HOW HUMANS EVOLVED

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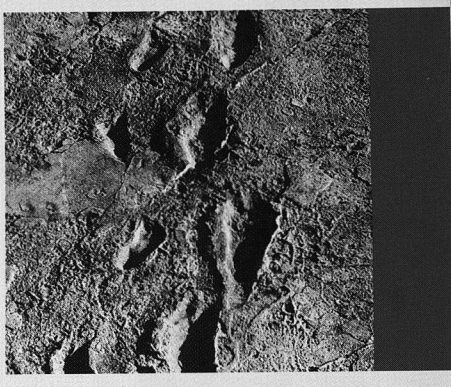

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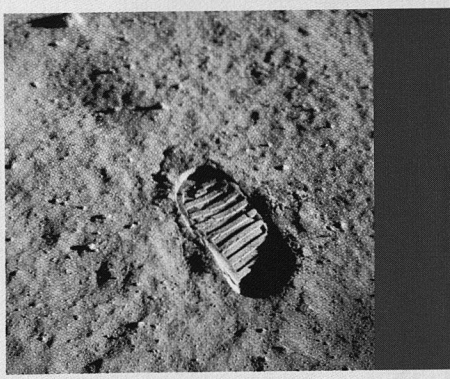
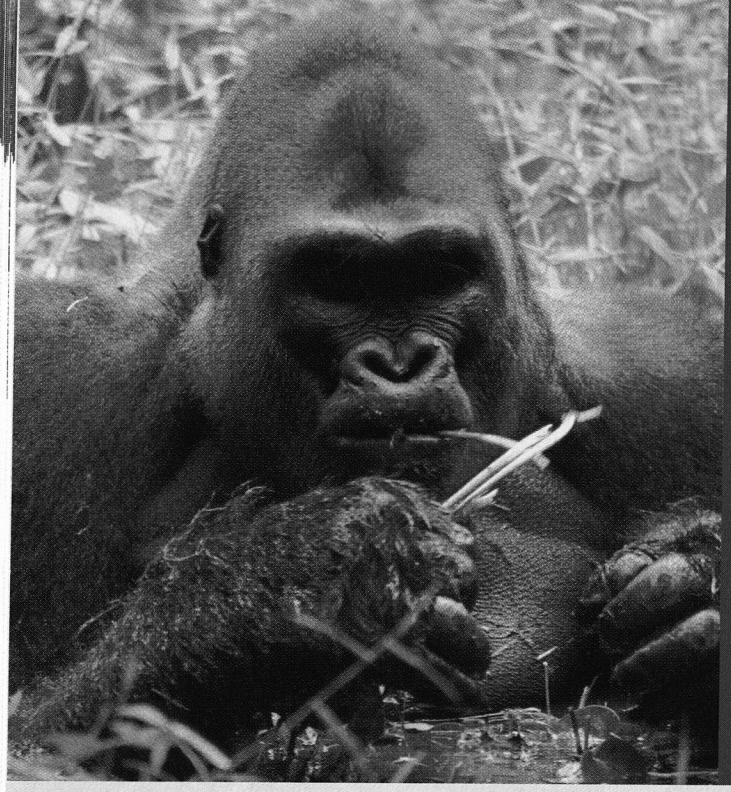




CHAPTER 5

INTRODUCTION TO THE PRIMATES

TWO REASONS TO STUDY PRIMATES

The chapters in Part Two focus on the behavior of living nonhuman primates. Studies of nonhuman primates help us understand human evolution for two complementary but distinct reasons. First, closely related species tend to be similar morphologically. As we saw in Chapter 4, this similarity is due to the fact that closely related species retain and share traits acquired through descent from a common ancestor. For example, **viviparity** (bearing live young) and lactation are traits that all placental and marsupial mammals share, and these traits distinguish mammals from other taxa, such as reptiles. The existence of such similarities means that

studies of living primates often give us more insight about the behavior of our ancestors than do studies of other organisms. This approach is called "reasoning by homology." The second reason we study primates is based on the idea that natural selection leads to similar organisms in similar environments. By assessing the patterns of diversity in the behavior and morphology of organisms in relation to their environments, we can see how evolution shapes adaptation in response to different selective pressures. This approach is called "reasoning by analogy."

