

Fossil of a dragonfly (*Cordulagomphus tuberculatus*) from the Cretaceous period, discovered in Ceara Province, Brazil.

## STUDY PLAN

### 22.1 The Fossil Record

Fossils form when organisms are buried by sediments or preserved in oxygen-poor environments

The fossil record provides an incomplete portrait of life in the past

Scientists assign relative and absolute dates to geological strata and the fossils they contain

Fossils provide abundant information about life in the past

### 22.2 Earth History, Biogeography, and Convergent Evolution

Geological processes have often changed Earth's physical environment

Historical biogeography explains the broad geographical distributions of organisms

Convergent evolution produces similar adaptations in distantly related organisms

### 22.3 Interpreting Evolutionary Lineages

Modern horses are living representatives of a once-diverse lineage

Evolutionary biologists debate the mode and tempo of macroevolution

### 22.4 Macroevolutionary Trends in Morphology

The body size of organisms has generally increased over time

Morphological complexity has also generally increased over time

Several phenomena trigger the evolution of morphological novelties

### 22.5 Macroevolutionary Trends in Biodiversity

Adaptive radiations are clusters of related species with diverse ecological adaptations

Extinctions have been common in the history of life

Biodiversity has increased repeatedly over evolutionary history

### 22.6 Evolutionary Developmental Biology

Most animals share the same genetic tool kit that regulates their development

Evolutionary changes in developmental switches may account for much evolutionary change

Courtesy Lowcountry Geologic



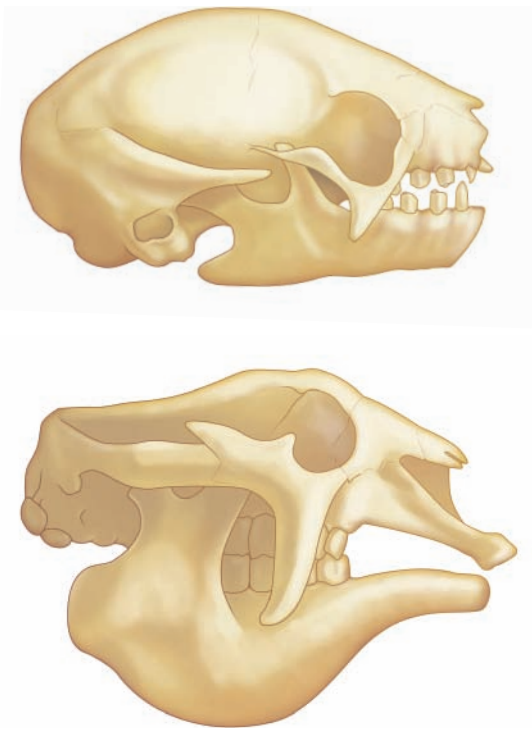
## 22 Paleobiology and Macroevolution

### WHY IT MATTERS

In January 1796, Georges Cuvier surprised his audience at the National Institute of Sciences and Arts in Paris by suggesting that fossils were the remains of species that no longer lived on Earth. Natural historians had long recognized the organic origin of fossils, but they did not believe that any creature could become extinct. They thought that the species preserved as fossils still lived in remote and inaccessible places.

Cuvier realized that he could not use the abundant fossils of small marine animals to demonstrate the reality of extinction: these species might still live in the deep sea or other unexplored regions. However, he reasoned that the world was already so well explored that scientists were unlikely to discover any new large terrestrial mammals. Thus, if he could show that fossilized mammals were different from living mammals, he could logically conclude that the fossilized species were truly extinct.

Now credited as the founder of comparative morphology, Cuvier thought that animals were essentially like machines. Each anatomical structure was a crucial part of a perfectly integrated whole. For example, a carnivore requires limbs to pursue prey, claws to catch it, teeth



**Figure 22.1**  
Comparing living organisms to fossils. Georges Cuvier compared the skull of a living sloth (top) to a fossilized skull from Paraguay (bottom). The fossilized skull has been reduced in size to facilitate the comparison.

to tear its flesh, and internal organs to digest meat. Thus, from the study of a few critical parts, a knowledgeable anatomist could make reasonable inferences about an animal's overall structure.

Cuvier is also recognized as the founder of paleobiology because he used the anatomy of living species to analyze fossils, which are rarely complete. Paleobiologists often use their knowledge of comparative morphology to make inferences about missing parts. Thus, when asked to analyze a large fossilized skull from Paraguay, Cuvier compared it to specimens in the museum and declared it to be a sloth (**Figure 22.1**). But living sloths are small, whereas this specimen was gigantic, so Cuvier concluded that it was extinct. If such a large species were still living, naturalists would surely have discovered it while exploring South America.

Cuvier studied fossils of other large mammals, especially elephants and rhinoceroses. In every case, he demonstrated that fossilized species were anatomically different from living species. And because no one had seen living examples of the fossilized species, Cuvier concluded that they must be extinct. In 1812, he produced a multivolume treatise in which he acknowledged Earth's great age and documented the appearance and disappearance of species over time. He even noted that fossils lying near the ground surface more closely resembled living species than did

those that were deeply buried. Despite these extraordinary insights, Cuvier never embraced the concept of evolution. If all anatomical features of an animal's body were perfectly integrated, as he believed, how could any part change without upsetting that delicate functional balance?

Cuvier was an early student of macroevolution, the large-scale changes in morphology and diversity that characterize the 3.8-billion-year history of life. Macroevolution has occurred over so vast a span of time and space that the evidence for it is fundamentally different from that for microevolution and speciation. In this chapter we consider what paleobiology and the new field of evolutionary developmental biology tell us about macroevolutionary patterns.

## 22.1 The Fossil Record

Paleobiologists discover, describe, and name new fossil species and analyze the morphology and ecology of extinct organisms. Because fossils provide physical evidence of life in the past, they are our primary sources of data about the evolutionary history of many organisms.

### Fossils Form When Organisms Are Buried by Sediments or Preserved in Oxygen-Poor Environments

Most fossils form in sedimentary rocks. Rain and runoff constantly erode the land, carrying fine particles of rock and soil downstream to a swamp, a lake, or the sea. Particles settle to the bottom as sediments, forming successive layers over millions of years. The weight of newer sediments compresses the older layers beneath them into a solid-matter matrix: sand into sandstone and silt or mud into shale. Fossils form within the layers when the remains of organisms are buried in the accumulating sediments.

The process of fossilization is a race against time because the soft remains of organisms are quickly consumed by scavengers or decomposed by microorganisms. Thus, fossils usually preserve the details of hard structures, such as the bones, teeth, and shells of animals and the wood, leaves, and pollen of plants. During fossilization, dissolved minerals replace some parts molecule by molecule, leaving a fossil made of stone (**Figure 22.2a**); other fossils form as molds, casts, or impressions in material that is later transformed into solid rock (**Figure 22.2b**).

In some environments, the near absence of oxygen prevents decomposition, and even soft-bodied organisms are preserved. Some insects, plants, and tiny lizards and frogs are embedded in amber, the fossilized resin of coniferous trees (**Figure 22.2c**). Other organisms are preserved in glacial ice, coal, tar pits, or the highly acidic water of peat bogs (**Figure**

22.d). Sometimes organisms are so well preserved that researchers can examine their internal anatomy, cell structure, and food in their digestive tracts. Biologists have even analyzed samples of DNA from a 40-million-year-old magnolia leaf.

a. Petrified wood



George H. Huey/Corbis

b. An invertebrate



Neville Pledge/South Australian Museum

c. Insects in amber



Jack Kovulsa/Photo Researchers, Inc.

d. Mammoth in permafrost



Novosti/Photo Researchers, Inc.

**Figure 22.2**

Fossils. (a) Petrified wood, from the Petrified Forest National Park in Arizona, formed when minerals replaced the wood of dead trees molecule by molecule. (b) The soft tissues of an invertebrate (genus *Dickinsonia*) from the Proterozoic era were preserved as an impression in very fine sediments. (c) This 30-million-year-old fly (above) and wasp were trapped in the oozing resin of a coniferous tree and are now encased in amber. (d) A frozen baby mammoth (genus *Mammonteus*) that lived about 40,000 years ago was discovered embedded in Siberian permafrost in 1989.

## The Fossil Record Provides an Incomplete Portrait of Life in the Past

The 300,000 described fossil species represent less than 1% of all the species that have ever lived. Several factors make the fossil record incomplete. First, soft-bodied organisms do not fossilize as easily as species with hard body parts. Moreover, we are unlikely to find the fossilized remains of species that were rare and locally distributed. Finally, fossils rarely form in habitats where sediments do not accumulate, such as mountain forests. The most common fossils are those of hard-bodied, widespread, and abundant organisms that lived in swamps or shallow seas, where sedimentation is ongoing.

Most fossils are composed of stone, but they don't last forever. Many are deformed by pressure from overlying rocks or destroyed by geological disturbances like volcanic eruptions and earthquakes. Once they are exposed on Earth's surface, where scientists are most likely to find them, rain and wind cause them to erode. Because the effects of these destructive processes are additive, old fossils are much less common than those formed more recently.

## Scientists Assign Relative and Absolute Dates to Geological Strata and the Fossils They Contain

The sediments found in any one place form distinctive strata (layers) that differ in color, mineral composition, particle size, and thickness (Figure 22.3). If they have not been disturbed, the strata are arranged in the order in which they formed, with the youngest layers on top. However, strata are sometimes uplifted, warped, or even inverted by geological processes.

Geologists of the early nineteenth century deduced that the fossils discovered in a particular sedimentary stratum, no matter where it is found, represent organisms that lived and died at roughly the same time in the past. Because each stratum formed at a specific time, the sequence of fossils in the lowest (oldest) to the highest (newest) strata reveals their *relative ages*. Geologists used the sequence of strata and their distinctive fossil assemblages to establish the geological time scale (Table 22.1).

Although the geological time scale provides a relative dating system for sedimentary



David Noble/PPG/Getty Images

**Figure 22.3**

Geological strata in the Grand Canyon. Millions of years of sedimentation in an old ocean basin produced layers of rock that differ in color and particle size. Tectonic forces later lifted the land above sea level, and the flow of the Colorado River carved this natural wonder.

**Table 22.1** The Geological Time Scale and Major Evolutionary Events

Eons (Duration drawn to scale)		Eons		Era		Period	Epoch	Millions of Years Ago	Major Evolutionary Events				
Phanerozoic	Cenozoic	Phanerozoic	Cenozoic	Cenozoic	Quaternary	Holocene	0.01	Origin of humans; major glaciations					
	Mesozoic					Pleistocene							
	Paleozoic					Pliocene							
Proterozoic	Proterozoic	Phanerozoic	Cenozoic	Cenozoic	Tertiary	Miocene	5.2	Angiosperms and mammals further diversify and dominate terrestrial habitats					
						Oligocene	23						
						Eocene	33.4						
					Cretaceous	Mesozoic	Mesozoic	Mesozoic	Mesozoic	Paleocene	55	Grasslands and deciduous woodlands spread; modern birds and mammals diversify; continents approach current positions	
											65		
					Triassic	Mesozoic	Mesozoic	Mesozoic	Mesozoic	Jurassic	144	Many lineages diversify: angiosperms, insects, marine invertebrates, fishes, dinosaurs; asteroid impact causes mass extinction at end of period, eliminating dinosaurs and many other groups	
											206		
											251		
													Predatory fishes and reptiles dominate oceans; gymnosperms dominate terrestrial habitats; radiation of dinosaurs; origin of mammals; Pangaea starts to break up; mass extinction at end of period



## Figure 22.4 Research Method

### Radiometric Dating

#### PROTOCOL:

1. Knowing the approximate age of a rock or fossil, select a radioisotope that has an appropriate half-life. Because different radioisotopes have half-lives ranging from seconds to billions of years, it is usually possible to choose one that brackets the estimated age of the sample under study. For example, if you think that your fossil is more than 10 million years old, you might use uranium-235. The half-life of  $^{235}\text{U}$ , which decays into the lead isotope  $^{207}\text{Pb}$ , is about 700 million years. Or if you think that your fossil is less than 70,000 years old, you might select carbon-14. The half-life of  $^{14}\text{C}$ , which decays into the nitrogen isotope  $^{14}\text{N}$ , is 5730 years.

