not fit this description, but is known to have quarreled with the victim, has the victim's blood on his clothes, and has no alibi for the time when the victim died. Most people would guess that the second suspect committed

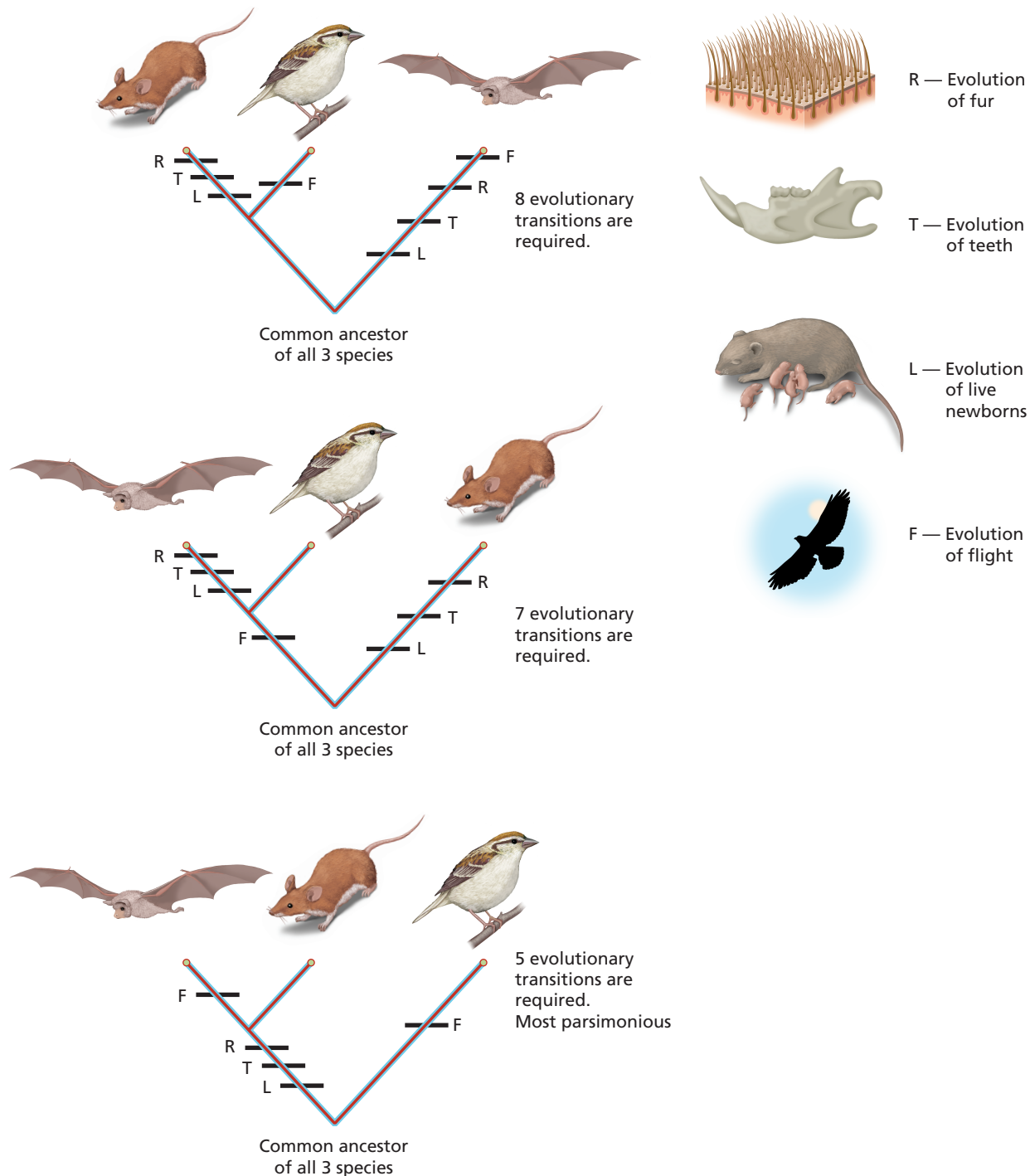


FIGURE 2.5A Alternative Evolutionary Trees

the crime, because there is only one piece of information that doesn't fit him, whereas the first suspect fits the crime profile in only one respect. Otherwise, a complex explanation would have to be provided to explain away the three points of evidence that implicate the second suspect. Such complex explanations are sometimes found in trials. For example, it could be discovered that the first suspect managed to frame the second suspect. In the absence of such exculpatory explanations for incriminating evidence, it is more parsimonious to indict the second suspect.

We can apply this same type of reasoning to evolutionary relationships. Let's say that you are from Mars, studying the animals of Earth. You have used your spaceship's tractor beam to catch three small animals: a mouse, a bat, and a sparrow. Being a Darwinian extraterrestrial, you wonder which of these three species are more closely related. There are three possibilities: mouse and sparrow closely related with bat distantly related; bat and sparrow closely related with mouse distantly related; or mouse and bat closely related with sparrow distantly related. These three possibilities are shown as three different evolutionary trees in Figure 2.5A.

How to decide? Consider a set of five characters, as listed in the table of Figure 2.5B: fur (vs. feathers); live offspring (vs. eggs); flight (vs. walking); warm-blooded (vs. cold-blooded); and teeth (vs. no teeth). All three animals are warm-blooded, so that character gives us no information, and we can ignore it. Obviously, bats and sparrows share the dramatic character of flight. But for three characters (teeth, fur, and live offspring),




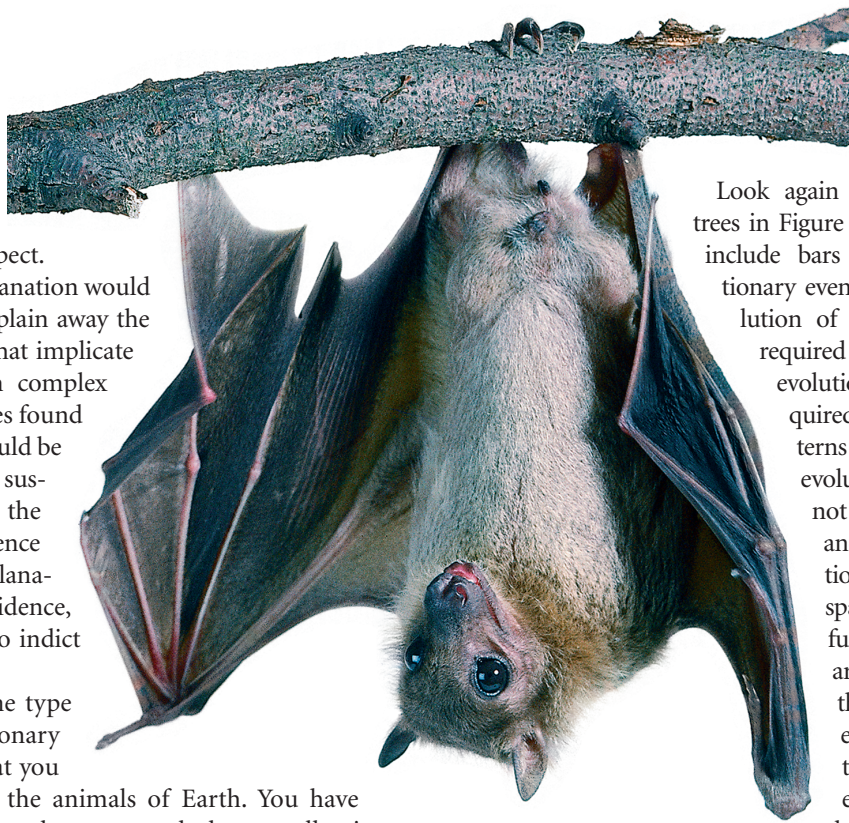
		Species		
				
Character	Teeth	yes	no	yes
	Flight	no	yes	yes
	Warm-blooded	yes	yes	yes
	Fur	yes	no	yes
	Live offspring	yes	no	yes

FIGURE 2.5B Character by Species Table for Classification



only bats and mice have the same attributes.

Look again at the evolutionary trees in Figure 2.5A. Note that they include bars representing evolutionary events—such as the evolution of fur—that would be required for each tree. These evolutionary events are required to explain the patterns of each tree. If these evolutionary events did not occur, we would have anomalies in our evolutionary trees, such as sparrows with teeth and fur. The first evolutionary tree, at the top of the diagram, requires eight separate evolutionary events to generate the differences between bat, sparrow,

and mouse. The next tree down requires seven evolutionary events. The bottom tree requires only five evolutionary events to account for the observed distribution of characters. That is the most parsimonious tree, so most evolutionary biologists would accept the evolutionary tree in which bats and mice are most closely related.

This example shows us how to determine the most parsimonious tree. (1) We create a matrix that associates particular character states with particular species. (2) We draw all possible evolutionary trees. (3) We place on each of these trees the evolutionary events required to generate the observed matrix of species characteristics. (4) We score the parsimony of an evolutionary tree as the number of distinct evolutionary transitions that have to be hypothesized to generate the observed pattern of differentiation among species (Figure 2.5A gives the number of hypothesized evolutionary transitions required for each tree in our example). (5) We compare the number of evolutionary transitions associated with each tree to discover which tree has the fewest transitions. That tree is the most parsimonious.

It is at least conceivable, however, that the most parsimonious tree is not the correct one. One problem is that an inappropriate collection of characters may have been chosen. For example, the extraterrestrial biologist might have chosen only those characters involved in the evolution of flight, in which case parallel selection for efficient flight in both bat and sparrow might have led to their parsimonious assignment to a common branch of evolution, separate from that of the mouse. In short, trees constructed using maximum parsimony are often better trees, though they may still be incorrect in some of the inferred branches. Adding more species to an evolutionary tree, and more characters, should improve the reliability of a tree.

SOME IMPORTANT TREES

2.6 The origin of life and the three domains

The origin of life seems like an inherently impossible topic for a scientific inquiry. After all, no biologists were around at the time. But it is precisely under such difficult conditions that tree making can reveal evolutionary history. In this case, the evolutionary history lies at the foundations of life itself.

For a long time, biologists divided life into two main groups: prokaryotes and eukaryotes. **Prokaryotes** are single-celled microbes that lack nuclei and other cell organelles. **Eukaryotes** are both single-celled and multicellular, with nuclei and other organelles. Crudely speaking, prokaryotes were seen as simple and eukaryotes were seen as complex. Naturally, the origin of life was posed as a problem in the early evolution of prokaryotes, with eukaryote evolution seen as the next major step in the evolution of life.

Figure 2.6A provides the crude timeline for the evolution of life on Earth. A striking feature of this timeline is the small amount of time between the origin of Earth and the first evolution of life. Another striking feature of the timeline is the late evolution of animals and plants. Most of the time, the evolution of life has been microbial.

A major area of biological research has concerned how life first evolved. One of the earliest findings was that amino acids and other components of cells arise randomly when water, hydrogen, methane, and ammonia are mixed together and subjected to electrical sparks. This result showed that the carbon molecules that are basic to life probably arose from chemical accidents alone.

Interest has shifted to how simple proteins and nucleic acids formed the first cells. One idea is that ribonucleic acid (RNA) may have been the first molecule of heredity, because it is simpler than deoxyribonucleic acid (DNA) and it can function as a catalyst for chemical reactions, like proteins do. Another proposal is that natural selection could have acted on cell components before full cellular integration, because durable or self-replicating cell constituents would tend to last longer. Finally, it has been suggested that complex cells ultimately evolved because of cooperation among components that evolved separately first.

One of the bigger surprises in the study of early evolution has been the realization that life is divided into three major branches, or **domains**. Two of these were already well known. The **Bacteria** are the familiar prokaryotes—including *Escherichia coli*, which inhabits our guts. The **Eukarya** are the well-known eukaryotes—from protozoa, to fungi, to plants, to animals. The third major domain is made up of the **Archaea**, formerly the archaeobacteria. The Archaea have a mix of attributes. Like Bacteria, they have no nuclei or organelles. But they differ from Bacteria in that they have histone proteins associated with their DNA and introns in some genes, like Eukarya. The Archaea have hydrocarbons that are not found in Bacteria or Eukarya, and, in some species, the ability to survive at very high temperatures. An

evolutionary tree for the three domains is shown in Figure 2.6B. Due to the great diversity of each domain, modern tree builders like to identify multiple **kingdoms** within each taxonomic domain.