Primates Are Our Closest Relatives

The fact that humans and other primates share many characteristics means that other primates provide valuable insights about early humans.

We humans are more closely related to nonhuman primates than we are to any other animal species. The anatomical similarities among monkeys, apes, and humans led the Swedish naturalist Carolus Linnaeus to place humans in the order Primates in the first scientific taxonomy, *Systema Naturae*, published in 1735. Later, naturalists such as Georges Cuvier and Johann Blumenbach placed humans in their own order because of our distinctive mental capacities and upright posture. In *The Descent of Man*, however, Charles Darwin firmly advocated reinstating humans in the order Primates; he cited biologist Thomas Henry Huxley's essay enumerating the many anatomical similarities between us and apes, and he suggested that "if man had not been his own classifier, he would never have thought of founding a separate order for his own reception." Modern systematics unambiguously confirms that humans are more closely related to other primates than to any other living creatures.

Because we are closely related to other primates, we share with them many aspects of morphology, physiology, and development. For example, like other primates, we have well-developed visual abilities and grasping hands and feet. We share certain features of our life history with other primates as well, including an extended period of juvenile development, and primates as a whole have larger brains in relation to body size than the members of most other taxonomic groups have. Homologies between humans and other primates also extend to behavior, since the physiological and cognitive structures that underlie human behavior are more similar to those of other primates than to members of other taxonomic groups. The existence of this extensive array of homologous traits, the product of the common evolutionary history of the primates, means that nonhuman primates provide useful models for understanding the evolutionary roots of human morphology and for unraveling the origins of human nature.

Primates Are a Diverse Order

Diversity within the primate order helps us to understand how natural selection shapes behavior.

During the last 30 years, hundreds of researchers from a variety of academic disciplines have spent thousands of hours observing many different species of nonhuman primates in the wild, in captive colonies, and in laboratories. All primate species have evolved adaptations that enable them to meet the basic challenges of life, such as finding food, avoiding predators, obtaining mates, rearing young, and coping with competitors. At

the same time, there is great morphological, ecological, and behavioral diversity among species within the primate order. For example, primates range in size from the tiny mouse lemur, who weighs less than 30 g (about 1 oz) to male gorillas weighing about 160 kg (350 lb). Some species live in dense tropical forests; others are at home in open woodlands and savannas. Some subsist almost entirely on leaves; others rely on an omnivorous diet that includes fruits, leaves, flowers, seeds, gum, nectar, insects, and small animal prey. Some species are solitary, and others are highly gregarious. Some are active at night (**nocturnal**); others are active during daylight hours (**diurnal**). One primate, the fat-tailed dwarf lemur, enters a torpid state and sleeps for six months each year. Some species actively defend territories from incursions by other members of their own species (**conspecifics**); others do not. In some species, only females provide care of their young; in others, males participate actively in this process.

This variety is inherently interesting. Researchers who study primates tend to be so absorbed in the lives of their subjects that they are motivated to endure the hardships of fieldwork, the frustrations of attempting to obtain a share of ever-shrinking research funds, and the puzzlement of family and friends who wonder why they have chosen such an odd occupation. However, evidence of diversity among closely related organisms living under somewhat different ecological and social conditions also helps researchers to understand how evolution shapes behavior. Animals that are closely related to one another phylogenetically tend to be very similar in morphology, physiology, life history, and behavior. Thus, differences observed among closely related species are likely to represent adaptive responses to specific ecological conditions. At the same time, similarities among more distantly related creatures living under similar ecological conditions are likely to be the product of convergence.

