

19 EVOLUTIONARY PATTERNS, RATES, AND TRENDS

Last of the Honeycreepers?

More than 5 million years ago, Kauai rose above the surface of the sea. It was the first of the big islands of the Hawaiian Archipelago. Several million years later, a few quite possibly terrified finches reached it after bobbing 4,000 kilometers (2,500 miles) across the open ocean. Were they unwilling pioneers, blown away from the mainland during a fierce storm? We may never know, but their chance geographic dispersal was the start of something big.

No predatory mammals had preceded the finches onto that isolated, volcanically born island. But tasty insects and plants that bore tender leaves, nectar, seeds, and fruits were already there. The finches thrived. Their descendants quickly radiated into habitats along the coasts, through dry lowland forests, and into rain forests of the highlands.

Between 1.8 million and 400,000 years ago, volcanic eruptions created the rest of the archipelago. Generation after generation, descendants of the first finches traveled on the winds to vacant habitats in the new islands. They foraged in many shrublands and forests, each with special food sources and nesting sites. Diverse agents of natural selection operated in each place, and differences in bill sizes and shapes, feather coloration and patterns, and territorial songs evolved. In this way, a spectacular family of birds, the Hawaiian honeycreepers, originated.

One existing Hawaiian honeycreeper has a bill that fits in the long, curving nectar tubes of *Lobelia* flowers (Figure 19.1). One probes tree bark with its sickle-shaped upper bill, then scoops out beetle larvae with its shovel-shaped lower bill. Other species use a thickened, strong, parrotlike bill to crush or pry open hard seed pods. The po'-ouli (Figure 19.2) is the only species that preferentially eats native tree snails.

Ironically, the very isolation that favored specialized adaptations to conditions in unique habitats made these birds vulnerable to extinction. When conditions changed, they had nowhere to go. They had no built-in defenses against predatory mammals and avian diseases of the mainland, against humans who coveted cloaks made of their eye-catching feathers, or against climate change.

Accompanying humans to the islands were brown tree snakes, rats, cats, and other voracious predators. People also imported chickens and other birds that happened to be infected with disease agents. Over time, people cleared more and more of the forests. Imported crop plants and plant-eating mammals became established. The Hawaiian honeycreeper habitats shrank. Today, with a long-term increase in global temperatures—global warming—the forests at higher elevations are not as cool as they once were. They have been infiltrated by mosquitoes, which



Figure 19.1 *Left*, the Hawaiian honeycreeper known informally as lii (*Vestiaria coccinea*). It evolved in the Hawaiian Archipelago (*right*), far from the mainland. It is a descendant of a spectacular adaptive radiation—one of the patterns explained in this chapter.

IMPACTS, ISSUES



Figure 19.2 Male po'ouli—rare, old, and missing one eye. Ecologists captured this small honeycreeper on the east slope of Haleakala, Hawaii, as part of a last-ditch effort to save the remaining population of three birds. This male was already suffering the effects of avian malaria, and it died in 2004. The perpetuation of its species—which was not even known about until 1973—now rests on the two remaining birds. The two have not been seen in many months.

thrive in warm climates. Mosquitoes happen to be vectors for pathogens that cause avian malaria and other diseases.

At one time there were approximately fifty species of Hawaiian honeycreepers. As many as twenty-four species colonized a single island. Half of the known species are extinct. The initial wave of extinction followed the arrival of the first Polynesians, and another ten species are now endangered. The remaining species are being studied in earnest, and efforts are under way to protect them. It may be a case of too little, too late; but time will tell.

How do we know so much about a group of birds on an island chain in the middle of the Pacific Ocean? Scientific theories and tools, particularly radiometric dating and automated gene sequencing, helped shine light on their rise and impending fall. The age of volcanic rocks on each island, as well as the DNA of different species, were among the clues. Such clues give us glimpses into **macroevolution**—the long-term patterns, rates, and trends in the origin and ultimate fate of Earth's many millions of species.



How Would You Vote?

*Often, when a species is on the brink of extinction, some individuals are captured and brought to zoos for captive breeding programs. Some people object to this practice. They say keeping a species alive in a zoo is a distraction from more meaningful conservation efforts, and captive animals seldom are successfully restored to the wild. Do you support captive breeding of highly endangered species? See *BiologyNow* for details, then vote online.*



Key Concepts

HOW DO SPECIES ARISE?

All sexually reproducing species consist of one or more populations of individuals that interbreed under natural conditions, produce fertile offspring, and are reproductively isolated from other such populations. [Section 19.1](#)

MODELS FOR SPECIATION

Speciation is a process that varies in details and duration among lineages. It starts when gene flow stops between populations of a species. Microevolutionary events occur independently in the reproductively isolated populations. The process ends when daughter species form. [Sections 19.2, 19.3](#)

PATTERNS IN THE HISTORY OF LIFE

The timing, rate, and direction of speciation differ among branches of a lineage and between lineages. Adaptive radiations and extinction punctuate the history of life. [Section 19.4](#)

CLASSIFICATION SYSTEMS

Patterns in life's history are being identified and interpreted. Taxonomy identifies, names, and then classifies species. Systematics infers evolutionary relationships by analytical methods. Phylogenetic classification systems are efficient tools for retrieving information about the history of life. [Section 19.5](#)

PIECING TOGETHER FAMILY TREES

Biologists construct evolutionary tree diagrams that use derived traits to determine branch points. A current tree subsumes six traditionally defined kingdoms into three domains: Bacteria, Archaea, and Eukarya. It reveals how all species interconnect through shared ancestors, some remote, others recent. [Sections 19.6–19.9](#)



Links to Earlier Concepts

Before starting this chapter, be sure you understand how gene flow can help keep populations of the same species genetically similar by countering the impact of mutation, natural selection, and genetic drift (Sections 18.1, 18.8). You will be applying your knowledge of changes in chromosome structure and function (12.8 and 15.4). Quickly review how comparisons of morphology (17.7) and of genes and proteins of different lineages (17.9) yield clues to shared ancestry.

Also reflect on the major geologic forces. They have been a factor in the origin of many species, especially on island chains (17.2, 17.6). You also will be taking a closer look at the three-domain system of classification (1.3).

 HOW DO SPECIES ARISE?

19.1 Reproductive Isolation, Maybe New Species

LINKS TO SECTIONS
11.6, 18.1, 18.8



Speciation is a macroevolutionary process. It starts when a population becomes reproductively isolated from others of the species and ends when daughter species have formed.

WHAT IS A SPECIES?

Species is a Latin word that means “kind,” as in “one kind of plant.” This generic definition does not help much when we are trying to figure out whether, say, a population of plants in one place belongs to the same species as a population of plants somewhere else. You may see variations in traits between the populations and variation within them, because plants can inherit diverse combinations of alleles. Also, some individuals may grow in very different environments that cause changes in gene expression (Section 11.6 and Figure 19.3). In other words, we might not be able to identify a biological species on the basis of appearance alone.

Evolutionary biologist Ernst Mayr came up with a **biological species concept**: A species is one or more groups of individuals that interbreed, produce fertile offspring, and are reproductively isolated from other such groups. This definition is reasonable for species that reproduce sexually—which most species do. It does not apply to asexual reproducers, and it cannot be used to interpret the fossil record.

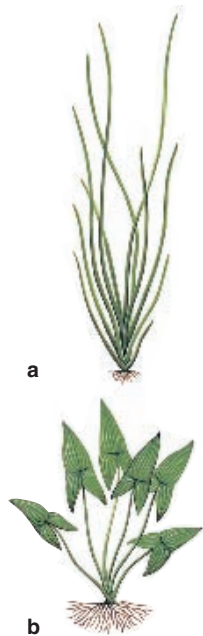


Figure 19.3 Morphological differences between plants of the same species (*Sagittaria sagittifolia*) growing (a) in water and (b) on land. The leaf shapes are responses to different environmental conditions, not to different genetic programs.

Figure 19.4 *Animated!* (a) Mechanical isolation. Few pollinating insects fit as well as wasps on a zebra flower. Petals form a landing platform below stamens.

(b) Temporal isolation. *Magicicada septendecim*, a periodical cicada that matures underground and emerges to reproduce every seventeen years. Its populations often overlap the habitats of a sibling species (*M. tredecim*), which reproduces every thirteen years. Adults live only a few weeks.

(c) Behavioral isolation. Courtship displays precede sex among many kinds of birds, including these albatrosses. Individuals recognize tactile, visual, and acoustical signals, such as a prancing dance followed by back arching, a skyward pointing bill and an exposed throat, and wing spreading.

A more recent definition has wider applicability: A **species** is one or more populations of individuals that share at least one structural, functional, or behavioral trait—the *legacy of a common ancestor*—that sets them apart from other species. This definition is based on comparative morphology, biochemistry, and the fossil record. It applies to sexually or asexually reproducing species. Unlike the biological species concept, it does not directly address how a species attains and then maintains its separate identity. That clue, for sexual reproducers at least, is *reproductive isolation*—the end of gene exchanges between populations.

REPRODUCTIVE ISOLATING MECHANISMS

Gene flow, recall, is the movement of alleles into and out of a population (Section 18.8). Speciation begins when gene flow, or the potential for it, ends between natural populations. Once it stops, gene pools start to change and populations undergo **genetic divergence**, because mutation, natural selection, and genetic drift are free to operate independently in each one (Section 18.8). As you will see later, speciation may result from gradual genetic divergence. It also may be completed within a few generations, as commonly occurs among flowering plants.

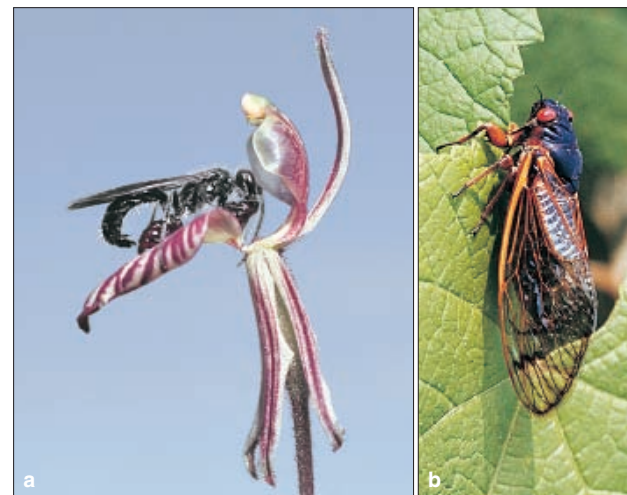


Figure 19.5 Animated! When certain reproductive isolating mechanisms prevent interbreeding. There are barriers to (a) getting together, mating, or pollination, (b) successful fertilization, and (c) survival, fitness, or fertility of hybrid embryos or offspring.

