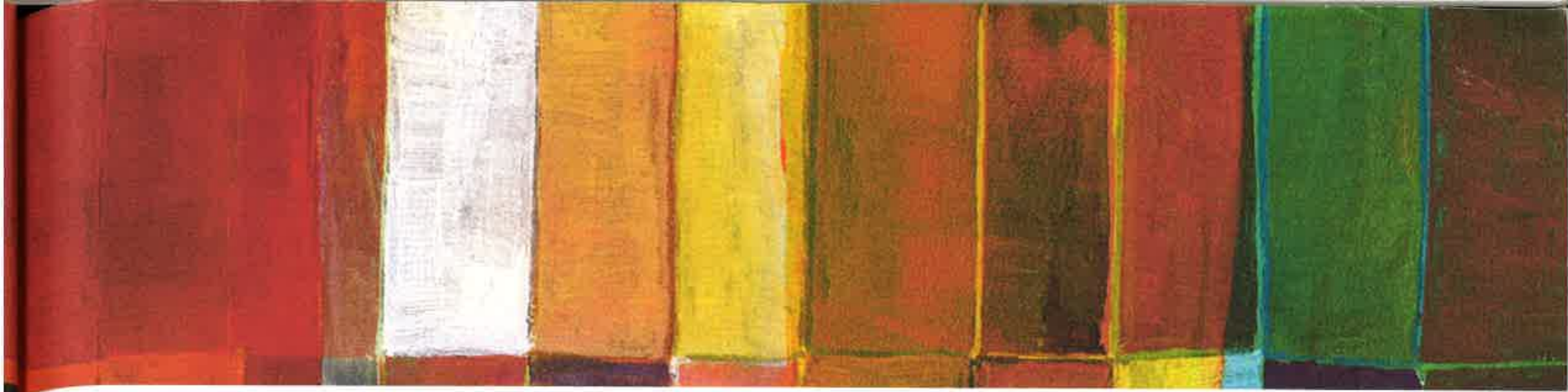

anthropology

what does it mean to be human?

FOURTH EDITION

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2018

New York Oxford
OXFORD UNIVERSITY PRESS

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What can the study of primates tell us about human beings?

Our closest animal relatives are the primates. This chapter introduces you to the richness and variety of primate ways of life and provides an overview of primate evolution. Primates are fascinating in their own right but also can help us understand more about what it means to be human.

CHAPTER OUTLINE

Primatologist Jane Goodall interacts with a chimpanzee.

Human beings are primates, and the evolution of human beings constitutes one strand of the broader evolutionary history of the primate order. Because knowledge of living primate species offers important clues to their evolutionary past, this chapter begins with an overview of what we know about living nonhuman primates. Because modern nonhuman primates have their own evolutionary history but also share an evolutionary history with human beings, we then turn to a brief look at their evolution.

What Are Primates?

Western Europeans first learned about African apes in the seventeenth century. Ever since, these animals have been used as a mirror to reflect on and speculate about human nature. But the results of this exercise have been contradictory. The physical characteristics that humans share with other primates have led many observers to assume that these primates also share our feelings and attitudes. This is called **anthropomorphism**, the attribution of human characteristics to nonhuman animals. In the twentieth century alone, Westerners vacillated between viewing primates as innocent and comical versions of themselves (Curious George) and as brutish and degraded versions of themselves (King Kong, Figure 3.1). When studying nonhuman primates, we must remain aware of how our own human interests can distort what we see (Haraway 1989). If you think humans are basically kind and generous, nonhuman primates will look kind and generous; if you think humans are basically nasty and selfish, nonhuman primates will look nasty and selfish. Primatologists have an obligation to avoid either romanticizing or demonizing primates if they are to understand these animals in their own right.

FIGURE 3.1 In the West, nonhuman primates are often portrayed in ways that embody human fears and anxieties. In the 1930s, the giant ape in the original *King Kong* (*a*) embodied a racial threat to the power of white males and the sexual virtue of white females. Since that time, the popularization of Jane Goodall's chimpanzee research and Dian Fossey's gorilla research, as well as worries about the extinction of wild ape populations, seems to have reshaped the recent remake of *King Kong* (*b*), in which the white human heroine and the giant ape become allies in an effort to evade greedy, abusive, and exploitative white males.

How Do Biologists Classify Primates?

The first step in understanding primates is to address the variety they exhibit. Primatologists, like other biologists, turn for assistance to modern biological **taxonomy**, the foundations of which were laid by Linnaeus in the eighteenth century. Today, taxonomists group organisms together on the basis of morphological traits, behavioral traits, and geographical distribution (Mayr 1982, 192). The laboratory technique of DNA hybridization allows researchers to combine single strands of DNA from two species to see how closely they match. When human DNA is combined with the DNA of other primates, they all match very closely, with the closest match being between humans and chimpanzees. As we will see in Chapter 4, these kinds of comparisons no longer are limited to the DNA of living primates. New laboratory techniques that permit the recovery of ancient DNA from fossilized bones tens of thousands of years old are making it possible to reconstruct evolutionary

anthropomorphism The attribution of human characteristics to nonhuman animals.

taxonomy A biological classification of various kinds of organisms.

continuity and divergence as measured in similarities and differences in the DNA of living species and their extinct relatives (Brown and Brown 2013).

Taxonomists classify organisms by assigning them to groups and arranging the groups in a hierarchy based on the seven levels originally recognized by Linnaeus: kingdom, phylum, class, order, family, genus, and species. Biologists continue to assign Latin names to species (e.g., *Homo sapiens*). The species name consists of (1) a generic name (always capitalized) that refers to the genus in which the species is classified and (2) a specific name that identifies particular species (any distinguishing name will do, including the Latinized name of the person who first identified the species). Genus and species names are always italicized. The taxonomy recognized by modern biologists is an *inclusive hierarchy*. That is, related lower groups are combined to make higher groups: related species make up a genus, related genera make up a family, and so on. Each species—and each set of related species grouped at any level of the hierarchy—is called a **taxon** (plural, *taxa*). For example, *H. sapiens* is a taxon, as is Hominoidea (the superfamily to which humans and apes belong) and Mammalia (the class to which primates and all other mammals belong).

Contemporary taxonomies are designed to reflect the evolutionary relationships that modern biologists believe were responsible for similarities and differences among species, and taxonomists debate which kinds of similarities and differences they ought to emphasize. Traditional evolutionary taxonomies focused on the **morphology** of organisms—the shapes and sizes of their anatomical features—and related these to the adaptations the organisms had developed. Organisms that seemed to have developed similar adaptations at a similar level of complexity in similar environments were classified together in the same evolutionary *grade*. Primates are classified into four evolutionary grades: the least complex grade is represented by prosimians ("premonkeys") and includes lemurs, lorises, and tarsiers; anthropoids (monkeys, apes, and humans) represent a more advanced grade; followed by the hominoids (apes and humans); the most advanced grade is the hominins (humans). The lesser apes (gibbons and siamangs) are distinguished from the great apes (gorillas, chimpanzees, and orangutans) on the grounds that the great apes had achieved a more complex adaptation than the lesser apes. For the same reason, the great apes were grouped together on the grounds that their adaptations were more similar to one another than any of them were to human beings.

The traditional approach to taxonomy has much to recommend it—especially to paleontologists because fossils are often so few and so incomplete that any classification more precise than "grade" is likely to be misleading. As we will discuss in Chapter 5, paleontologists face numerous challenges in the systematic classification of fossil organisms that biologists studying living species usually do not encounter. Paleontologists realize that adaptive morphological similarity by itself is not a foolproof indicator of evolutionary relatedness. This is because similarity can arise in one of two ways. Sometimes, members of different species have inherited common features from a common ancestor (a phenomenon called **homology**); in other cases, members of different species have common features, but do not share a recent common ancestor (a phenomenon called **homoplasy**). Homoplasy is the result of convergent, or parallel, evolution, as when two species with very different evolutionary histories develop similar physical features as a result of adapting to a similar environment. Examples include wings in birds and in bats and long, hydrodynamic body shapes in fishes and in whales.

To avoid confusing homology with homoplasy, some twentieth-century taxonomists developed an alternative taxonomic method called *cladistics* that is based on homology alone (that is, on evolutionary relatedness alone). Cladistics attempts to reconstruct the degrees of similarity and difference that result from **cladogenesis** (the formation of one or more new species from an older species). First, cladists must distinguish between homologous and analogous physical traits, focusing on homologous traits only. Then, they must determine which of the homologous traits shared by a group of organisms belonged to the ancestral population out of which they all evolved. These are called "primitive traits."

To trace later evolutionary developments, cladists identify phenotypic features shared by some, but not all, of the descendant organisms. A group of organisms possessing such a set of *shared, derived* features constitutes a natural group called a *clade* that must be recognized in the taxonomy. Finally, if cladists find derived features that are unique to a given group, this too requires taxonomic recognition. A group of organisms sharing a set of unique, derived features that sets them apart from other such groups within the same genus would qualify as a species (Figure 3.2). This way of defining species exemplifies the *Phylogenetic Species Concept*, to be discussed in

taxon Each species, as well as each group of related species, at any level in a taxonomic hierarchy.

morphology The physical shape and size of an organism or its body parts.

homology Genetic inheritance resulting from common ancestry.

homoplasy Convergent, or parallel, evolution, as when two species with very different evolutionary histories develop similar physical features as a result of adapting to a similar environment.

cladogenesis The birth of a variety of descendant species from a single ancestral species.