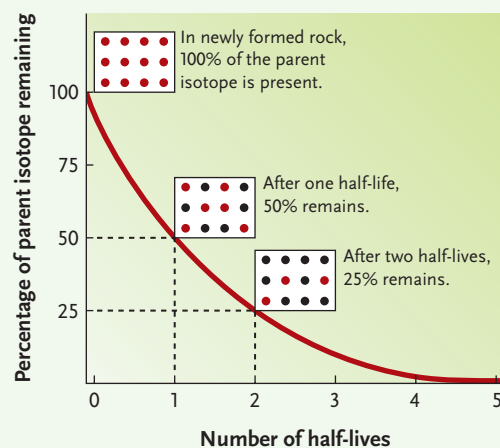
**PURPOSE:** Radiometric dating allows researchers to estimate the absolute age of a rock sample or fossil.

#### Radioisotopes Commonly Used in Radiometric Dating

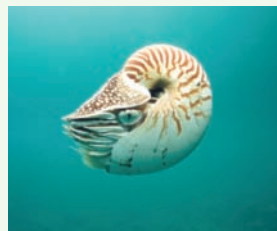
Radioisotope (Unstable)	More Stable Breakdown Product	Half-Life (Years)	Useful Range (Years)
Samarium-147	Neodymium-143	106 billion	>100 million
Rubidium-87	Strontium-87	48 billion	>10 million
Thorium-232	Lead-208	14 billion	>10 million
Uranium-238	Lead-206	4.5 billion	>10 million
Uranium-235	Lead-207	700 million	>10 million
Potassium-40	Argon-40	1.25 billion	>100,000
Carbon-14	Nitrogen-14	5730	<70,000

2. Prepare a sample of the material and measure the quantities of the parent radioisotope and its more stable breakdown product.

**INTERPRETING THE RESULTS:** Compare the relative quantities of the parent radioisotope and its breakdown product (or some other stable isotope) to determine what percentage of the original parent radioisotope remains in the sample. Then use a graph of radioactive decay for that isotope to determine how many half-lives have passed since the sample formed.



Knowing the number of half-lives that have passed allows you to estimate the age of the sample.



A living mollusk absorbed trace amounts of  $^{14}\text{C}$ , a rare radioisotope of carbon, and large amounts of  $^{12}\text{C}$ , which is the more stable and common isotope of carbon.



When the mollusk died, it was buried in sand and fossilized. From the moment of its death, the ratio of  $^{14}\text{C}$  to  $^{12}\text{C}$  began to decline through radioactive decay. Because the half-life of  $^{14}\text{C}$  is 5730 years, half of the original  $^{14}\text{C}$  was eliminated from the fossil in 5730 years and half of what remained was eliminated in another 5730 years.



After the fossil was discovered, a scientist determined that its  $^{14}\text{C}$  to  $^{12}\text{C}$  ratio was one-eighth of the  $^{14}\text{C}$  to  $^{12}\text{C}$  ratio in living organisms. Thus, radioactive decay had proceeded for three half-lives—or about 17,000 years—since the mollusk's death.

strata, it does not tell us how old the rocks and fossils actually are. But many rocks contain radioisotopes, which, from the moment they form, begin to break down into other, more stable elements. The breakdown proceeds at a steady rate that is unaffected by chemical reactions or environmental conditions such as temperature or pressure. Using a technique called **radiometric dating**, scientists can estimate the age of a rock by noting how much of an unstable “parent” isotope has decayed to another form. By measuring the relative amounts of the parent radioisotope and its breakdown products and comparing this ratio with the isotope’s **half-life**—the time it takes for half of a given

amount of radioisotope to decay—researchers can estimate the *absolute age* of the rock (**Figure 22.4**). Table 22.1 presents these age estimates along with the major geological and evolutionary events of each period.

Radiometric dating works best with volcanic rocks, which form when lava cools and solidifies. But most fossils are found in sedimentary rocks. To date sedimentary fossils, scientists determine the age of volcanic rocks from the same strata. Using this method, investigators have linked fossils to deposits that are hundreds of millions of years old.

Fossils that still contain organic matter, such as the remains of bones or wood, can be dated directly by mea-

asuring their content of the radioactive carbon isotope  $^{14}\text{C}$ , which decays to  $^{14}\text{N}$ . Living organisms absorb traces of  $^{14}\text{C}$  and large quantities of  $^{12}\text{C}$ , a stable carbon isotope, from the environment and incorporate them into biological molecules. As long as an organism is still alive, its  $^{14}\text{C}$  content remains constant because any  $^{14}\text{C}$  that decays is replaced by the uptake of other  $^{14}\text{C}$  atoms. But as soon as the organism dies, no further replacement occurs and  $^{14}\text{C}$  begins its steady radioactive decay. Scientists use the ratio of  $^{14}\text{C}$  to  $^{12}\text{C}$  present in a fossil to determine its age, as explained in Figure 22.4.

To develop a feeling for geological time, imagine the 4.5-billion-year history of Earth scaled onto an annual calendar; each day represents a little over 12 million years. The planet was formed on January 1. Animal life originated in mid-November, dinosaurs lived between December 14 and December 26, and the primate ancestors of modern humans appeared during the last 4 hours of December 31.

### Fossils Provide Abundant Information about Life in the Past

Imperfect as it is, the fossil record provides our only direct information about life in the past. Fossilized skeletons, shells, stems, leaves, and flowers tell us about the size and appearance of ancient animals and plants. The fossil record also allows scientists to see how structures were modified as they became adapted for specialized uses (see Figure 19.3). Moreover, fossils chronicle the proliferation and extinction of evolutionary lineages and provide data on their past geographical distributions.

Fossils can also provide indirect data about behavior, physiology, and ecology. For example, the fossilized footprints of some dinosaurs suggest that adults surrounded their young when the group moved, perhaps to protect them from predators. Complex scrolls of bone in the nasal passages of early mammals suggest that they had a well-developed sense of smell, and fossilized teeth and dung provide data about the diets of extinct animals. The study of fossilized pollen allows paleobiologists to reconstruct the vegetation and climate of ancient sites. The changing arrays of fossils that document biological evolution partly reflect large-scale shifts in Earth's physical environments, a topic that we explore in the next section.

### STUDY BREAK

1. What biological materials are the most likely to fossilize?
2. Why does the fossil record provide an incomplete portrait of life in the past?
3. What sort of information can paleobiologists discern from the fossil record?

## 22.2 Earth History, Biogeography, and Convergent Evolution

Organisms interact constantly with their environments. Some of these interactions have caused fundamental changes in Earth's physical environment, such as the development of an oxidizing atmosphere (see Chapter 24). In this section we consider other aspects of Earth's history and their profound effects on living systems.

### Geological Processes Have Often Changed Earth's Physical Environment

Long-term shifts in geography and climate—as well as brief but catastrophic events—have significantly altered environments on Earth. Major geological and climatic shifts occur because the planet's crust is in motion.

According to the theory of **plate tectonics**, Earth's crust is broken into irregularly shaped plates of rock that float on its semisolid mantle (**Figure 22.5**). Currents in the mantle cause the plates—and the continents embedded in them—to move, a phenomenon called **continental drift**. About 250 million years ago, Earth's landmasses coalesced into a single supercontinent called Pangaea; continental drift later separated Pangaea into a northern continent, Laurasia, and a southern continent, Gondwana. Laurasia and Gondwana subsequently broke into the continents we know today (**Figure 22.6**).

The drifting continents induced global changes in Earth's climate. For example, the movement of continents toward the poles encouraged the formation of glaciers, which caused temperature and rainfall to decrease worldwide. As a result of complex continental movements, Earth's average temperature has fluctuated widely. During one geologically recent cold spell (about 20,000 years ago), the northern polar ice cap extended into southern Indiana and Ohio.

Unpredictable events have also changed physical environments on Earth. Massive volcanic eruptions and asteroid impacts have occasionally altered the planet's atmosphere and climate drastically. These cataclysmic events have sometimes caused many forms of life to disappear over relatively short periods of geological time.

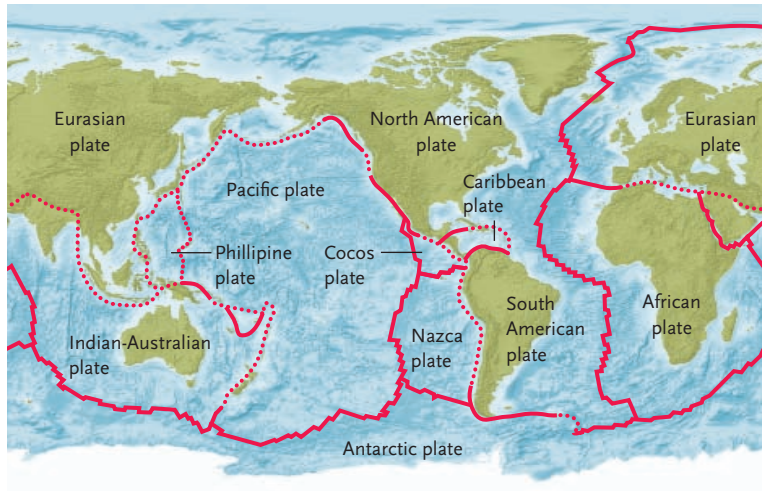
### Historical Biogeography Explains the Broad Geographical Distributions of Organisms

More than a century after Darwin published his observations, the theory of plate tectonics refocused attention on biogeography. Historical biogeographers try to explain how organisms acquired their geographical distributions over evolutionary time.

**Continuous and Disjunct Distributions.** Many species have a **continuous distribution**: they live in suitable habitats throughout a geographical area. For example, herring gulls (*Larus argentatus*) live along the coastlines of all northern continents. Continuous distributions usually require no special historical explanation.