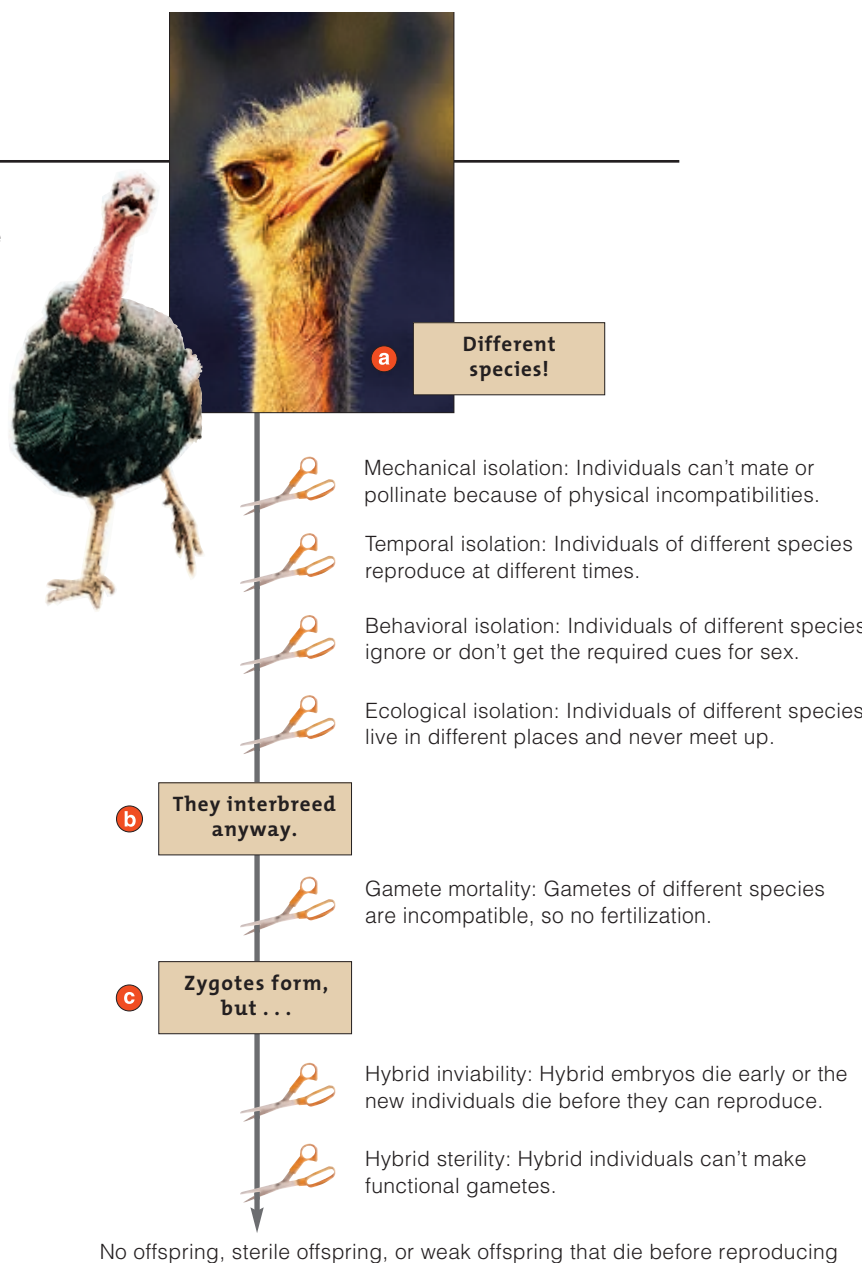
Either way, **reproductive isolating mechanisms** evolve. All of these heritable aspects of body form, function, or behavior block interbreeding between populations. *Prezygotic* mechanisms, as in Figure 19.4, stop cross-pollination or cross-breeding, the formation of gametes, or fertilization. *Postzygotic* mechanisms kill hybrids or make them weak or infertile. Let us start off with the prezygotic isolating mechanisms listed in Figure 19.5a,b.

Mechanical isolation. The body parts of a species are not a physical match with those of a species that could otherwise serve as a mate or pollinator. Figure 19.4a shows the fit between a zebra plant and its preferred pollinator. Similarly, the pollen-bearing stamens of the flowers of one sage species extend above petals that act as a landing platform. Big-bodied pollinators get a dusting of pollen when they land and collect nectar. Pollen-gathering bees are not large enough to brush against these stamens. But the other sage species has its stamens poised above a bee-sized platform that is too small and fragile to hold big, heavy pollinators.

Temporal isolation. Diverging populations cannot interbreed when their timing of reproduction differs. Cicada species that differ in form and behavior often live in the same habitat in the eastern United States. They all mature underground and feed on juicy roots. Every 17 years, three species emerge and reproduce (Figure 19.4b). Each one has a *sibling* species of similar form and behavior. But siblings emerge on a 13-year cycle. This means that each species and its sibling do not get together except once every 221 years!

Behavioral isolation. Behavioral differences bar gene flow between related species. Before male and female birds copulate, they may engage in courtship displays (Figure 19.4c). A female bird is genetically prewired to recognize the singing, wing spreading, prancing, or head bobbing of a male of her species as an overture to sex. Females of different species usually do not.

Ecological isolation. Populations occupying different microenvironments may be ecologically isolated. Two manzanita species live in seasonally dry foothills of the Sierra Nevada, one at elevations between 600 and 1,850 meters, the other between 750 and 3,350 meters. They hybridize rarely, and only where the two ranges overlap. Water-conserving mechanisms operate in dry seasons. But one species is adapted to sites where water stress is not intense. The other lives in drier, exposed sites on rocky hillsides, so cross-pollination is unlikely.



Gamete mortality. Gametes of different species may have molecular incompatibilities. Example: If pollen lands on a plant of another species, it usually does not respond to the plant's molecular signals to germinate.

Postzygotic isolating mechanisms act in an embryo (Figure 19.5c). Unsuitable interactions among genes or gene products cause early death, sterility, or weak hybrids with low survival rates. Certain hybrids are sturdy but sterile. Mules, which are the offspring of a female horse and male donkey, are infertile hybrids.

A species is one or more populations of individuals having a unique common ancestor. Its individuals share a gene pool, produce fertile offspring, and remain reproductively isolated from individuals of other species.

Speciation is the process by which daughter species form from a population or subpopulation of a parent species. The process varies in its details and duration, but all modes of speciation are based on reproductive isolation.

19.2 The Main Model for Speciation

LINKS TO
SECTIONS
17.2, 17.6, 17.9



Three models for speciation differ in their basic premise of how populations become reproductively isolated.

START WITH GEOGRAPHIC ISOLATION

The genetic changes leading to a new species usually begin with *physical separation* between populations, so allopatry might be the most common speciation route. By a model for **allopatric speciation**, physical barriers stop gene flow among populations or subpopulations of a species. (*Allo-* means different; *patria* can be taken to mean the homeland.) In both groups, reproductive isolating mechanisms develop. In time, speciation is complete. Interbreeding is no longer possible even if daughter species come into contact with one another.

Whether a geographic barrier can block gene flow depends on an organism's means of travel (deliberate or accidental), how fast it can travel, and whether it is inclined to disperse. Populations of most species are some distance apart, and gene flow is intermittent. Barriers may arise abruptly and end the flow entirely. In the 1800s, a major earthquake buckled part of the Midwest and the Mississippi River changed course. It cut through the habitats of populations of insects that could not swim or fly. It ended the gene flow between those adjoining populations.

The fossil record suggests that geographic isolation generally happens slowly. For example, it happened after vast glaciers advanced into North America and Europe during the ice ages and cut off populations of plants and animals from one another. After glaciers

retreated and the descendants of related populations met, some were no longer reproductively compatible. They were separate species. Genetic divergence was not as great between other separated populations, so descendants still interbred. In their case, reproductive isolation was incomplete; speciation did not follow.

Also, remember how Earth's crust is fractured into gigantic plates? Slow, colossal movements inevitably alter the configurations of land masses (Section 17.6). As Central America formed, part of an ancient ocean basin was uplifted, and it became a land bridge—now called the Isthmus of Panama. Some camelids crossed the bridge into South America. Geographic separation led to new species: llamas and vicunas (Figure 19.6).

THE INVITING ARCHIPELAGOS

An **archipelago** is an island chain some distance from a continent. Many chains are so close to the mainland that gene flow is more or less unimpeded, so there is little if any speciation. The Florida Keys are like this. As you read earlier, the Hawaiian Islands, Galápagos Islands, and other remote, isolated archipelagos favor adaptive radiations and speciation (Figures 17.3 and 19.1). The islands are only the tops of volcanoes that started building up on the seafloor. In time they broke the surface of the ocean. We can therefore assume that their fiery surfaces were initially barren, with no life.

In one view, winds or ocean currents carry a few individuals of some mainland species to such islands, as shown in Figure 19.7*a*. Descendants colonize other

Figure 19.6 Allopatric speciations. The earliest camelids, no bigger than a jackrabbit, evolved in the Eocene grasslands and deserts of North America. By the end of the Miocene, they included the now-extinct *Procamelus*. The fossil record and comparative studies indicate that this may have been the common ancestral stock for llamas (**a**), vicunas (**b**), and camels (**c**). One of the descendant lineages dispersed into Africa and Asia and evolved into modern camels. A different lineage, ancestral to the llamas and vicunas, dispersed into South America after gradual crustal movements formed a land bridge between the two continents.