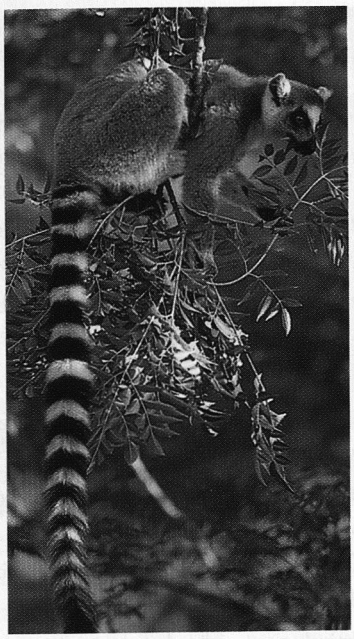
This approach, sometimes called the "comparative method," has become an important form of analysis as researchers attempt to explain the patterns of variation in morphology and behavior observed in nature. The same principles have been borrowed to reconstruct the behavior of extinct hominins, early members of the human lineage. Because behavior leaves virtually no trace in the fossil record, the comparative method provides one of our only objective means of testing hypotheses about the lives of our hominin ancestors. For example, the observation that there are substantial differences in male and female body size, a phenomenon called **sexual dimorphism**, in species that form nonmonogamous groups suggests that highly dimorphic hominins in the past were not monogamous. In Part Three we will see how the data and theories about behavior produced by primatologists have played an important role in reshaping our ideas about human origins.

FEATURES THAT DEFINE THE PRIMATES

The primate order is generally defined by a number of shared, derived characters, but not all primates share all of these traits.

The animals pictured in Figure 5.1 are all members of the primate order. These animals are similar in many ways: they are covered with a thick coat of hair, they have four limbs, and they have five fingers on each hand. However, they share these ancestral features with all mammals. Beyond these ancestral features, it is hard to see what this group of animals have in common that makes them distinct from other mammals. What distinguishes a ring-tailed lemur from a mongoose or a raccoon? What features link the langur and the aye-aye?

(a)



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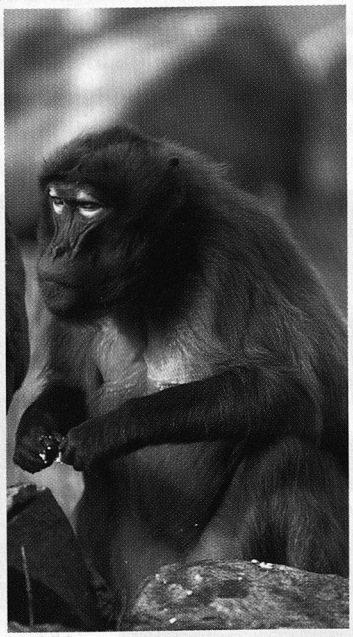


(e)