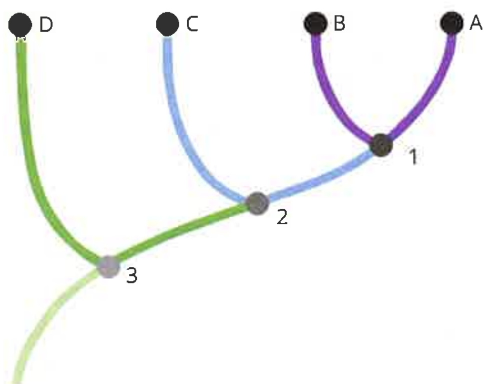

FIGURE 3.2 This cladogram shows the relationships among four hypothetical species. *A, B, C,* and *D* are assigned separate species status on the basis of unique, derived traits. *A* and *B* together possess shared, derived traits not found among *C* or *D*, indicating that *A* and *B* share a recent common ancestor *(1)*. *A, B,* and *C* together possess shared, derived traits that distinguish them from D, indicating that they, too, share a common—but more distant—ancestor *(2)*. *A, B, C,* and *D* are grouped together for analysis on the basis of shared, primitive traits common to them all or shared, derived traits that distinguish their common ancestor *(3)* from an out-group not shown in the cladogram.

Chapter 5. In recent years, cladistic methods have been widely adopted by primatologists and human paleontologists, and the following discussion uses cladistic categories.

How Many Categories of Living Primates Are There?

Nonhuman primates are found today in all the major rain forests of the world, except those in New Guinea and northeastern Australia. Some species, such as the Japanese macaque, have moved out of the tropics and into temperate climates. Primates are unusual, however, because, unlike most mammalian groups, their many and varied species are nearly all found in the tropics. Primates are studied in laboratories, in captive populations in zoos or research facilities, and in the wild. Primatologists must gather and compare information from all these settings to construct a picture of primate life that does justice to its richness and diversity.

And primate life is tremendously diverse. Different species live in different habitats, eat different kinds of food, organize themselves into different kinds of social configurations, and observe different patterns of mating and raising offspring. In light of all this diversity, most primatologists would probably caution against taking any single primate species as a model of early human social life (Cheney et al. 1987, 2). Alison Jolly (1985) points out that any species' way of life—what it eats and how it finds mates, raises its young, relates to companions, and protects itself from predators—defines that species' **ecological niche**. And, she adds, "With primates, much of the interest lies in guessing how our ancestors evolved from narrow confinement in a particular niche into our present cosmopolitan state."

Strepsirrhines

Strepsirrhini include lemurs and lorises (see Figures 3.3 and 3.4), the prosimians that have a *rhinarium*, or upper lip, attached to the gums by a web of skin. Other shared, derived features that unite Strepsirrhines include the *tooth comb* (forward-tilting lower incisors and canine teeth used for grooming), a *grooming claw* on the second digit of their feet, and an ankle bone (or *talus*) that flares to the side (Fleagle 2013, 57). Strepsirrhine **dentition** (the sizes, shapes, and numbers of their teeth) displays the dental formula 2.1.3.3 (that is, each side of both upper and lower jaws has two incisors, one canine, three premolars, and three molars). Females have a bicornate ("two-horned") uterus and a primitive form of placenta in which the blood of the mother and the blood of the fetus are more separated from one another than they are in other primates. Ancient and contemporary DNA comparisons indicate that all the Madagascar species (including the mouse lemur, the smallest living primate) form a clade separate from lorises and galagos, although more detailed relations among many species remain unclear (Fleagle 2013, 82).

Today lemurs are found only on the island of Madagascar, off the east coast of Africa, where they were isolated from competition from later-evolving primate species on the African mainland. They have been classified into 2 superfamilies, 5 families, and 15 *genera* (plural of genus) (Fleagle 2013, 5). There is evidence that different species of brown lemur are able to successfully interbreed with one another, although they have different numbers of chromosomes; different species of sportive lemurs are also able to interbreed despite chromosome differences that distinguish them (Fleagle 2013, 63, 67). Humans first arrived in Madagascar about 2000 years ago, and it appears that they were responsible for the extinction of a number of large-bodied lemur species, either by hunting or by destruction of their habitats (Fleagle 2013, 73).

Lorises are found in Africa and Asia, and their close relatives, the galagos, are found in Africa. These groups all share the same three strepsirrhine features as lemurs,

ecological niche Any species' way of life: what it eats and how it finds mates, raises its young, relates to companions, and protects itself from predators.

dentition The sizes, shapes, and number of an animal's teeth.

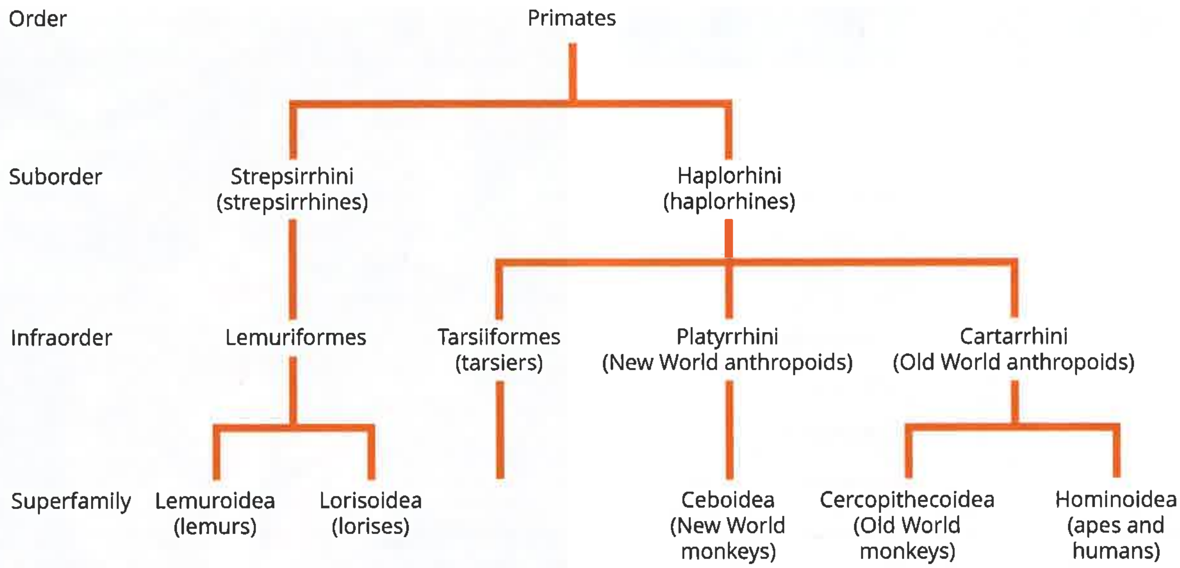

FIGURE 3.3 Cladistic taxonomy of the primates (Relethford 1996, 175).

FIGURE 3.4 Lemurs are native only to the island of Madagascar, off the east coast of Africa. They managed to avoid competition from later-evolving monkeys and apes in Africa thanks to their geographical isolation.

but in addition possess features in their cranium that differentiate them from lemurs. Both groups live in trees and are **nocturnal** (active at night), but differ in their characteristic styles of movement: lorises are slow climbers, whereas galagos are leapers (Fleagle 2013, 78).

Haplorhines

Haplorhini includes tarsiers and anthropoids, primates whose upper lips are not attached to their gums. Some taxonomies emphasize the features all Haplorhini share, and recognize three Haplorhini infraorders: Tarsiiformes (tarsiers), Platyrrhini (New World anthropoids), and Catarrhini (Old World anthropoids) (see Figure 3.3). Other taxonomists, who judge that anthropoids have more in common with each other than they do with tarsiers, treat Haplorhini and Anthropoidea as semiorders, place Tarsiiformes in Haplorhini, and classify Platyrrhini and Catarrhini as two infraorders in Anthropoidea (see Table 3.1).

Tarsiers Tarsiers are small nocturnal primates (Figure 3.5) that eat only animal food, such as insects, birds, bats, and snakes. Tarsiers used to be grouped with lemurs and lorises, but cladists have argued persuasively that they belong in the same clade as anthropoids. This is because they share a number of derived traits with the anthropoids, including dry noses, detached upper lips, a similarly structured placenta (and heavier infants), and a structure in their skulls

nocturnal Describes animals that are active during the night.

TABLE 3.1 Classification of *Homo sapiens*

Kingdom	Animal
Phylum	Chordata
Class	Mammalia (mammals)
Order	Primates (primates)
Semiorder	Haplorhini
Suborder	Anthropoidea
Infraorder	Catarrhini
Superfamily	Hominoidea
Family	Hominidae
Subfamily	Homininae
Genus	*Homo*
Species	*Homo sapiens*

A modern biological classification of our species, *Homo sapiens*, using Linnaean principles, based on Fleagle (2013, 5).

FIGURE 3.5 Although tarsiers used to be grouped together with lemurs and lorises on phenetic grounds, cladists point out that tarsiers share a number of derived traits with the anthropoids.

called the "postorbital partition" (Bearder 1987; Aiello 1986). Tarsier body morphology—a tiny body and enormous eyes and feet—is quite distinctive. Tarsier dentition is also unusual: tarsiers have no tooth comb, but resemble lemurs and lorises in the upper jaw (2.1.3.3), although not the lower jaw (1.1.3.3). In other respects, tarsier tooth morphology resembles that of anthropoids (Fleagle 2013, 85).