Late Eocene paleomap, before a land bridge formed between North and South America. At that time, North America and Eurasia were still connected by a land bridge

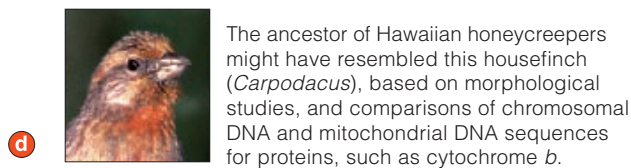
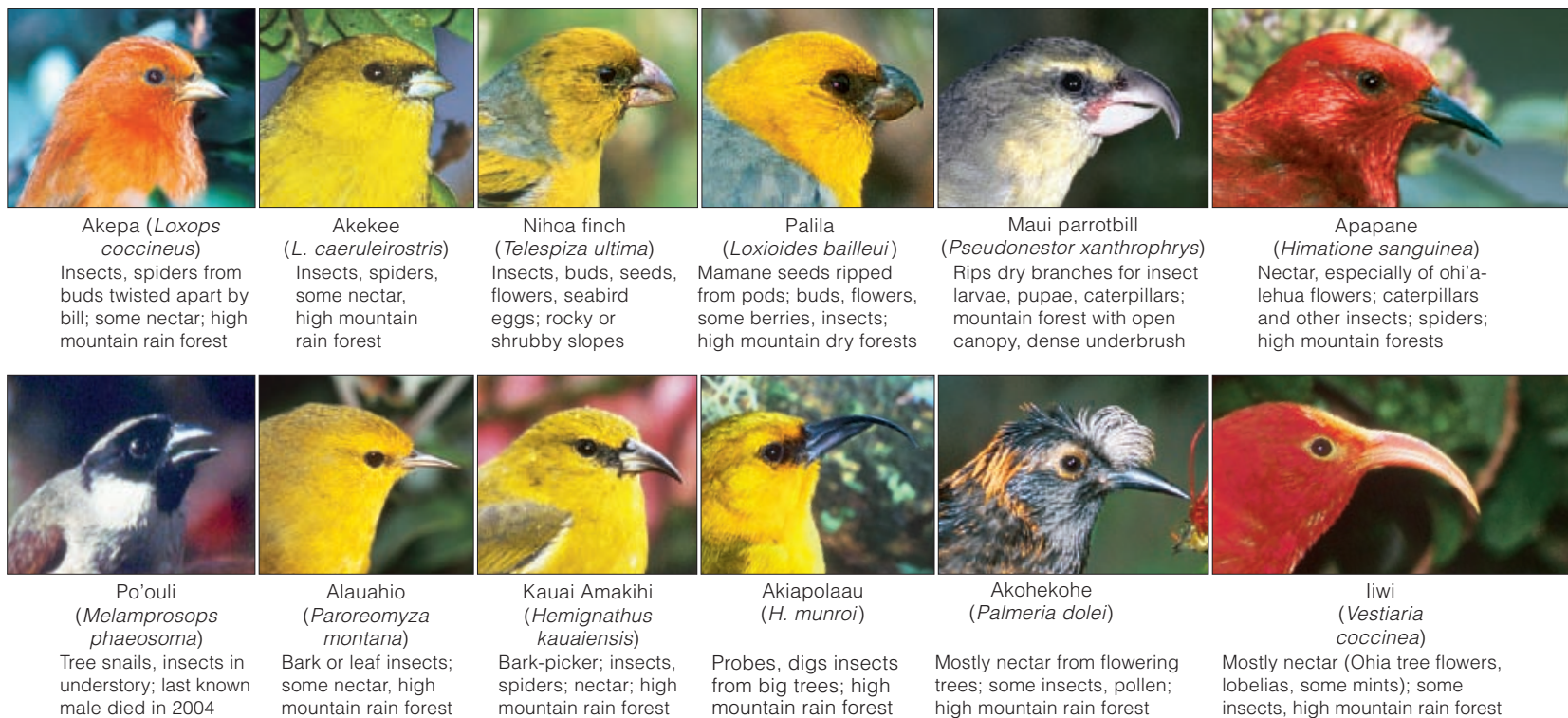


Figure 19.7 Animated! (a–c) Allopatric speciation on an isolated archipelago. (d) Twelve of fifty-seven known species and subspecies of Hawaiian honeycreepers, with a sampling of their dietary and habitat preferences. Honeycreeper bills are adapted to diverse foods, such as insects, seeds, fruits, and nectar in floral cups.

islands that form in the chain. Habitats and selection pressures differ within and between these islands, so allopatric speciation proceeds by way of divergences. Later, new species may even invade islands that were colonized by their ancestors. Distances between islands in archipelagos are enough to favor divergence but not enough to stop the occasional colonizers.

The big island of Hawaii formed less than 1 million years ago. Its habitats range from old lava beds, rain forests, and grasslands to snow-capped volcanoes. The first birds to colonize it found a buffet of fruits, seeds, nectars, tasty insects, and few competitors for them. The near absence of competition spurred rapid speciations into vacant adaptive zones. Figure 19.7d

shows some of the Hawaiian honeycreepers described earlier. Like thousands of other species of animals and plants, they are unique to this island. As still another example of their potential for speciation, the Hawaiian Islands combined make up less than 2 percent of the world's land masses. Yet they are the original home of 40 percent of all species of fruit flies (*Drosophila*).

By one allopatric speciation model, some type of physical barrier intervenes between populations or subpopulations of a species and prevents gene flow among them. Gene flow ends, and genetic divergences give rise to daughter species.

19.3 Other Speciation Models

LINKS TO
SECTIONS 4.10,
12.8, 15.4, 17.9



There is evidence that some species have arisen and are being maintained by less common mechanisms in which environmental barriers do not play a role.

ISOLATION WITHIN THE HOME RANGE

By the model for **sympatric speciation**, a species may form *within* the home range of an existing species, in the absence of a physical barrier. *Sym-* means together with, as in “together with others in the homeland.”

Evidence From Cichlids in Africa In Cameroon, West Africa, many species of freshwater fishes called cichlids may have arisen by sympatric speciation. The fish live in lakes that formed in the collapsed cones of small volcanoes (Figure 19.8). The cichlids probably colonized the lakes before volcanic action severed the inflow from a nearby river system.



Figure 19.8 A small, isolated crater lake in Cameroon, West Africa, where different species of cichlids may have originated by way of sympatric speciation.

Figure 19.9 Love those polyploids! Among them are several cotton species (including the kind shown here), sugarcane, seedless watermelons, bananas, plums, sweet potatoes, coffee plants with 22, 44, 66, or 88 chromosomes, and marigolds, azaleas, and lilies.



Remember how gene sequences can be compared (Section 17.9)? Ulrich Schliewen looked at differences in nuclear DNA and mitochondrial DNA for eleven cichlid species in Barombi Mbo, one of the small crater lakes. He also compared the samples with DNA from cichlid species in nearby lakes and rivers. He found that cichlid species in Barombi Mbo are more closely related to one another than to neighboring species. He concluded that all of the Barombi Mbo cichlids are descended from the same ancestral species—and that speciation must have occurred *within* this lake.

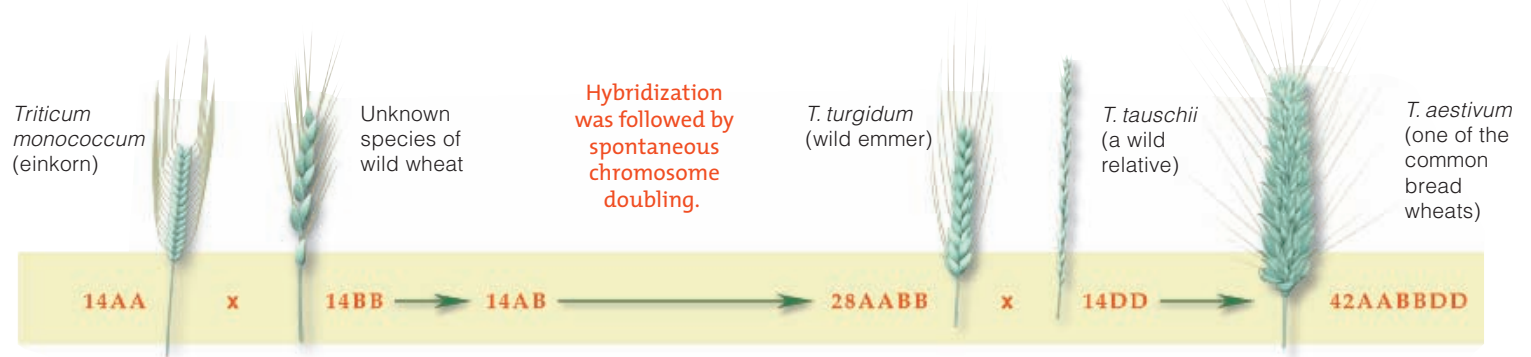
What could have cause the divergences that led to speciation? The lake is only 2.5 kilometers across, so it is not likely that cichlid populations were separated from one another by any type of barrier. Also, physical and chemical conditions are uniform throughout the lake. Another point: Cichlids are good swimmers, so individuals of different species often meet up.

However, the Barombi Mbo species do show some *ecological* separation. Feeding preferences put species in different places. Some feed in open waters, others at the lake bottom. Yet they all breed close to the lake bottom, in sympatry. Was this small-scale ecological separation enough to promote sexual selection among potential mates? Possibly. Over time, it may have led to reproductive isolation, then speciation.

Ploidy's Impact Reproductive isolation might happen within a few generations through **polyploidy**, in which individuals inherit three or more sets of the chromosomes characteristic of their species (Section 12.8). Either a somatic cell fails to divide mitotically after its DNA is duplicated, or nondisjunction occurs at meiosis and results in an unreduced chromosome number in gametes. Offspring usually cannot breed or mate successfully with the parent species, but they may be able to reproduce asexually.

Autopolyploids arise by a doubling of the parental chromosome number. This event arises spontaneously in nature but can be artificially induced in plant breeding laboratories. Breeders expose dividing plant cells to colchicine which, recall, stops microtubular spindles from forming during mitosis (Section 4.10). Without the spindle, duplicated chromosomes do not separate, and cells with the unreduced chromosome number may function as gametes.

