FIGURE 13.1 A coevolved interaction. The orchid *Angraecum sesquipedale* bears nectar in an exceedingly long spur and is pollinated by the long-tongued sphinx moth *Xanthopan morganii praedicta*. The moth was discovered about 40 years after Darwin predicted its existence. Each of the species in this mutualism is adapted to obtain something from the other.

Coevolution and Interactions among Species

Every species is subjected to natural selection from its biotic environment: the complex of other organisms with which it interacts. Most of these species can be classified as resources (used as nutrition or habitat), competitors (for resources such as food and space), enemies (predators or parasites), or mutualists. In mutualistic interactions, each species obtains a benefit from the other. (**Symbiosis**, meaning "living together," describes intimate associations between species that may be either mutualists or parasite and host. An endosymbiont lives within the other organism's body.) The community of other species with which a species interacts is complex and variable—both the identity and genetic composition of interacting species vary in time and place. Thus, a plant species may be pollinated or attacked by many species of insects, and be inhabited by any of hundreds of species of fungi and bacteria that live on or in its leaves and roots. Similarly, the natural environment of humans includes a variable "human microbiome": the trillions of bacteria, including thousands of species—mostly harmless and some even beneficial—that occupy the gut, skin, nostrils, and other microhabitats [15, 34, 55].

Some of the most familiar examples of natural selection, such as industrial melanism in the peppered moth and the sickle-cell polymorphism in human hemoglobin, entail biological agents (predaceous birds and malarial parasites, respectively) (see Chapter 5). In many such interactions, the evolution of one species has been affected by the other, but not vice versa. **Coevolution**, strictly defined, is reciprocal genetic change in interacting species, owing to natural selection imposed by each on the other. Not all adaptations of one species to other species are necessarily coevolved.

The nature and strength of an interaction between two species may vary depending on genotype, environmental conditions, and other species with which those species interact. For example, populations of the limber pine in areas where squirrels eat the seeds have cones that reduce squirrel depredation, but are also less favorable for the Clark's nutcracker, a bird that the pine depends on for seed dispersal (**FIGURE 13.2**). Thus the selection that species exert on each other may differ among populations, resulting in a geographic mosaic of coevolution that differs from one place to another [73].

The term "coevolution" includes several concepts [28, 72]. In its simplest form, called *specific coevolution*, two species evolve in response to each other (**FIGURE 13.3A**). Darwin's *Angraecum* orchid and its specialized pollinating moth are an example. *Diffuse coevolution* occurs when several species are involved and their effects are not independent (**FIGURE 13.3B**). For example, genetic variation in the resistance of a host to two different species of parasites might be correlated [35]. In *escape-and-radiate coevolution*, a species evolves a defense against enemies and is thereby enabled to radiate into diverse descendant species, to which different enemies may later adapt (**FIGURE 13.3C**).

A few cases have been described in which the phylogeny of a group of organisms matches the phylogeny of a group of its parasites or symbionts. An example is the association between aphids and endosymbiotic bacteria (*Buchnera*) that live in special aphid cells and supply the essential amino acid tryptophan to their hosts. The completely concordant phylogenies of the aphids and bacteria (**FIGURE 13.4**)