Anthropoids Anthropoids include New World monkeys, Old World monkeys, apes, and humans. New World monkeys are called *platyrrhines*, a term referring to their broad, flat noses; Old World monkeys, apes, and humans are called *catarrhines* in reference to their downward-pointing nostrils (Figure 3.6). Platyrrhines (Figure 3.7) also differ from catarrhines in dentition: the platyrrhine dental formula is 2.1.3.3, whereas the catarrhine dental formula is 2.1.2.3. Some platyrrhines have **prehensile**, or grasping, tails, whereas no catarrhines do. Finally, all platyrrhines are tree dwellers, whereas some catarrhine species live permanently on the ground. John Fleagle (2013, 90) reminds us that all these anthropoid features did not appear at once, but evolved in a piecemeal fashion over millions of years.

New World monkeys are the only clade of anthropoids in Central and South America; neither apes nor strepsirrhines are found there. It happens that some New World monkeys have evolved lemur-like adaptations and some have evolved ape-like adaptations, but other adaptations are unique (Fleagle 2013, 92). Platyrrhini are classified into 2 superfamilies, 7 subfamilies, and 18 genera (Fleagle 2013, 5). Titi monkeys are the least specialized of all New World monkeys and may bear the closest resemblance to the earliest platyrrhines (Fleagle 2013, 93). Capuchins (or organ-grinder monkeys) are well known outside their habitats in the South American rainforest. Some populations in open habitats in Brazil have been observed walking on their hind legs and using tools to break open palm nuts (Fleagle 2013, 104). Owl monkeys, found throughout South America, are the only nocturnal anthropoid species (Fleagle 2013, 106). The largest New World monkeys are atelids like the spider monkey, which have prehensile tails. Their tails function much like a fifth limb, helping them to suspend themselves in the trees. These are the New World monkeys whose adaptations most resemble those of Old World apes (Fleagle 2013, 98). Overall, the adaptive diversity of New World monkeys is impressive. There is no evidence of hybridization among species of New World monkeys (Fleagle 2013, 116).

prehensile The ability to grasp, with fingers, toes, or tail.

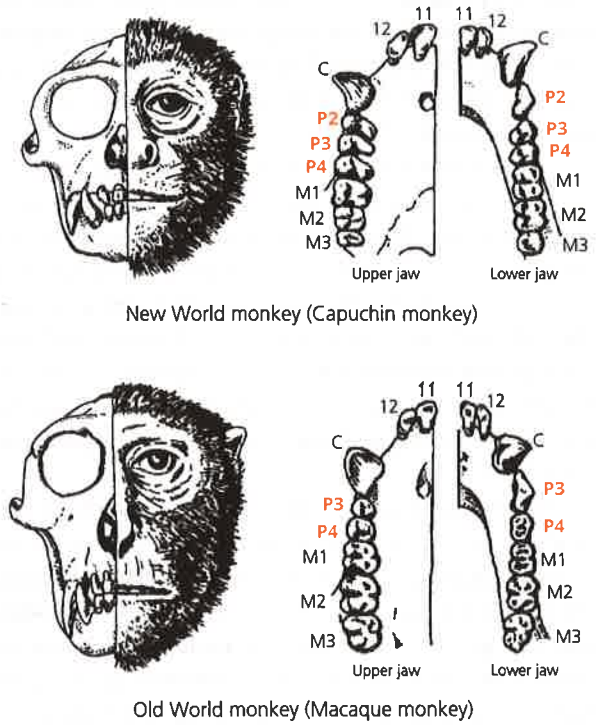

FIGURE 3.6 New World monkeys, such as the capuchin, have flat noses with nostrils pointing sideways and three premolars (P2, P3, and P4). By contrast, Old World anthropoids, including Old World monkeys such as the macaque, have noses with downward-pointing nostrils and only two premolars (P3 and P4).

FIGURE 3.7 A well-known species of New World monkeys is the spider monkey. This monkey was photographed in the Guatemalan rain forest.

Old World monkeys include two major groups: the colobines and the cercopithecines. *Colobines*, including the langurs of Asia (Figure 3.8) and the red colobus monkeys of Africa, are all **diurnal** (active during the day) and primarily adapted to arboreal life, although they have been observed to travel on the ground between tracts of forest. Colobines have four-chambered stomachs, presumably an adaptation to a heavy diet of leaves (Struhsaker and Leland 1987). Sorting out the phylogenetic connections among colobines in Africa and Asia has been difficult; it appears that much hybridization has occurred among them in the past (Fleagle 2013, 135). Indeed, hybridization seems to have happened regularly among many Old World monkey species, which makes it difficult for taxonomists to agree about how to classify them (Fleagle 2013, 148). *Cercopithecines* include some species adapted to live in the trees and others adapted to live on the ground. Those species living in forests, such as African guenons, are often found in one-male breeding groups; females remain in the groups where they were born, whereas males ordinarily transfer out at puberty. Groups of more than one species are often found feeding and traveling together (Cords 1987).

Ground-dwelling cercopithecines include several species of baboons, perhaps the best known of all Old World monkeys. Hamadryas baboons (*Papio hamadryas*) and gelada baboons (*Theropithecus gelada*) are found in Africa (Figure 3.9). Although they belong to different genera, they both live in social groups that possess a single breeding male. However, this superficial similarity turns out to be the result of very different social processes. Hamadryas males build up their one-male units by enticing females away from other units or by "adopting" immature females and caring for them until they are ready to breed. They carefully police the females in their units, punishing those that stray with a ritualized neck bite. In addition, hamadryas males thought to be kin form bonds to create a higher-level social unit known as a "clan." Several one-male units, several clans, and some individual males congregate in a band to forage together; and three or four bands may sleep together at night in a

diurnal Describes animals that are active during the day.

FIGURE 3.8 Gray langurs are Old World colobine monkeys. Some primatologists have described events in which all-male langur groups "invade" one-male langur groups. Invading males have been reported to deliberately kill unweaned offspring of resident females. Whether this behavior should be interpreted as adaptive or maladaptive has been one of the great controversies of contemporary primatology.

troop. By contrast, gelada baboons construct their one-male units on a core of strongly bonded female relatives that are closely influenced by the dominant female and that stay together even if the male of their group is removed (Stammbach 1987).

The most widely distributed primate genus in the world is *Macaca*—or the macaques—of which there are 20 species, ranging from Gibraltar and North Africa to Southeast Asia. All macaque species live in large multimale groups with complex internal social structures. They do well in a wide variety of habitats and have been especially successful living in habitats disturbed by human populations, with whom they have a long history of interaction in many parts of the world (Fleagle 2013, 123).

Hominoidea is the superfamily of catarrhines that includes apes and humans (see Table 3.1). Apes can be distinguished from Old World monkeys by morphological features such as dentition (reduced canine size, changes in jaw shape and molar shape) and the absence of a tail. Traditional taxonomies divide living apes into three grades, or families: the lesser apes (gibbons and siamangs), the great apes (orangutans, gorillas, and chimpanzees), and the hominids (humans). As we noted earlier, this taxonomic judgment was based on the differences in the kinds of adaptations each grade of anthropoid had developed. In recent years, however, many cladists have argued that classification within the great ape and human categories must be revised to reflect the results of biochemical and DNA testing, which show that humans and African apes (gorillas and chimpanzees) are far more closely related to one another than

FIGURE 3.9 Both hamadryas baboons (*a*) and gelada baboons (*b*) are ground-dwelling Old World cercopithecine monkeys. Although both species live in social groups with a single breeding male, hamadryas groups are created when the male entices females away from other groups, whereas gelada groups construct their one-male units on a core of closely related females.

they are to orangutans. Moreover, because chimpanzees and humans share more than 98% of their DNA, more and more taxonomists have concluded that these genetic similarities require placing chimpanzees and humans together in the same family, Hominidae; humans and their immediate ancestors are then grouped into a subfamily called Homininae and are called **hominins** (Goodman et al. 1990). This usage, now adopted by many leading authorities (e.g., Klein 2009, 74–75; Stringer and Andrews 2005, 16), will be followed in this book.

However, some biological anthropologists object that using genetics alone to determine taxonomy ignores important evolutionary information. For instance, emphasizing the genetic similarities between chimps and humans ignores wide adaptive differences between these taxa that illustrate Darwinian "descent with modification." These differences help explain why chimps and other apes are on the verge of extinction, largely as a consequence of human adaptive success. Biological anthropologist Jonathan Marks (2013) asks:

> Who would say "nature" is reducible to "genetics" (aside from self-interested geneticists)? Certainly not the evolutionary "synthetic theorists" of the mid-twentieth century (Huxley 1947, Simpson 1949). If "evolution" refers to the naturalistic production of difference, then to say that we are apes is equivalent to denying that we have evolved. Or to put it another way, if evolution is descent with modification, then our ape identity implies descent without modification. (251)

Both traditionalists and cladists agree that gibbons (Figure 3.10) belong in their own family, Hylobatidae. Gibbons, the smallest of the apes, are found in the tropical rain forests of southeastern Asia. Most primate species show **sexual dimorphism** in size; that is, individuals of one sex (usually the males) are larger than individuals of the other sex. Gibbons, however, show no sexual dimorphism in size, although in some species males and females have different coat colors. Gibbons are monogamous, neither male nor female is consistently dominant, and males contribute a great deal of care to their offspring. Gibbon groups usually comprise the mated pair and one or two offspring, all of whom spend comparatively little time in social interactions with one another. Gibbon pairs defend their joint territory, usually by vocalizing together to warn off intruders but occasionally with physical encounters. Establishing a territory appears to be difficult for newly mated pairs, and there is some evidence that parents may assist offspring in this effort. Evidence also suggests that some young male gibbons inherit the territory of their parents by pairing with their widowed mothers, although these pairs do not seem to breed (Leighton 1987).