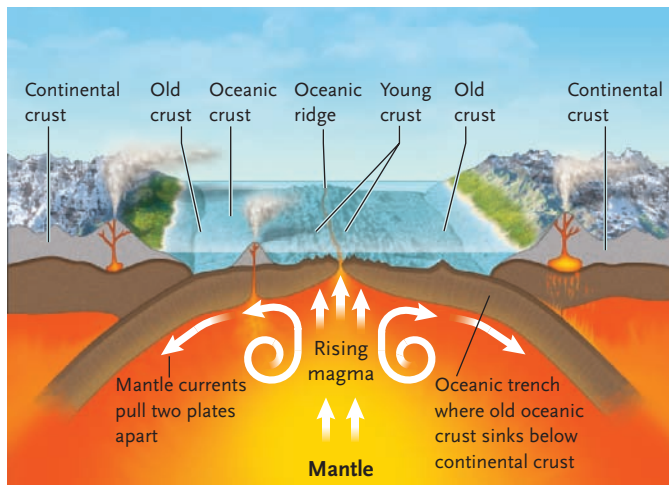
Other groups exhibit **disjunct distributions**, in which closely related species live in widely separated locations. For example, magnolia trees (*Magnolia* species)

**a. Earth's crustal plates**



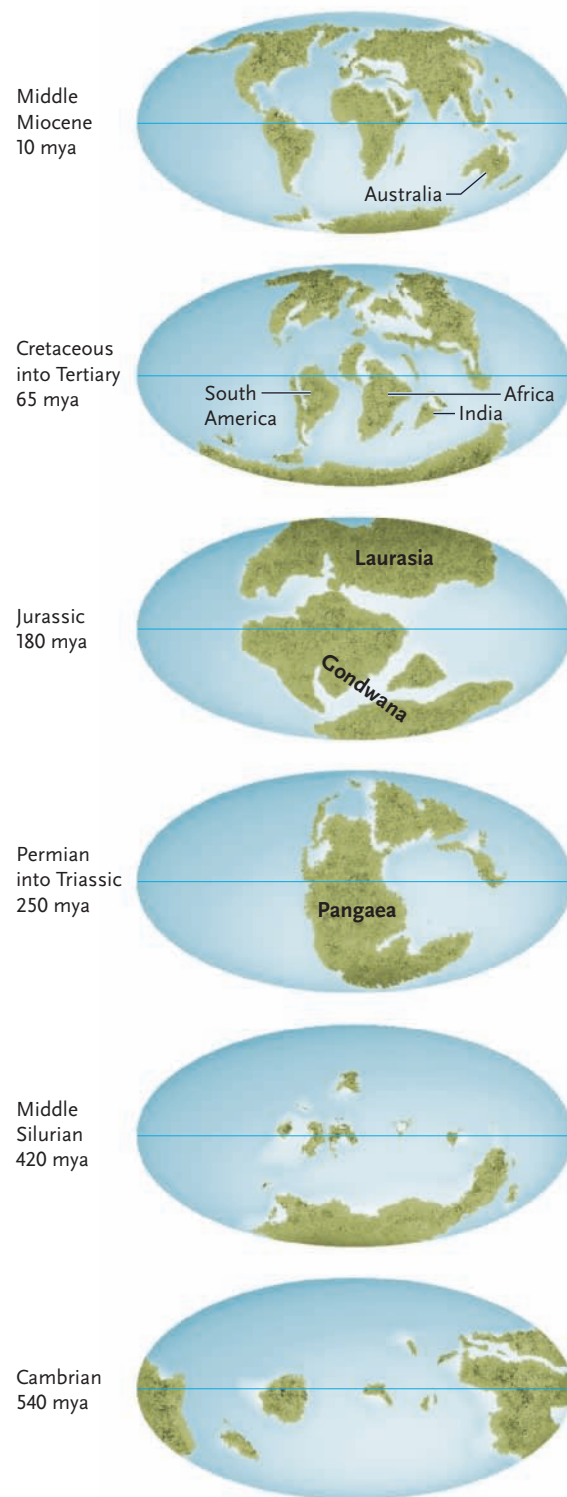
**KEY**  
 — Oceanic ridge    ..... Oceanic trench

**b. Model of plate tectonics**



**Figure 22.5**

**Plate tectonics. (a)** Earth's crust is broken into large, rigid plates. New crust is added at oceanic ridges, and old crust is recycled into the mantle at oceanic trenches. **(b)** Oceanic ridges form where pressure in the mantle forces magma (molten rock) through fissures in the sea floor. Mantle currents pull the plates apart on either side of the ridge, forcing the sea floor to move laterally away from the ridge. This phenomenon, seafloor spreading, is widening the Atlantic Ocean about 3 cm per year. Oceanic trenches form where plates collide. The heavier oceanic crust sinks below the lighter continental crust, and it is recycled into the mantle, a process called subduction. The highest mountain ranges (including the Rockies, Himalayas, Alps, and Andes) formed where subduction uplifted continental crust. Earthquakes and volcanoes are also common near trenches.



**Figure 22.6**

**History of long-term changes in the positions of continents.** Earth's many landmasses coalesced during the Permian period, forming the supercontinent Pangaea. About 180 million years ago (mya), Pangaea separated into Gondwana and Laurasia. Then Gondwana began to break apart. Africa and India pulled away first, opening the South Atlantic and Indian Oceans. Australia separated from Antarctica about 55 million years ago and slowly drifted northward. South America separated from Antarctica shortly thereafter. Laurasia remained nearly intact until 43 million years ago when North America and Greenland together separated from Europe and Asia. Movement of the continents also changed the shapes and the sizes of the oceans.



occur in parts of North, Central, and South America as well as in China and Southeast Asia, but nowhere in between.

Two phenomena—dispersal and vicariance—create disjunct distributions. **Dispersal** is the movement of organisms away from their place of origin; it can produce a disjunct distribution if a new population becomes established on the far side of a geographical barrier. **Vicariance** is the fragmentation of a continuous geographical distribution by external factors. Over the course of evolutionary history, dispersal and vicariance have together influenced the geographical distributions of organisms on a very grand scale (see *Focus on Research*).

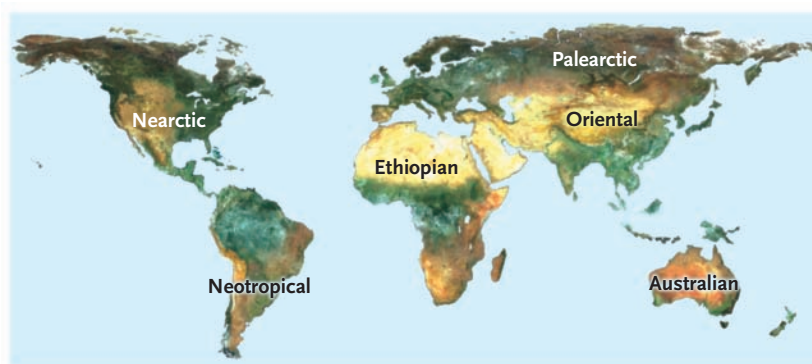
**Biogeographical Realms.** For species that were widespread in the Mesozoic era, Pangaea’s breakup was a powerful vicariant experience. The subsequent geographical isolation of continents fostered the evolution of distinctive regional **biotas** (all organisms living in a region). Alfred Russel Wallace used the biotas to define six **biogeographical realms**, which we still recognize today (**Figure 22.7**).

The Australian and Neotropical realms, which have been geographically isolated since the Mesozoic, contain many **endemic species** (those that occur nowhere else on Earth). The Australian realm, in particular, has had no complete land connection to any other continent for approximately 55 million years. As a result, Australia’s mammalian fauna (all the mammals living in the region) is unique, made up almost entirely of endemic marsupials. Few native placental mammals occur in Australia because the placental lineage arose elsewhere after Australia had become isolated.

The biotas of the Nearctic and Palearctic realms are, by contrast, fairly similar. North America and Eurasia were frequently connected by land bridges; eastern North America was attached to Western Europe until the breakup of Laurasia 43 million years ago, and northwestern North America had periodic contact with northeastern Asia over the Bering land bridge during much of the past 60 million years.

### Convergent Evolution Produces Similar Adaptations in Distantly Related Organisms

Distantly related species living in different biogeographical realms are sometimes very similar in appearance. For example, the overall form of cactuses in the Americas is almost identical to that of spurges in Africa (**Figure 22.8**). But these lineages arose independently long after those continents had separated; thus, cactuses and spurges did not inherit their similarities from a shared ancestor. Their overall resemblance is the product of **convergent evolution**, the evolution of similar adaptations in distantly related organisms that occupy similar environments.



**Figure 22.7**  
Wallace’s biogeographical realms. Each realm contains a distinctive biota.

Convergent evolution also creates similarities in distantly related animals that use the same mode of locomotion. Some marine fishes, birds, and mammals have torpedo-shaped bodies and appendages modified for swimming in strong ocean currents (**Figure 22.9**). Even entire faunas can develop convergent morphologies. For example, the marsupial mammals of Australia and placental mammals of North America—groups that arose long after the breakup of Pangaea—include many pairs of morphologically convergent species that also occupy similar habitats and feed on similar foods. To understand convergent evolution as well as most other macroevolutionary patterns, biologists must analyze the evolutionary history of individual lineages, a sometimes-controversial activity that we consider next.

### STUDY BREAK

1. How did the process of continental drift affect the geographical distributions of organisms?
2. Why do some distantly related species that live in different biogeographical realms sometimes resemble each other?

a. Cactus



Edward S. Rioss

b. Spurge



Edward S. Rioss

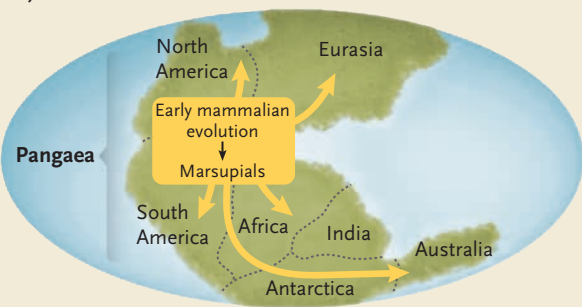
**Figure 22.8**

Convergent evolution in plants. (a) *Echinocereus* and other North American cactuses (family Cactaceae) are strikingly similar to (b) *Euphorbia* and other African spurges (family Euphorbiaceae). Convergent evolution adapted both groups to desert environments with thick, water-storing stems, spiny structures that discourage animals from feeding on them, CAM photosynthesis (see Section 9.4), and stomata that open only at night.

## FOCUS ON RESEARCH

### Basic Research: The Great American Interchange

#### a. Jurassic Period



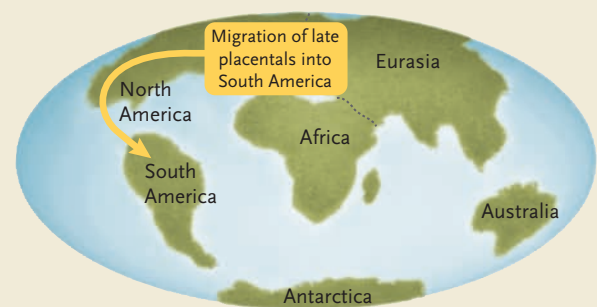
#### b. Cretaceous Period



#### c. Miocene Epoch



#### d. Pliocene Epoch



#### Figures a–d

Dispersal and vicariance changed the geographical distributions of marsupial and placental mammals.

Paleobiologists reconstruct the biogeographical history of a lineage by dating its fossils and mapping their geographical distributions at specific times in the past. The complex evolutionary history of mammals, especially in North and South America, illustrates the effects of dispersal and vicariance.