Allopolyploids originate through (1) spontaneous or induced hybridization between closely related species and (2) doubling of the chromosome number. Figure 19.9 is one example. As genome studies reveal, many stable allopolyploids originated long ago. The kinds produced in the laboratory may or may not prove to



a By 11,000 years ago, humans were cultivating wild wheats. Einkorn has a diploid chromosome number of 14 (two sets of 7). It probably hybridized with another wild wheat species having the same number of chromosomes.

b About 8,000 years ago, the allopoloid called wild emmer originated from an AB hybrid wheat plant in which the chromosome number doubled. Wild emmer is tetraploid, or AABB; it has two sets of 14 chromosomes.

c An AABB plant probably hybridized with *T. tauschii*, a wild relative of wheat. Its diploid chromosome number is 14 (two sets of 7 DD). Common bread wheats have a chromosome number of 42 (six sets of 7 AABBDD).

be stable and fertile. Attempts are more successful if the species are close relatives.

Plant speciation is rapid when polyploids produce fertile offspring by self-fertilizing or cross-fertilizing with an identical polyploid. The ancestor of common bread wheat apparently was a wild species, *Triticum monococcum*, which spontaneously hybridized about 11,000 years ago with another wild species (Figure 19.10). Much later in time, a spontaneous chromosome doubling gave rise to *T. turgidum*, an allopoloid species with two sets of chromosomes (AABB). Later still, another hybridization resulted in *T. aestivum*, a bread wheat with a chromosome number of 42.

About 95 percent of fern species and 30–70 percent of flowering plants are polyploid species. So are a few conifers, mollusks, insects, and other arthropods, as well as fishes, amphibians, and reptiles. What about mammals? In 1999, a polyploid species of rat with a chromosome number of 102 was found in Argentina.

ISOLATION AT HYBRID ZONES

Parapatric speciation might proceed when different selection pressures operating across a broad region affect populations that are in contact along a common border. Hybrids that form in the contact zone are less fit than individuals on either side of it. Because the hybrids are being selected against, they appear in the hybrid zone only (Figure 19.11).

By a sympatric speciation model, daughter species arise from a group of individuals within an existing population. Polyploid flowering plants probably formed this way.

By a parapatric speciation model, populations maintaining contact along a common border evolve into distinct species.

Figure 19.10 Animated! Presumed sympatric speciation in wheat. Wheat grains 11,000 years old and diploid wild wheats have been found in the Near East, and chromosome analysis indicates that they hybridized. Later, in a self-fertilizing hybrid, homologous chromosomes failed to separate at meiosis, and it produced fertile polyploid offspring. A polyploid descendant hybridized with a wild species. We make bread from grains of their hybrid descendants.

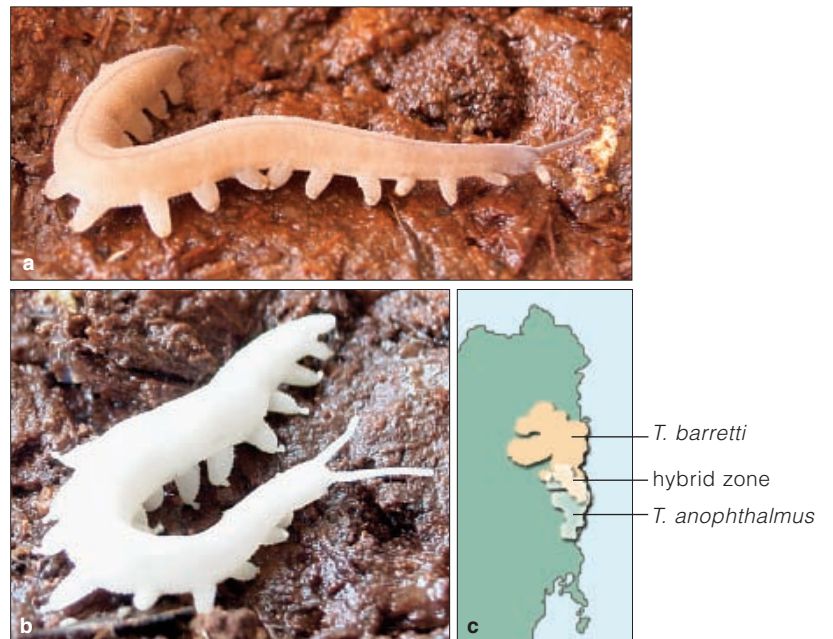


Figure 19.11 Example of parapatric speciation on the island of Tasmania, directly south of eastern Australia.

(a) Giant velvet worm, *Tasmanipatus barretti* and (b) blind velvet worm, *T. anophthalmus*.

(c) Both of these rare species of velvet walking worms live in adjoining regions of northeastern Tasmania. Their habitats overlap in a hybrid zone. Hybrid offspring are sterile, which may be the main reason these two species are maintaining separate identities in the absence of an obvious physical barrier between their habitats.

19.4 Patterns of Speciation and Extinction

LINK TO
SECTION
17.7



All species, past and present, are related by descent. They share genetic connections through lineages that extend back in time to the molecular origin of life.

BRANCHING AND UNBRANCHED EVOLUTION

The fossil record reveals two patterns of evolutionary change, one branching, the other unbranched. The first is known as **cladogenesis** (from *klados*, branch; and *genesis*, origin). In this pattern, a lineage splits when one or more of its populations become reproductively isolated and diverge genetically. It might be the main speciation pattern. It is the one introduced earlier, in Section 19.1.

In the second pattern, **anagenesis**, changes in allele frequencies and morphology accumulate in a single line of descent. (In this context, *ana-* means renewed.) Directional change is confined within that lineage, as gene flow continues among its populations. In time, allele frequencies and morphology shift so much that the new type differs significantly from the ancestral type, so it is classified as a separate species.

RATES OF CHANGE IN FAMILY TREES

Evolutionary trees summarize information on the relationships among groups. Figure 19.12 can start you thinking about how to construct these tree diagrams. Each branch represents one line of descent from a common ancestor. A *branch point* represents a time of genetic divergence.

When plotted against time, a branch that ends before the present (the treetop) signifies that the lineage is extinct. A dashed line signifies that we know something about the lineage but not exactly where it fits in the tree.

The **gradual model of speciation** holds that species originate by slight morphological changes over long time spans. The model fits with many fossil sequences. For example, sedimentary rock layers often hold vertical sequences of fossilized shells of foraminiferans, as in Figure 19.13. The sequence reflects gradual morphological change.

The **punctuation model of speciation** offers a different explanation for patterns of speciation. Most morphological changes are said to evolve

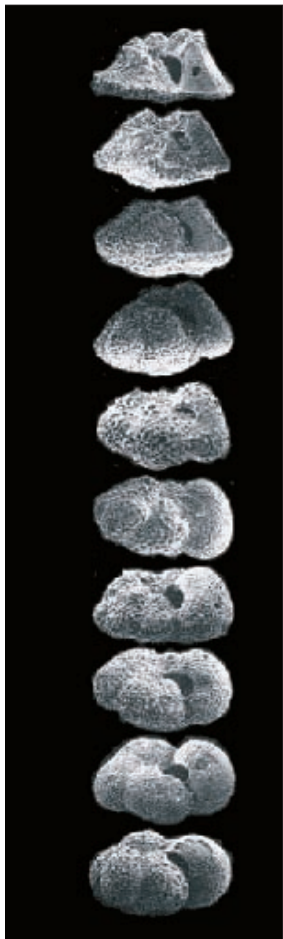


Figure 19.13 Fossilized foraminiferan shells from a vertical sequence of sedimentary rock layers. The first shell (*bottom*) is 64.5 million years old. The most recent (*top*) is 58 million years old. Analysis of shell patterns confirm that the evolutionary order matches the geological sequence.

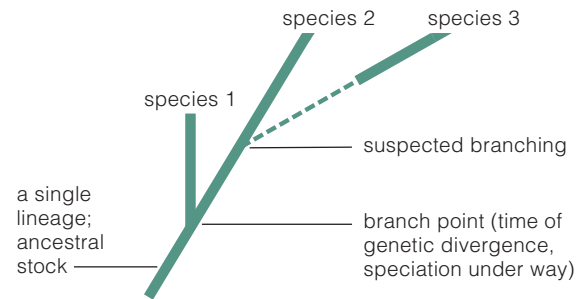


Figure 19.12 Some elements of evolutionary tree diagrams.

in a relatively brief geologic period, within the tens to hundreds of thousands of years when populations are starting to diverge. Directional selection, genetic drift, the founder effect, bottlenecks, or some combination of them favor rapid speciation. The daughter species recover fast from the adaptive wrenching, then they change very little over long periods.

The fossil record shows that stability prevailed for all but 1 percent of the history of most lineages, but it also reveals episodes of abrupt change. As it turns out, both models help explain speciation patterns. Changes have been gradual, abrupt, or both. Species originated at different times and have differed in how long they last. Some did not change much over millions of years; others were the start of adaptive radiations.

ADAPTIVE RADIATIONS

An **adaptive radiation** is a burst of divergences from a single lineage that leads to many new species. This is the pattern that gave rise to the family of Hawaiian honeycreepers. It requires **adaptive zones**, or a set of niches that come to be filled by a group of usually related species. Think of a *niche* as a way of life, such as “burrowing into seafloor sediments” or “catching winged insects in the air at night.” Either the lineage enters a vacant adaptive zone or it competes with the resident species well enough to displace them.