FIGURE 3.10 Gibbons are the smallest of the apes. Unlike most primate species, gibbons are monogamous, and male and female gibbons show no sexual dimorphism in size.

Orangutans (Figure 3.11) are found today only in the rain forests of Sumatra and Borneo in southeastern Asia. Their dentition is different from that of chimpanzees and gorillas. Orangutans are an extremely solitary species whose way of life has made them difficult to study in the wild. Adult female orangutans and their offspring occupy overlapping ranges that also overlap the ranges of more than one male. Orangutan males come in two different adult forms, unflanged and flanged. Unflanged males are the size of females, whereas flanged males grow protruding fleshy jowls, called flanges, and may be twice as large. Some orangutan populations have been documented demonstrating cultural differences in tool use and vocalization (Fleagle 2013, 158–59).

hominins Humans and their immediate ancestors.

sexual dimorphism The observable phenotypic differences between males and females of the same species.

IN THEIR OWN WORDS

The Future of Primate Biodiversity

In a recent collection presenting the latest research on primates, Karen Strier writes about one of the most critical concerns for all who work with primates: conservation.

Between the inevitable effects of global warming on the world's endangered ecosystems and the ongoing expansion of human populations in and around the world's biodiversity hotspots, it is difficult to foresee how the future of primates—and other animals—that are threatened with extinction can be protected. Global losses of biodiversity and ecosystem changes are predicted to occur by 2050, and major primate extinctions may occur even sooner than this because rates of deforestation in countries such as Indonesia and Madagascar are so high. . . .

There is no question that human pressures are accelerating the extinction risks for many primate taxa. Whether through direct actions, such as unsustainable hunting and habitat destruction, or indirect activities, such as the far-reaching effects of atmospheric pollution on global climate, the impact of humans on other primates today is much greater than it has been in the past. . . . Yet, despite the depressing forecast for primates, increased awareness about the status of the world's endangered primates has fueled intensified international conservation efforts. It is too soon to tell whether these efforts will ultimately succeed in securing the futures of all endangered taxa, but there is no doubt that they are helping gain essential time in what for many primates is now an urgent race against extinction.

Ten years after Strier published her warning, matters have not improved. On January 18, 2017, science writer Carl Zimmer of the *New York Times* reported that "a team of 31 primatologists has analyzed every known species of primate to judge how they are faring. The news for man's closest animal relatives is not good. Three-quarters of primate species are in decline, the researchers found, and about 60 percent are now threatened with extinction. From gorillas to gibbons, primates are in significantly worse shape now than in recent decades because of the devastation from agriculture, hunting and mining."

Echoing the findings of ethnoprimatologists, the researchers Zimmer interviewed reported mixed outcomes, depending on the primate species; for example, generalist species that do well in a range of habitats are doing better than species that are dependent on highly specific resources. The decrease in primate numbers, however, affects more than the survival of individual species. Scientists now know that the activities of primate species keep tropical forests healthy. Zimmer quotes one of the coauthors of the study, biological anthropologist Katherine C. MacKinnon, who observed that "People used to think of primates as icing on the cake, as not being vital for ecosystems. . . . But now we know they are."

Some conservation efforts have been successful. For example, Anthony Rylands, another coauthor of the study, told Zimmer about a project to conserve golden lion tamarins, whose numbers were greatly reduced when the coastal forests of Brazil were cut down to make way for agriculture. Begun in 1983, the project has succeeded in preserving a small, stable population of this species in the wild. Still, conservation faces severe challenges: as Rylands pointed out, "the immensity of the destruction of tropical forests makes it very difficult."

Sources: Strier 2007, 506; Zimmer 2017.

There are five living subspecies of gorillas, all of which are found in Africa: the western lowland gorilla, the Cross River gorilla, Grauer's gorilla, the Bwindi gorilla, and the mountain gorilla. The rarest subspecies, the mountain gorilla, is probably the best known, thanks to the work of Dian Fossey (Figure 3.12), whose experiences have been popularized in books and film. Mountain gorillas eat mostly leaves. Like the New World howler monkeys, both male and female gorillas transfer out of the group in which they were born before they start breeding. The transfer, which does not appear forced, may occur more than once in a female's life. An adult female gorilla may produce three surviving offspring in her lifetime. Gorillas are highly sexually dimorphic, and the dominant male often determines group activity and the direction of travel. Immature gorillas are attracted to dominant males, who ordinarily treat them with tolerance and protect them in dangerous situations (Stewart and Harcourt 1987; Whitten 1987).

Chimpanzees (*Pan troglodytes*) are probably the most studied of all the apes (Figure 3.13). Jane Goodall and her associates in Gombe, Tanzania, have followed some chimpanzee groups for 50 years. Other long-term field research on chimpanzees has been carried out

FIGURE 3.11 Orangutans are an extremely solitary species that lives deep in the rain forests of Sumatra and Borneo.

FIGURE 3.12 The mountain gorilla of central Africa is the rarest of the living species of gorilla found in Africa.

FIGURE 3.13 Chimpanzees are probably the most studied of all the apes.

elsewhere in eastern and western Africa as well (Boesch-Achermann and Boesch 1994). In recent years, a second species belonging to the genus *Pan, Pan paniscus*, known as the "pygmy chimpanzee" or bonobo (Figure 3.14), has received increasing attention, both in the wild and in captivity. Bonobos are found only in central Africa south of the Zaire River and may number fewer than 100,000; forest destruction, human predation, and capture for illegal sale all threaten their survival (de Waal 1989, 177). The two species differ morphologically: bonobos have less rugged builds, shorter upper limbs, and longer lower limbs than chimpanzees and sport a distinctive coiffure. Both species share a fluid social structure; that is, temporary smaller groups form within the framework of a larger community (de Waal 1989, 180; Nishida and Hiraiwa-Hasegawa 1987, 172). Their patterns of social interactions differ, however. Bands of unrelated adult males are common among chimpanzees but rare among bonobos. Bonds formed between unrelated females are relatively weak among chimpanzees but strong among bonobos. Bonds between the sexes are much stronger among bonobos as well. This means that female bonobos play a more central role in their society than female chimpanzees play in theirs (de Waal 1989, 180).

Chimpanzees and bonobos eat both plant and animal foods. Indeed, one of Goodall's famous early discoveries was that chimpanzees deliberately make tools to help them find food. They have been observed preparing sticks to fish for insects in termite mounds or anthills, using leaf sponges to obtain water from tree hollows, and using rocks to smash open nuts. Indeed, patterns of tool use seem to vary regionally, suggesting the existence of separate cultural traditions in different chimpanzee

FIGURE 3.14 Social interactions among bonobos are highly eroticized, apparently to manipulate social relationships rather than to increase reproductive rates. Female bonobos play a more central role in their society than female chimpanzees play in theirs.

groups. Male chimpanzees have been observed hunting for meat and sharing their kill with other members of the group; interestingly, forest-dwelling chimpanzees are more likely to hunt in groups, presumably because the foliage makes their prey harder to secure (Boesch-Achermann and Boesch 1994).

Bonobos have never been observed using tools (Nishida and Hiraiwa-Hasegawa 1987, 166). However, the sexual life of chimpanzees cannot compare with the highly eroticized social interactions typical of bonobos. Bonobo females are able and willing to mate during much of their monthly cycle, but researchers have also observed a high degree of mounting behavior and sexual play between all members of bonobo groups, young and old, involving individuals of the same sex and of the opposite sex. Studying a captive colony of bonobos in the San Diego Zoo, Frans de Waal and his assistants observed 600 mounts, fewer than 200 of which involved sexually mature individuals. Although this might be a function of life in captivity, it does not appear to be contradicted by data gathered in the wild. Nishida and Hiraiwa-Hasegawa (1987), who refer to material gathered under both conditions, conclude that elaborate bonobo sexual behavior is "apparently used to manipulate relationships rather than to increase reproductive rates" (173). de Waal (1989) agrees, suggesting that "conflict resolution is the more fundamental and pervasive function of bonobo sex" (212). Wolfe (1995) notes that same-sex mounting behavior has been observed in 11 different primate species.

When we try to summarize what makes primate life unique, we are struck by its flexibility, resilience, and creativity. Primates can get by under difficult circumstances, survive injuries, try out new foods or new social arrangements, and take advantage of the random processes of history and demography to do what none has done before (Jolly 1985, 80–81, 242, 319). Simplistic models of primate behavior assuming that all primates are fundamentally alike, with few behavioral options, are no longer plausible. Mary Ellen Morbeck (1997) observes that "Most current models are inadequate when applied to the complex lives of large-bodied, long-lived, group-living mammals, primates, and humans with big brains and good memories" (14). Overall, it seems quite clear that flexibility is the hallmark of primate adaptations.