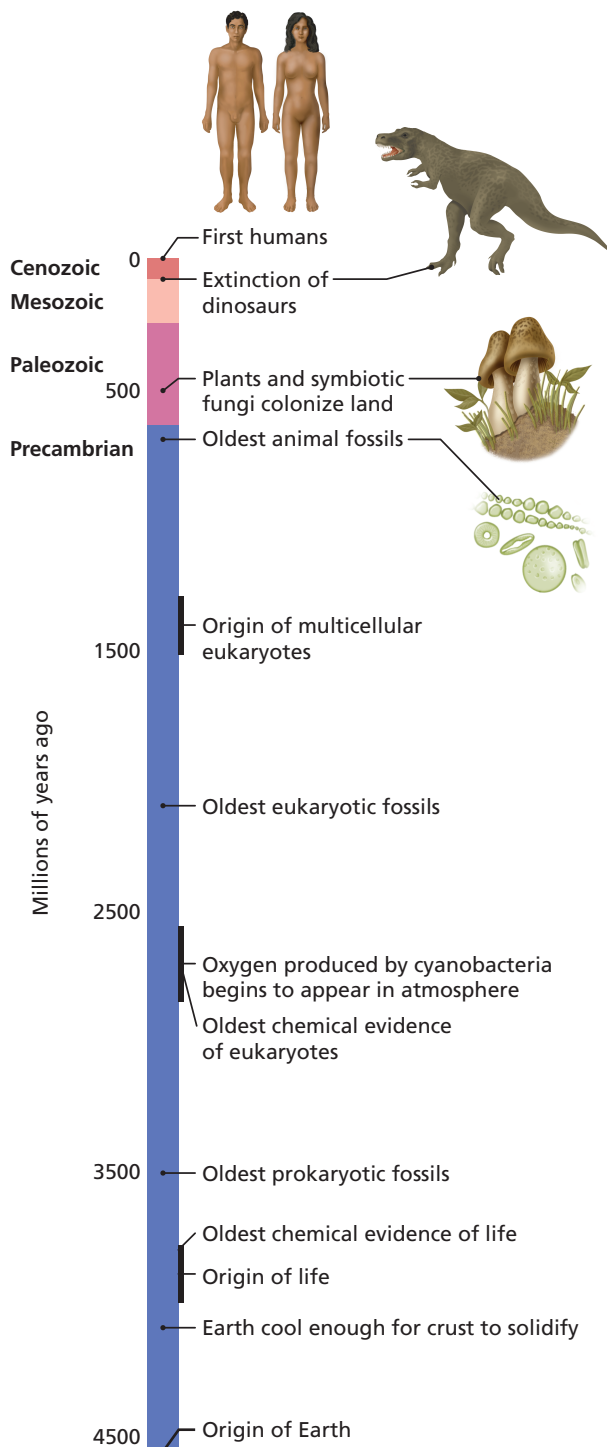
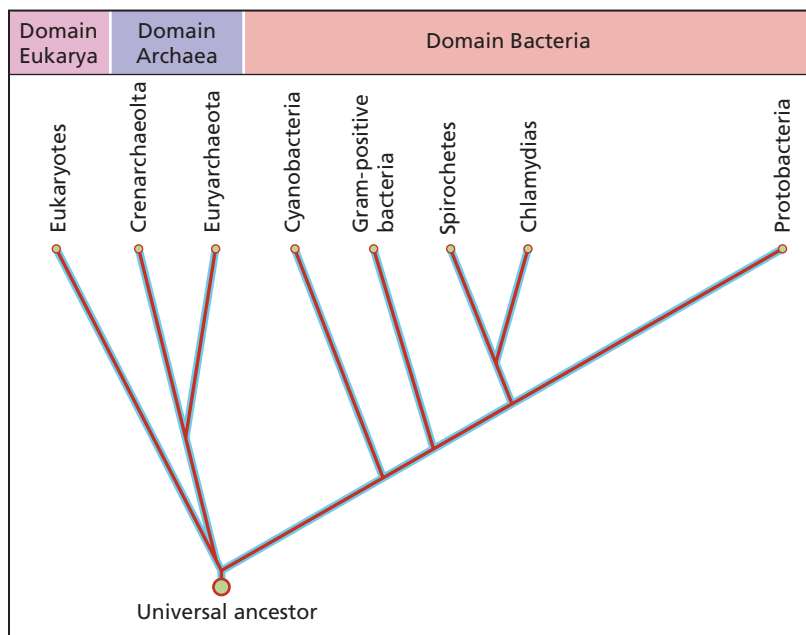


FIGURE 2.6A Timeline of the History of Life

**FIGURE 2.6B** Major Branches of the Tree of Life

2.7 Eukaryotic life evolved from endosymbiosis

The most important example of anastomosis in the evolution of life was the origin of the eukaryotes. For some time it had been noticed that mitochondria, the power plant of the eukaryotic cell, and chloroplasts, the photosynthesizing organelle of plants, were similar to bacterial cells. Figure 2.7A shows pictures of mitochondria and chloroplasts alongside free-living cyanobacteria. Mitochondria and chloroplasts have closed circles of DNA, like bacteria, and they are usually small, like bacteria. These features suggested to some biologists, like Lynn Margulis, that the eukaryotic cell might have evolved from the symbiotic combination of bacterial cells. This was called the **endosymbiont** theory of eukaryotic evolution.

But most biologists were not convinced by the cytology of eukaryotic cells, that is their crude features under a microscope. Fortunately, tree construction would persuade virtually everyone that the endosymbiont theory is correct.

There are two basic possibilities for the position of organelles in a phylogenetic tree. The first is that eukaryotes evolved their organelles from within. All the genes in organelles should then be closely related to the genes found in the nucleus. In this scenario, the eukaryotes evolved using their own resources, with no major contribution from bacteria.

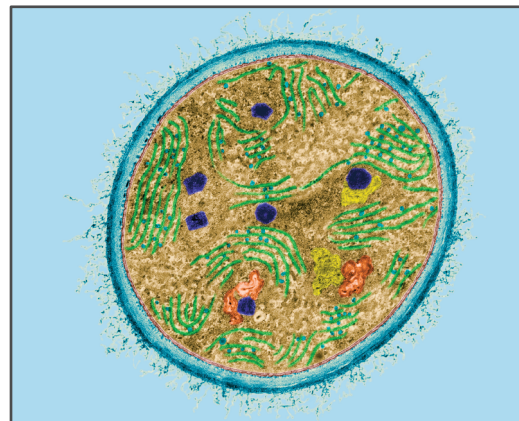
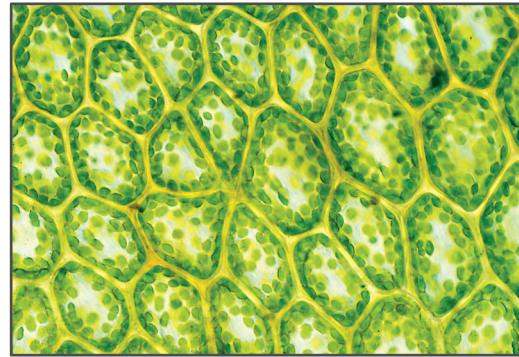
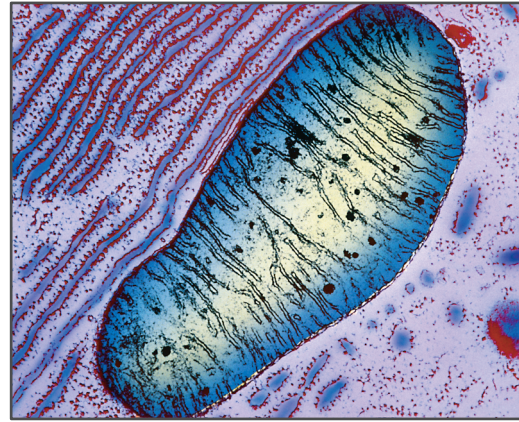
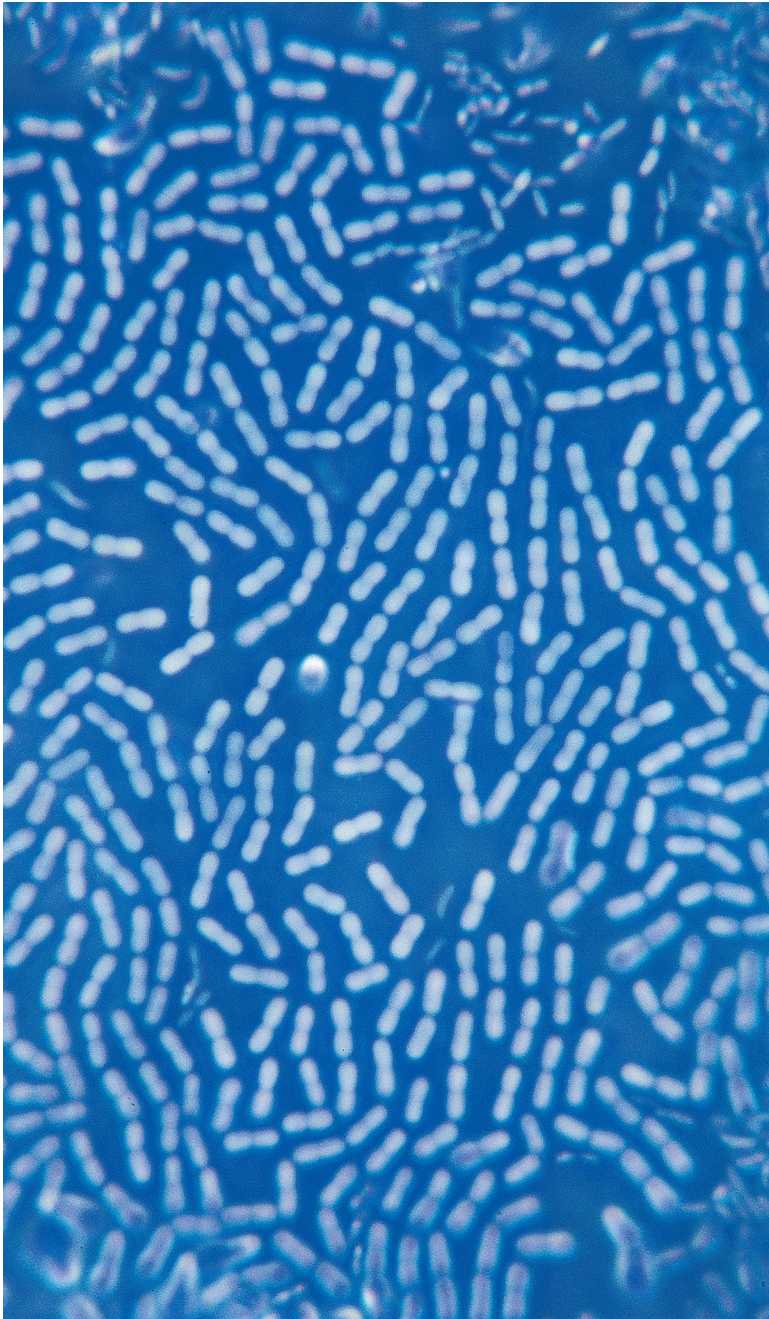


FIGURE 2.7A Mitochondria, Chloroplasts, and Cyanobacteria Related to Chloroplasts, proceeding from Top to Bottom

The second basic possibility is that eukaryotic organelles were evolutionarily derived from bacterial cells that had originally evolved on their own. If this is correct, then most genes in organelles should be closely related to the genes found in bacteria, not the nuclei of eukaryotes.

Based on tree structure, the first hypothesis would place eukaryotic nuclei and organelle genes on the same branch of the tree of life. The second hypothesis would place eukaryotic nuclei on one main branch, with prokaryote and organelle genomes together on the other branches of the evolutionary tree.

The actual tree is shown in Figure 2.7B. As the figure reveals, eukaryotic nuclei do not share recent ancestors with the genes of their organelles. Instead, those organelles are closely related to bacterial genomes. This finding dramatically supports the endosymbiont theory for the origin of eukaryotes.

A second point that emerges from this result is that the origin of eukaryotes depended critically on symbiosis. This fact suggests that, in general, symbiosis may be as important as competition and predation in the evolution of life. ♦

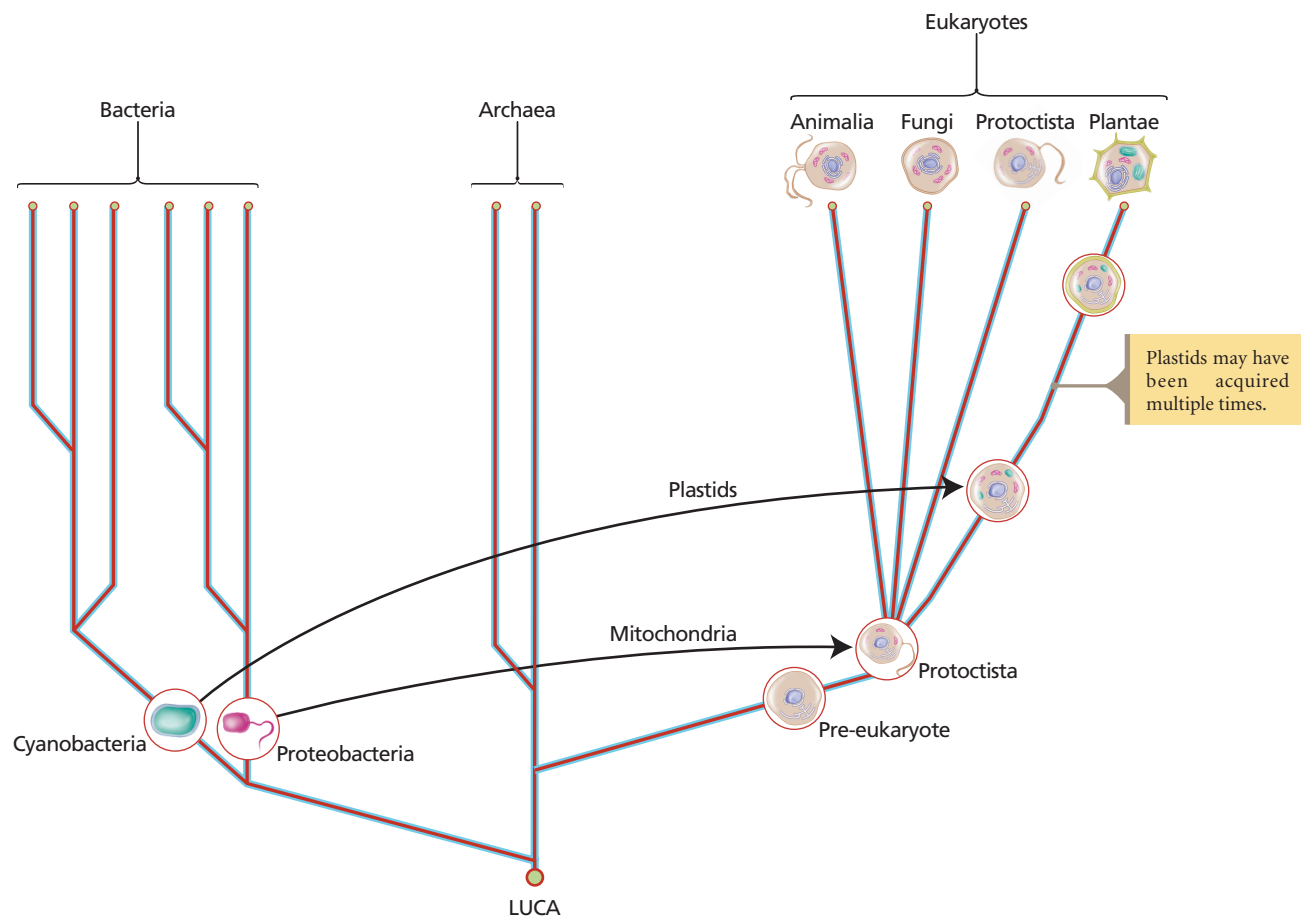


FIGURE 2.7B Evolutionary Tree of Eukaryotic Nuclei, Bacteria, and Eukaryotic Organelles

2.8 The trees of prokaryotic life

There are many things to learn about prokaryotes. Most important is the considerable diversity among prokaryotic groups. The most profound feature of this diversity is the evolutionary split between Bacteria and Archaea, already discussed. But there is also considerable diversity within these two domains.