You will read more about niches in Chapter 46, in the context of community structure. For now, be aware of two concepts. First, a species must have physical access to a niche when it opens up. Mammals were once distributed in the uniformly tropical regions of Pangea. That supercontinent broke up into huge land

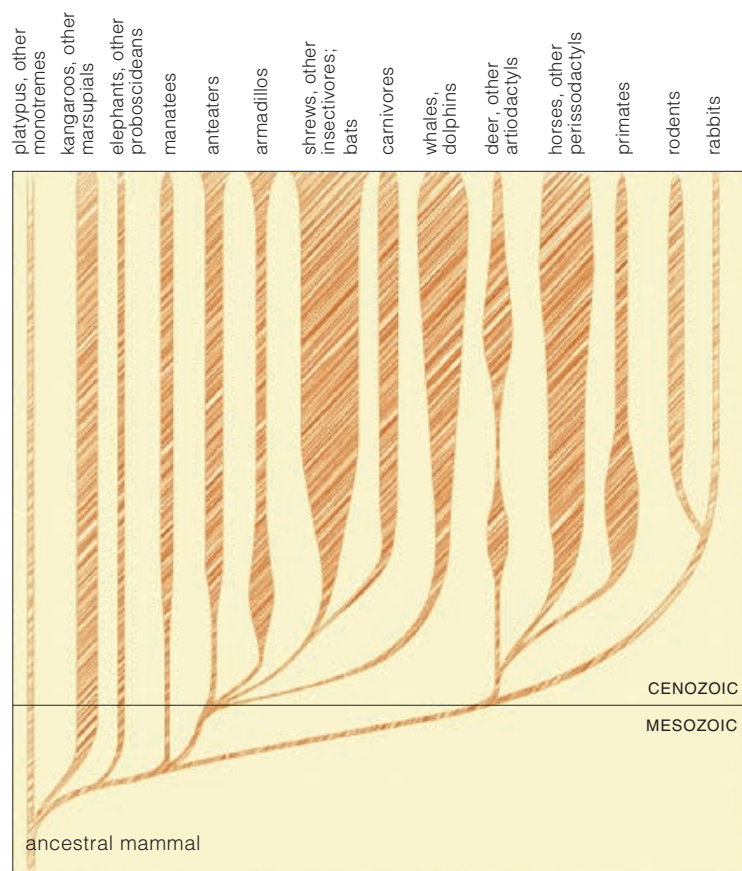


Figure 19.14 Adaptive radiation of mammals. Branch widths indicate the range of biodiversity at different times. Mammals arose 220 million years ago but did not start a great radiation until after the K–T impact removed the last of the dinosaurs (page 260). Not all lineages are shown. The 4,000 existing species include shrews, bats, and giant whales.

The photograph shows a fossil of *Eomaia scansoria* (Greek for ancient mother climber). About 125 million years ago, this insectivore crawled on low shrubs and branches. At this writing, it is the earliest placental mammal we know about.

masses, which drifted apart. Habitats and resources changed in different ways, in different places, and set the stage for independent radiations (Figure 19.14).

Second, a species may enter an adaptive zone by a **key innovation**: A chance modification in some body structure or function gives it the opportunity to exploit the environment more efficiently or in a novel way.

Once a species has entered an adaptive zone, genetic divergences can give rise to other species, which can fill a variety of niches within the zone. For example, when the forelimbs of certain vertebrate evolved into wings, novel niches opened up for the ancestors of modern birds and bats (Section 17.7).

EXTINCTIONS—THE END OF THE LINE

An **extinction** is the irrevocable loss of a species. By some estimates, more than 99 percent of all species that ever lived are extinct. The chapter introduction gave examples of typical causes, including imports of new predators and climate change.

In addition to ongoing, small-scale extinctions, the fossil record indicates there were at least twenty or more **mass extinctions**, or catastrophic losses of entire families or other major groups. They differed in size.

For example, 250 million years ago, 95 percent of all known species were abruptly lost. At other times, fewer groups were lost. Afterward, biodiversity slowly recovered as new species filled vacant adaptive zones.

Luck, again, had a lot to do with it. Many species were wiped out by global climate change. When one asteroid struck Earth and the last dinosaurs vanished, mammals were among the survivors that could radiate into vacated adaptive zones. Asteroids, imperceptibly drifting continents, climatic change—all contributed to past patterns of major extinctions and recoveries. In the next unit, you will have plenty of examples.

Lineages have changed gradually, abruptly, or both. Their member species originated at different times and have differed in how long they have persisted.

An adaptive radiation is the rapid origin of many species from a single lineage. It happens when an adaptive zone, a set of similar niches, opens up and the lineage has physical, evolutionary, and ecological access to it.

Repeated and often large extinctions happened in the past. After times of reduced biodiversity, new species originated and occupied new or vacated adaptive zones.

19.5 Organizing Information About Species

LINK TO
SECTION
1.3



So far, you have been thinking about what a species is, how it originates, and what has become of the many, many millions of them that originated. Turn now to what taxonomists do with the information.

SETS OF ORGANISMS—THE HIGHER TAXA

One field of biology, *taxonomy*, deals with identifying, naming, and classifying species. It goes hand in hand with *systematics*, or the study of relationships among organisms. Any organism that has been identified as representing a new species is assigned a unique two-part scientific name, the first part being the genus. As outlined in Chapter 1, species are grouped into more inclusive categories, such as families, orders, classes, phyla (or divisions, which is an equivalent ranking). Figure 19.15 has a few examples.

Each set of organisms in a given category is called a **taxon** (plural, taxa). The sets above the species level are known as the higher taxa, which are the units of classification systems. Most classification systems are now phylogenetic, meaning that they reflect perceived evolutionary connections within and between higher taxa as well as patterns of evolutionary change.

A **six-kingdom classification system** promoted by Robert Whittaker prevailed for some time. It assigned all of the prokaryotic species to kingdoms Eubacteria and Archaea, and all single-celled eukaryotes (as well as many multicelled species) to kingdom Protista. It

bestowed separate kingdom status on animals, plants, and fungi. Figure 19.16 shows the six kingdoms of this system. Section 1.3 sketched out a few defining traits for their representatives, which are topics of the next unit of the book.

New fossil finds, and new insights from geology, morphological studies, and biochemical comparisons, caused many researchers to rethink the six-kingdom system. Most decided to subsume the groups into a **three-domain system**, in which the three highest taxa are Bacteria, Archaea, and Eukarya (Figure 19.16).

Why the change? Ongoing research revealed that many of the taxa in earlier classification schemes are not monophyletic, or a “single tribe.” A **monophyletic group** includes only the descendants from an ancestral species in which a unique feature first evolved. Said another way, the branchings in each taxon should be outgrowths from a single stem.

One problem with the six-kingdom system was that no one could find a single stem for the thousands of diverse single-celled and multicelled eukaryotic species of “kingdom Protista.” Research is now clarifying their evolutionary connections with remarkable speed.

A CLADISTIC APPROACH

Think of each set of species descended from just one ancestral species as a **clade** (from *klados*, a Greek word for branch or twig). A cladistic classification system

					
KINGDOM	Bacteria	Plantae	Plantae	Animalia	Animalia
PHYLUM	Proteobacteria	Coniferophyta	Anthophyta	Arthropoda	Chordata
CLASS	Epsilonproteobacteria	Coniferopsida	Monocotyledonae	Insecta	Mammalia
ORDER	Campylobacterales	Coniferales	Asparagales	Diptera	Primates
FAMILY	Helicobacteraceae	Cupressaceae	Orchidaceae	Muscidae	Hominidae
GENUS	<i>Helicobacter</i>	<i>Juniperus</i>	<i>Vanilla</i>	<i>Musca</i>	<i>Homo</i>
SPECIES	<i>H. felis</i>	<i>J. occidentalis</i>	<i>V. planifolia</i>	<i>M. domestica</i>	<i>H. sapiens</i>
COMMON NAME	none	western juniper	vanilla orchid	housefly	human

Figure 19.15 Taxonomic classification of five species. Each species has been assigned to ever more inclusive sets of organisms—in this case, from species to kingdom.

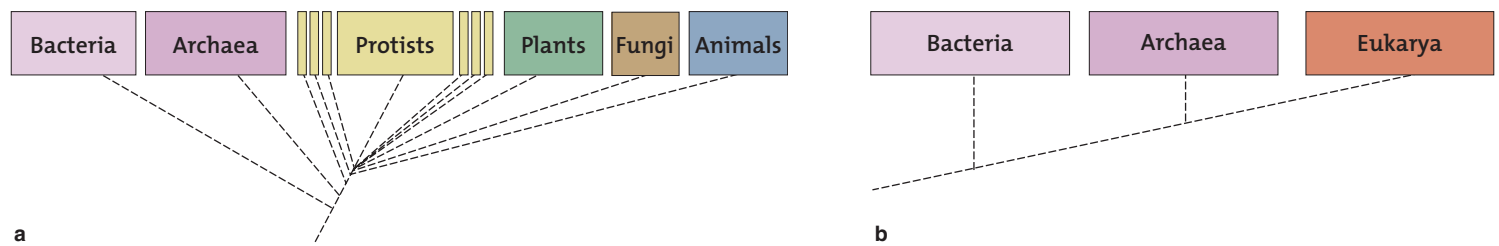


Figure 19.16 Animated! (a) Six-kingdom system of classification. In time, protists may be divided into more kingdoms. (b) The more recent three-domain system of classification. Protists, plants, fungi, and animals share features that unite them in domain Eukarya.

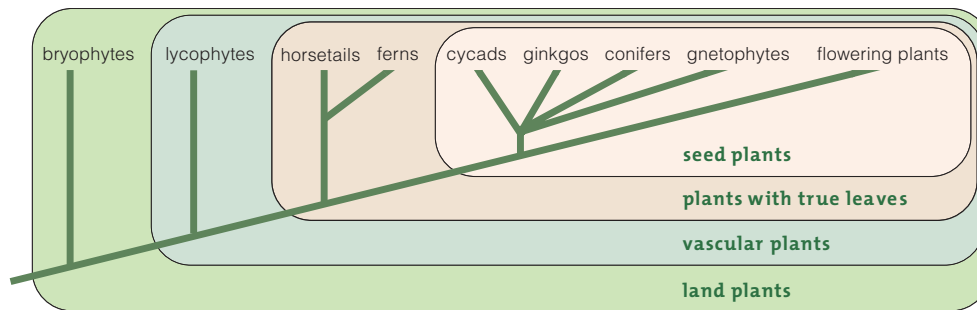


Figure 19.17 Evolutionary tree for land plants, with monophyletic groups nested as sets within sets. All but bryophytes have vascular tissues. All but bryophytes and lycophytes have true leaves. All but bryophytes, lycophytes, horsetails, and ferns produce seeds.

defines clades in terms of the history of divergences, or branch points in time. Only species that share traits derived from the last common ancestor are in the same clade. A **derived trait** is a novel feature that evolved in one species and is present only in its descendants. This emphasis means the descendants within a clade can differ—sometimes exuberantly so—in other traits.