Mammals first arose in western Pangaea (now part of North America), where they diverged into several evolutionary lineages. The earliest marsupials (whose young complete development in a pouch on the mother's belly) dispersed to the future Eurasia, Africa, South America, Antarctica, and Australia during the Jurassic period (**Figure a**). Somewhat later, but before the continents completely separated during the Cretaceous period, the earliest placentals (whose young complete development within the mother's uterus) also dispersed from North America into Eurasia, Africa, and South America (**Figure b**).

The breakup of Pangaea did not destroy all of these dispersal paths immediately. Persistent land connections allowed many organisms to migrate freely between North America and Eurasia throughout the Cretaceous period. Modern placentals further diversified in Eurasia during the Miocene epoch, and these new forms quickly dispersed back into North America (**Figure c**). As a result, the mammalian faunas of these continents have always been very similar.

By contrast, Australia and South America experienced substantial geographical isolation, particularly after the breakup of Gondwana. In South America, a distinctive mammalian fauna evolved from the marsupials and early placentals that had arrived during the Mesozoic. Small marsupials fed primarily on insects and other invertebrates, but larger species, including a marsupial saber-toothed cat, ate other vertebrates. The early South

American placentals gave rise to many large ungulates (hoofed herbivorous mammals) as well as to armadillos, sloths, and anteaters, some of which still live in South America today.

Periodic dispersal events slowly added to South America's mammal fauna. For example, rodents and primates first arrived about 25 million years ago, during the Oligocene epoch. They probably came from Africa by island-hopping across the slowly widening South Atlantic. These rodents eventually gave rise to guinea pigs and their relatives, and these primates to all the living New World monkeys. South America then began to drift northwest toward North America. By the late Miocene epoch, 6 million to 8 million years ago, North American rodents and raccoons were able to disperse into South America across the narrow water gap. By about 3 million years ago, in the Pliocene epoch, the Panamanian land bridge was established between North and South America, allowing mammals to migrate in both directions (**Figure d**).

A group of paleobiologists led by Larry G. Marshall of the Field Museum of Natural History in Chicago and S. David Webb of the Florida State Museum and the University of Florida have determined that about 10% of the mammal species on each continent dispersed across the land bridge to the other side. But North America—with its greater size and long-standing connections to Eurasia—had a greater variety of mammals than South America. Thus, more different types of mammals moved from north to south than in the opposite direction. Dispersal was so extensive during the Pliocene that paleobiologists describe these movements as the Great American Interchange.

The dispersal of so many northern mammals into South America fundamentally changed its ecological communities. Carnivorous cats, dogs, and

weasels and herbivorous camels, deer, elephants, horses, rabbits, and tapirs swept into the continent. Many new arrivals were wildly successful, apparently because they ate resources that native South American mammals were not using. Moreover, the northern immigrants had high rates of speciation, producing numerous descendant species.

As climates periodically cooled during the Pleistocene epoch, many mammals became extinct on both continents. Descendants of the northern immigrants have fared well over the long term: about half the mammals in South America today—including all the cats, llamas, tapirs, and many

rodents—are the descendants of northern ancestors. Most South American species that moved north were not as successful. Perhaps they could not adapt to physical conditions in the north, especially during the Pleistocene glaciations; or perhaps they could not prevail in competition with mammals that were already there. Today, relatively few mammals of southern origin persist in North America. Armadillos, monkeys, and anteaters are restricted to the southernmost parts. Only one opossum species (*Didelphis virginiana*, **Figure e**) and one porcupine species (*Erethizon dorsatum*) have moved further north.



Jack Dermid

**Figure e** Opossums (*Didelphis virginiana*) are among the few mammals of South American origin that are successful in North America.

**a. Shark**



Douglas P. Wilson/Eric and David Hosking

**b. Penguin**



Superstock, Inc.

**c. Porpoise**



E. R. DeGinger

**Figure 22.9** Convergent evolution in marine vertebrates. Convergent evolution produced similar body forms and appendages in distantly related marine predators: **(a)** sharks, which are cartilaginous fishes; **(b)** penguins, which are birds; and **(c)** porpoises, which are mammals. The resemblances are superficial, however. The tails of sharks are vertical, whereas those of penguins and porpoises are horizontal. Penguins also lack fins along their backs.

## 22.3 Interpreting Evolutionary Lineages

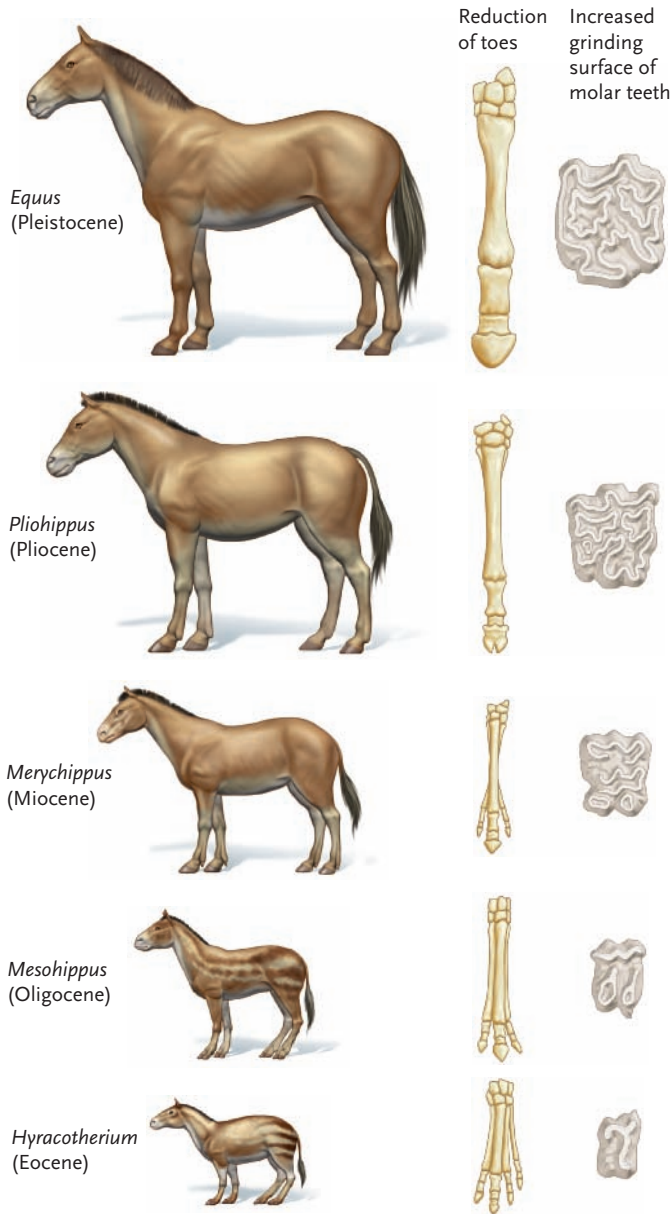
As newly discovered fossils demand the reinterpretation of old hypotheses, biologists constantly refine their ideas about the history of life. The evolution of horses is a case in point.

### Modern Horses Are Living Representatives of a Once-Diverse Lineage

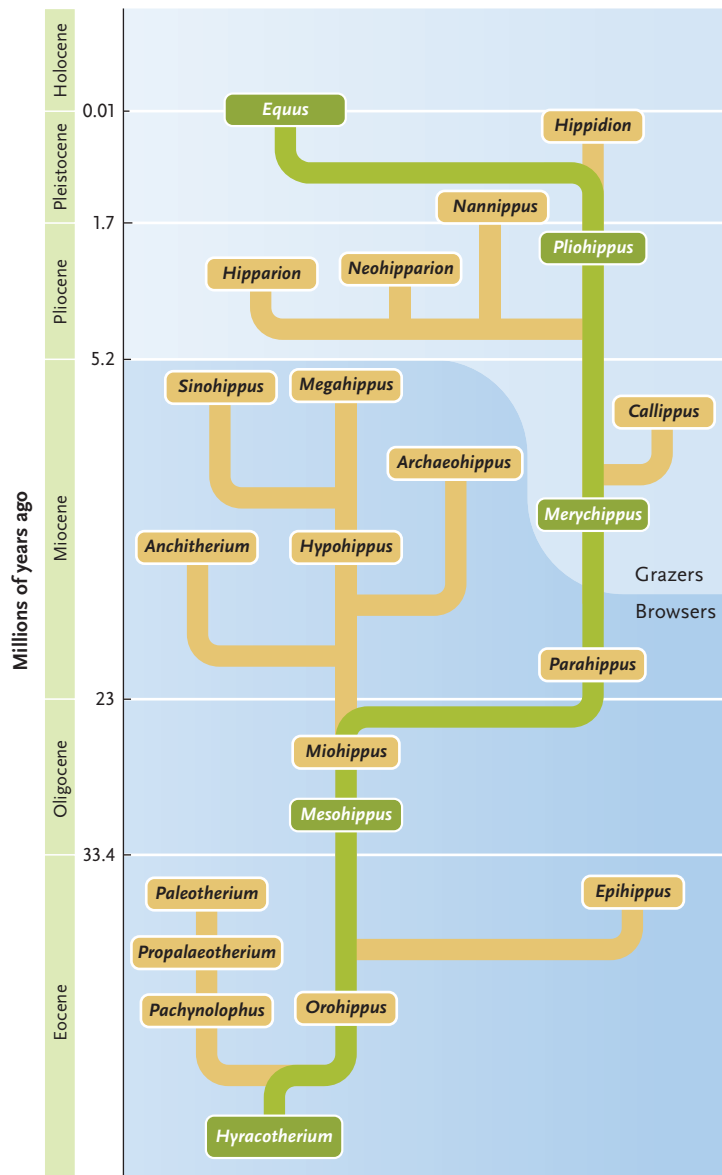
The earliest known ancestors of modern horses were first identified by Othniel C. Marsh of Yale University just a year after Darwin published *On the Origin of Species*. These early horses, *Hyracotherium*, stood 25 to 50 cm high and weighed no more than 20 kg. Their toes (four on the front feet and three on the hind) were each capped with a tiny hoof, but the animals walked on soft pads as dogs do today. Their faces were short, their teeth were small, and they browsed on soft leaves in woodland habitats.

In 1879, Marsh published his analysis of 60 million years of horse family history. He described the evolution of this group of mammals as a sequence of stages from the tiny *Hyracotherium* through intermediates represented by *Mesohippus*, *Merychippus*, and *Pliohippus* to the modern *Equus* (**Figure 22.10a**). (Each of these names refers to a genus, a group of closely related species.) Marsh inferred a pattern of descent characterized by gradual, directional evolution in several skeletal features. Changes in the legs and feet allowed horses to run more quickly, and changes in the face and teeth accompanied a switch in diet from soft leaves to tough grasses.