Figure 2.8A shows the phylogeny of the Archaea, together with photos of some particular species from this group. The range of environments inhabited by Archaea is their most impressive feature. The **methanogens** live in anaerobic environments, like swamps and animal guts, where they use carbon dioxide and hydrogen to produce energy, with methane as a by-product. They are thereby responsible for the characteristic fragrance that bubbles out of such habitats. **Halophilic** species live in environments with a lot of salt, such as salt lakes. **Thermophiles** live in or near hot springs, on land as well as in oceans. Other Archaea live in less extreme environments.

Figure 2.8B shows the phylogeny of the Bacteria. These are the most abundant prokaryotes. The main groups of Bacteria have been given kingdom status. Each of the bacterial kingdoms is probably more ancient than either the plant or animal kingdoms. Bacteria take on many ecological roles, but they are best known to us as pathogens. *Bdellovibrio* causes cholera; *Helicobacter pylori* infects stomachs, where it causes ulcers; and *Chlamydia trachomatis* causes both venereal and eye diseases. Other bacteria are symbiotic, the best known being the *Rhizobium* bacteria, which take nitrogen from the atmosphere and supply it to the plants in which they live.

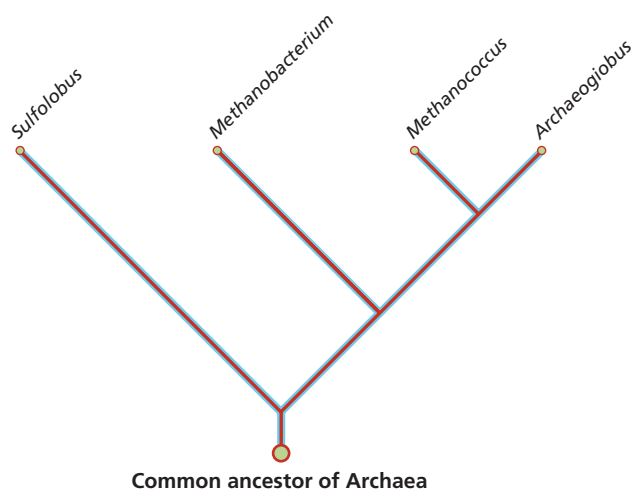
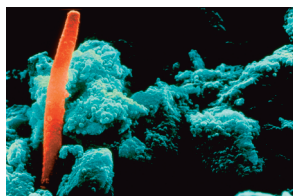
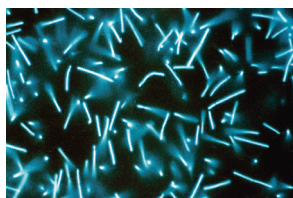


FIGURE 2.8A Evolutionary Tree of the Archaea

Still other bacteria are free living. Some of the extremely small mycoplasma species live in soil. Other free-living bacteria form multicellular fruiting bodies that produce spores. Cyanobacteria are able to photosynthesize. Their relatives evolved into chloroplasts.

An important feature of prokaryotic evolution is that horizontal gene transfer between species is common. Prokaryotes have several forms of parasexuality: **conjugation**, **transduction**, and **transformation**. During conjugation, one cell receives a plasmid from another cell. During transduction, DNA is transmitted between cells by a virus. Transformation occurs when linear molecules of DNA are excreted by one cell and ingested by another cell, where they are recombined with the genome of the recipient cell. All of these forms of sex are considerably less particular than eukaryotic sex. (They are discussed further in Chapter 18.) Useful genes may be passed from one species to another during any of these three parasexual processes. The best-known example of this process is the spread of antibiotic resistance genes among bacteria, a major problem for public health discussed further in Chapter 22. However, the long-term importance of horizontal gene transfer for bacterial evolution is hard to evaluate. Unlike the endosymbiotic origin of eukaryotes, which is now fairly obvious, the exchange of only one or a few genes during bacterial evolution is far harder to detect. But this difficulty of detection does not mean that gene transfer has been unimportant in bacterial evolution. ❖

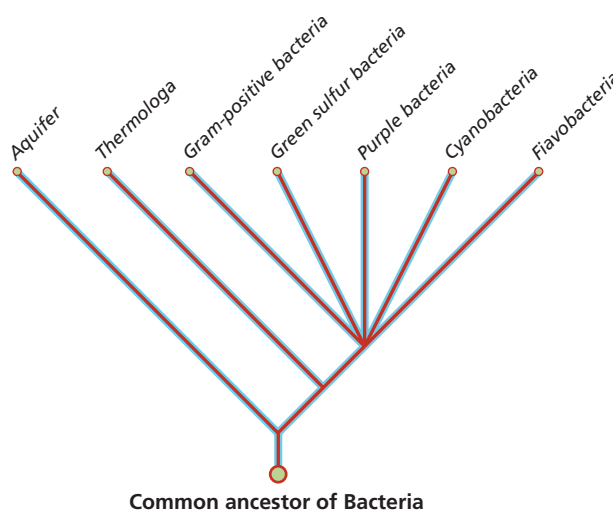


FIGURE 2.8B Evolutionary Tree of the Bacteria

The trees of eukaryotic life 2.9

The traditional classification of eukaryotes was a tree based on a protistan base primarily made up of single-celled organisms, with fungi, plants, and animals radiating out from those species. This image is shown in Figure 2.9A. It is almost entirely incorrect.

A better view of evolution in Eukarya is supplied by Figure 2.9B. Based on long-standing evolutionary differentiation, many protist groups are worthy of the designation kingdom. This viewpoint is not too surprising, because there was a long evolutionary period of protistan evolution before animals, fungi, or plants evolved.

The diversity of protistan forms needs to be appreciated. Diplomonads and parabasalids lack mitochondria. However, this may be a secondary loss during the evolution of these species, rather than a failure to acquire mitochondria during evolution. Protistans also vary considerably with respect to their locomotion. Some move their bodies in waves, others have long flagella, and still others have cilia. There are still more variations on these themes. The ciliates are a major group of protists that have cilia. The reproductive systems of protists vary too. Some are asexual (e.g., some *Ameoba* species), some have sexual processes where entire cells fuse to form zygotes (e.g., *Chlamydomonas*), and some ciliate species have a complex sexual process involving different types of nuclei within each cell.

Some of the first land plants to evolve were the bryophytes, which include the liverworts, hornworts, and mosses. These plants lack a complex vascular system and do not produce seeds. Vascular systems evolved later among the ferns and horsetails, among other groups. Seed production evolved among the ancestors of the gymnosperms (e.g., conifers) and angiosperms, the flowering plants. Most plant evolution has occurred during the last 600 million years.

Animal evolution has occurred primarily during the last billion years or so. Although animal evolution is commonly taught in relation to the evolution of the main vertebrate groups (jawless fish, cartilaginous fish, bony fish, amphibians, reptiles, birds, and mammals), vertebrates are actually a

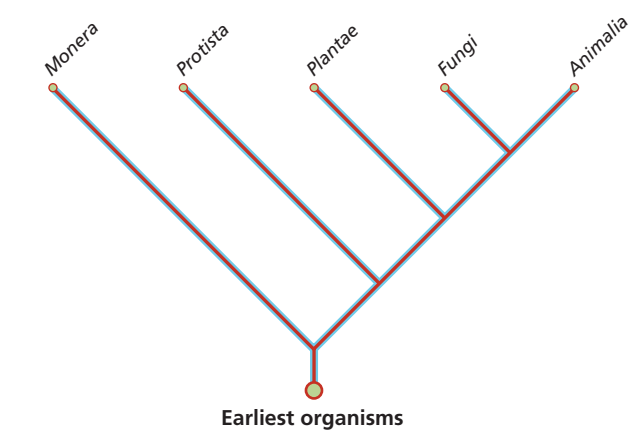


FIGURE 2.9A Historical Division of Eukaryotes into Protozoa, Fungi, Plants, and Animals

minor group of animals, with few species and few individual organisms. The most abundant animal group is the arthropods, made up of insects, spiders, crustaceans, and so on. There are far more arthropod species than vertebrate species.

Finally, we come to the fungi, once grouped with plants and now recognized as an independent group of organisms. Fungi are primarily known for their major role in decomposition. This sounds like a relatively passive ecological role. But some fungi actively catch animals for food, while still other species have flagella and can locomote. A number of fungi attack plants, including agricultural crops. In humans, fungal infections cause irritating disorders like athlete's foot as well as persistent lung infections that can kill.

The spectrum of eukaryotic life is vast. Students of biology have to be careful not to let their biases and practical interests distract from the important patterns of evolution. However interesting we may find dinosaurs, they were a tiny part of the tree of life. There have been far more parasitic wasp species than dinosaur species in the history of life, and those parasitic wasps have probably been more important in the ecology of the planet. ♦

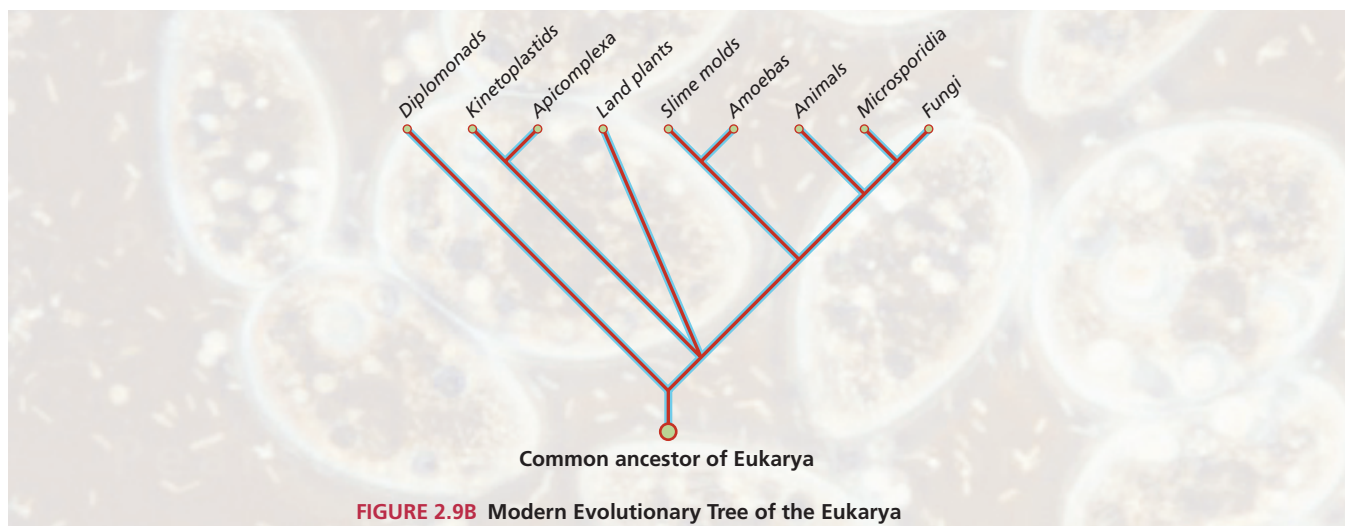


FIGURE 2.9B Modern Evolutionary Tree of the Eukarya

USING TREES TO STUDY EVOLUTION

2.10 The classification of species can be explained elegantly with Darwin's evolutionary tree concept

The classification of species has roots in classical Greek thinking, especially the theory of ideal types that we know best from Plato. Originally classification was an entirely non-evolutionary tool for grouping living things. But it provides us with some of the best evidence in favor of evolution.

It is an obvious fact about life that organisms can be grouped together. A large number of birds weigh several pounds, have entirely black feathers, and call with a distinctive sound, which can be rendered roughly as “caw! caw!” In everyday English, these birds are called crows (Figure 2.10A). We will see hundreds of them in our lives. There are a number of species of crow, from carrion crows to ravens to rooks. But they all have easily recognizable plumage, shape, and call.

To a Platonic thinker, these birds all share an inner “crow-ness.” For this reason, all these birds are grouped together in the genus *Corvus*. Different species, such as *Corvus graculous*, are recognized for their differences from other crows. Crows are also examples of birds, and for that reason they are placed in the taxonomic class called Aves, which brings together all animals with two walking feet, wings (usable for flight or not), and feathers.

There are several notable things about conventional **biological classification**: (1) It groups very similar organisms into a species. (2) It goes on to cluster species together in larger and larger aggregations: genus, family, order, class, phylum, and **kingdom**. As shown in Figure 2.10B, this clustering gives a kind of Chinese box structure to biological classification. (3) Some of the affiliations of organisms become fairly subtle. For example, humans, crocodiles, and the wormlike *Amphioxus* (Figure 2.10C) are all grouped as members of the Phylum Chordata. This grouping is based on a structure called a *notochord*, a proto-backbone that appears in the development of chordates. This obscure structure is not as obvious as the milk of a mammal or the feathers of a bird. (4) This classification approach is not based on evolutionary theory. Indeed, there is no deep theory to traditional biological classification. It is based entirely on mere similarity.