Evolutionary tree diagrams called **cladograms** use the position of branch points from the last shared ancestor to convey inferred evolutionary relationships (phylogenies) among taxa. A cladogram is an estimate of “who came from whom.” It has no time bar with absolute dates, so it cannot convey differences in rates of evolution among taxa. Even so, a cladistic approach has already reinforced part of the fossil record, and it is making us reevaluate interpretations of the past.

A tree of life only looks like a simple stick drawing. Many thousands of morphological and biochemical traits were analyzed during the attempts to make its evolutionary connections. For example, as you will see in the next unit of the book, detailed comparisons of genes and ribosomal RNAs have revealed sometimes surprising similarities and differences among groups. The evolutionary tree of life in Section 19.6 is based on such combined evidence.

The derived traits used to construct a cladogram also help us visualize different monophyletic groups as *sets within sets*. For example, Figure 19.17 shows a cladogram for major sets of land plants that have been

nested into ever larger categories. We assume that the cycads, ginkgos, conifers, gnetophytes, and flowering plants form one set, because only they have a common ancestor that was the first seed-producing plant. The seed plants are nested in a larger set—plants with true leaves—that includes horsetails and ferns but excludes lycophytes and bryophytes. Only the bryophytes are not nested in the still-larger set called vascular plants; they do not have tubelike tissues that deliver water and solutes throughout the plant body.

The section to follow shows you how to construct a cladogram. It provides a closer look at the advantages and some of the pitfalls of a cladistic approach.

Taxonomists identify, name, and classify sets of organisms into ever more inclusive categories, the higher taxa.

Classification systems organize and simplify the retrieval of information about species. Phylogenetic systems attempt to reflect evolutionary relationships among species.

Reconstructing the evolutionary history of a given lineage is based on detailed understanding of the fossil record, morphology, life-styles, and habitats of its representatives, and on biochemical comparisons with other groups.

Recent evidence, especially from comparative biochemistry, favors the grouping of organisms into a three-domain system of classification—Archaea, Bacteria, and Eukarya (protists, plants, fungi, and animals).

19.6 How To Construct a Cladogram

 LINK TO
SECTION
17.6


In case you would like to know how a cladogram can be constructed, here is a step-by-step approach.

Suppose you want to make a cladogram for vertebrates. You select an *ingroup* of organisms with traits that suggest they might be related—in this case, jaws and paired appendages. You focus on sharks, mammals, crocodiles, and birds because they also differ clearly in some morphological, physiological, and behavioral traits, or characters. Now you must select a different vertebrate that can be used as a reference point for estimating evolutionary distances within the ingroup.

To keep things simple, you check for the presence (+) or absence (–) of seven traits and tabulate them, as in Figure 19.18a. After scanning Chapter 26, you decide that lampreys are only distantly related to the other four vertebrates. For instance, although a tubular structure called a notochord forms in its embryos, as it does for all other vertebrates, only lampreys have no jaws or paired appendages, such as lateral fins and legs. They can be the *outgroup*, the one with the fewest derived traits when compared to the others.

Derived traits, recall, are evidence of morphological divergence and branching in an evolutionary tree. In Figure 19.18b, each zero (0) across the columns of traits for each vertebrate indicates an ancestral condition. Each numeral one (1) means the vertebrate shows the derived trait.

Now you look for derived traits that the selected groups do or do not share. For example, the crocodile, mammal, and bird share five derived traits, but the bird and the shark share only three. You can now make a simple cladogram, although systematists often use many traits of many taxa. Typically they use a computer to analyze data and find the pattern that is best supported by a lot of information.

Figure 19.18c–g shows how a cladogram develops as you keep adding information to it. Start with the presence or absence of jaws and paired appendages, two traits that all

groups except lampreys derived from a common ancestor. What about lungs? Like lampreys, sharks do not have them, so you have identified another branch point in vertebrate evolution. Past that branch point, only mammals have hair, only crocodiles and birds have some form of gizzard. Only birds and their immediate ancestors have feathers.

How do you “read” the final cladogram? Remember, it is an estimate of *relative* relatedness, which implies common ancestry. Birds are more closely related to crocodiles than they are to mammals. Crocodiles are not the ancestor of birds (they are modern organisms, too), but both share a more recent common ancestor than either does with mammals. Birds, crocodiles, and mammals are closer to one another evolutionarily than they are to the shark.

The higher up a branch point is on a family tree, the more derived traits are shared. The lower the position of the branch point between two groups in the diagram, the fewer traits are shared with other groups being investigated.

A few words of caution: Interpretations of evolutionary relationships are more reliable when many traits are used, and there must be strong evidence that shared traits are derived. This helps counter the impact of a bad choice, such as including a trait that is a result of morphological convergence rather than divergence (Section 17.6).

The choice of derived traits is essential. If you were to select body size, for instance, you might wrongly perceive an evolutionary connection between *Sauroposeidon* (a dinosaur that weighed 60 tons), blue whales (mammals that weigh 200,000 pounds), quaking aspen (one plant has 50,000 stems and weighs an estimated 13 million pounds), and a honey mushroom that has been growing for 2,400 years (its underground body extends through 2,200 acres).

Cladograms are only as good as the choices made for their construction—and good choices start with a broad, deep knowledge of life.

Figure 19.18 (a) Charting out a selection of traits among vertebrate groups that can be used for the construction of a simple cladogram.

(b) A trait's absence in an outgroup or ingroup indicates an ancestral state (here indicated by a zero). Its presence in the set of vertebrates selected as the ingroup is taken to mean it is a derived trait, indicated by a numeral one.

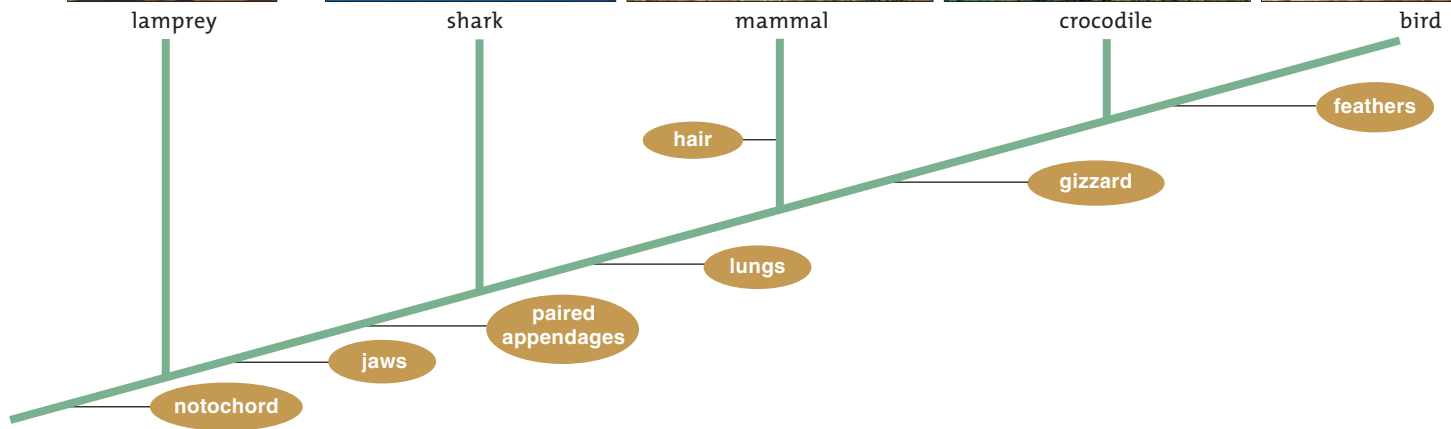
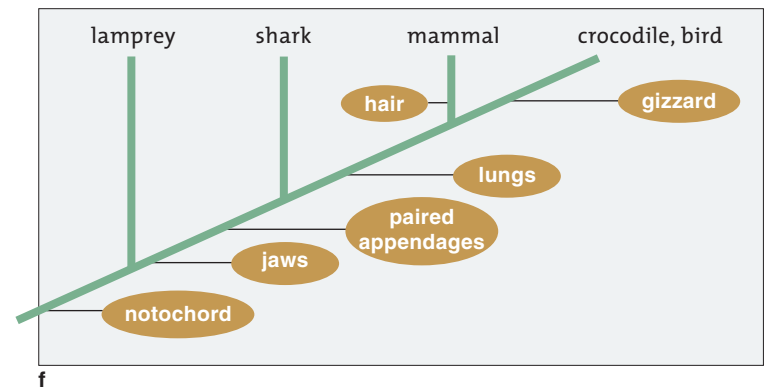
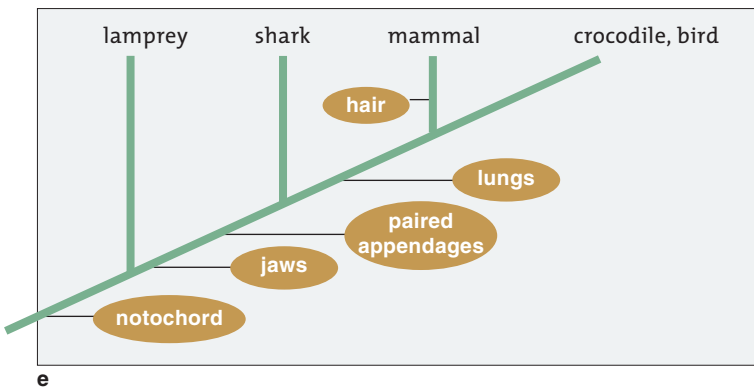
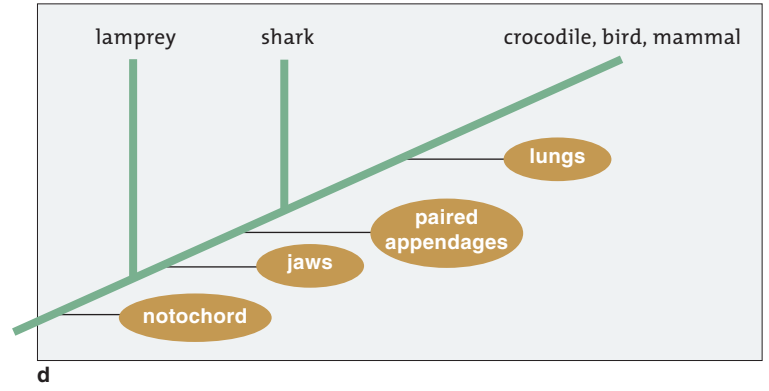
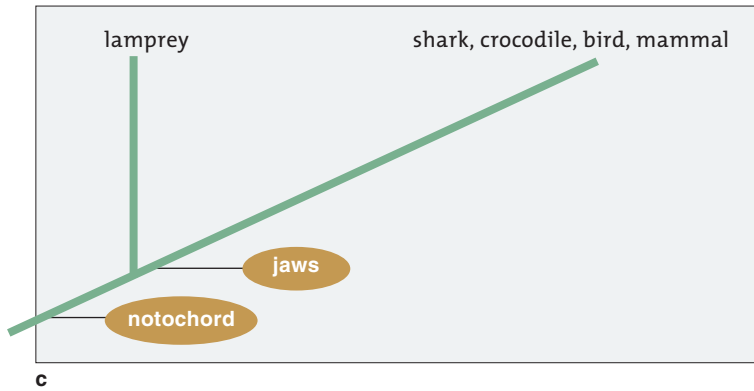
(c–g) Step-by-step construction of a cladogram, as explained in the text.