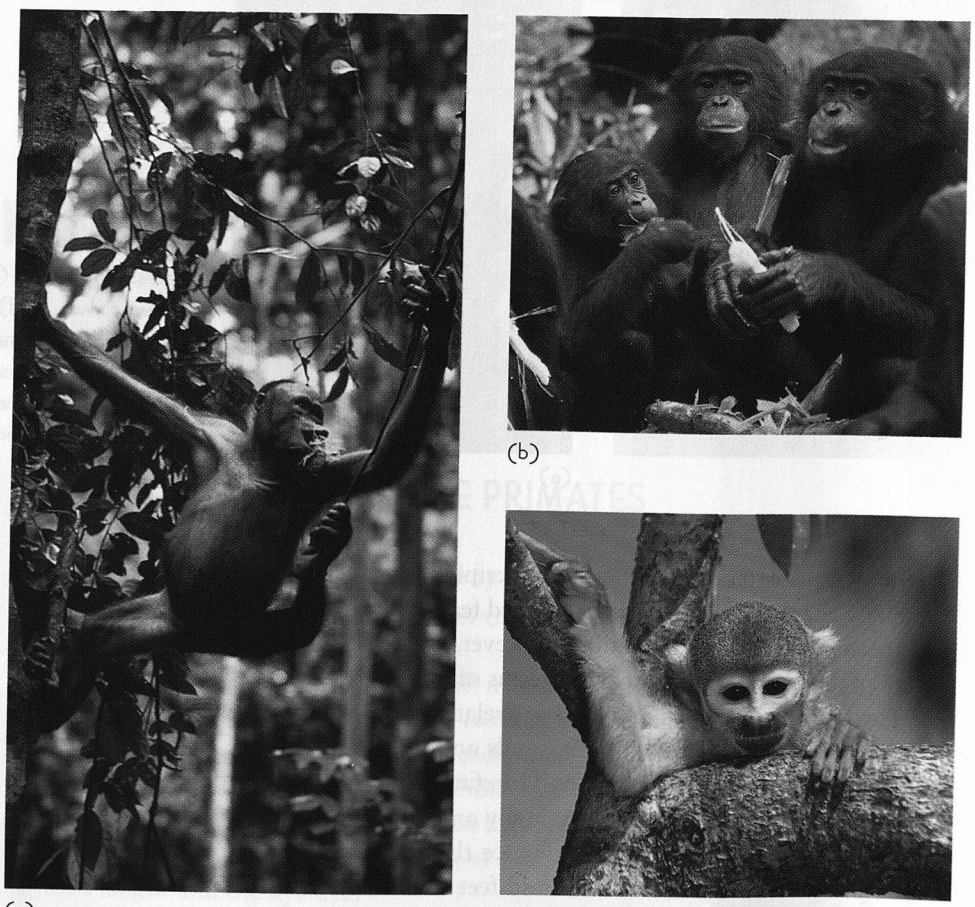
FIGURE 5.1 All of these animals are primates: (a) aye-aye, (b) ring-tailed lemur, (c) langur, (d) howler, (e) gelada baboon. Primates are a diverse order and do not possess a suite of traits that unambiguously distinguish them from other animals.

In fact, primates are a rather nondescript mammalian order that cannot be unambiguously characterized by a single derived feature shared by all members. In his extensive treatise on primate evolution, however, University of Chicago biologist Robert Martin defines the primate order in terms of the derived features listed in Table 5.1.

The first three traits in Table 5.1 are related to the flexible movement of hands and feet. Primates can grasp with their hands and feet (Figure 5.2a), and most monkeys and apes can oppose their thumb and forefinger in a precision grip (Figure 5.2b). The flat nails, distinct from the claws of many animals, and the tactile pads on the tips of primate fingers and toes further enhance their dexterity (Figure 5.2c). These traits enable primates to use their hands and feet differently than most other animals do.

TABLE 5.1 Definition of the primate order. See the text for more complete descriptions of these features.

1. The big toe on the foot is **opposable,** and hands are **prehensile.** This means that primates can use their feet and hands for grasping. The opposable big toe has been lost in humans.
2. There are flat nails on the hands and feet in most species, instead of claws, and there are sensitive tactile pads with "fingerprints" on fingers and toes.
3. Locomotion is **hindlimb-dominated,** meaning the hindlimbs do most of the work, and the center of gravity is nearer the hindlimbs than the forelimbs.
4. There is an unspecialized **olfactory** (smelling) apparatus that is reduced in diurnal primates.
5. The visual sense is highly developed. The eyes are large and moved forward in the head, providing stereoscopic vision.
6. Females have small litters, and gestation and juvenile periods are longer than in other mammals of similar size.
7. The brain is large compared with the brains of similarly sized mammals, and it has a number of unique anatomical features.
8. The **molars** are relatively unspecialized, and there is a maximum of two **incisors,** one **canine,** three **premolars,** and three molars on each half of the upper and lower jaw.
9. There are a number of other subtle anatomical characteristics that are useful to systematists but are hard to interpret functionally.