The incredible thing about biological classification is that it works so often. Organisms do cluster fairly well, with further clustering within larger clusters. There are no bats with feathers. There are no insects

with calcified bones. Living things obey unseen rules that make classification work. Why?

The answer is evolution, the tree of life. As shown in Figure 2.10D, we can make sense of the clustering of organisms in relation to their descent from **common ancestors**. In the figure, each genus of the imaginary Family Treeidae shares a common ancestor. Common features of the members of the Genus Luckius that are not shared with other members of the Family Treeidae can be explained evolutionarily as deriving from the features of the common ancestor of



FIGURE 2.10A A Crow



that particular genus. Thus a Darwinian would explain unique characters that are shared among groups of organisms as a result of derivation from a common ancestor that possessed those characters. The descendants of such common ancestors then evolve into multiple descendant species that differentiate from each other in many respects, yet share features that were retained from their common ancestor.

In other words, biological classification is a reflection of evolutionary history. Because evolutionary history follows Darwinian rules, some of the critical assumptions of biologi-

cal classification are guaranteed. Species are not members of more than one genus, family, order, class, or phylum. And multiple characters can be used to identify organisms as belonging to species, genera, families, and so on.

The explanation of biological classification is an application of the evolutionary tree concept that supports the foundations of the science of biology. Before the tree concept came along, biological classification was based on convenient similarities. Now biological classification actually makes sense. ❖

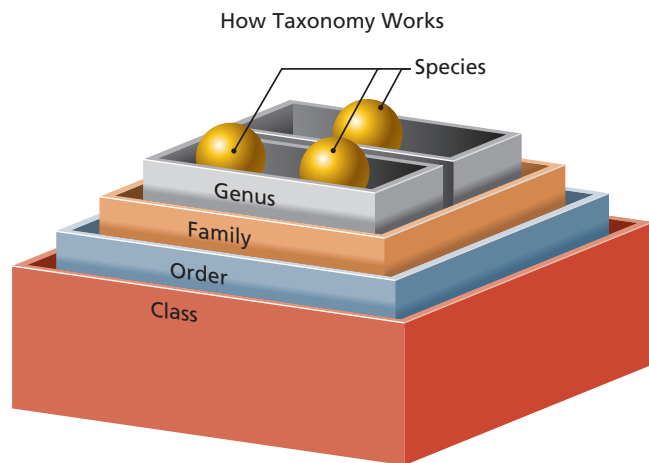


FIGURE 2.10B Taxonomy Works like Chinese Boxes

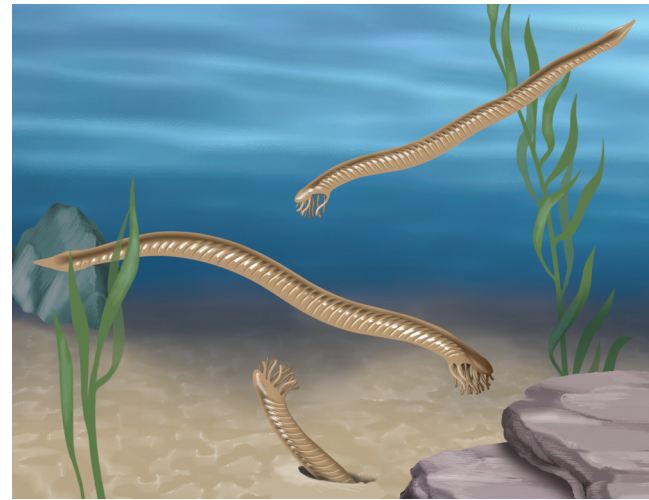


FIGURE 2.10C *Amphioxus* in Its Natural habitat

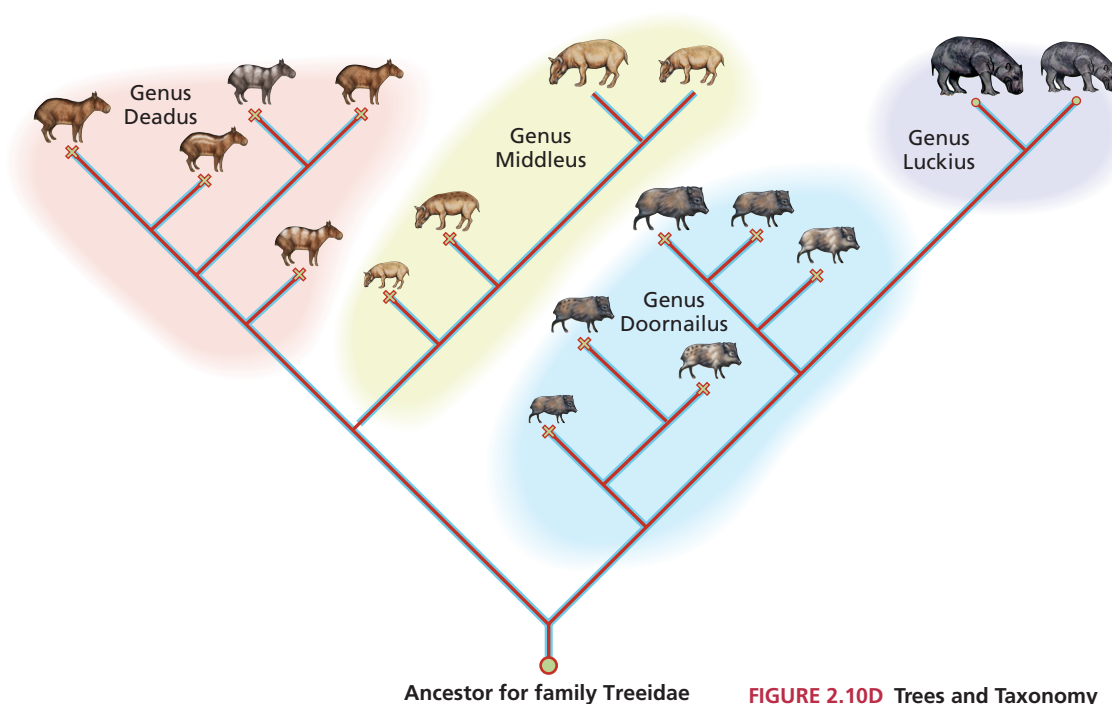


FIGURE 2.10D Trees and Taxonomy

2.11 Fossil differentiation often follows tree patterns

Fossil specimens are used to construct evolutionary trees, when they are available. The hard structures of many animals can become fossils. That is, sedimentary and other slow geological processes convert shells and bones into rocks that retain the original shape of these hard structures. In some rare cases, geological events allow the fossilization of softer body parts. This occurred at the Burgess Shale site in the Canadian Rockies (Figure 2.11A). This one fossil deposit has told us more about the early evolution of animals than any other. Some illustrations of these animals are shown on the book cover. But for most animals, only thick shells, like those of mollusks, or bones, like those of vertebrates, fossilize.

In taxonomic groups with hard structures, we can follow the evolution of these hard structures using reasoning based on the tree concept. With abundant fossil specimens, it is often possible to reconstruct in detail the evolutionary sequences linking one species with another, especially when the fossils can be accurately dated. Entirely novel structures may evolve, allowing us to identify either the branching off of new species or profound evolutionary change within an unbranching part of the evolutionary tree.

Evolutionary biologists sometimes physically array fossil specimens into tree patterns. Consider Figure 2.11B. The fossils placed at the bottom of the evolutionary tree come from the oldest, usually deepest, fossil strata or layers. Species that evolved somewhat later come from the middle layers of geological deposits. The species that have evolved most recently will either come from the fossils nearest the surface of the Earth, or they will be represented by living organisms.

Fossils can reveal specific features of the evolutionary process. Instead of speculating about the properties of common ancestors based on present-day forms of life, evolutionary biologists may be able to examine fossils from deep strata that show hypothesized features. Such fossils provide a glimpse of the evolutionary process at a point in time when the common ancestor might have lived.

Fossils can also reveal the speed with which hard structures evolve. One of the more spectacular examples of rapid evolution is the expansion of the human cranium over the last 2 million years. The human skull is an excellent structure for fossil studies, because it fossilizes well. On the other hand, humans have only recently become abundant. For most of our evolution, humans were relatively rare animals—compared to pigs, for example—thus impeding the search for our fossils. Figure 2.11D gives a human evolutionary tree. (We will consider this example of evolution in some detail in Chapter 21.) Paleontologists, the scientists who study fossils, have many interesting stories to tell about human evolution.

Dinosaurs and humans are the most famous concerns of **paleontology**, but there are many other taxonomic groups with which we have made considerable scientific progress. One of the most-studied groups is the hard-shelled Foraminifera. These small oceanic creatures make extremely durable shells that are among the most common microfossils in the world. Ironically, the seemingly obscure study of “foram” fossils is valuable in prospecting for oil, one of the most remunerative businesses of modern times. ❖



FIGURE 2.11A The Animals of the Burgess Shale, a Traditional View

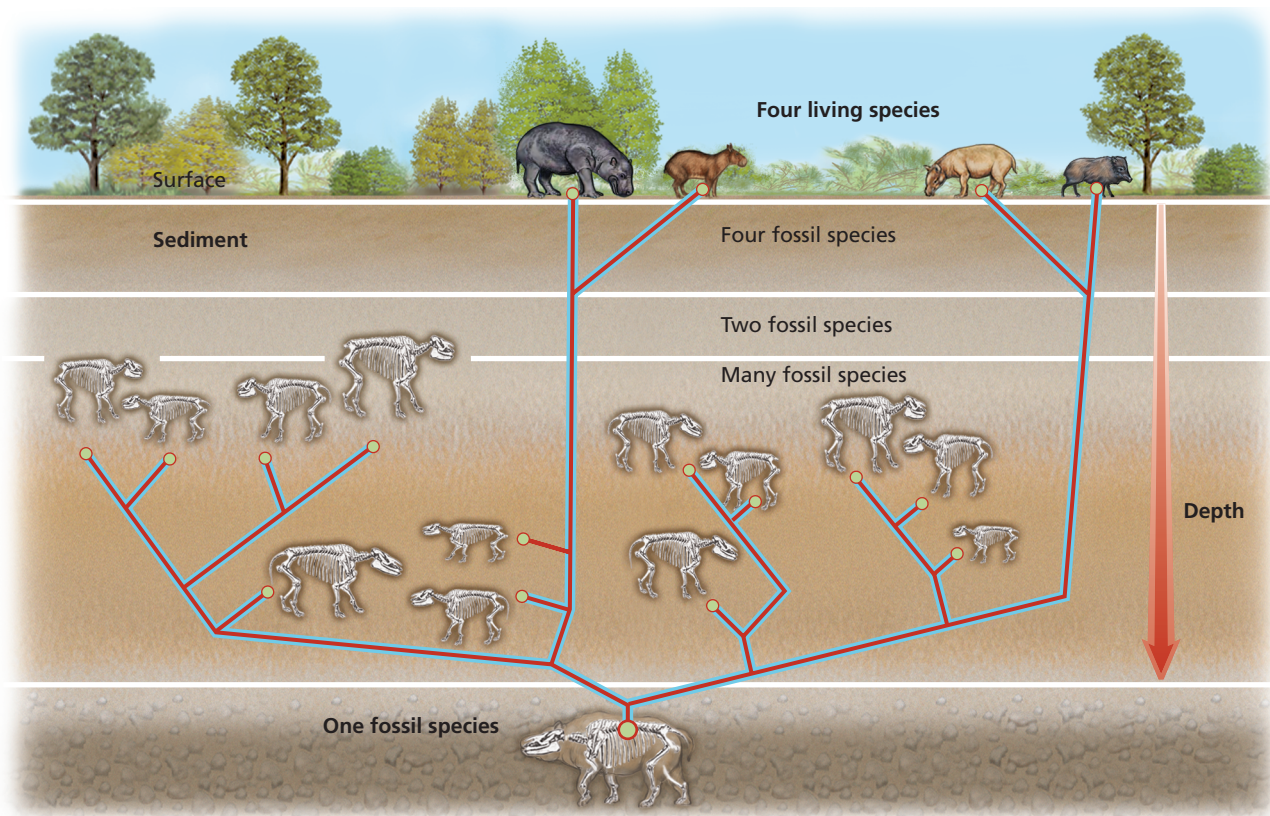


FIGURE 2.11B Trees and Fossils

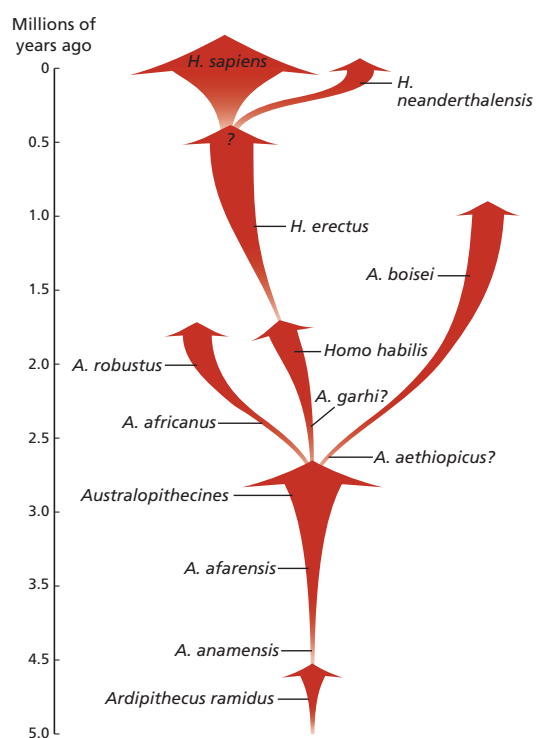


FIGURE 2.11C Evolutionary Tree Based on Human Fossils This tree is revised frequently by paleoanthropologists.