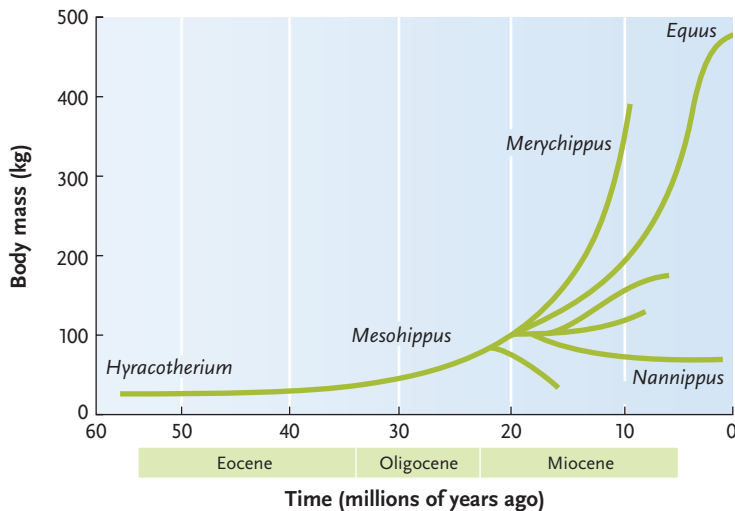
a. Marsh's reconstruction of horse evolution



b. Modern reconstruction of horse evolution



c. Changes in body size of horse species over time



**Figure 22.10**

Evolution of horses. **(a)** Marsh depicted the evolution of horses as a linear pattern of descent characterized by an increase in body size, a reduction in the number of toes, increased fusion of the bones in the lower leg, elongation of the face, and an increase in the size of grinding teeth at the back of the mouth. **(b)** Recent studies revealed that the horse family includes numerous evolutionary branches with variable morphology. The horses in Marsh's analysis are highlighted in green. **(c)** Although many branches of the lineage evolved a larger body size, some remained as small as the earliest horses.

The fossil record for horses is superb, and we now have fossils of more than 100 extinct species from five continents. These data reveal a macroevolutionary history very different from Marsh's interpretation. *Hyracotherium* was not gradually transformed into *Equus* along a linear track. Instead, the evolutionary tree for horses was highly branched (Figure 22.10b), and *Hyracotherium*'s descendants differed in size, number of toes, tooth structure, and other traits. Although many branches of this lineage lived in the Miocene and Pliocene epochs, all but one are now extinct. The species of the genus *Equus* living today (horses, donkeys, and zebras) are the surviving tips of that one branch.

When we study extinct organisms, we tend to focus on traits that characterize modern species. Marsh, for example, assumed that the differences between *Hyracotherium* and *Equus* were typical of the changes that characterized the group's evolutionary history. But not all fossil horses were larger (Figure 22.10c), had fewer toes, or were better adapted to feed on grass than their ancestors. And if a branch other than *Equus* had survived, Marsh's description of trends in horse evolution would have been very different. All evolutionary lineages have extinct branches, and any attempt to trace a linear evolutionary path—as Marsh did for horses and many people do for humans—imposes artificial order on an inherently disorderly history.

### Evolutionary Biologists Debate the Mode and Tempo of Macroevolution

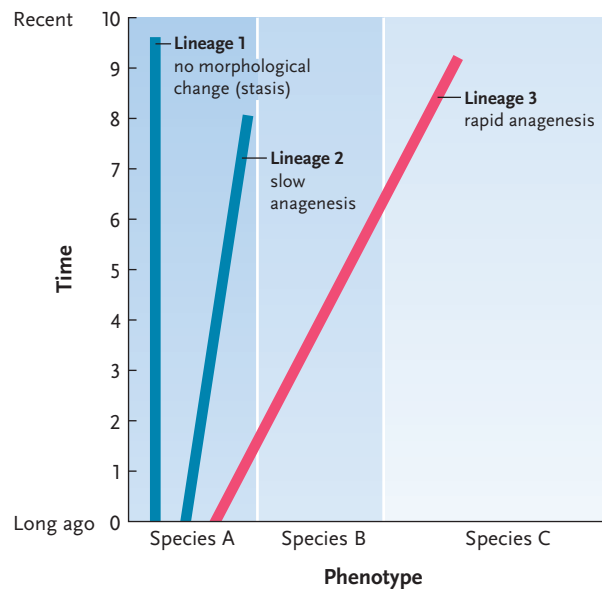
What evolutionary processes produce the numerous branches of a lineage such as the horse lineage, and over what time scale does a lineage evolve?

**Modes of Evolutionary Change.** The species that paleobiologists identify may arise by one of two modes, or processes of change, called anagenesis and cladogenesis. **Anagenesis** refers to the accumulation of changes in a lineage as it adapts to changing environments. If morphological changes are large, we may give the organisms different names at different times in their history. One might say, for example, that Species A from the late Mesozoic era had evolved into Species B from the middle Cenozoic era (Figure 22.11a). Anagenesis does not increase the number of species—it is the evolutionary transformation of an existing species rather than the production of new ones.

**Cladogenesis** refers to the evolution of two or more descendant species from a common ancestor. If the fossilized remains of the descendants are distinct, paleobiologists will recognize them as different species (Figure 22.11b). Cladogenesis does increase the number of species on Earth.

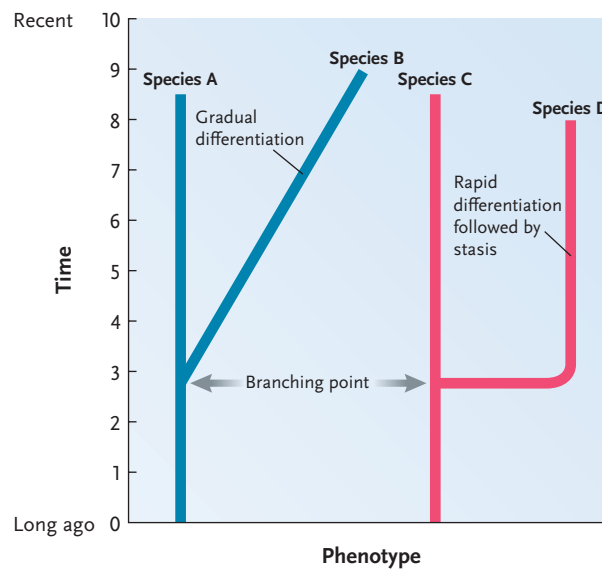
**Tempo of Morphological Change.** Macroevolutionists have developed two alternative hypotheses to describe the tempo, or timing, of morphological change.

#### a. Anagenesis



Three lineages begin with the same phenotype, identified as fossil Species A, at time 0. The rate of evolutionary change is shown by the angle of the line for each lineage: lineage 1 undergoes no change over time, lineage 2 changes slowly, and lineage 3 changes so rapidly that its phenotype shifts far to the right in the graph. Paleobiologists might assign different names to the fossils of lineage 3 at different times in its history—Species A at time 1, Species B at times 2 through 6, and Species C at times 7 through 9—even though no additional species evolved. By contrast, fossils of lineages 1 and 2 change so little over time that they would be identified as Species A throughout their evolutionary history.

#### b. Cladogenesis



Each branching point represents a new line of descent. The branching may show either gradual (left) or rapid (right) morphological differentiation from the parent species.

**Figure 22.11**

**Patterns of evolution.** In these hypothetical examples, the vertical axis represents geological time and the horizontal axis represents variation in phenotypic traits.

## Figure 22.12 Observational Research

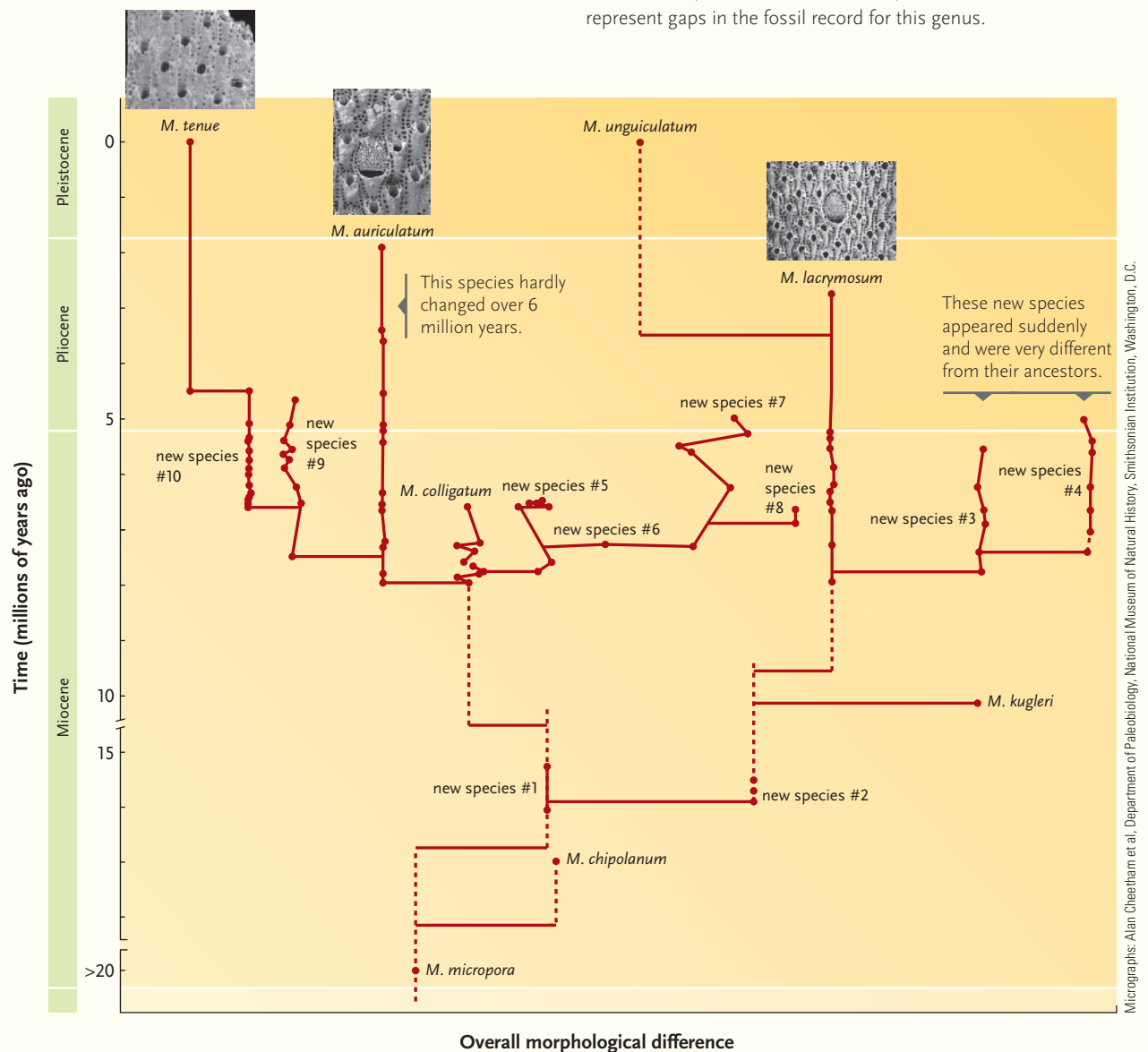
### Evidence Supporting the Punctuated Equilibrium Hypothesis

**METHOD:** Cheetham examined numerous fossilized samples of populations of a small marine invertebrate, the ectoproct *Metrarabdotos*, from the Dominican Republic. He measured 46 morphological characters in populations representing 18 species and then used a complex statistical analysis to summarize how morphologically different the species are.

**HYPOTHESIS:** The punctuated equilibrium hypothesis states that most morphological change within evolutionary lineages appears during periods of rapid speciation.