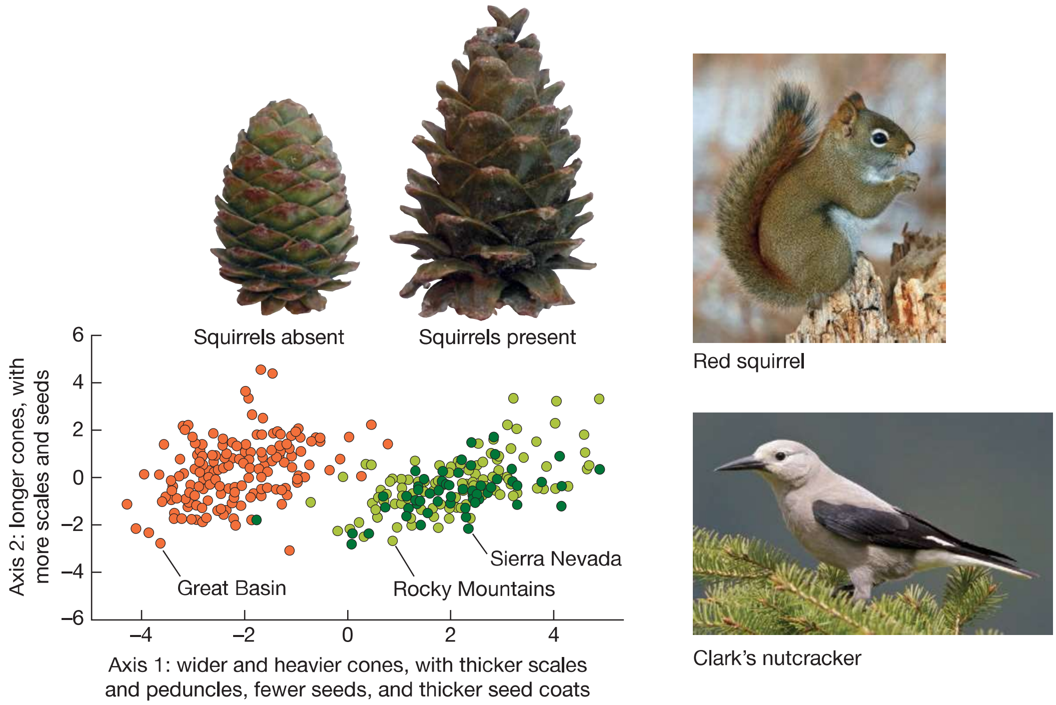

FIGURE 13.2 A geographic mosaic of interactions. Typical cones of limber pine (*Pinus flexilis*) populations that (at right) are adapted to resist seed-eating squirrels or (at left) are adapted for seed dispersal by Clark's nutcracker where squirrels are absent. The graph of two variables, each of which combines several measurements of cones and seeds, shows that pines in an area without squirrels (Great Basin, orange dots) differ from those in two areas with squirrels (Sierra Nevada and Rocky Mountains, dark and light green dots, respectively). Each dot represents one tree. (After [67]; pine cone photos from [67].)

show that this association dates from the origin of the aphids, and that the bacteria have diverged in concert with speciation in their hosts. The explanation is simple: the bacteria are transmitted from mother aphids to their offspring just as if they were mitochondria. By themselves, matching phylogenies should not be considered coevolution, because there need not have been any reciprocal adaptation. A match can arise simply because the parasite or endosymbiont has had little or no opportunity to be transmitted between different hosts. The phylogeny

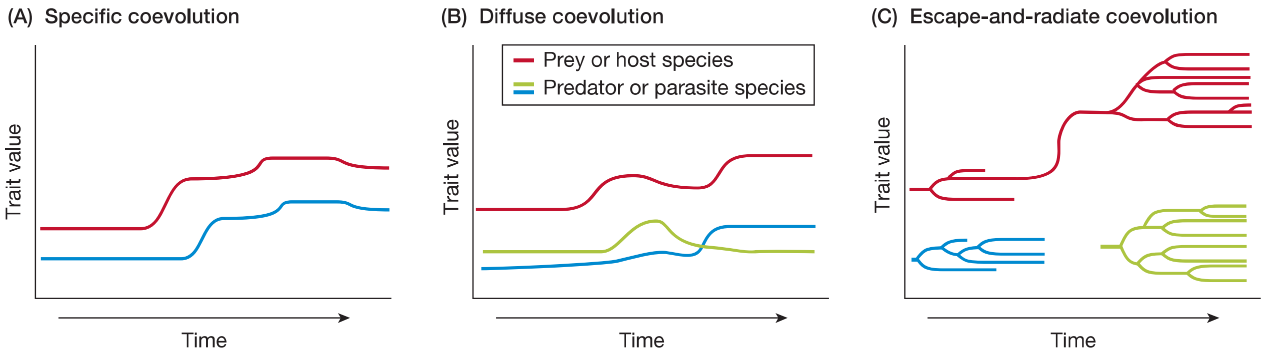

FIGURE 13.3 Three kinds of coevolution. In each graph, the horizontal axis represents evolutionary time, and the vertical axis shows the state of a character in a species of prey or host and one or more species of predators or parasites. (A) Specific coevolution. (B) Diffuse coevolution, in which a prey species interacts with two or more predators, can take many paths. In this case, a prey species becomes better defended against two predators, only one of which (blue curve) becomes better able to capture the prey. (C) Escape-and-radiate coevolution. A prey or host species evolves a major new defense, escapes association with a predator or parasite, and diversifies. Later, a different predator or parasite adapts to the host clade and diversifies.