(a) (b) (c)

FIGURE 5.2 (a) Primates have grasping feet, which they use to climb, cling to branches, hold food, and scratch themselves. (b) Primates can oppose the thumb and forefinger in a precision grip—a feature that enables them to hold food in one hand while they are feeding, to pick small ticks and bits of debris from their hair while grooming, and (in some species) to use tools. (c) Most primates have flat nails on their hands and sensitive tactile pads on the tips of their fingers.

Primates are able to grasp fruit, squirming insects, and other small items in their hands and feet, and they can grip branches with their fingers and toes. During grooming sessions, they delicately part their partner's hair and use their thumb and forefinger to remove small bits of debris from the skin.

Traits 4 and 5 in Table 5.1 are related to a shift in emphasis among the sense organs. Primates are generally characterized by a greater reliance on visual stimuli and a reduced reliance on olfactory stimuli than other mammals are. Many primate species can perceive color, and their eyes are set forward in the head, providing them with binocular, stereoscopic vision (Figure 5.3). **Binocular vision** means that the fields of vision of the two eyes overlap so that both eyes perceive the same image. **Stereoscopic vision** means that each eye sends a signal of the visual image to both hemispheres in the brain to create an image with depth. These trends are not uniformly expressed within the primate order; for example, olfactory cues play a more important role in the lives of prosimian primates than in the lives of anthropoid primates. As we will explain shortly, the **prosimian** primates include the lorises and lemurs, and the **anthropoid** primates include the monkeys and apes.

FIGURE 5.3 In most primates, the eyes are moved forward in the head. The field of vision of the two eyes overlaps, creating binocular, stereoscopic vision. (Photograph courtesy of Carola Borries.)

Features 6 and 7 in Table 5.1 result from the distinctive life history of primates. As a group, primates have longer pregnancies, mature at later ages, live longer, and have larger brains than other animals of similar body size do. These features reflect a progressive trend toward increased dependence on complex behavior, learning, and behavioral flexibility within the primate order. As the noted primatologist Alison Jolly points out, "If there is an essence of being a primate, it is the progressive evolution of intelligence as a way of life." As we will see in the chapters that follow, these traits have a profound impact on the mating and parenting strategies of males and females and the patterns of social interaction among members of the order Primates.

The eighth feature in Table 5.1 concerns primate dentition. Teeth play a very important role in the lives of primates and in our understanding of their evolution. The utility of teeth to primates themselves is straightforward: teeth are necessary for processing food and are also used as weapons in conflicts with other animals. Teeth are also useful features for those who study living and fossil primates. Primatologists sometimes rely on tooth wear to gauge the age of individuals, and they use features of the teeth to assess the phylogenetic relationships among species. As we will see, paleontologists often rely on teeth, which are hard and preserve well, to identify the phylogenetic relationships of extinct creatures and to make inferences about their developmental patterns, their dietary preferences, and their social structure. Box 5.1 describes primate dentition in greater detail.

Although these traits are generally characteristic of primates, you should keep two points in mind. First, none of them makes primates unique. Dolphins, for example, have large brains and extended periods of juvenile dependence, and their social behavior may be just as complicated and flexible as that of any nonhuman primate (Figure 5.4). Second, not every primate possesses all of these traits.

FIGURE 5.4 A high degree of intelligence characterizes some animals besides primates. Dolphins, for example, have very large brains in relation to their body size, and their behavior is quite complex.

BOX 5.1

What's in a Tooth?

To appreciate the basic features of primate dentition, you can consult Figure 5.12, or you can simply look in a mirror, since your teeth are much like those of other primates. Teeth are rooted in the jaw. The jaw holds four different kinds of teeth; in order, they are first the incisors at the front, then the canines, premolars, and the molars in the rear. To understand what each kind of tooth does, imagine yourself eating a sandwich. You bite into the sandwich with your incisors and canines and use your front teeth to detach a piece. The incisors are relatively small, peg-shaped teeth. The canines are dagger-shaped. The upper canines are usually considerably longer than the other teeth, and the upper canine is sharpened on the lower premolar. The incisors and canines are involved mainly in getting food into the mouth and preparing food for further processing by the molars and premolars. The molars and premolars have broad surfaces, covered by a series of enamel bumps, or **cusps**, connected by crests or ridges. The molars and premolars are mainly used to crush, shred, and chew food before it is swallowed. In Chapter 6 we will show how the size and shape of the teeth are related to the types of foods primates eat.