What Is Ethnoprimatology?

More than 20 years ago, in *Primate Visions* (1989), Donna Haraway showed how human ambivalence about race and gender had shaped much traditional Western scientific thinking about nonhuman primates. Today, many primatologists are focusing their research on the complex and often contradictory interconnections between human and nonhuman primates. As a result, they increasingly insist that field studies of primates must be connected with conservation activities that take into consideration the welfare not only of the animals themselves, but also of the ecosystems and human communities with which they are inextricably interconnected (e.g., Strier 1997; Jolly 2004; SAGA 2005; see In Their Own Words, page 70). These concerns have become central to a new specialty within primatology that is called *ethnoprimatology*.

Ethnoprimatology has been defined as the "theoretically and methodologically interdisciplinary study of the multifarious interactions and interfaces between humans and other primates" (Fuentes 2012, 102). As Agustín Fuentes explains, humans and other primates have long coexisted successfully in many global settings, but human activities now threaten the survival of many primate species in the wild. Indeed, ethnoprimatologists call into question the very notion of "the wild," given mounting knowledge that human niche construction is responsible for vast modifications of the living and nonliving world. Some scientists argue that this human-generated (or *anthropogenic*) environmental modification has been extensive enough to initiate a new geological epoch, which they call the *Anthropocene:* "the current geological epoch wherein anthropogenic agency is one of the prominent forces affecting global landscapes and climates" (Fuentes 2012, 102).

To study human–primate interactions in the Anthropocene requires reconfiguring the focus of primatological field research and broadening the kinds of questions researchers ask. For instance, if we all live in the Anthropocene, ethnoprimatologists must give up on the idea that there are any settings on the planet where primates are able to live beyond the influences of human activity. Acknowledging these multiple entanglements means that ethnoprimatologists must also explore a range of issues that go beyond their traditional focus on predator–prey relations. Overall, "Ethnoprimatology rejects the idea that humans are separate from natural ecosystems and mandates that anthropological and multiple stakeholder approaches be included in behavioral ecological and conservation research on other primates" (Fuentes 2012, 102) (see In Their Own Words, page 70).

Fuentes, a biological anthropologist, was an early advocate of ethnoprimatological research, which now involves field primatologists, primate conservationists, and sociocultural anthropologists interested in human–animal interactions. These concerns have led to the writing of "multispecies ethnographies" in which relations of humans to nonhuman others are a central concern (Haraway 2008; Kirksey and Helmreich 2010). Ethnoprimatology is also beginning to have an impact on other disciplines, such as *anthrozoology*, a field in which veterinarians, public health researchers, psychologists, and psychiatrists study a variety of human–animal interactions; it even promises to engage members of the animal welfare movement who in the past have been critical of the work of primatologists (Fuentes 2012, 104).

In some parts of the world human relations with nonhuman primates have provoked conflict. Early ethnoprimatological studies focused on situations where crops planted by humans were subject to raiding by primates living in nearby forests. Other studies look at the increasing importance of primates as tourist attractions (see In Their Own Words, "Chimpanzee Tourism," page 74). In recent decades, ethnoprimatological research projects have been undertaken in a number of sites in Southeast Asia and Africa. Some ethnoprimatological research projects are multisited undertakings, similar to multisited projects that have become common in ethnographic research on human populations. For example, macaques are found in parts of Europe, Africa, and Asia and have established a variety of long-standing relationships with local human populations in a range of types of human settlement. Comparison of the similarities and differences in these relationships across different sites allows ethnoprimatologists to document successes and challenges faced by all parties to these encounters. For instance, ongoing multiple encounters between humans and nonhuman primates seem to have shaped the evolution and transmission of disease-causing microorganisms, relationships that are increasingly affected by human migration and tourism (Gumert et al. 2011; Radhakrishna et al. 2013).

How have different primate populations fared in their encounters with humans? The great apes seem to face the greatest threats: gorillas, chimpanzees, and orangutans all require large areas of forest to meet their dietary needs and reproduce at slow rates. They are threatened by forest destruction by human settlement and logging, as well as by hunters who capture infants for the exotic pet trade or prize the flesh of these animals as "bushmeat." By comparison, macaques and baboons seem able to coexist with humans on much better terms. These monkeys are generalist foragers who seem to thrive in areas disturbed by human settlement and are becoming important draws for tourists in Southeast Asia and South Africa (Fuentes 2012, 111).

In many situations, Fuentes (2012) argues, "ethnoprimatological projects provide a particularly robust arena for the (re) integration of sociocultural and biological perspectives in anthropology" (106). This reintegration of perspectives is clear in situations where ethnoprimatologists work with conservationists and local communities to find ways of managing human–nonhuman primate relations more successfully. Indeed, Fuentes reports, programs of this kind "that incorporate anthropological orientations and multistakeholder approaches show the most potential, although in some cases it appears that the human social and economic crises will overwhelm attempts to find sustainable solutions that benefit alloprimates as well as humans" (109–10).

IN THEIR OWN WORDS

Chimpanzee Tourism

Thirty years ago, the closest human neighbors of the Gombe chimpanzees were African villagers and Jane Goodall's research team. Today, human encroachment on chimpanzee territory is an everyday fact of life, with negative consequences.

Gombe National Park in Tanzania, the locus of most of Jane Goodall's studies, has been inundated by the most intrepid tourists who find their own way there, on foot or by water taxi, camp on the beach, and attempt to make their own arrangements with the underpaid park staff. This situation compromises the research program at Gombe and also endangers the chimpanzees, who are even more susceptible than gorillas to human diseases. In 1966, a polio epidemic that began among the human population in Kigoma district killed about 10–15% of the Gombe chimpanzee population in one year, and in 1988, an additional 14 animals died from an introduced respiratory infection. Bacteria, parasites, and other infectious organisms can be transmitted both by tourists and by resident staff.

In Burundi, Jane Goodall has been working to help set up a tourism program in a small vestige of forest that has been turned into a sanctuary for chimpanzees confiscated from poachers and dealers. Given the demand for chimpanzees as medical research subjects, the threat of illegal recapture is constant. One group of 30 vagabond animals is followed around full-time by ten armed guards. Goodall and others involved in this conservation effort hope that the greater visibility of the chimpanzees and daily contact with tourists when the program is well-established will help deter poachers.

One of the greatest problems with marketing chimpanzee tourism is delivering the chimpanzee experience on a predictable daily schedule. Chimpanzees are much more mobile than gorillas, and unlike gorillas, live in fluid social groupings whose membership is changing constantly. Not only do individuals move up to 25 km per day, but they often travel above ground level, leaving little or no trail for an earthbound tourist to follow.

Source: Brooks and Smith 1991, 14.

Are There Patterns in Primate Evolution?

How do we begin to trace evolutionary developments within the primate order? The first step is to create a framework for comparison. For example, to trace the evolution of the mammalian skeleton, paleontologists collect samples of fossil mammal bones that span a long stretch of geological time, and they distinguish the bones of the animal's head—the skull, or **cranium** (plural, *crania*), and lower jaw, or **mandible**—from the rest of the animal's bones, its **postcranial skeleton**. Homologous bones of different ages can then be compared for similarities and differences. The fossilized and living species grouped together in the primate order share no single attribute that sets all of them apart from other living creatures (Figure 3.15). What does distinguish primates, living and extinct, are three different sets of features: ancestral characteristics (often called "primitive characteristics"), past evolutionary trends, and unique features. In addition, primates are unusual because they are "distinguished mainly by a tendency to retain specific parts that other animals have lost during their evolution" (Klein 2009, 68). This is why primates are often described as *generalized* organisms.

Ancestral characteristics that primates inherited from earlier, nonprimate, mammalian ancestors appear in their generalized postcranial skeletons. These characteristics include the following:

- The presence of five digits on the hands and feet
- The presence of the clavicle, or collar bone, allowing for flexibility in the shoulder joint
- The use of the palms of the hand and foot (rather than the toes) for walking, called *plantigrade locomotion*

W. E. LeGros Clark (1963) identified four evolutionary trends that can be traced across the primate order since the first primates evolved away from their primitive mammalian ancestors:

cranium The bones of the head, excluding the jaw.

mandible The lower jaw.

postcranial skeleton The bones of the body, excluding those of the head.