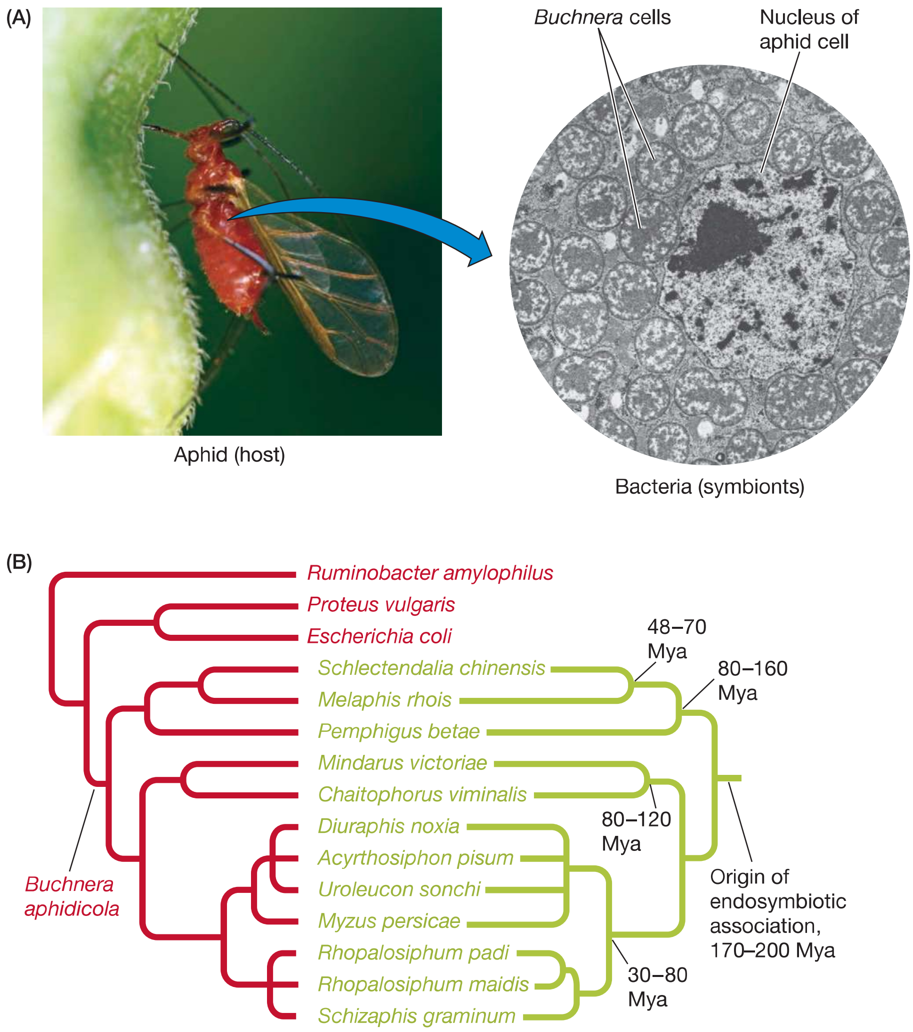

FIGURE 13.4 (A) *Buchnera aphidicola* bacteria are endosymbionts of aphids. The electron micrograph (at right) shows bacterial cells living inside a specialized aphid cell (bacteriocyte). (B) The phylogeny of endosymbiotic bacteria included under the name *Buchnera aphidicola* is perfectly congruent with that of their aphid hosts. Several related bacteria (names in red) were included as outgroups in this analysis. Names of the aphid hosts of the *Buchnera* lineages are given in green. The estimated ages of the aphid lineages are based on fossils and biogeography. These *Buchnera* lineages are as old as the aphid lineages that carry them. (After [53]; electron micrograph courtesy of N. Moran and J. White.)

of free-living parasites and mutualists seldom matches the host phylogeny very closely [29, 57, 82].

The Evolution of Enemies and Victims

Interactions between enemies and victims include predators and their prey, parasites and their hosts, and herbivores and their host plants. Such interactions are often unstable, because enemies can extinguish victim populations, or reduce them to the point that the enemy population becomes extinct for lack of food. Many species of Australian marsupials were driven to extinction by introduced foxes and feral cats [19]; a chytrid fungus has extinguished some species of frogs and threatens many other amphibians [12]. Because the future does not affect the action of natural selection (see Chapter 3), the possibility that the prey or host might be killed off does not cause enemies to evolve restraint that might preserve prey populations. Victims and their enemies coexist only if their interactions are stabilized by ecological and evolutionary factors, including adaptations to escape or resist enemies.