**PREDICTION:** The fossil record will reveal that most species experienced relatively little morphological change for long periods of time, but that new, morphologically distinctive species arose suddenly.

**RESULTS:** The morphology of most *Metrarabdotos* species changed very little over millions of years, but new species, morphologically very different from their ancestors, often appeared suddenly in the fossil record. Each dot in the graph represents a sample of a population from the fossil record. The horizontal axis reflects the overall morphological difference between samples of one species over time or between samples of ancestral species and descendant species. The dashed lines represent gaps in the fossil record for this genus.



**CONCLUSION:** The *Metrarabdotos* lineage exhibits a pattern of morphological evolution that is consistent with the predictions of the punctuated equilibrium hypothesis.

According to the **gradualist hypothesis**, large changes result from the slow, continuous accumulation of small changes over time. If this hypothesis is correct, we might expect to find a series of transitional fossils that document gradual evolution. In fact, we rarely find evidence of perfectly gradual change in any lineage. Most species appear suddenly in a particular stratum, persist for some time with little change, and then disappear from the fossil record. Then another species with different traits suddenly appears in the next higher stratum.

In the early 1970s, Niles Eldredge of the American Museum of Natural History and Stephen Jay Gould of Harvard University published an explanation for the absence of transitional forms, or “missing links.” Their **punctuated equilibrium hypothesis** suggested that speciation usually occurs in isolated populations at the edge of a species’ geographical distribution. Such populations experience substantial genetic drift and distinctive patterns of natural selection (as described in Section 21.3). According to this hypothesis, morphological variations arise rapidly during cladogenesis. Thus, most species exhibit long periods of morphological equilibrium or stasis (little change in form), punctuated by brief periods of cladogenesis and rapid morphological evolution. If this hypothesis is correct, transitional forms live only for short periods of geological time in small, localized populations—the very conditions that discourage broad representation in the fossil record. Darwin himself used this line of reasoning to explain puzzling gaps in the fossil record: new species appear as fossils only after they become abundant and widespread and begin a period of morphological stasis.

Some evolutionists point to flaws in the punctuated equilibrium hypothesis. First, rapid morphological evolution frequently occurs without cladogenesis. For example, in North America, variations in the body size of house sparrows evolved within 100 years without the appearance of new sparrow species (see Figure 21.5). Furthermore, geographical variation in most widespread species (see Section 21.1) provides compelling evidence of morphological evolution without speciation.

Second, critics challenge the hypothesis’ definition of rapid morphological change, particularly given our inability to resolve time precisely in the fossil record. To a paleobiologist with a geological perspective, “instantaneous” events occur over tens or hundreds of thousands of years. But to a population geneticist, those time scales may encompass thousands of generations, ample time for gradual microevolutionary change.

Third, examples of evolutionary stasis may not be as static as they appear. Alternating periods of directional selection that favor opposite patterns of change could produce the appearance of stasis. For example, if natural selection favored slight increases in body size

for 2000 years and then favored slight decreases for the next 2000 years, paleobiologists would probably detect no change in body size at all.

The fossil record provides some support for both hypotheses. A punctuated pattern is evident in the evolutionary history of *Metrarabdotos*, a genus of ectoprocts from the Caribbean Sea. Ectoprocts are small colonial animals that build hard skeletons (see Figure 29.15a), the details of which are well preserved in fossils. Alan Cheetham of the Smithsonian Institution measured 46 morphological traits in fossils of 18 *Metrarabdotos* species. He then used a summary statistic to describe the morphological difference between populations of a single species over time and between ancestral species and their descendants. His results indicate that most species did not change much over millions of years, but new species, which were morphologically different from their ancestors, often appeared quite suddenly (**Figure 22.12**).

By contrast, a study of Ordovician trilobites supports the gradualist hypothesis of evolution. The number of “ribs” in their tail region changed continuously over 3 million years. The change was so gradual that a sample from any given stratum was almost always intermediate between samples from the strata just above and below it. The changes in rib number probably evolved without cladogenesis (**Figure 22.13**).

The punctuationalist and gradualist hypotheses represent extremes on a continuum of possible macroevolutionary patterns. The mode and tempo of evolution vary among lineages, and both viewpoints are validated by data on some organisms but not others. Although some biologists still question the punctuated equilibrium hypothesis, its publication rekindled interest in paleobiology and macroevolution, inspiring much new research. Some of the most interesting results have focused on morphological changes within lineages and on long-term changes in the number of living species.

## STUDY BREAK

1. Did the horse lineage undergo a steady increase in body size over its evolutionary history?
2. How do the predictions of the gradualist and the punctuationalist hypotheses differ?

## 22.4 Macroevolutionary Trends in Morphology

Some evolutionary lineages exhibit trends toward larger size and greater morphological complexity, and others are marked by the development of novel structures.

Figure 22.13 Observational Research

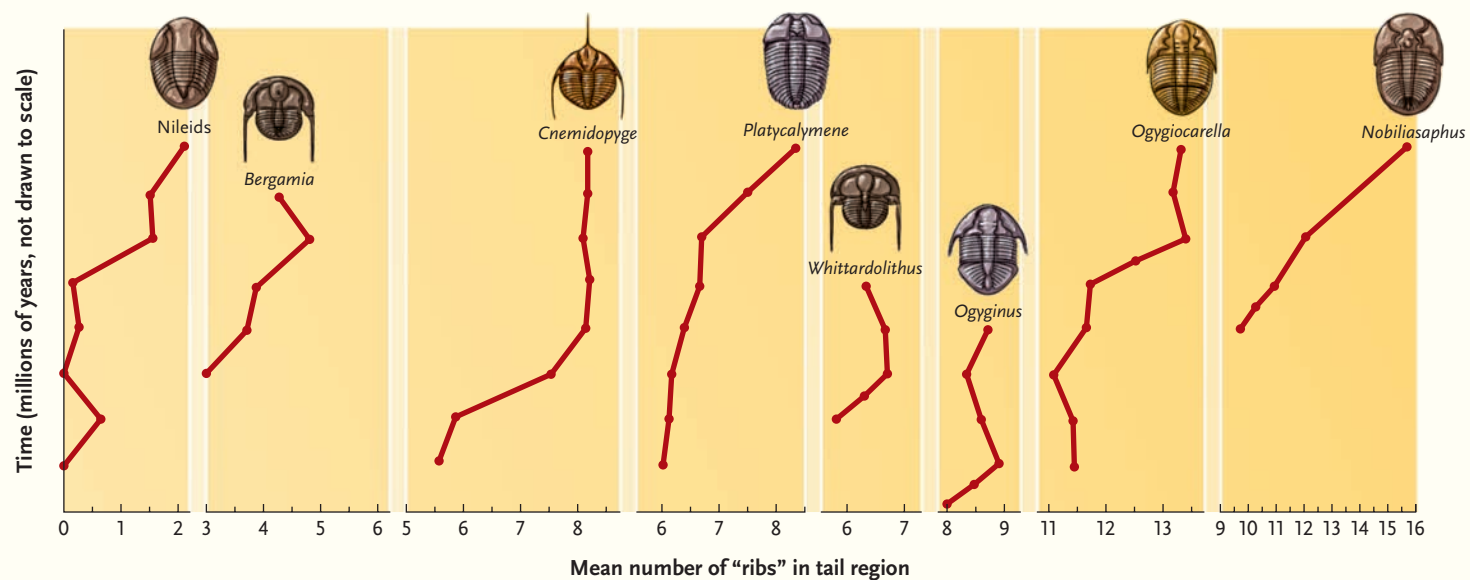
## Evidence Supporting the Gradualist Hypothesis

**HYPOTHESIS:** The gradualist hypothesis states that most morphological change within evolutionary lineages results from the accumulation of small, incremental changes over long periods of time.

**PREDICTION:** The fossil record will reveal that the morphology of fossils from a given stratum will be intermediate between those of fossils from the strata immediately below and above it.

**METHOD:** Peter R. Sheldon of Trinity College, Dublin, Ireland, counted the number of “ribs” in the tail region of the exoskeletons of approximately 15,000 trilobite fossils from central Wales, United Kingdom. The fossils had formed over a span of about 3 million years during the Ordovician period. Sheldon plotted the mean number of ribs found in successive samples of each lineage.

**RESULTS:** Sheldon’s data reveal gradual changes in the mean number of “ribs” in these animals with no evidence of speciation.



**CONCLUSION:** Morphological changes in Ordovician trilobites from central Wales are consistent with the predictions of the gradualist hypothesis.

## The Body Size of Organisms Has Generally Increased over Time

Body size affects most aspects of an organism’s physiology and ecology. When we look at the entire history of life, organisms have generally become larger over time. The earliest organisms were tiny, as most still are today. But the change from replicating molecules to acellular, unicellular, and finally multicellular organization must have demanded an increase in body size.

Within evolutionary lineages, increases in body size are not universal, but they are common. The nineteenth-century paleobiologist Edward Drinker Cope first noted this trend toward larger body size, now known as *Cope’s Rule*, in vertebrates. Although Cope’s Rule also applies to some invertebrate and plant lineages, no one has conducted a truly broad survey to test the generality of the hypothesis. Insects, for example,

are a major exception to Cope’s Rule. Most insects have remained small since their appearance in the Devonian, probably because of the constraints imposed by an external skeleton (see Section 29.7).

We can readily imagine why natural selection may sometimes favor larger size. Large organisms maintain a more constant internal environment than small ones. They may also have access to a wider range of resources, harvest resources more efficiently, and be less likely to be captured by predators. Moreover, larger females may produce more young, and larger males may have greater access to mates. Unfortunately, we cannot test such hypotheses about extinct life forms directly. We can only analyze past events with an understanding of how natural selection affects organisms living today.

In the 1970s, Steven Stanley of Johns Hopkins University proposed an explanation for how macroevolu-



tionary trends may develop. He suggested that certain traits might make some species more likely to undergo speciation than others. This mechanism, called **species selection**, is analogous to natural selection. In natural selection, the evolutionary success of an individual is measured by the number of its surviving offspring. In species selection, the evolutionary success of a species is measured by the number of its descendant species. Thus, the traits of species that frequently undergo cladogenesis become more common, establishing a trend within a lineage. For example, if large species leave more descendant species than small ones do, the number of large species will increase faster than the number of small species. As a result, the average size of species in the lineage will increase over time. Stanley's hypothesis has not been widely tested.

### Morphological Complexity Has Also Generally Increased over Time

In general, the evolutionary increase in size has been accompanied by an increase in morphological complexity. Among contemporary organisms, for example, species with large body size have a greater variety of cell types than do species with small body size. We can probably assume that new cell types arose when larger organisms first evolved.

However, under some circumstances, natural selection has simplified traits. The single toe and fused leg bones of modern horses are stronger, but mechanically less complex, than the ancestral structures in *Hyracotherium*. Similarly, snakes, which evolved from lizards with well-developed legs, have lost their limbs entirely. These changes, which increase the efficiency of locomotion, represent decreases in morphological complexity.

### Several Phenomena Trigger the Evolution of Morphological Novelties

Sometimes a trait that is adaptive in one context turns out to be advantageous in another. Natural selection may then modify the trait to enhance its new function. Such **preadaptations** are just lucky accidents; they never evolve *in anticipation* of future evolutionary needs.