2.12 Biogeographic patterns can be explained in relation to geology, migration, and evolutionary history

All evolution is local. New species evolve from already existing species at particular times and places. This small point has important implications for our understanding of the geography of life.

In some cases, the biology of evolving species obscures the evolutionary basis of **biogeography**, the distribution of species over the Earth. Birds that have evolved in one locale may be able to fly over most of the Earth's surface. Albatross (species of the genus *Diomedea*), for example, are very strong long-distance fliers, able to travel over thousands of miles of ocean, so their present-day distribution on Earth does not reveal much about where they evolved. Likewise, some moths and butterflies can fly thousands of miles during their migrations. The monarch butterfly (*Danaus plexippus*), for example, seasonally migrates between Mexico, the midwestern and northeastern areas of North America, and the southern states of the United States. Oceanic species, like some of the whales, swim between the poles, as do many bony fishes. Even plants may have pollen that can be carried on winds over hundreds of

miles. The ubiquity of the dandelion (*Taraxacum officinale*) is just one example of the effects of aerial dispersal. Even if evolution is local, dispersal may obscure that fact. (The biology and impact of dispersal is considered further in Chapter 11.)

But some species reveal their evolutionary history in their distribution—especially their distribution before humans started deliberately and accidentally dispersing species from continent to continent. The classic example is the abundance of marsupial mammals in Australia. Elsewhere, marsupials are extremely rare, the most notable group outside of Australia being the opossums of America (*Didelphis marsupialis*). Before humans arrived in Australia some 30,000 to 60,000 years ago, the only significant group of placental mammals on that continent were the bats (Order Chiroptera), which could have reached Australia readily by flight.

How can we explain the biogeography of this distribution? The standard evolutionary explanation involves the isolation of Australia due to continental drift. Marsupial mammals evolved before placental mammals and spread over the surface

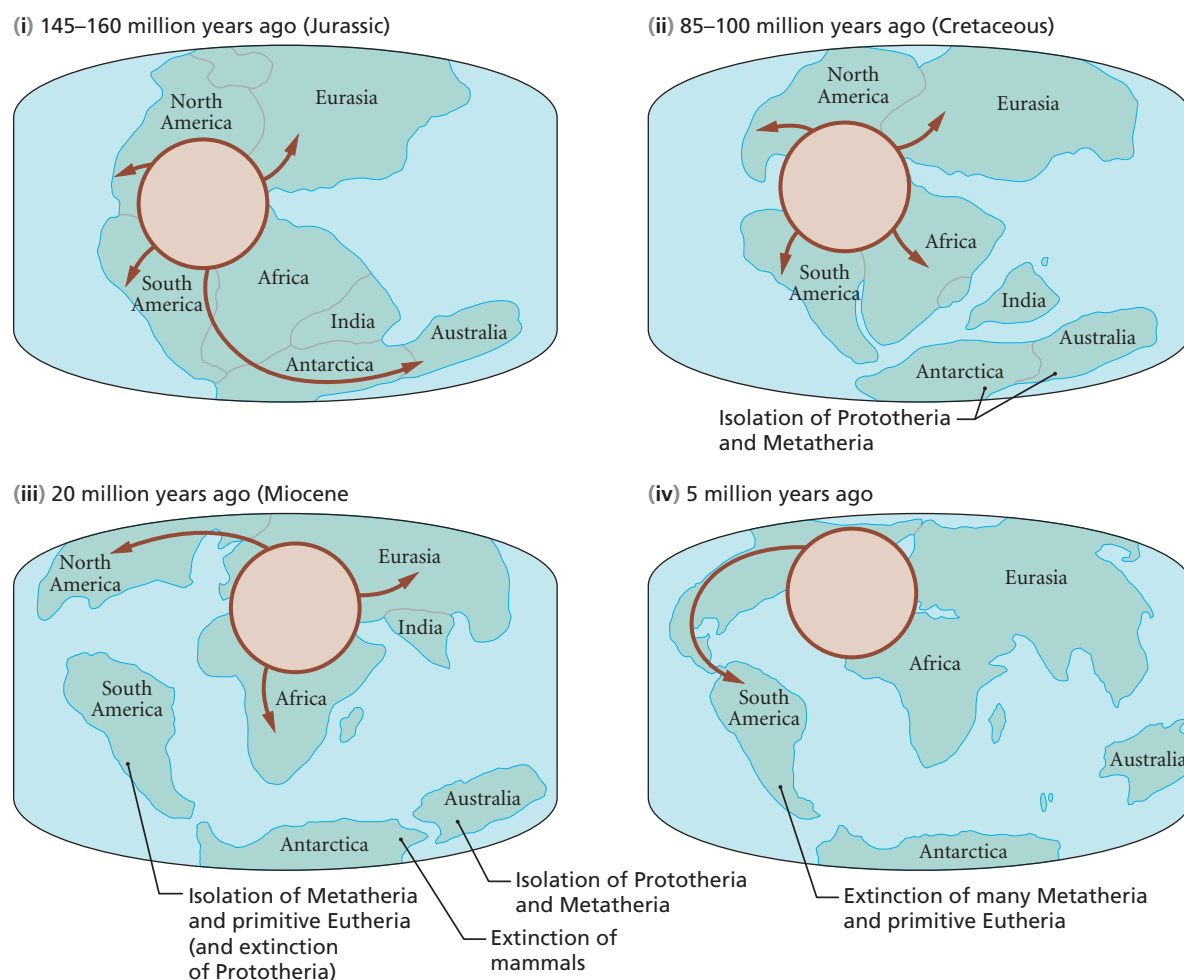


FIGURE 2.12A The Biogeography of Mammalian Evolution The disk shows the main line of mammalian evolution that eventually produced the Eutheria, the placental mammals.

of the world when the continents had not drifted too far apart. Placental mammals evolved later, but the terrestrial mammal species could not reach Australia due to the absence of land bridges—such as those that have connected all the other continents—in the last 50 million years. The isolation of Australia protected the marsupials there from ecological elimination by the placental mammals. This biogeographical hypothesis is illustrated in Figure 2.12A.

The ultimate corroboration of this model is supplied by the animals of New Zealand. Before humans arrived around 800 years ago, the fossil record of New Zealand shows no evidence of colonization by any type of terrestrial mammal. Instead, the birds that reached New Zealand apparently evolved to take on ecological roles similar to those of terrestrial mammals. One example of this is nighttime ground foraging by kiwis (genus *Apteryx*) instead of rodents. A number of New Zealand bird species are completely flightless (see Figure 2.12B). Some of these birds were small and timorous, like kiwis. Others were quite large, like the moa, a group of bird species driven to extinction by the first human colonists of New Zealand, the Maori. Some moas weighed several hundred pounds, remarkable for a bird. The ecology and evolution of the moa must have hinged on the complete absence of terrestrial mammals in New Zealand. The extinction of the moa after human colonization and the absence of birds like them elsewhere in the world suggests that moas could not have survived with dogs, cattle, and monkeys as competitors. Ostriches, for example, are not as large as the big moa species and probably much better at running.

Another way to look at biogeography is to realize that it shows the imperfection of evolution by natural selection. By

accidents both constraining and fortuitous, new species evolve from other local species in response to local ecological conditions. Evolution works with the materials at hand, like the birds of New Zealand, not with the species best suited to the ecological circumstances—presumably, placental mammals in the case of New Zealand. If evolution were perfect, it is arguable that the kiwis should have been rodents. But we don't expect evolution to be perfect. ♦



FIGURE 2.12B Flightless Birds of New Zealand



2.13 Developmental patterns can be explained using evolutionary trees

Figure 2.13A, below, shows one of the famous features of life. The embryos of many groups of organisms often show considerable similarity when they are very young. The example shown is a drawing of vertebrate embryonic development. (Illustrations of this kind are not regarded as entirely reliable by biologists, but they were important in convincing biologists of the conservation of patterns of development.) This is one of the most surprising facts in biology, if you are not an evolutionary biologist.

Darwin offered an explanation for this pattern in the *Origin*. His argument distinguished two cases. In the first case, the embryo lies within a protective structure during development. An eggshell is an example of such a protective structure, and so is the uterus of a placental mammal. Another example is a seed. In all these cases, the developing embryo will not be shaped by natural selection for a particular type of locomotion, feeding, or growth. Therefore, there will be no immediate selection for the embryo to resemble the adult. The embryonic stage is not shaped by the selection imposed on the free-living, unprotected life stages. Therefore, natural selection is likely to leave the embryo relatively unchanged from the features in the common ancestor of the taxonomic group to which the embryo's species belongs.

One way to look at the embryos of vertebrates as diverse as fish, reptiles, birds, and mammals is that all these embryos develop in protected environments, whether inside an egg or inside a uterus. These embryos live in a manner that is not as different from that of the ancestral wormlike aquatic chordate as the ways of life of many vertebrates today, which may fly, run on legs, and so forth. Thus Darwin essentially argued that many embryos reflect ancestral features largely unchanged by natural selection.

The key test of Darwin's interpretation, as he realized himself, lay in the second case that he distinguished—the embryology of species in which larvae are free living. Free-living larvae may be subject to selection for feeding, avoiding predation or herbivory (if they are plants), and so on. Under these conditions, Darwin predicted that natural selection would tend to obscure an organism's evolutionary ancestry.

A good example of this principle is the larval stages of butterflies, moths, flies, and other insects. Most larval development in these species takes place during a free-living stage in which food must be found and eaten, predators avoided, and so on. Caterpillars, for example, take on a wide range of sizes, coloration, "hairiness," and so on. Instead of

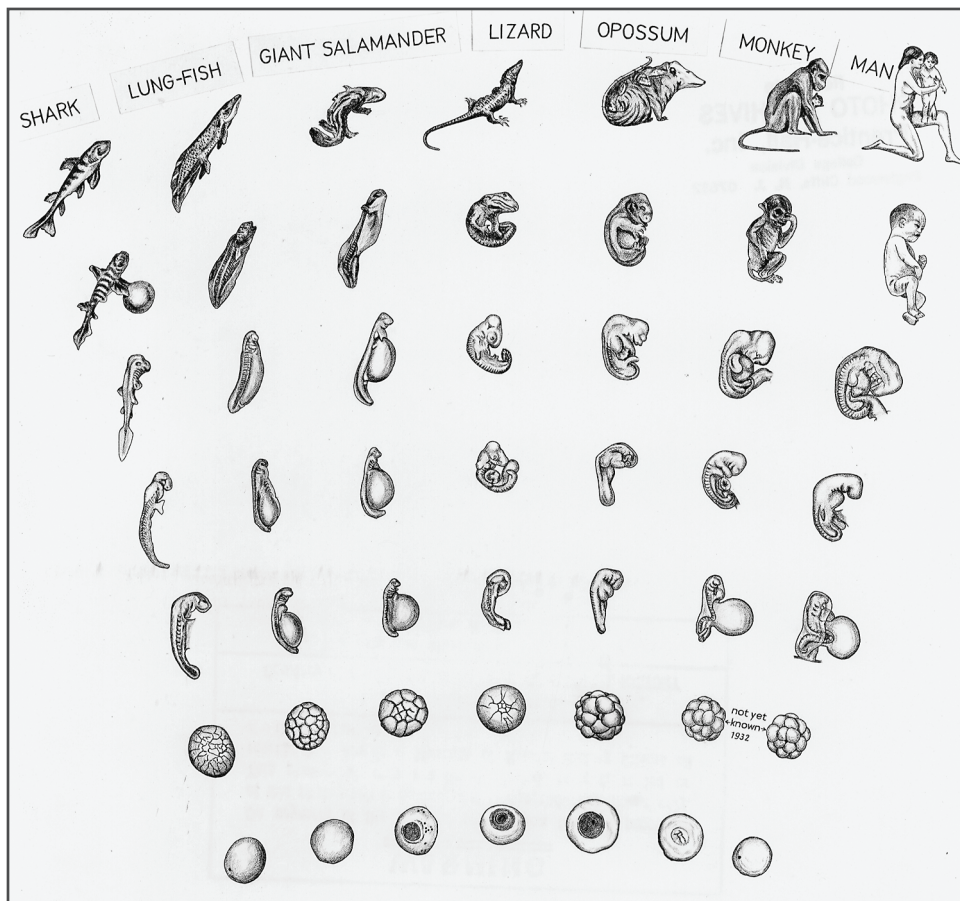


FIGURE 2.13A Somewhat Misleading Figure Illustrating Parallel Development in Vertebrate Embryos