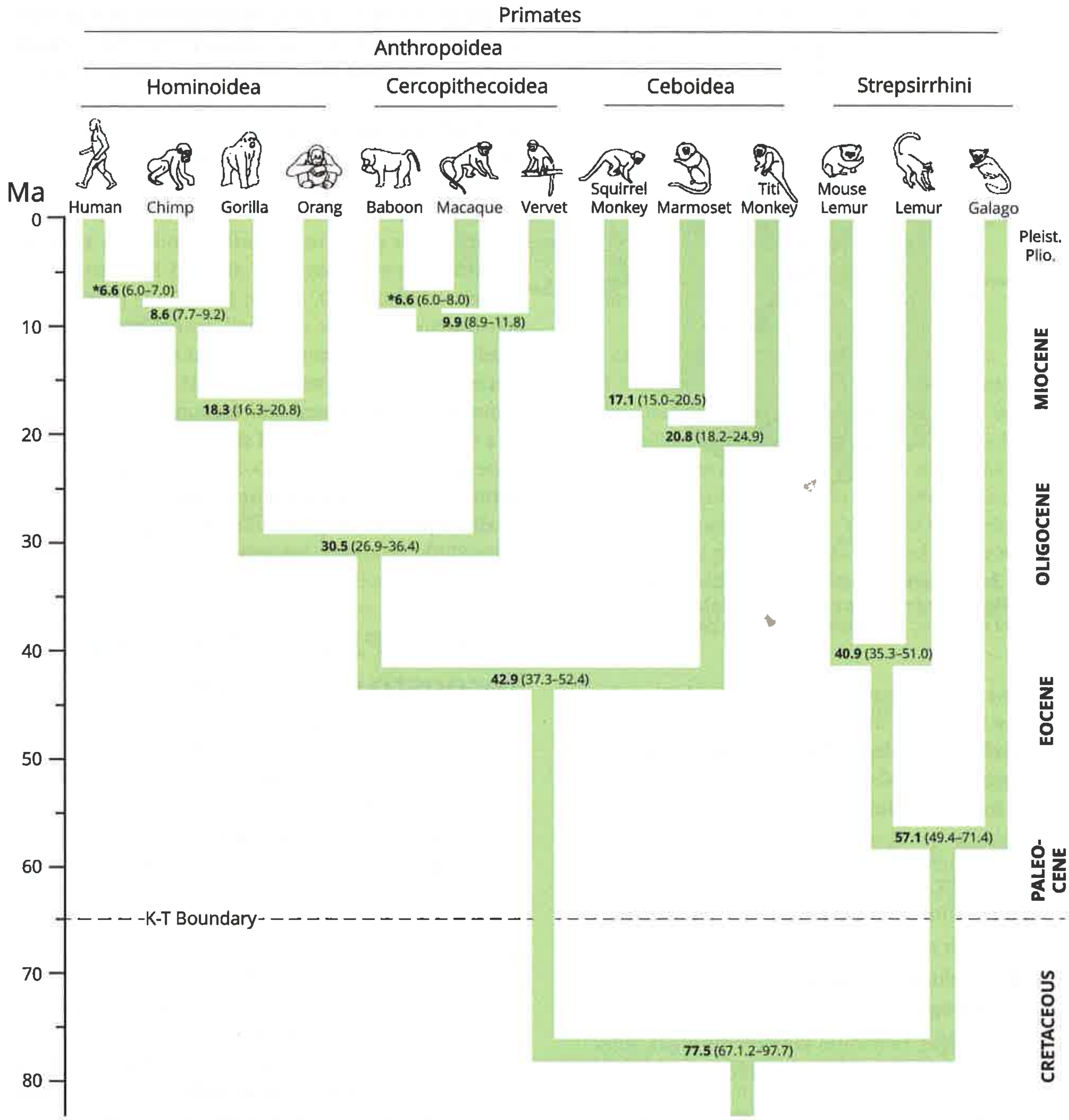

FIGURE 3.15 This timeline arranges the major fossil primate taxa by date and geological epoch and indicates estimated divergence dates in millions of years.

1. An increase in brain size, relative to body size, and an increase in the complexity of the neocortex (or new brain)
2. A reduction of both the projection of the face and the reliance on the sense of smell
3. An increasing dependence on the sense of sight, resulting in the relocation of the eyes onto the same plane on the front of the face so that the visual field of each eye overlaps, producing depth perception (or **stereoscopic vision**) (Figure 3.16)
4. A reduction in the number of teeth

stereoscopic vision A form of vision in which the visual field of each eye of a two-eyed (binocular) animal overlaps with the other, producing depth perception.

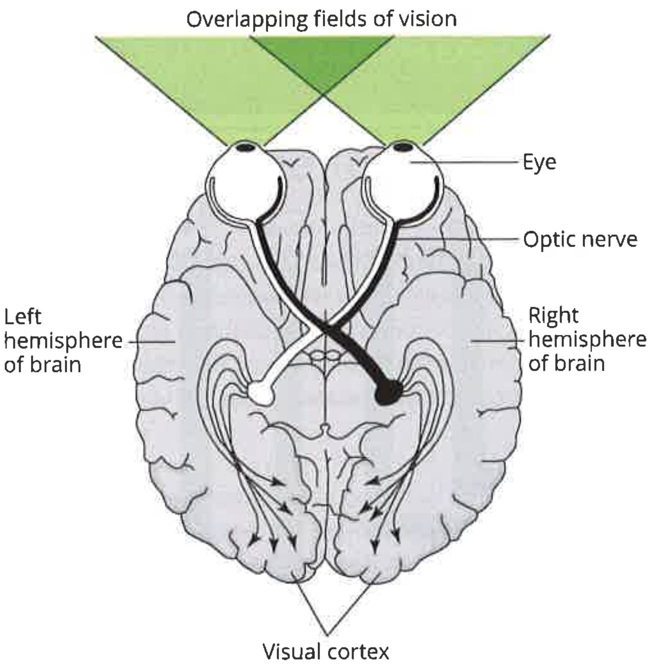

FIGURE 3.16 Stereoscopic vision. The fields of vision overlap, and the optic nerve from each eye travels to both hemispheres of the brain. The result is true depth perception.

Some scholars have suggested two additional evolutionary trends: an increasing period of infant dependence and a greater dependence on learned behavior.

Finally, primates' unique prehensile morphological features include the following:

1. Opposable thumbs and great toes (i.e., the thumb is opposite the other fingers and can be "opposed to" the other fingers for grasping)
2. Nails rather than claws on at least some digits
3. Pads at the tips of fingers and toes that are rich in nerve endings
4. Dermal ridges, or friction skin, on the digits, soles, palms, and underside of prehensile tails

LeGros Clark (1963) argued that primate evolutionary trends and unique features were the outcome of an arboreal adaptation—that is, adaptation to life in the trees. In his view, creatures with excellent grasping abilities, acute binocular vision, and a superior brain are well suited to an arboreal habitat. However, many other organisms (e.g., squirrels) have adapted to life in the trees without having evolved such traits. Matt Cartmill (1972) offered the "visual predation hypothesis." He suggested that many of these traits derive from an ancestral adaptation to feeding on insects at the ends of tree branches in the lower levels of tropical forests. Selective pressure for improved vision resulted from the fact that these ancestral primates fed at night and relied on sight to locate their prey. More recently, Robert Sussman (1991) and Katherine Milton (1993) have argued that switching from insect predation to consumption of edible plant parts set the stage for future primate evolution leading to grasping hands, visual acuity (including color vision), larger brains, and increased behavioral flexibility.

It is important to remember that while past evolutionary trends apply to the primate order as a whole, all primate species were not affected by these trends in the same way. R. D. Martin (1986, 13) pointed out that lessened reliance on smell probably only developed in primates that were diurnal rather than those that were nocturnal (active at night). Some living primates are still nocturnal and continue to rely heavily on a well-developed sense of smell. These matters continue to be debated, but, as Fleagle concludes, "Unfortunately, until we have a better fossil record . . . the details of primate origins will remain hidden" (Fleagle 2013, 225).

How Do Paleoanthropologists Reconstruct Primate Evolutionary History?

The following survey of primate evolution is organized in terms of the five geological divisions, or epochs, recognized in the Tertiary period of the geological era called the Cenozoic. The Cenozoic began 65 mya, about the same time as the primates did.

Primates of the Paleocene

The Paleocene lasted from about 65 to 55 mya. Evidence about early primate evolution in this period is growing, but remains complex and subject to debate. Based on DNA evidence from living mammals, it now seems that primates, tree shrews, and so-called "flying lemurs" (gliding mammals from Southeast Asia with tooth combs) are more closely related to one another than they are to other mammals. All three have been placed together into the superorder Euarchonta, which also includes a group of Paleocene fossils known as *plesiadapiforms* (Fleagle 2013, 212). Plesiadapiforms were numerous, varied, and successful during the Paleocene and early Eocene of Europe and North America (Fleagle 2013, 213–14). But taxonomists disagree about their connection to primates, and the relation of Euarchonta to primates remains unclear (Fleagle 2013, 224). The best current candidate for the oldest probable primate is *Altiatlasius*, whose fragmentary fossils have been found in late Paleocene deposits

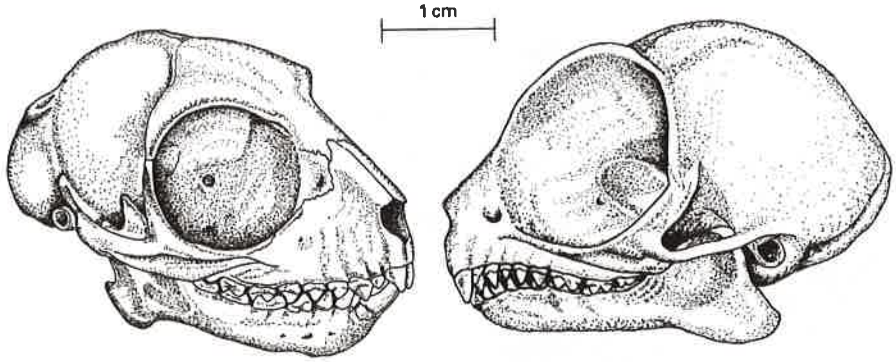

FIGURE 3.17 The fossil omomyid *Necrolemur* (*left*) belongs to the superfamily Omomyoidea, thought to be ancestral to the modern tarsier (*right*).

in North Africa. Too little is known about *Altiatlasius*, however, to relate it clearly to later primate taxa; indeed, exactly where the first primates evolved is still unknown (Rose 1994; Fleagle 2013, 231).