Taxon	Traits, or Characters						
	Notochord in Embryo	Jaws	Paired Appendages	Lungs	Hair	Gizzard	Feathers
Lamprey	+	–	–	–	–	–	–
Shark	+	+	+	–	–	–	–
Crocodile	+	+	+	+	–	+	–
Mammal	+	+	+	+	+	–	–
Bird	+	+	+	+	–	+	+

a

Taxon	Traits, or Characters						
	Notochord in Embryo	Jaws	Paired Appendages	Lungs	Hair	Gizzard	Feathers
Lamprey	1	0	0	0	0	0	0
Shark	1	1	1	0	0	0	0
Crocodile	1	1	1	1	0	1	0
Mammal	1	1	1	1	1	0	0
Bird	1	1	1	1	0	1	1

b



g The completed diagram, livened up with photographs of representative species.

19.7 Preview of Life's Evolutionary History

Figure 19.19, a tree of life, shows the macroevolutionary links among major groups of organisms, as described in the next unit. Each set of organisms (taxon) has living representatives. Each branch point represents the last

common ancestor of the set above it. The small boxes within domains Archaea and Eukarya highlight taxa that are currently being recognized as the equivalent of kingdoms in earlier classification systems.

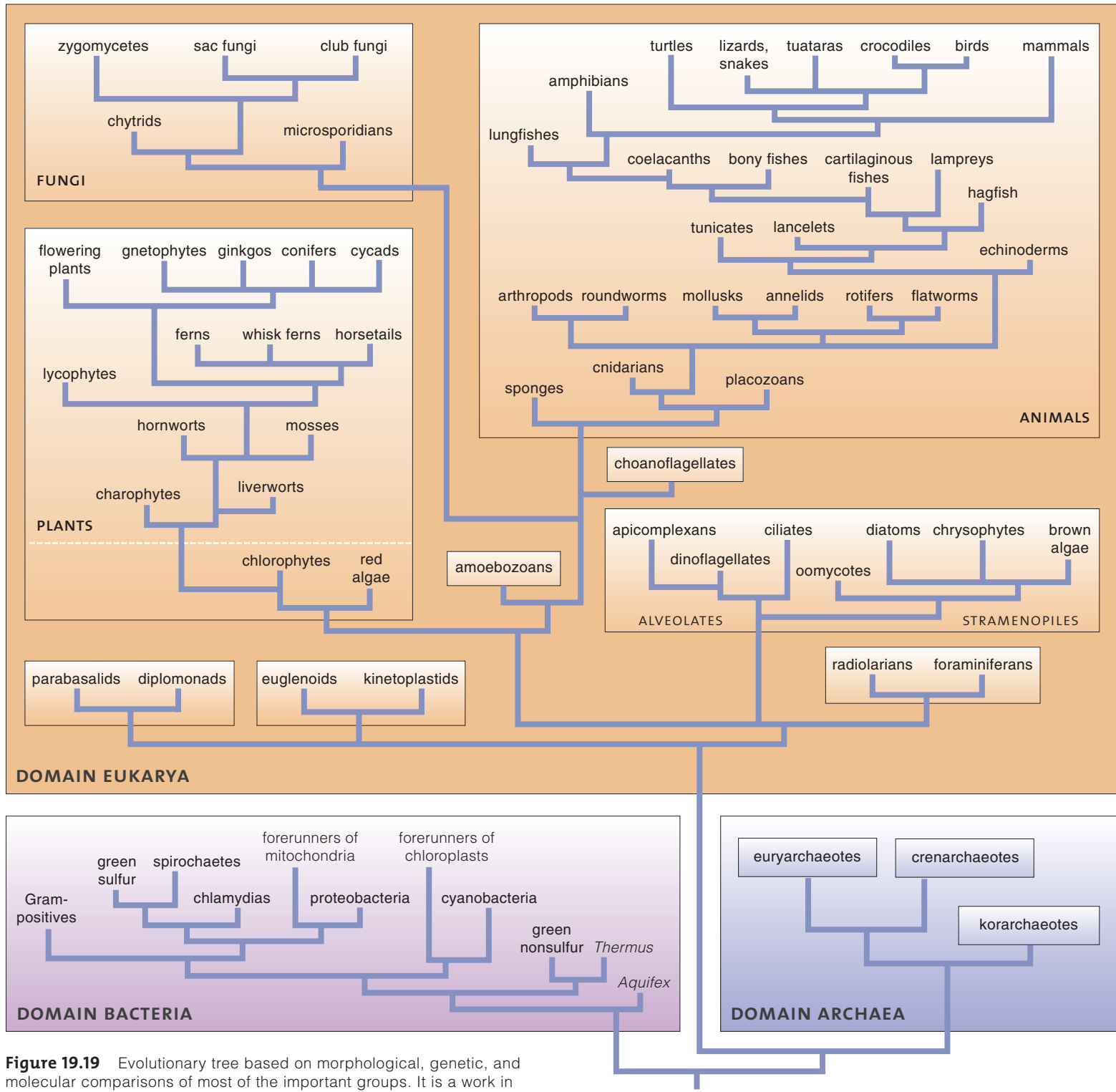


Figure 19.19 Evolutionary tree based on morphological, genetic, and molecular comparisons of most of the important groups. It is a work in progress, subject to refinements as more information comes in.

biochemical and molecular origin of life

19.8 Madeleine's Limbs

CONNECTIONS

So what does macroevolution have to do with you and me? Everything.

In August of 1994, about 900 million years after the first animals appeared on Earth, Madeleine made *her* entrance. Her grandmothers and aunts made a quick count—arms, legs, ears, and eyes, two of each; fully formed mouth and nose—just to be sure these were present and accounted for. One grandmother, having been too long in the company of biologists, had an epiphany as she witnessed Madeleine's birth. In that instant she sensed ancestral connections between the distant past and, through this child, the future.

Madeleine's body plan did not emerge out of thin air. Thirty-five thousand years ago, people just like us were having children just like Madeleine. If we are reading the fossil record correctly, then five million years ago, the offspring of individuals on the road to modern humans resembled her in some respects but not others. Sixty million years ago, primate ancestors of those individuals were giving birth precariously, up in the trees. Two hundred fifty million years ago, the mammalian ancestors of those primates were giving birth—and so on back in time to the very first animals, which had no limbs or eyes or noses at all.

We know little about the very first animals. Yet one thing is clear. By the dawn of the Cambrian, they had given rise to all major groups of invertebrates and to

Madeleine's backboneed, jawed ancestors. We know this from fossils. For example, one Cambrian community flourished 530 million years ago in, on, and above the dimly lit mud in a submerged basin between a steep reef and the coast of an early continent. About 500 feet below the surface, the water was oxygenated and clear (Figure 19.20). Like a castle built from wet sand, their home was unstable and an underwater avalanche buried them. Over great time spans, compaction and chemical change transformed those small, flattened animals into fossils. By 1909, tectonic activity had moved the fossils high into the eastern mountains of British Columbia, and there a fossil hunter found them.

In the next unit, you will compare body plans of diverse organisms. Such comparisons give insight into evolutionary relatedness and help us construct family trees. As you poke through the tree branches, make use of the evolutionary perspective. At each branch point, the processes of microevolution gave rise to workable changes in body plans. Your collection of conserved and modified traits, and Madeleine's, evolved earlier in countless generations of vertebrates and, even before them, in ancient invertebrate forms.

Our family tree is a record of conserved and derived traits.