Although all primates have the same kinds of teeth, species vary in how many of each kind of tooth they have. For convenience, these combinations are expressed in a standard format called the **dental formula**, which is commonly written in the following form:

$$\frac{2.1.3.3}{2.1.3.3}$$

The numerals separated by periods tell us how many of each of the four types of teeth a particular species has (or had) on one side of its jaw. Left to right, the four types are given for the front of the mouth (incisors) to the rear (molars). The top line of numbers represents the teeth on one side of the upper jaw (**maxilla**), and the bottom line represents the teeth on the corresponding side of the lower jaw (**mandible**). Hence this species—which happens to be the common ancestor of all primates—had two incisors, one canine, three premolars, and three molars each on one side of the upper and lower jaws. Usually, but not always, the formula is the same for both upper and lower jaws. Like most other parts of the body, our dentition is **bilaterally symmetrical**, which means that the left side is identical to the right side.

The ancestral pattern shown here has been modified in various primate taxa, as the total number of teeth has been reduced (Table 5.2).

The dental formulas among living primates vary. Prosimians have the most variable dentition. The lorises, pottos, galagos, and a number of lemurids have retained the primitive dental formula, but other groups have lost incisors, canines, or premolars. Tarsiers have lost one incisor on the mandible but retained two on the maxilla. Dentition is generally less variable among the anthropoid primates than among the prosimians. All of the New World monkeys, except the marmosets and tamarins, have retained the primitive dental formula; the marmosets and tamarins have lost one molar. The Old World monkeys, apes, and humans have reduced the number of premolars from three to two.

TABLE 5.2 Primates vary in the numbers of each type of tooth that they have. The dental formulas here give the number of incisors, canines, premolars, and molars on each side of the upper and lower jaws. For example, lorises have two incisors, one canine, three premolars, and three molars on each side of their upper and lower jaws.

Primate Group	Dental Formula
Prosimians	
Lorises, pottos, and galagos	$\frac{2.1.3.3}{2.1.3.3}$
Dwarf lemurs, mouse lemurs, and true lemurs	$\frac{2.1.3.3}{2.1.3.3}$
Indris	$\frac{2.1.2.3}{2.0.3.3}$
Aye-ayes	$\frac{1.0.1.3}{1.0.0.3}$
Tarsiers	$\frac{2.1.3.3}{1.1.3.3}$
New World monkeys	
Most species	$\frac{2.1.3.3}{2.1.3.3}$
Marmosets and tamarins	$\frac{2.1.3.2}{2.1.3.2}$
All Old World monkeys, apes, and humans	$\frac{2.1.2.3}{2.1.2.3}$

Humans have lost the grasping big toe that characterizes other primates, and some prosimians have claws on some of their fingers and toes.

PRIMATE BIOGEOGRAPHY

Primates are generally restricted to tropical regions of the world.

The continents of Asia, Africa, and South America and the islands that lie near their coasts are home to most of the world's primates (Figure 5.5). A few species remain in Mexico and Central America. Primates were once found in southern Europe, but no natural populations survive there now. There are no natural populations of primates in Australia or Antarctica, and none occupied these continents in the past.

Primates are found mainly in tropical regions, where the fluctuations in temperature from day to night greatly exceed fluctuations in temperature over the course of the year. In the tropics the distribution of resources that primates rely on for subsistence is affected more strongly by seasonal changes in rainfall than by seasonal changes in temperature. Some primate species extend their ranges into temperate areas of Africa and Asia, where they manage to cope with substantial seasonal fluctuations in environmental conditions.