Primates of the Eocene

The first undisputed primates appeared during the Eocene epoch, which lasted from about 55 to about 38 mya. Most of the fossils are jaws and teeth, but skulls, limb bones, and even some nearly complete skeletons have also been recovered. The best-known Eocene primates fall into two basic groups. The first group, *adapids*, looks a lot like living lemurs. However, a number of morphological features—dentition in particular—distinguish them from their modern counterparts. Eocene adapids had four premolars, whereas modern lemurs have only three, and their lower incisors and canines were generalized, whereas modern lemurs possess a specialized tooth comb. The second group, the *omomyids*, resembles living tarsiers (Figure 3.17). Most omomyids were much smaller than adapids. Adapted for climbing, clinging, and leaping, omomyids appear to have been nocturnal, feeding on insects, fruit, or gum (Rose 1994). A tiny primate from the Early Eocene of Mongolia called *Altanius orlovi* may be ancestral to both adapoids and omomyoids (Fleagle 2013, 231). Linking later omomyoid fossils to living tarsiers, however, is not straightforward because different features evolved at different times, and parallel evolution seems to have been common. "Nevertheless, omomyoids, tarsiers and anthropoids all share a number of features that lead almost all researchers to group them together in the semiorder Haplorhini" (Fleagle 2013, 256). Currently, taxonomists are working to reconcile contradictions between older biomolecular estimates of the period that strepsirrhines split from haplorhines with more recent dates provided from the fossil record (Fleagle 2013, 259).

The early ancestors of later anthropoids began to appear in the period of transition between the late Eocene and early Oligocene, perhaps 44 to 40 mya (Martin 1993; Simons and Rasmussen 1994). The parapithecoids are the most primitive early anthropoid group from this period, with a dental formula of 2.1.3.3., which, as we saw, is found in platyrrhines (Fleagle 2013, 267). However, parapithecoids may well not be direct ancestors of New World monkeys because this and other shared attributes may be primitive traits retained from earlier ancestors (Fleagle 2013, 273). We still do not know how the earliest platyrrhines reached the New World (Fleagle 2013, 291).

Primates of the Oligocene

The Oligocene epoch lasted from about 38 to about 23 mya. Temperatures cooled and environments dried out. Those adapids whose ancestors made it to the island of Madagascar unwittingly found a safe refuge from evolutionary competition elsewhere and evolved into modern lemurs. Elsewhere, the early anthropoids and their descendants flourished.

Oligocene layers at the Fayum, in Egypt, dating from between 35 and 31 mya have long been our richest source of information about anthropoid evolution. The best represented group of early anthropoids is the *propliopithecids*, which were larger than the parapithecids and had the 2.1.2.3 dental formula characteristic of all later catarrhines. However, many features of their anatomy are more primitive than those found in Old World monkeys and apes (Fleagle 2013, 273).

Aegyptopithecus zeuxis, the largest of the Oligocene anthropoideans, is well known from numerous fossilized teeth, skulls, and limb bones and appears ancestral to later Old World anthropoids, or *catarrhines* (Figure 3.18). *A. zeuxis* lived 35 mya and looked very much like a primitive monkey (Simons 1985, 40). The bones of its lower jaw and upper cranium are fused along the midlines, and the eye orbits are closed off from the brain by a bony plate. Nevertheless, its limb bones show none of the features that allow modern apes to hang upright or swing from the branches of trees. Its cranium

FIGURE 3.18 *Aegyptopithecus zeuxis* is the largest of the Oligocene fossil anthropoids and may be ancestral to all catarrhines (Old World monkeys, apes, and humans).

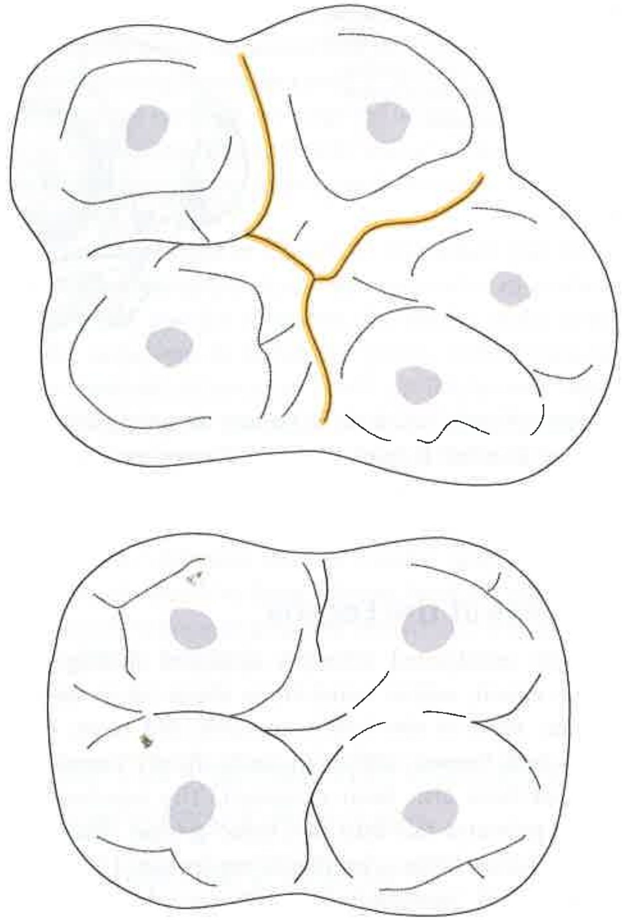

FIGURE 3.19 The upper molar shows the characteristic Y-5 pattern of apes and humans; the lower molar exhibits the bilophodont pattern of Old World cercopithecoid monkeys. Current evidence suggests that the Y-5 molar was primitive for all Old World anthropoids and that the bilophodont molar of the cercopithecoids developed later.

also shows some primitive characteristics: its brain was smaller, its snout projected more, its eye orbits did not face as fully to the front, and its ear was not as fully developed. Propliopithecids like *A. zeuxis* have long been described as primitive apes, but recent work suggests that the anatomical traits they share with apes are primitive catarrhine traits, rather than shared, derived ape specializations (Fleagle 2013, 276).

A. zeuxis had two premolars (a diagnostic catarrhine [Old World anthropoid] feature), and it also had Y-5 molars. A *Y-5 molar* is a tooth with five cusps that are separated by a "Y"-shaped furrow (Figure 3.19). Later Old World monkeys (cercopithecoids) have *bilophodont molars* with four cusps arranged in pairs, each of which is joined by a ridge of enamel called a "loph." Early Miocene fossils, 17–19 million years old, of undoubted cercopithecoid monkeys have molars with a fifth cusp and incomplete lophs. Thus, "the bilophodont teeth of Old World monkeys are derived from an ancestor with more ape-like teeth" (Fleagle 2013, 348), and the Y-5 pattern was primitive for all Old World anthropoids, making *A. zeuxis* and other Oligocene catarrhines likely ancestors of both Old World monkeys and hominoids (apes and humans) (Fleagle 2013, 273; Stringer and Andrews 2005, 84).

The earliest known hominoid fossils date from the middle to late Oligocene (29 mya) and come from western Saudi Arabia and northern Kenya (Fleagle 2013, 313). It was during the Miocene, however, that hominoid evolution took off.

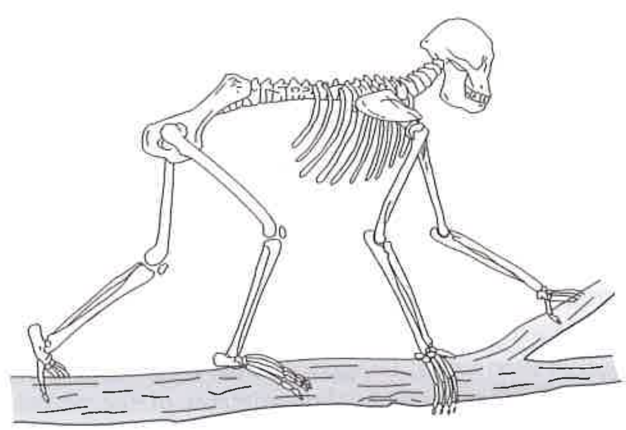

FIGURE 3.20 *Proconsul*, perhaps the best known of the earliest African hominoids. Some argue that *Proconsul* is generalized enough in its morphology to have been ancestral to later hominoids, including modern apes and human beings, although this is debated.

Primates of the Miocene

The Miocene lasted from about 23 to about 5 mya. Between 18 and 17 mya, the continents finally arrived at their present positions, when the African plate (which includes the Arabian Peninsula) contacted the Eurasian plate. This helps explain why fossil hominoids from the early Miocene (about 23–16 mya) have been found only in Africa. More recent fossil hominoids have been found from western Europe to China, presumably because their ancestors used the new land bridge to cross from Africa into Eurasia. During the middle Miocene (about 16–10 mya), hominoid diversity declined. During the late Miocene (about 9–5 mya), cercopithecoid monkeys became very successful, many hominoid species became extinct, and the first members of a new lineage, the hominins, appeared.