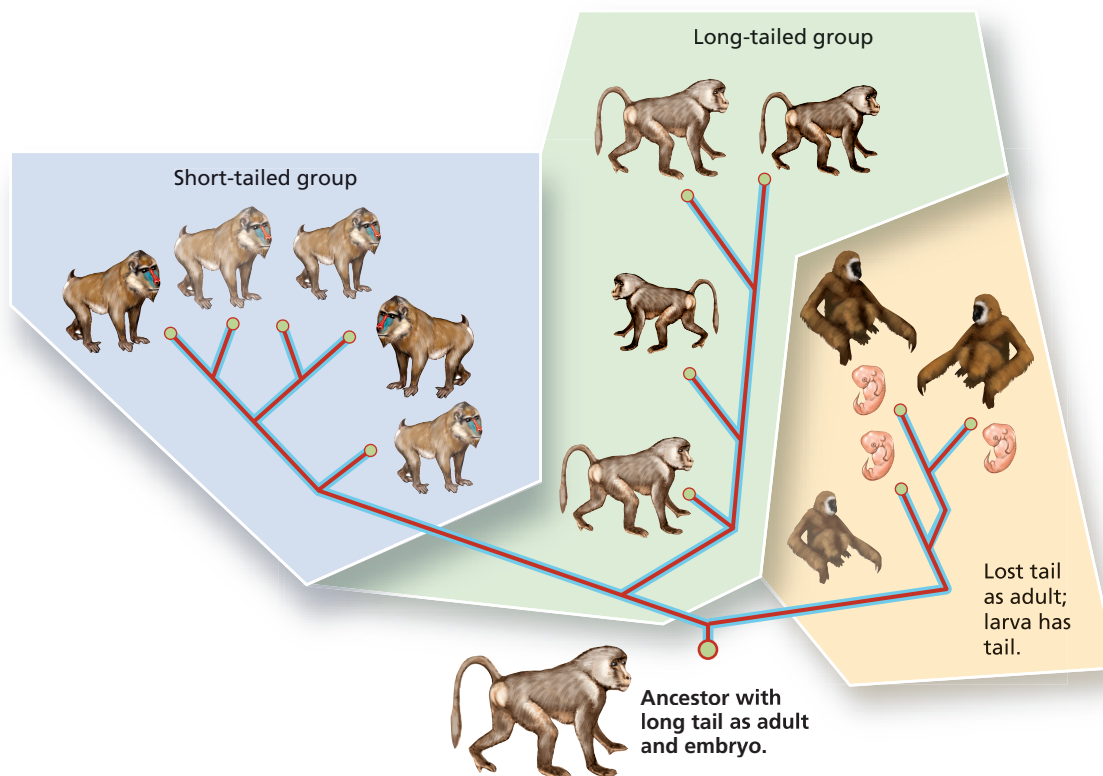
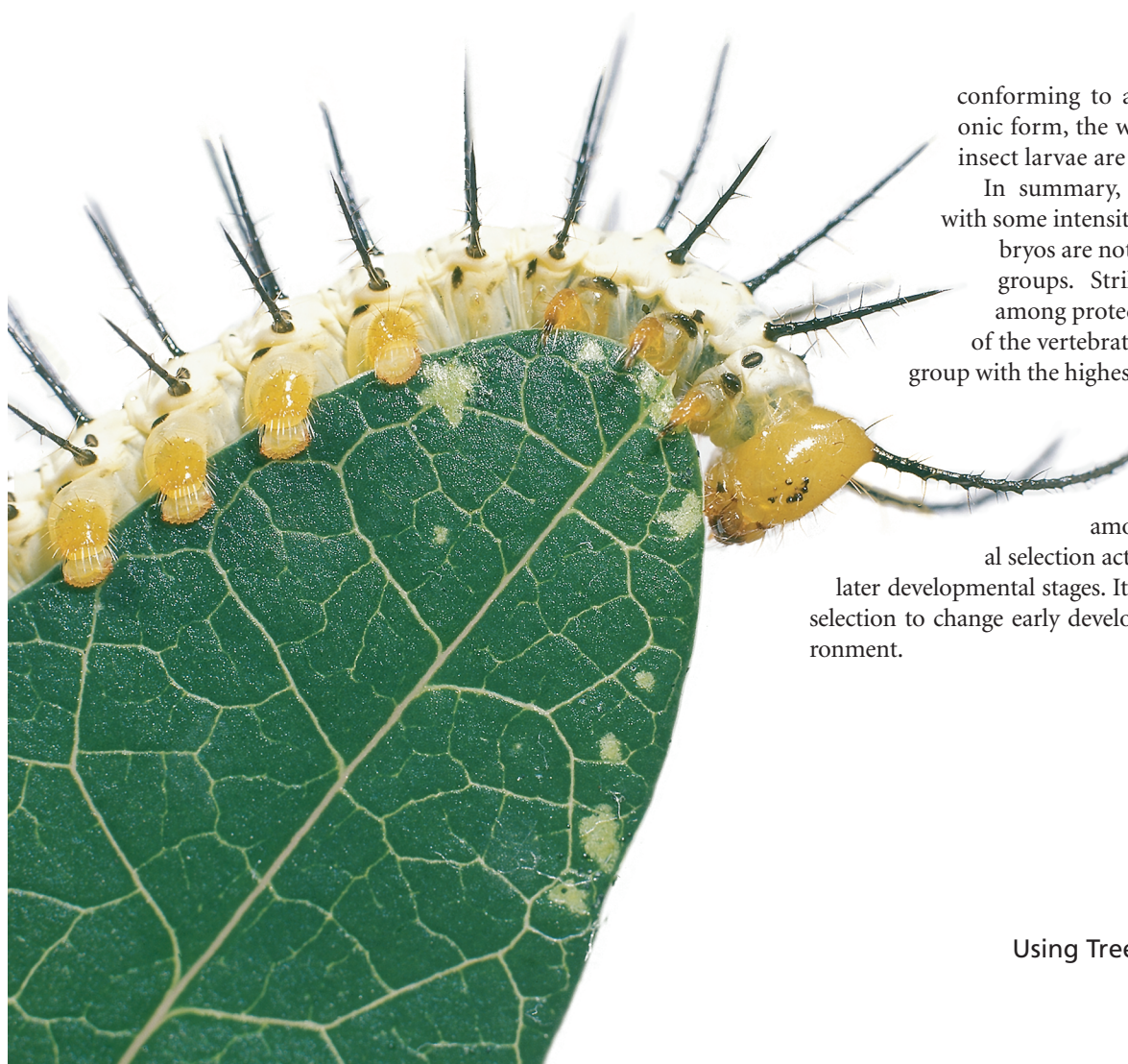


FIGURE 2.13B Trees and Development Evolutionary history leaves traces in development.



conforming to a general primordial embryonic form, the way vertebrates do, free-living insect larvae are wildly diverse.

In summary, when natural selection acts with some intensity on an embryonic form, embryos are not similar across heterogeneous groups. Striking similarity occurs only among protected embryos, especially those of the vertebrates, which make up the animal group with the highest degree of embryonic shelter.

Figure 2.13B illustrates the general principles of the Darwinian explanation of similarity among protected embryos. Natural selection acts to differentiate the species at later developmental stages. It just happens that there is less selection to change early development arising from the environment. ♦

THE COMPARATIVE METHOD

2.14 The comparative method uses the pattern of adaptation among species and their environments to infer the evolutionary causes of particular adaptations

The **comparative method** is one of the venerable parts of evolutionary biology. Indeed, it is such an obvious biological idea that ancient Greek scientists, such as Aristotle, often used it, despite the lack of scientific foundations for it in Greek science. Closely allied to the comparative method is the idea of **adaptation**. Adaptations are the products of natural selection, while adaptation is the response to the process of natural selection. Normally these two meanings of the term *adaptation* are quite close, but sometimes they are different.

Nothing is more natural than explaining the features of organisms as adaptations produced by natural selection. The wings of flying animals are adaptations that permit efficient flight. The roots of plants are adaptations that extract moisture

from the ground. The sticky surfaces of pathogens enable these organisms to bind to the tissues of their hosts. There is really no limit to our ability to invent stories of this kind, whether they are right or wrong.

The problem is that it is not obvious how to separate correct Darwinian explanations from incorrect ones. For example, it might be supposed that six legs are adaptations to insect life, which explains why almost all adult insects have six legs instead of two, four, or ten. Then the eight legs of spiders could be explained as particularly well suited to the spider way of life. But are these really valid explanations? Can every feature of life be explained well by the comparative method?



FIGURE 2.14A Wings and Related Structures Used in Flight and Gliding



Take coughing as an example. It is easy to speculate that coughing is an adaptation produced by natural selection on humans that enables us to clear our throats and lungs of debris when food has entered our respiratory tract. We cough to get the food out. But we cough even more when we have viral and other respiratory tract infections; and some of this coughing is “dry hacking,” which produces very little fluid or mucus. Some biologists have suggested that behavior such as coughing may be produced by microbes to help them spread to new hosts. Or it could be that we are attempting to remove microbes from our respiratory tract, especially our lungs, to forestall suffocation. It is not our concern, right now, to decide between these explanations for coughing. Both could be right. (We discuss this type of problem further in Chapter 22.) But they illustrate the problem that there may be more than one way to use the concept of natural selection to generate a reasonable explanation for an organismal feature.

The tool that biologists have tried to use in resolving this problem is the comparative method. With the comparative

method, as it was traditionally employed, biologists sought to associate particular environments with both natural selection and adaptations. To use a fairly obvious example, a biologist might note that animals that fly typically have morphological structures that produce aerodynamic lift forces. This is true of bird and bat wings. It is also true of insect wings, flying squirrel fur, and the highly modified fins of flying fish. Even some plant seeds have structures that supply aerodynamic lift. All of the structures shown in Figure 2.14A are associated with flight.

To finish off a traditional comparative analysis, a biologist might then point to moles, flightless insects, plants that produce immobile seeds, and other nonflying species, noting that these species do not have structures like wings. This observation would be offered as comparative evidence that wings are indeed adaptations for flight in species whose way of life depends on such locomotion.

But what about the exceptions? Some birds, like ostriches and penguins, have wings but do not fly (see box). Perhaps wings are used for things other than flight. For example, many birds and insects use wings as part of their courtship, the right motion being required to arouse the opposite sex. Some male insects even use their wings to produce a humming sound during mating. In these cases, is the wing still “for” flight? ♦

Why Does the Ostrich Still Have Wings?

One solution to the problem of why ostriches still have wings is to suppose that the development of birds tends to lead to the growth of wings. Originally, wings might have evolved as an adaptation for flight. Or they might already have existed for other reasons, such as selection for body covering, and then later were selected for use in flight. Either way, we might suppose that the common ancestor of birds evolved wings that were efficient for flight, so that almost all members of the bird, or avian, group used wings for flight. Now suppose that some birds became so large that they couldn't fly anymore. Suppose that they lived in dense jungles where flight was not efficient. They might still keep their wings, possibly much smaller than before. In other words, wings might be vestiges of earlier evolution.

There are three ways in which evolutionary history can account for wings in flightless animals:

1. The wings could be used for something other than flight. Courtship has already been mentioned as an alternative use for

wings, a use that would be important for reproduction. This use might have been established before the loss of flight.

2. Developmental changes that would eliminate wings might have detrimental secondary effects, such as bad leg development. In other words, wings aren't useful anymore, but getting rid of them creates other problems.
3. Having wings is just irrelevant to natural selection, so they are kept for no functional reason. This type of evolution is discussed more in Chapter 3.

Whichever pattern explains the wings of the ostrich, note that all of these hypotheses hinge on the interaction between history and selection in the comparative biology of adaptations. History can provide a resolution. Our next interest is how historical information can be efficiently and objectively incorporated in comparisons of species.

2.15 Evolutionary trees can be used to test hypotheses of adaptation objectively

The comparative method can be used objectively to test hypotheses of adaptation. The key is to employ evolutionary trees. Good evolutionary trees define the biological history of a taxonomic group. From these trees we can easily see how history makes the adaptations of different species depend on the derivation of these species from common ancestors.

Consider Figure 2.15A. If we have four species of a particular type, say four primitive birds, they could all have evolved wings for flight independently. This first possibility is shown in the tree to the left in Figure 2.15A. Or, the four bird species could all have descended from an ancestral bird species that had already evolved flight. This second possibility is shown in the tree on the right in Figure 2.15A. In the first case, winged flight evolves four times. In the second case, winged flight evolves only once. Evidently the case where flight evolves once is more parsimonious. But that is not our concern here.

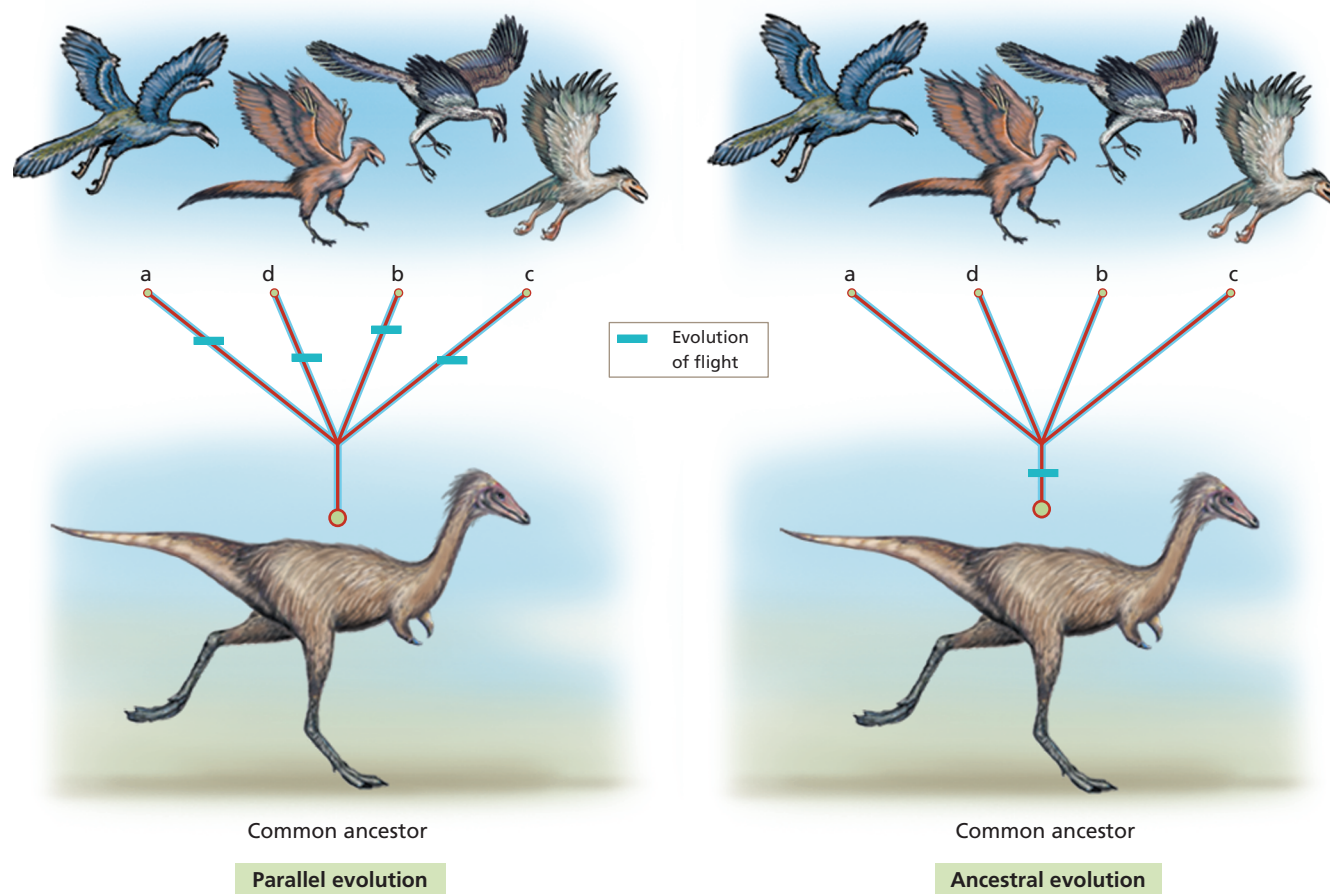


FIGURE 2.15A Trees and Adaptation

When these evolutionary tree patterns are used comparatively, the correct choice of tree is very important. For example, if the ancestral species changed its ecology from ground dwelling to tree dwelling, then its evolution of wings for flight might be explained by living in trees. On the other hand, if the ancestral species moved into trees but did *not* evolve flight, with winged flight evolving in the four descendant species, then it would be less reasonable to suppose that winged flight evolved because of tree dwelling.