John Ostrom of Yale University described how some carnivorous dinosaurs, the immediate ancestors of *Archaeopteryx* and modern birds, were preadapted for flight (see Figure 19.12). These small, agile creatures were bipedal with lightweight hollow bones and long forelimbs to capture prey; some even had rudimentary feathers that may have retained body heat. But all these traits evolved because they were useful adaptations in highly active and mobile predators, not because they would someday allow flight.

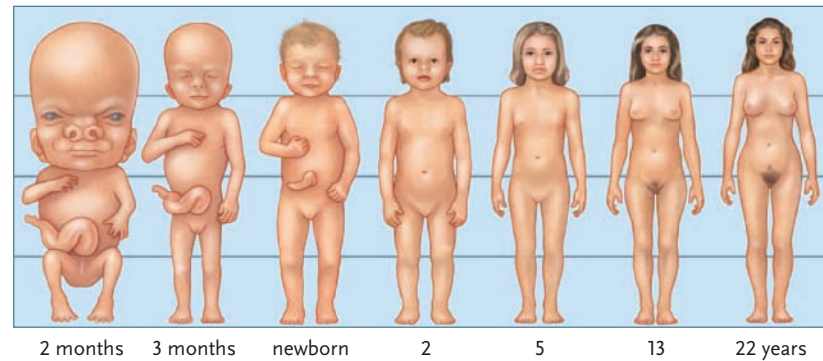
The morphology of individuals sometimes changes over time because of **allometric growth** (*allo* = different;

*metro* = measure), the differential growth of body parts. In humans, for example, the relative sizes of different body parts change because human heads, torsos, and limbs grow at different rates (**Figure 22.14a**).

Allometric growth can also create morphological differences in closely related species. For example, the skulls of chimpanzees and humans are similar in newborns, but markedly different in adults (**Figure 22.14b**). Some regions of the chimp skull grow much faster than others, while the proportions of the human skull

**Figure 22.14**  
Examples of allometric growth.

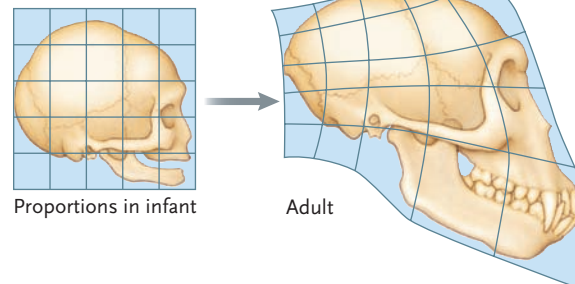
#### a. Allometric growth in humans



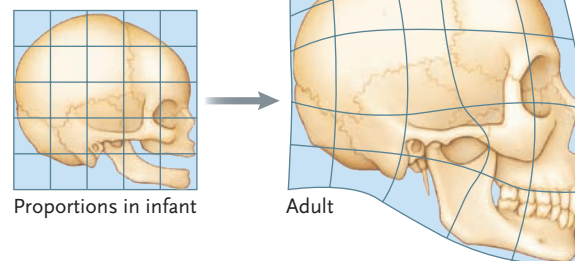
Humans exhibit allometric growth from prenatal development until adulthood. Our heads grow more slowly than other body parts; our legs grow faster.

#### b. Differential growth in the skulls of chimpanzees and humans

##### Changes in chimpanzee skull



##### Changes in human skull



Although the skulls of newborn humans and chimpanzees are remarkably similar, differential patterns of growth make them diverge during development. Imagine that the skulls are painted on a blue rubber sheet marked with a grid. Stretching the sheet deforms the grid in particular ways, mimicking the differential growth of various parts of the skull.



David Scott/SERL

**Figure 22.15**

Paedomorphosis in salamanders. Some small-mouthed salamanders (*Ambystoma talpoideum*) undergo metamorphosis, losing their gills and developing lungs (left). Others are paedomorphic: they retain juvenile morphological characteristics, such as gills, after attaining sexual maturity (right).

change much less. Differences in the adult skulls may simply reflect changes in one or a few genes that regulate the pattern of growth.

Changes in the timing of developmental events, called **heterochrony** (*hetero* = different; *chronos* = time), also cause the morphology of closely related species to differ. **Paedomorphosis** (*paedo* = child; *morpho* = form), the development of reproductive capability in an organism with juvenile characteristics, is a common form of heterochrony.

Many salamanders, for example, undergo metamorphosis from an aquatic juvenile into a morphologically distinct terrestrial adult. However, populations of several species are paedomorphic—they grow to adult size and become reproductively mature without changing to the adult form (**Figure 22.15**). The evolutionary change causing these differences may be surprisingly simple. In amphibians, including salamanders, the hormone thyroxine induces metamorphosis (see Chapter 40). Paedomorphosis could result from a mutation that either reduces thyroxine production or limits the responsiveness of some developmental processes to thyroxine concentration.

Changes in developmental rates also influence the morphology of plants (**Figure 22.16**). The flower of a larkspur species, *Delphinium decorum*, includes a ring of petals that guide bees to its nectar tube and structures on which bees can perch. By contrast, *Delphinium nudicaule*, a more recently evolved species, has tight flowers that attract hummingbird pollinators, which can hover in front of the flowers. Slower development in *D. nudicaule* flowers causes the structural difference: a mature flower in the descendant species resembles an unopened (juvenile) flower of the ancestral species.

Novel morphological structures, such as the wings of birds, often appear suddenly in the fossil record. How do novel features evolve? Scientists have identified several mechanisms including preadaptation, allometric growth, and heterochrony. We describe new research about the genetic basis of some morphological innovations in the last section of this chapter.

## STUDY BREAK

1. How have the sizes of organisms changed since life first appeared?
2. What processes can trigger the evolution of morphological novelties?

## 22.5 Macroevolutionary Trends in Biodiversity

The number of species living on Earth—its overall **biodiversity**—changes over time as a result of both adaptive radiation and extinction.

### Adaptive Radiations Are Clusters of Related Species with Diverse Ecological Adaptations

In some lineages, rapid speciation produces a cluster of closely related species that occupy different habitats or consume different foods; we describe such a lineage as an **adaptive radiation**. The Galápagos finches (**Figure 22.17**) and the Hawaiian fruit flies described in Chapter 21 are examples of adaptive radiations.

Adaptive radiation usually occurs after an ancestral species moves into an unfilled **adaptive zone**, a general way of life. Browsing on soft leaves in the forest is the adaptive zone that early horses occupied, and grazing on grass in open habitats is the adaptive zone that horses occupy today. Feeding on plastic in landfills might become an adaptive zone in the future if some organism develops the ability to digest that now-abundant resource.

An organism may move into a new adaptive zone after the chance evolution of a key morphological innovation that allows it to use the environment in a unique way. For example, the dehydration-resistant eggs of early reptiles enabled them to complete their life cycle on land, opening terrestrial habitats to them. Similarly, the evolution of flowers that attract insect pollinators was a key innovation in the history of flowering plants.

An adaptive zone may also open up after the demise of a successful group. Mammals, for example, were relatively inconspicuous during their first 150 million years on Earth, presumably because dinosaurs dominated terrestrial habitats. But after dinosaurs declined in the late Mesozoic era, mammals underwent an explosive adaptive radiation. Today they are the dominant vertebrates in many terrestrial habitats.

### Extinctions Have Been Common in the History of Life

Increased biodiversity is counteracted by **extinction**, the death of the last individual in a species or the last species in a lineage. Paleobiologists recognize two dis-

tinct patterns of extinction in the fossil record, background extinction and mass extinction.

Species and lineages have been going extinct since life first appeared. We should expect species to disappear at some low rate, the **background extinction rate**; as environments change, poorly adapted organisms will not survive and reproduce. In all likelihood, more than 99.9% of the species that have ever lived are now extinct. David Raup of the University of Chicago has suggested that, on average, as many as 10% of species go extinct every million years and that more than 50% go extinct every 100 million years. Thus, the history of life has been characterized by an ongoing turnover of species.

On at least five occasions, extinction rates rose well above the background rate. During these **mass extinctions**, large numbers of species and lineages died out over relatively short periods of geological time (**Figure 22.18**). The Permian extinction was the most severe: more than 85% of the species alive at that time—including all trilobites, many amphibians, and the trees of the coal swamp forests—disappeared forever. During the last mass extinction, at the end of the Cretaceous, half the species on Earth, including most dinosaurs, became extinct. A sixth mass extinction, potentially the largest of all, may be occurring now as a result of human degradation of the environment (see Chapter 53).

Different factors were responsible for the five mass extinctions. Some were probably caused by tectonic activity and associated changes in climate. For example, the Ordovician extinction occurred after Gondwana moved toward the South Pole, triggering a glaciation that cooled the world's climate and lowered sea levels. The Permian extinction coincided with a major glaciation and a decline in sea level induced by the formation of Pangaea.

Many researchers believe that an asteroid impact caused the Cretaceous mass extinction. The resulting dust cloud may have blocked the sunlight necessary for photosynthesis, setting up a chain reaction of extinctions that began with microscopic marine organisms. Geological evidence supports this hypothesis. Rocks dating to the end of the Cretaceous period (65 million years ago) contain a highly concentrated layer of iridium, a metal that is rare on Earth but common in asteroids. The impact from an iridium-laden asteroid only 10 km in diameter could have caused an explosion equivalent to that of a billion tons of TNT, scattering iridium dust around the world. Geologists have identified the Chicxulub crater, 180 km in diameter, on the edge of Mexico's Yucatán peninsula as the likely site of the impact.

Although scientists agree that an asteroid struck Earth at that time, many question its precise relationship to the mass extinction. Dinosaurs had begun their decline at least 8 million years earlier, but many persisted for at least 40,000 years after the impact. More-

## Figure 22.16 Observational Research

### *Paedomorphosis in Delphinium Flowers*

**HYPOTHESIS:** The narrow tubular shape of the flowers of *Delphinium nudicaule*, which are pollinated by hummingbirds, is the product of paedomorphosis, the retention of juvenile characteristics in a reproductive adult.

**PREDICTION:** The flowers of *D. nudicaule* grow more slowly and mature at an earlier stage of development than those of *Delphinium decorum*, a species with broad, open flowers that are pollinated by bees.