In the early Miocene, eastern Africa was covered with tropical forest and woodland. One well-known collection of early Miocene primate fossils has been assigned to the hominoid genus *Proconsul*. The best evidence, including a nearly complete skeleton, exists for the smallest species, *Proconsul heseloni* (formerly *P. africanus*) (Figure 3.20), which was about the size of a modern gibbon (Klein 2009, 117). *Proconsul heseloni* is very apelike in its cranium, teeth, and shoulder and elbow joints. However, its long trunk, arm, and hand resemble those of modern monkeys. It appears to have been a fruit-eating, tree-dwelling, four-footed (four-handed?) protoape that may have lacked a tail. Some argue that it is also generalized enough in its morphology to have been ancestral to later hominoids, including modern apes and human beings, although this is debated (Fleagle 1995). *Proconsul* and other early Miocene hominoids were confined to Africa and the Arabian Peninsula.

Most taxonomists agree, however, that *P. heseloni* and other early-Miocene hominoids were outside the modern hominoid clade (Fleagle 2013, 320). They also retained many primitive catarrhine features lost by later cercopithecoid monkeys, showing that "Old World monkeys are a very specialized group of higher primates" (Fleagle 2013, 322).

The land bridge connecting Africa to Eurasia was formed during the middle Miocene (16–10 mya). The earliest fossils assigned to the modern hominoid clade first date to the middle and late Miocene (10–5 mya) and come mostly from Africa, although one genus, *Kenyapithecus*, is also represented by a second species from Turkey (Fleagle 2013, 320). Once hominoids made it out of Africa, they experienced a rapid radiation throughout many parts of the Old World, and their fossils remain difficult to classify (Fleagle 2013, 326). Unfortunately, very few African hominoid fossils of any kind date from the late Miocene (10–5 mya) or early Pliocene (5–2.5 mya) (Benefit and McCrossin 1995, 251).

In the absence of hard data, attempts to identify either the last common ancestor of the African apes and human beings or the earliest ancestors of chimpanzees and gorillas must be based on educated speculation (Stringer and Andrews 2005, 114). Nevertheless, we know that it was during the late Miocene that the first ancestors in our own lineage appeared. Tracing their evolutionary history is the topic of the next chapter.

Chapter Summary

1. If we avoid anthropomorphism, careful comparison between human beings and other primate species offers enormous insight into our evolutionary past. Primatologists attempt to make sense of primate diversity by creating a primate taxonomy. Traditional taxonomies of primates compared the phenotypes and adaptations of primates and recognized four primate grades. Cladistic taxonomies ignore adaptation and the fossil record and classify organisms only on the basis of homologous evolutionary traits found in living species. Many primatologists combine features of both kinds of taxonomies to demonstrate relations of evolutionary relatedness between species.
2. Strepsirrhines include lemurs and lorises. Haplorhines include tarsiers and anthropoids. Anthropoids include New World and Old World forms. New World monkeys evolved separately from Old World anthropoids and differ from them in nose shape and the number of premolars; in addition, some New World monkeys evolved prehensile tails. All New World monkey species are tree dwellers.
3. Old World anthropoids include species of monkeys and apes, as well as human beings: all share the same nose shape and the same number of premolars. Apes are distinguished from Old World monkeys by dentition, skeletal shape and size, and the absence of a tail. The African apes are far more closely related to one another than they are to gibbons or orangutans, and human beings are more closely related to chimpanzees than to any other ape species. Chimpanzees deliberately make simple tools

(continued on next page)

Chapter Summary *(continued)*

to help them find food. Bonobos, or pygmy chimpanzees, are known for their highly eroticized social interactions and for the central role females play in their society.

4. Primates show at least six evolutionary trends of their own and four unique features associated with prehensility. These evolutionary trends have not affected all primate species in the same way.

5. Paleontologists assign primate fossils to various categories after examining and comparing cranial and postcranial skeletal material. They have concluded that the first undisputed primates appeared during the Eocene. The best-known Eocene primates are the adapids, which resemble living lemurs, and the omomyids, which resemble living tarsiers. Anthropoideans, ancestral to all later monkeys, apes, and humans, appeared in the late Eocene and are known from sites in northern Africa and Asia. Some Oligocene primate fossils look like possible ancestors to modern New World anthropoids; others, like *Propliopithecus zeuxis*, appear ancestral to all later Old World anthropoids.

6. The first hominoids that evolved in Africa during the early Miocene are very diverse. One of the best-known examples is *Proconsul*, which is generalized enough to have been ancestral to later apes and human beings. During the middle Miocene, hominoids rapidly spread and diversified, and their fossils are found from Europe to eastern Asia. In the late Miocene, many hominoid species became extinct. Paleoanthropologists agree that chimpanzees, gorillas, and human beings shared a common ancestor in the late Miocene.

For Review

1. Summarize the discussion of taxonomy at the beginning of the chapter.
2. Distinguish between homology and analogy.
3. What are clades? Illustrate with examples.
4. Summarize the features used to distinguish different kinds of primates from each other. What is distinctive about the anthropoids?
5. Discuss the differences and similarities of chimpanzees and bonobos.
6. What are primate ancestral characteristics? evolutionary trends? unique morphological features?
7. What adaptive explanations do paleoanthropologists give for the unique features of primates?
8. Prepare a table or chart that displays what is currently known about key developments in primate evolution, from the Paleocene to the Miocene.

Key Terms

anthropomorphism 62
cladogenesis 63
cranium 74
dentition 64
diurnal 67
ecological niche 64
hominins 69
homology 63
homoplasy 63
mandible 74
morphology 63
nocturnal 65
postcranial skeleton 74
prehensile 66
sexual dimorphism 69
stereoscopic vision 75
taxonomy 62
taxon 63

Suggested Readings

All the World's Primates. http://www.alltheworldsprimates.org. *This website, which describes itself as "the comprehensive online resource for primate information," provides information on all primate species currently recognized by the International Union for Conservation of Nature. It also presents contributions by researchers on living and fossil primates, including Jane Goodall, Richard Leakey, and John Fleagle.*

Campbell, Christina, Agustín Fuentes, Katherine MacKinnon, Melissa Panger, and Simon Bearder. 2011. *Primates in prespective*, 2nd ed. New York: Oxford University Press. *A comprehensive overview of the primates and what we know about them.*

de Waal, Frans. 2003. *My family album: Thirty years of primate photography.* Berkeley: University of California Press.

In addition to being an influential primatologist, de Waal is a superb photographer. These images are an excellent visual introduction to the various primate species he has studied.

Fleagle, John G. 2013. Primate adaptation and evolution, 3rd ed. Amsterdam: Elsevier. *The third edition of a detailed, up-to-date, and engaging introduction to primatology. The chapters cover both living primates and the fossil record of primate evolution, including that of* Homo sapiens. *It also addresses current issues in primate conservation.*

Fossey, Dian. 1983. *Gorillas in the mist.* Boston: Houghton Mifflin. *Dian Fossey's account of research among the mountain gorillas of Rwanda over a 13-year period; includes many color photographs. Fossey was murdered at her field station in 1985. This book inspired a major motion picture of the same name.*

Goodall, Jane. 1986. *The chimpanzees of Gombe: Patterns of behavior.* Cambridge, MA: Harvard University Press. *This volume presents the results of a quarter of a century of scientific research among chimpanzees in Gombe, Tanzania.*

———. 1999. *Jane Goodall: 40 years at Gombe.* New York: Stewart, Tabori and Chang. *After 1986, Jane Goodall shifted the emphasis of her work from scientific observation to rescuing and rehabilitating laboratory animals and working for environmental causes, as have many primatologists concerned about threats to the continued viability of the species they have studied.*

Haraway, Donna. 1989. *Primate visions.* New York: Routledge. *This volume, a major landmark in primate studies, contains a series of essays by a feminist historian of science who describes the way Western cultural assumptions about gender, race, and nature have shaped American primatology. Chapters discussing how collections were made for the American Museum of Natural History and the symbolic significance of white female primatologists should be of particular interest to beginning students.*

International Union for Conservation of Nature. http://www.iucnredlist.org. *The International Union for Conservation of Nature (IUCN) manages a website that contains updated lists of endangered animal species, estimating the degree of endangerment and explaining the sources of endangerment. Entering "Primates" into their search engine brings up a list of endangered primate species. It also provides a wealth of information about the taxonomic status of primate species, their life histories, their habitats, and where their populations can be found.*

Smuts, Barbara, Dorothy Cheney, Robert Seyfarth, and Richard Wrangham, eds. 1987. *Primate societies.* Chicago: University of Chicago Press. *This volume is a classic, comprehensive survey of research on primates from all over the world and includes articles by 46 contributors.*

Tudge, Colin, with Josh Young. 2009. *The link.* New York: Little, Brown. *This volume was written in connection with a film,* The Link, *broadcast in May 2009 on the History Channel in the United States and on several other television channels worldwide. Science writer Colin Tudge wrote chapters 3–8, plus the epilogue, and he provides a brief, solid, reader-friendly introduction to contemporary work in primate evolution. Josh Young, who wrote chapters 1, 2, and 9, describes how fossils have become valuable commodities in twenty-first-century antiquities markets. He also shows the high stakes facing scientists who introduce new primate fossils to a media-saturated world—in this case, "Ida," a remarkably complete 47-million-year-old fossil prosimian from Germany.*