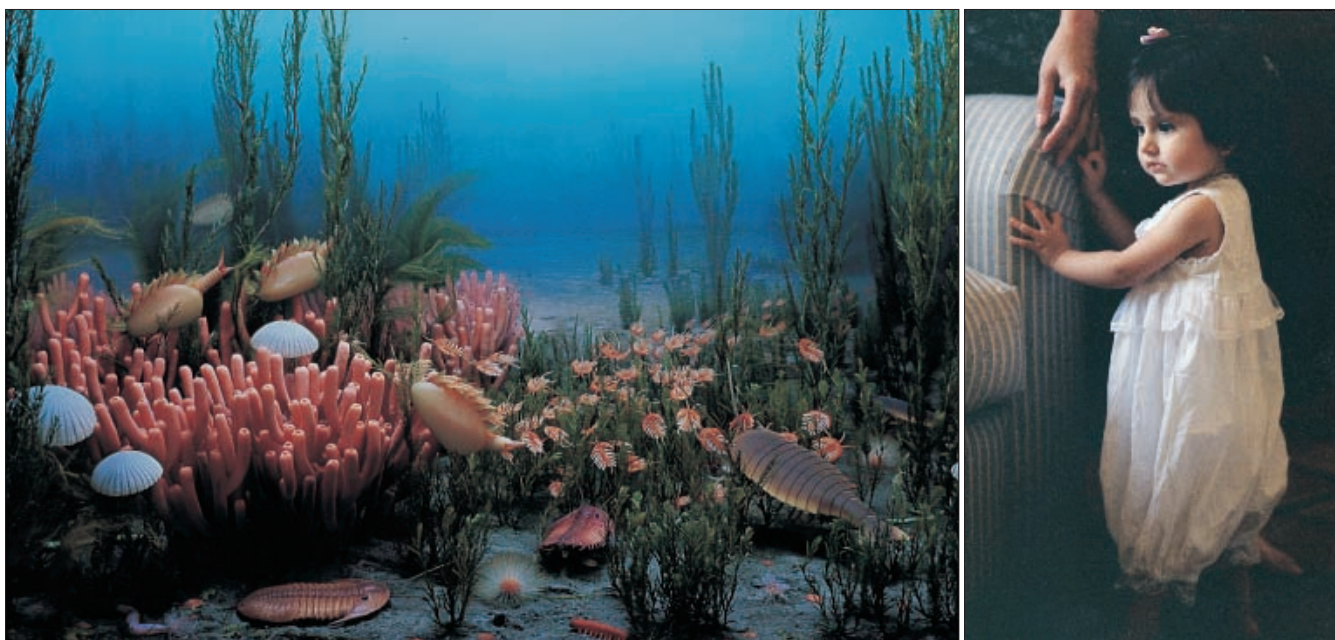


Figure 19.20 *Left*, reconstruction of a few Cambrian animals known from fossils of the Burgess Shale in British Columbia. *Right*, Madeleine.

<http://biology.brookscole.com/starr11>

Summary

Section 19.1 Populations of each species share at least one unique trait, a legacy of a common ancestor. In sexually reproducing species, individuals interbreed, produce fertile offspring under natural conditions, and are reproductively isolated from all other species.

If gene flow ends between populations, divergences may lead to new species. Mutation, natural selection, and genetic drift operate independently and may give rise to reproductive isolating mechanisms (Table 19.1). In some cases, reproductive isolation occurs in a few generations.

Prezygotic isolating mechanisms stop interbreeding. They include incompatibilities between reproductive parts or between gametes, differences in reproductive timing or behavior, and ecological restriction to different microenvironments in the same area. The postzygotic mechanisms lead to early death, sterility, or unfit hybrid offspring. They come into play after fertilization.

Biology Now

Use the animation and interaction on *BiologyNow* to explore how species become reproductively isolated.

Read the InfoTrac article “Tracking the Red-Eyed, Sluggish, and Ear-splitting,” Tabitha M. Powledge, *American Scientist*, July 2004.

Section 19.2 By the allopatric speciation model, a geographic barrier cuts off gene flow between two or more populations. Genetic divergence and reproductive isolation are favored and may result in a new species.

Biology Now

Learn more about speciation on an archipelago with the animation on *BiologyNow*.

Section 19.3 By a sympatric speciation model, populations in physical contact diverge from each other. Polyploid species of many plants and some animals have originated by chromosome doublings and hybridizations.

By a parapatric speciation model, different selection pressures across a broad region act on populations that are in contact along a common border. Unfit hybrids form in the contact zone, so populations on either side diverge independently from each other.

Biology Now

Explore the effects of sympatric speciation in wheat with the animation on *BiologyNow*.

Section 19.4 Macroevolution refers to the timing, duration, and direction of speciation in the history of life. These features differ among lineages. The major speciation patterns are unbranched (evolution within a single lineage) or branching (divergences from ancestral stock). Most lineages remain stable for long periods, but abrupt episodes of change also have occurred.

Radiations occur in adaptive zones, a similar set of niches that come to be filled by a (usually) related group of species. A niche is a way of life, such as catching insects in the air at night. Species must have physical, evolutionary, and ecological access to these zones.

A key innovation is a chance modification in some body structure or function that lets an organism exploit the environment more efficiently or in a novel way.

Most species are now extinct. Mass extinctions, slow recoveries, and adaptive radiations are major patterns.

Section 19.5 Each species has a unique, two-part scientific name. Taxonomy deals with identifying, naming, and classifying species. Systematics deals with reconstructing life’s evolutionary history (phylogeny). In classification systems, sets of organisms (taxa) are organized into ever more inclusive categories as a way to retrieve information about species.

A current three-domain classification system is based largely on phylogenetic evidence. It recognizes three domains: Bacteria, Archaea, and Eukarya. The Eukarya includes diverse lineages known informally as protists, as well as plants, fungi, and animals.

Biology Now

Review biological classification systems with the animation on *BiologyNow*.

Section 19.6 A cladistic classification system recognizes monophyletic groups. Each group is a clade, a set of species that includes only descendants that display a derived trait, inherited from an ancestor in which that trait first evolved. It is the equivalent of all branches growing from the same point on a stem.

Biology Now

Read the InfoTrac article “How Taxonomy Helps Us Make Sense Out of the Natural World,” Sue Hubbell, *Smithsonian*, May 1996.

Sections 19.7, 19.8 Representing life’s history as a tree with branchings from ancestral stems brings clarity to the view that all organisms are related by descent.

Table 19.1 Summary of Processes and Patterns of Evolution

Microevolutionary Processes		
Mutation	Original source of alleles	} Stability or change in heritable traits that define populations, and the species, is the outcome of balances or imbalances among all of these processes. Population size and prevailing conditions in the environment influence the outcome.
Gene flow	Preserves species cohesion	
Genetic drift	Erodes species cohesion	
Natural selection	Preserves or erodes species cohesion, depending on environmental pressures	
Macroevolutionary Processes		
Genetic persistence	The basis of the unity of life. The biochemical and molecular basis of inheritance extends from the origin of first cells through all subsequent lines of descent.	
Genetic divergence	Basis of life’s diversity, as brought about by adaptive shifts, branching, and radiations. Rates and times of change varied within and between lineages.	
Genetic disconnect	End of the line for a species. Mass extinctions are catastrophic events in which major groups abruptly and simultaneously are lost.	

Self-Quiz

Answers in Appendix II

- _____ can isolate one population from others.
 - Structural traits
 - Functional traits
 - Behavioral traits
 - all of the above
- Reproductive isolating mechanisms _____.
 - stop interbreeding
 - stop gene flow
 - reinforce genetic divergence
 - all of the above
- Most species originate by a (an) _____ route.
 - allopatric
 - sympatric
 - parapatric
 - parametric
- In evolutionary trees, a branch point represents a _____; and a branch that ends represents _____.
 - single species; incomplete data on lineage
 - single species; extinction
 - time of divergence; extinction
 - time of divergence; speciation complete
- Fossil evidence supports the _____ model of evolutionary change.
 - punctuation
 - gradual
 - both are correct
- Pinus banksiana*, *Pinus strobus*, and *Pinus radiata* are _____.
 - three families of pine trees
 - three different names for the same organism
 - three species grouped in the same genus
 - both a and c
- Individuals of a monophyletic group _____.
 - are all descended from an ancestral species
 - demonstrate morphological convergence
 - have a derived trait that first evolved in their last shared ancestor
 - both a and c
- A(n) _____ classification system reflects presumed evolutionary relationships.
 - epigenetic
 - tectonic
 - phylogenetic
 - both b and c
- In modern classification systems, groupings of sets of taxa range from _____ to _____.
 - kingdom; genera and species
 - kingdom; genera and domain
 - genera; domain and kingdom
 - species; kingdom and domain
- Match these terms suitably.

_____ phylogeny	a. now the most inclusive taxon
_____ extinction	b. tree of branching lineages
_____ domain	c. many lineages diverge from one in a new adaptive zone
_____ derived trait	d. end of a species or lineage
_____ cladogram	e. evolutionary history of species
_____ adaptive radiation	f. only in descendants of ancestor in which it first evolved

Additional questions are available on **Biology Now™**

Critical Thinking

- You notice several duck species in the same lake habitat, with no physical barriers hampering the ducks' movements. All the females of the various species look quite similar to one another. But the males differ in the



Figure 19.21
Rama the cama displaying his unexpected short temper.

patterning and coloration of their feathers. Speculate on which forms of reproductive isolation may be keeping each species distinct. How does the appearance of the male ducks provide a clue to the answer?

- Rama the cama*, a llama-camel hybrid, was born in 1997 (Figure 19.21). Camels and llamas have a shared ancestor but have been separated for 30 million years. Veterinarians collected semen from a male camel that weighed close to 1,000 pounds, then used it to artificially inseminate a female llama one-sixth his weight. The idea was to breed an animal having a camel's strength and endurance and a llama's gentle disposition.

Instead of being large, strong, and sweet, Rama is smaller than expected and has a camel's short temper. Rama resembles both parents, with a camel's long tail and short ears but no hump, and llama-like hooves rather than camel footpads. Now old enough to mate, he is too short to get together with a female camel and too heavy to mount a female llama. He has his eye on Kamilah, a female cama born in early 2002, but will have to wait several years for her to mature. The question is, will any offspring from such a match be fertile?

What does Rama's story tell you about the genetic changes required for irreversible reproductive isolation in nature? Explain why a biologist might not view Rama as evidence that llamas and camels are the same species.

- Speculate on what might have been a key innovation in human evolution. Describe how that innovation might be the basis of an adaptive radiation in environments of the distant future.
- Shannon thinks there are too many major taxa and sees no reason to make a new one for something as tiny as archaeans. "Keep them with the other prokaryotes!" she says. Taxonomists would call her a "lumper." But Andrew is a "splitter." He sees no reason to withhold separate status from archaeans simply because they are part of a microscopic world that not many people know about. Which may be the most useful: more or fewer boundaries between groups? Explain your answer.
- Richard Lenski uses bacterial populations in culture tubes to develop model systems for studying evolution. Bacteria produce several generations in a day. Researchers can store them in the deep freeze, then bring them back to active form, unaltered, to directly compare ancestors and their descendants. Are bacterial models relevant to any evolutionary studies of sexually reproducing organisms? Before you answer, read a short article by P. Raine and M. Travisano entitled "Adaptive Radiation in a Heterogeneous Environment" (*Nature*, July 2, 1998: 69–72).