*D. decorum*

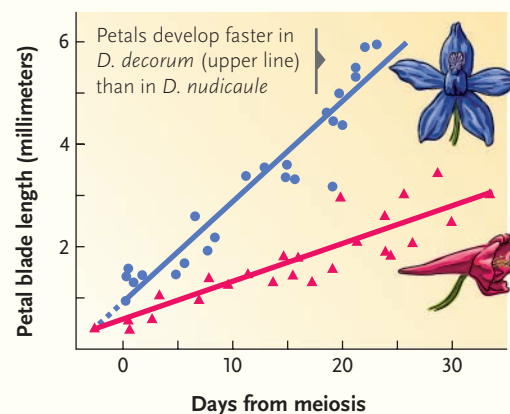


*D. nudicaule*

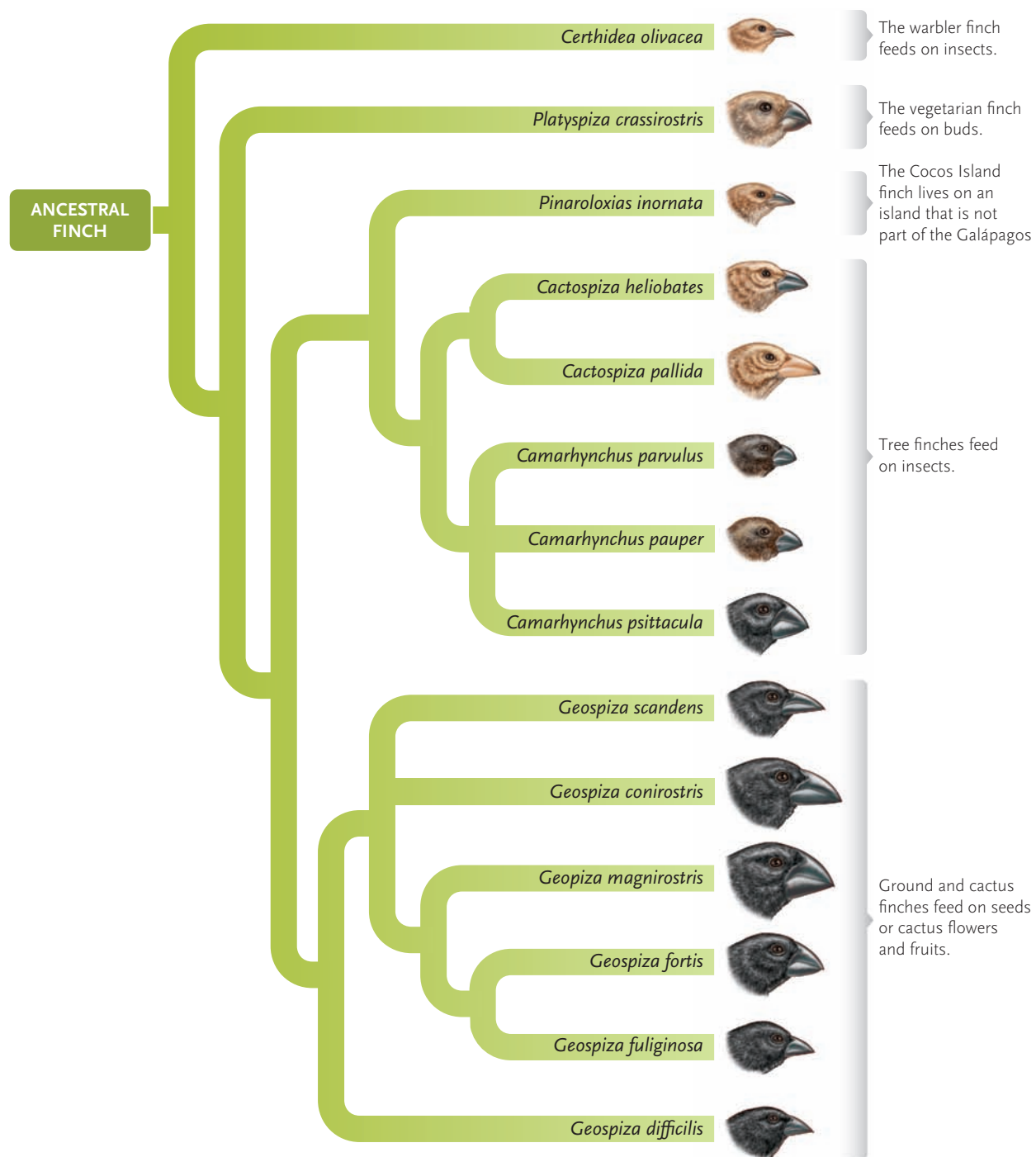


**METHOD:** Edward O. Guerrant of the University of California at Berkeley measured 42 bud and flower characteristics in *D. nudicaule* and *D. decorum* as their flowers developed and used the number of days since the completion of meiosis in pollen grains as a measure of flower maturity. He then used a complex statistical analysis to compare the characteristics of the buds and flowers of both species.

**RESULTS:** The mature flowers of *D. nudicaule* resemble the buds of both species more closely than they resemble the flowers of *D. decorum*. Although the time required for maturation of the reproductive structures is similar in the two species, the rate of petal growth (measured as petal blade length) is slower in *D. nudicaule*. As a result, the mature flowers of *D. nudicaule* do not open as widely as those of *D. decorum*. Because of these morphological differences, bees can pollinate flowers of *D. decorum*, but they can't land on the flowers of *D. nudicaule*, which are instead pollinated by hummingbirds.



**CONCLUSION:** The narrower and more tubular shape of *D. nudicaule* flowers, which mature at an earlier stage of development than *D. decorum* flowers, is the product of paedomorphosis.



**Figure 22.17**  
Adaptive radiation. The 14 species of Galápagos finches are descended from one ancestral species.

over, other groups of organisms did not suddenly disappear, as one would expect after a global calamity. Instead, the Cretaceous extinction took place over tens of thousands of years.

### Biodiversity Has Increased Repeatedly over Evolutionary History

Although mass extinctions temporarily reduce biodiversity, they also create evolutionary opportunities. Some species survive because they have highly adaptive traits, large population sizes, or widespread distributions. And some surviving species undergo adaptive

radiation, filling adaptive zones that mass extinctions made available.

Sometimes the success of one lineage comes at the expense of another. Although the diversity of terrestrial vascular plants has increased almost continuously since the Devonian period, this trend includes booms and busts in several lineages (**Figure 22.19**). Ferns and conifers recovered rapidly after the Permian extinction, maintaining their diversity until the end of the Mesozoic era. However, angiosperms, which arose and diversified in the late Jurassic and early Cretaceous periods, may have hastened the decline of these groups by replacing them in many environments.

The superb fossil record left by certain marine animals reveals three major periods of adaptive radiation (Figure 22.20). The first occurred during the Cambrian, more than 500 million years ago, when all animal phyla, the major categories of animal life, arose. Most of these phyla became extinct, and a second wave of radiations established the dominant Paleozoic fauna during the Ordovician period. A third evolutionary fauna emerged in the Triassic period, right after the great Permian extinction; it produced the immediate ancestors of modern marine animals. The diversity of marine animals has increased consistently since the early Triassic, in large measure because of continental drift. As continents and shallow seas became increasingly isolated, regional biotas diversified independently of one another, increasing worldwide biodiversity.

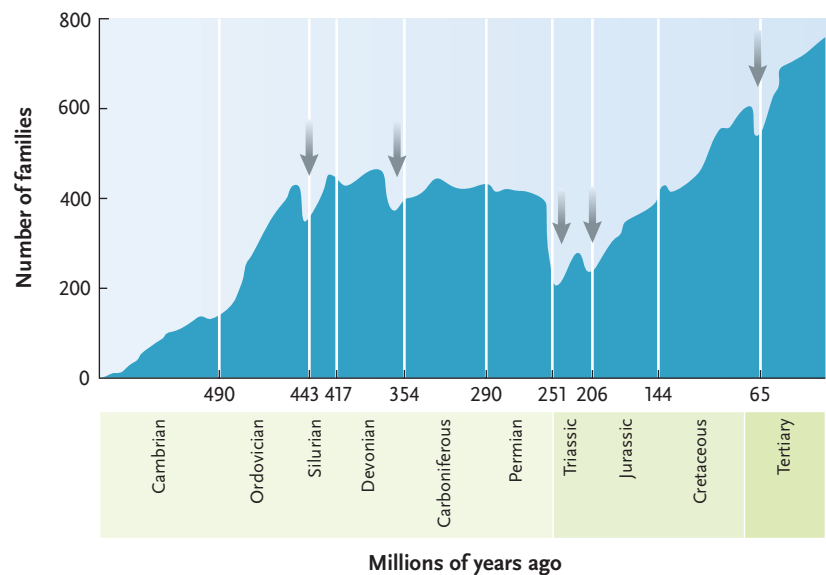
Historical increases in biodiversity can also be attributed to the evolution of ecological interactions. For example, the number of plant species found *within* fossil assemblages has increased over time, suggesting the evolution of mechanisms that allow more species to coexist. In addition, insects diversified dramatically in the Cretaceous period, possibly because the angiosperms created a new adaptive zone for them. New insect species then provided a novel set of pollinators that may have stimulated the radiation of angiosperms. Such long-term evolutionary interactions between ecologically intertwined lineages have played an important role in structuring ecological communities, which are described more fully in Chapter 50.

## STUDY BREAK

1. What factors might allow a population of organisms to occupy a new adaptive zone?
2. Did the mass extinction at the end of the Cretaceous period occur quickly or over a long period of time?
3. When did the first major adaptive radiation of animals occur?

## 22.6 Evolutionary Developmental Biology

Historically, evolutionary biologists compared the embryos of different species to study their evolutionary history (see Figure 19.13), but they often worked independently from scientists studying the embryonic development of organisms. As a result, evolutionary biologists were unable to construct a coherent picture of the specific developmental mechanisms that contributed to morphological innovations. Since the late 1980s, however, advances in molecular genetics have allowed scientists to explore the genomes of organisms in great detail, fostering a new approach to these stud-

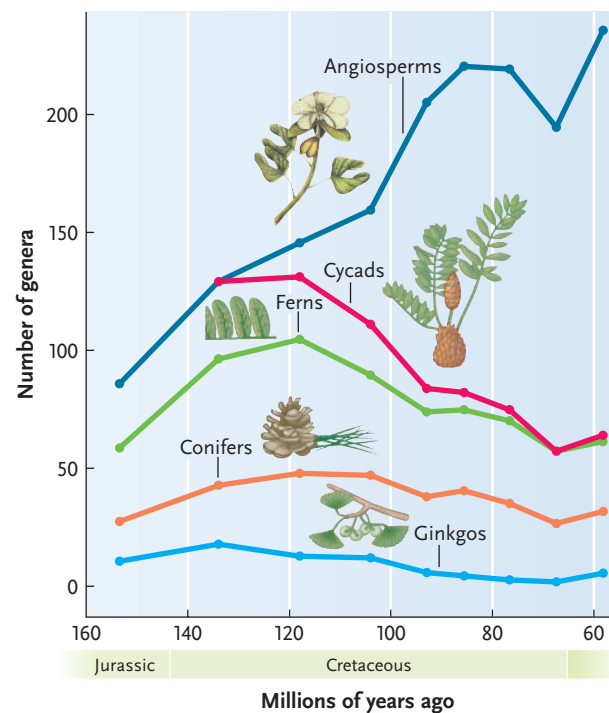


**Figure 22.18**

Mass extinctions. Biodiversity, indicated by the height of the dark blue area in the graph, was temporarily reduced by at least five mass extinctions (arrows) during the history of life. The data presented in this graph record the family-level diversity of marine animals. A family is a group of genera descended from a common ancestor.

ies. **Evolutionary developmental biology**—evo-devo, for short—asks how evolutionary changes in the genes regulating embryonic development can lead to changes in body shape and form.

The study of the genetics of embryonic development helps us understand macroevolutionary trends



**Figure 22.19**

History of vascular plant diversity. The diversity of angiosperms increased during the Mesozoic era as the diversity of other groups declined.