The ideal pattern for comparative inferences is that of Figure 2.15B. In Figure 2.15B, an adaptation (the purple bar) evolves multiple times. And in most of the cases when it evolves, it follows a well-defined ecological change (the turquoise bar).

In an evolutionary tree like that of Figure 2.15B, we have several types of important information:

- *Evolutionary relationships* We have the actual evolutionary relationships of the species. That is, we know the correct evolutionary tree.
- *Ecological events* We also know the major ecological events in the history of these species.
- *Timing of adaptations* And finally we know when the species involved actually evolved their particular adaptations.

Under conditions like these, we can make legitimate comparative inferences. We can even get an objective feeling for the validity of our inference, from the number of times an evolutionary transition occurs independently. The more times the same evolutionary transition occurs in response to a particular ecological transition, the more confidence we have in our conclusions. ♦

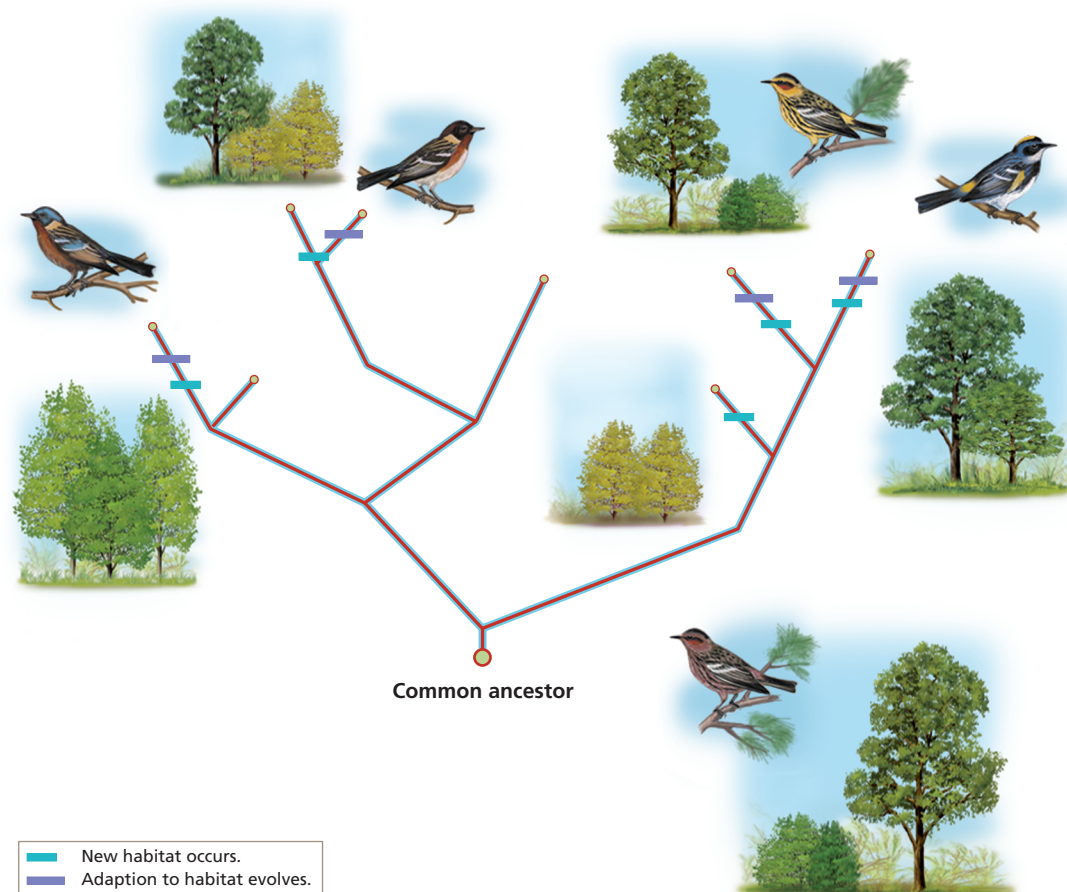


FIGURE 2.15B Repeated Adaptation to a New Habitat

2.16 Homology: When similar features among related species are inherited from their common ancestor

One of the most important patterns in evolutionary history is **homology**. Homology occurs when a structure present in an ancestral species is retained in descendant species, possibly with considerable evolutionary modification.

The qualitative pattern of homologous evolution is shown in Figure 2.16A. The ancestral species has a rib bone, call it A. The particular form of the rib bone in the ancestor is A1. In the species that descend from the common ancestor, A has been modified, taking on specific forms A2, A3, and A4. In one species, the structure has been completely lost. But this loss does not affect the homology involving the same structure in the other species. A homology may be involved in the evolution of a group of related species even if the structure is entirely lost in a few cases, although the species that lost the structure are not described as possessing the homology.

Figure 2.16B shows a well-known case of homology, the vertebrate forelimb. We humans experience this homology by having arms. Other vertebrates have fins and wings, but these structures are still homologous to our arms. There are many kinds of evidence for homology in a case like this. The best kind of evidence is illustrated by vertebrate fossils. Vertebrate bones fossilize well, so there is a good fossil record for the last 500 million years of vertebrate evolution. It is not difficult to follow the evolutionary expansion and shrinkage of particular bones, including the bones of the forelimb, in each of the vertebrate lineages. This information has left biologists confi-

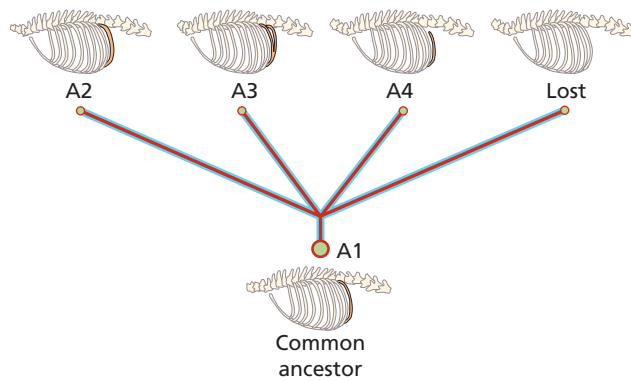


FIGURE 2.16A Evolution of Homologous Structures in the Descendants of a Common Ancestor

dent that the different vertebrate forelimbs all derive evolutionarily from the forelimbs of ancestral species.

Another type of evidence for homology comes from the idiosyncratic details of evolutionary history. These are the telltale clues that biologists use when they don't know as much about fossil history as we do with vertebrates. Homologies among organs that do not readily fossilize are usually inferred from the relative positions of structures. The vertebrate heart, for example, varies widely in its gross structure (Figure 2.16C). Some contemporary vertebrate hearts

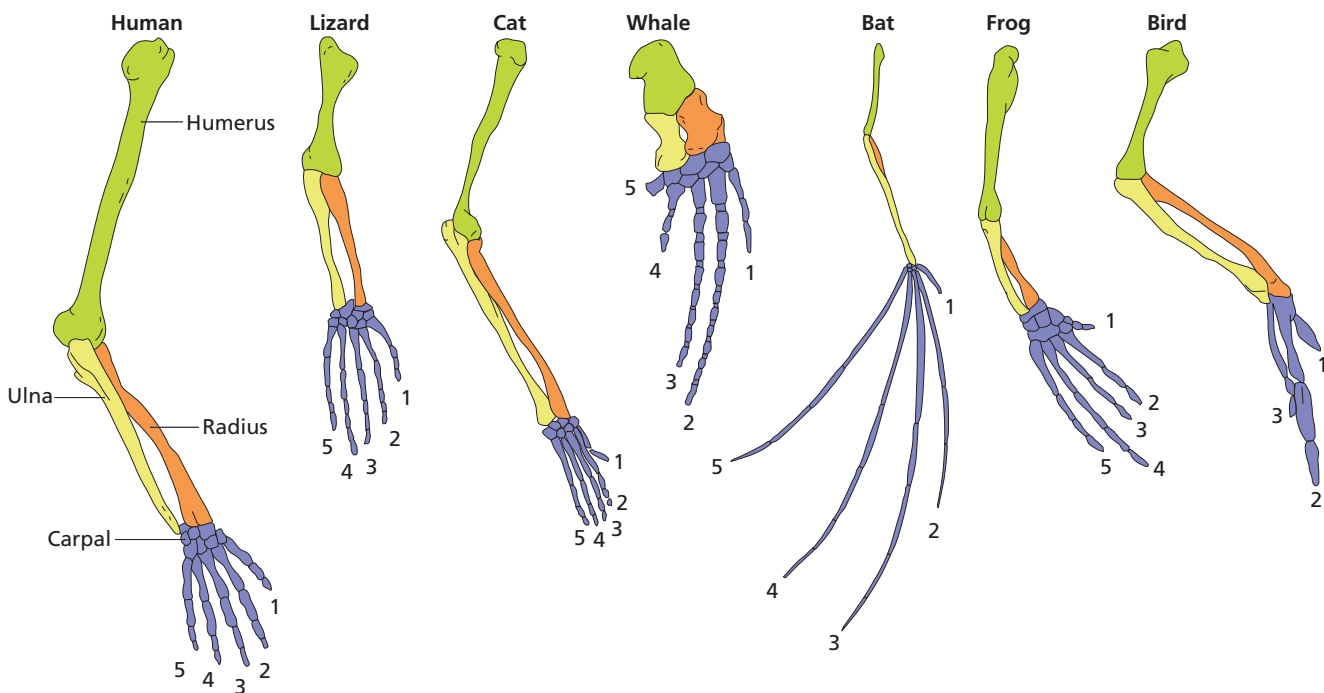


FIGURE 2.16B The skeletal structures of forelimbs in various vertebrate animals show the homologies among bones.

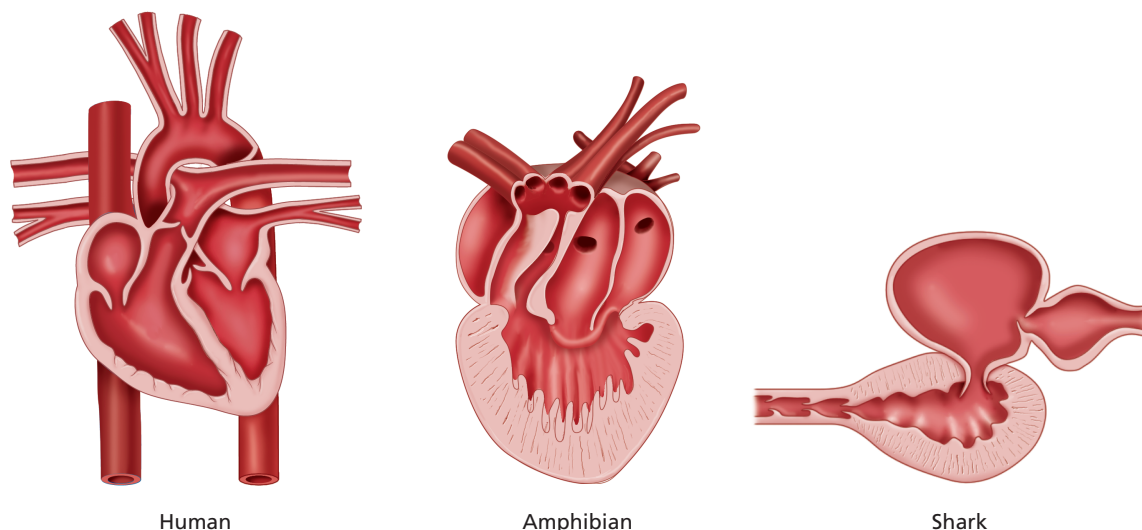


FIGURE 2.16C The Hearts of Different Vertebrate Species: Human, Amphibian, and Shark

have only one ventricle, the large pumping structure, while others have two ventricles. From the similar connections of ventricles to the heart's auricles and the arteries that lead from the heart, it is inferred that all vertebrate ventricles are homologous structures. Similar inferences are made about the components of the vertebrate brain—the medulla oblongata, the cerebellum, and the cortex—although fossil skulls sometimes give additional information. To revert to the forelimb example, vertebrate forelimbs usually have three main bones, called humerus, radius, and ulna. One humerus bone supports the first, proximal, part of the forelimb; but two bones, the radius and the ulna, support the second. This structural pattern serves as a clue that enables us to find the structural parallels between the vertebrate bones. Other cases are harder, but this general principle can be extended even as far as structural patterns of enzyme evolution.

An interesting variation on the homology concept is **serial homology**. Serial homology arises when a species has repeated structural features. When a common ancestral species has relatively simple repetitions of the same structural elements, it may be possible to detect the evolutionary divergence of individual segments in the descendant species.

The best-known example of serial homology is the structural evolution of the arthropod body plan, shown in Figure 2.16D. It is generally agreed that the ancestral arthropods had repeated segments, each bearing similar jointed limbs, like a centipede does today. In the descendant arthropod species, these segments diverged evolutionarily, producing antennae, jaws, other feeding structures, claws, walking legs, wings, swimmerets, and so on. These structures are homologous to each other because they are modifications of a common structure that was repeated serially in the ancestral species. The next time you eat a whole lobster or crayfish, you might look at its limbs, noticing how they vary down the length of the body. ♦

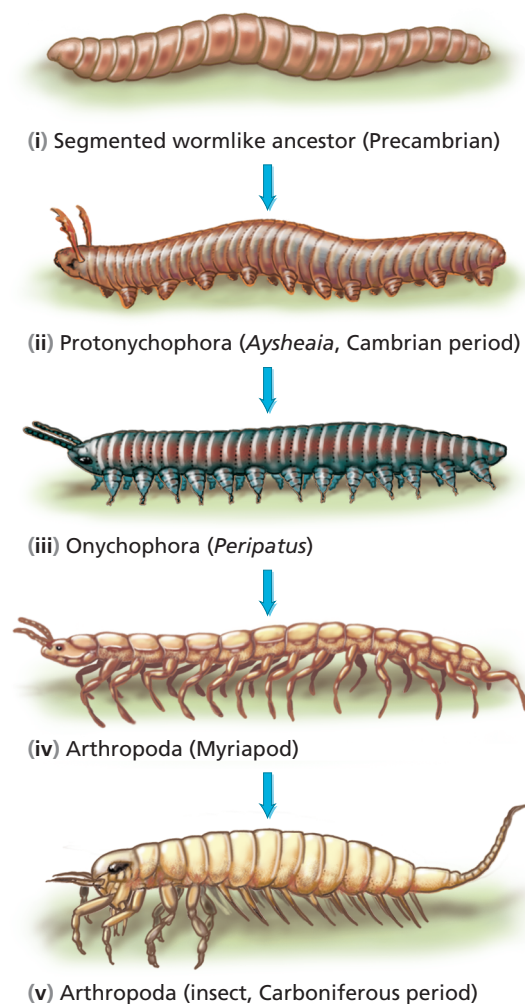


FIGURE 2.16D Homologous Segmentation of Various Arthropod Species

2.17 Homoplasy: Parallel patterns in evolution that are due to natural selection, not ancestry

The concept of **homoplasy** is the opposite of homology. With homology, derivation from a common ancestor is responsible for shared characteristics in a group of species. With homoplasy, similarity is produced in multiple evolutionary lineages by the action of natural selection specifically favoring the similar features. **Convergent evolution** is one case of homoplasy.

Bear in mind that evolution acts independently on each species, though of course they may have ecological interactions with each other. Nonetheless, homoplasy is fundamentally dif-

ferent from homology. Homoplasy can be thought of as the a product of natural selection. In the species of Figure 2.17A, there are a number of homoplasious patterns of evolution. The hallmark of homoplasy in evolutionary trees is the evolution of common features among species that have already evolved for some time *without* those common features. In other words, homoplasy produces similarity among species when homology cannot explain it.

Homoplasy supplies us with many of our most revealing examples of natural selection in action. An important historical

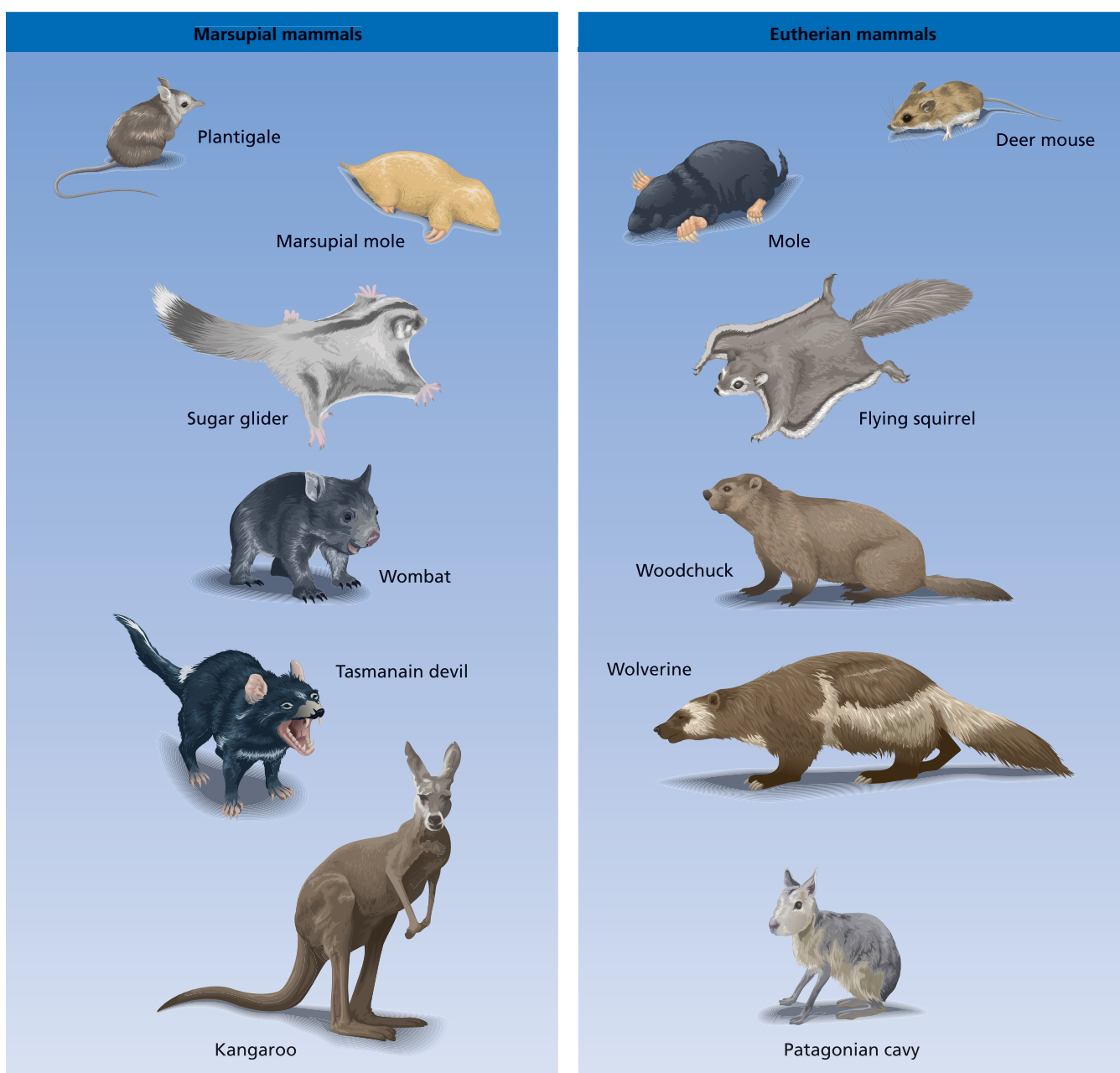


FIGURE 2.17A Homoplasious Adaptation in Eutherian and Marsupial Mammals

example is the evolution of industrial **melanism**, the dark coloration of many European butterflies and moths in the early twentieth century. A notable feature of this evolutionary event was that many species of butterflies and moths evolved darker coloration in parallel (Figure 2.17B). In the early nineteenth century, darker forms were little known in England. By the early twentieth century, darker forms were extremely common among many species found in the industrialized parts of England, where the surrounding forest had lost lichen from its bark.

Much of the habitat of the butterflies and moths became dark and sooty. For these insects to remain camouflaged, they had to evolve dark coloration. Many of them did so. We will discuss this case in detail in Chapter 4. But the homoplasious evolution of darker coloration in many butterfly and moth species that had been light-colored just two centuries ago told evolutionary biologists that natural selection, and not common ancestry, must have been involved. Homoplasy is very important in the comparative analysis of evolution by natural selection. ♦

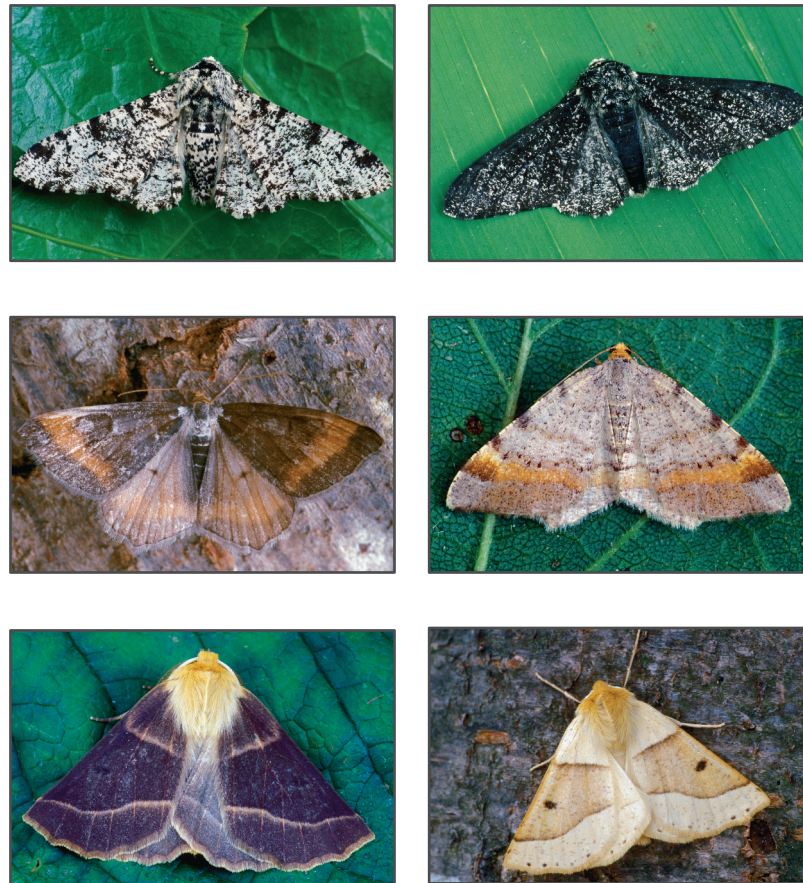


FIGURE 2.17B Dark Melanic Moths and Speckled Lighter Moths from Europe

SUMMARY

1. The evolutionary tree is one of the most important concepts in biology. With the evolutionary tree, we can conveniently represent evolutionary histories using diagrams that have many intuitive features. Evolutionary trees grow outward only, never doubling back. Just like real trees, they only rarely involve branches growing together. Extinctions are easily represented as truncated branches. Speciation is shown as forks, usually with two descendant species continuing onward, and thus upward.
2. Evolutionary trees are often constructed using the rule of maximum parsimony. Maximum parsimony is a rule that tells evolutionary biologists to prefer evolutionary histories with the fewest number of independent evolutionary events. Using parsimony, for example, a biologist does not suppose that fur independently evolved in each mammalian species. Instead, she assumes that the common ancestor of the mammalian species evolved fur, and it has since been retained by all the mammalian species that descend from their common ancestor.
3. The success of biological classification can be explained in relation to evolutionary history. Groups of organisms that share numerous attributes probably share common ancestors. Larger groups of organisms that share attributes are likely to have a relatively ancient common ancestor, compared to smaller groups that are similar to each other. Small, similar groups of species are likely to have had a recent common ancestor.
4. The geographical distribution of species indicates that species arise by local evolutionary processes, not by a global creation. Large, flying species are distributed throughout the world, because they can fly to distant areas once they have evolved in one region. But terrestrial animals have localized distributions that can be explained best in relation to local evolution.
5. In some groups, developmental patterns are conserved in protected larval or embryonic stages due to an absence of selection on them.
6. The comparative method contrasts species in order to understand adaptation. Recent applications of the comparative method have benefited from the use of evolutionary trees. Homology occurs when a structure evolves from a common ancestral feature, changing somewhat from one descendant species to another. Homoplasy occurs when similar characters evolve independently in separate species, homology not being involved.

REVIEW QUESTIONS

1. Are the fins of dolphins and sharks examples of homology or homoplasy?
2. Which evolved first, bacteria or fish?
3. Was the origin of eukaryotes an example of evolutionary tree branches terminating or fusing?
4. The terrestrial fauna of Australia illustrate which principles of biogeography?
5. Why are bats unusual among the mammals of Australia?
6. Why is Darwin's theory of evolution compatible with the system of biological classification?
7. Why does the principle of maximum parsimony help us to choose between evolutionary trees?
8. Extinction corresponds to what type of change in the evolutionary tree?
9. Does adaptation foster homology or homoplasy?

KEY TERMS

adaptation	conjugation	fossil record	paleontology
anastomosis	convergent evolution	halophile	prokaryote
Archaea	creationism	homology	serial homology
Bacteria	domain	homoplasy	speciation
biogeography	endosymbiosis	kingdom	thermophile
biological classification	Eukarya	maximum parsimony	transduction
common ancestor	eukaryote	melanism	transformation
comparative method	evolutionary tree	methanogen	

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