Within their ranges, primates occupy an extremely diverse set of habitats that includes all types of tropical forests, savanna woodlands, mangrove swamps, grasslands, high-altitude plateaus, and deserts. The vast majority of primates, however, are found in forested areas, where they travel, feed, socialize, and sleep in a largely arboreal world.

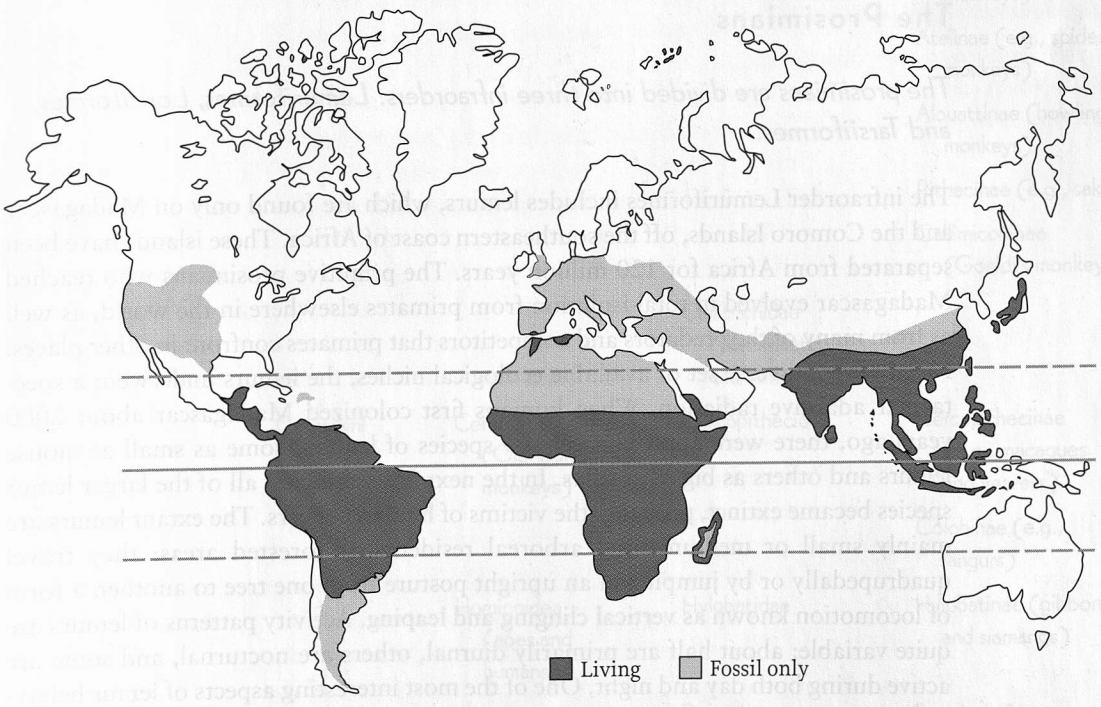


FIGURE 5.5 The distribution of living and fossil primates. Primates are now found in Central America, South America, Africa, and Asia. They are found mainly in tropical regions of the world. Primates were formerly found in southern Europe and northern Africa. There have never been indigenous populations of primates in Australia or Antarctica.

A TAXONOMY OF LIVING PRIMATES

The primates are divided into two groups: the prosimians and the anthropoids.

Scientists classify primates into two suborders: Prosimii and Anthropoidea (Table 5.3). Many of the primates included in the suborder Prosimii are nocturnal, and like some of the earliest primates who lived 50 mya, they have many adaptations to living in darkness, including a well-developed sense of smell, large eyes, and independently movable ears. By contrast, monkeys and apes, who make up the suborder Anthropoidea, evolved adaptations more suited to a diurnal lifestyle early in their evolutionary history. In the Anthropoidea, the traits related to increased complexity of behavior are most fully developed.

The classification of the primates into prosimians and anthropoids does not strictly reflect the patterns of genetic relationships among the animals in the suborders. Tarsiers are included in the prosimians because, like the lorises and lemurs, they are nocturnal creatures that have retained many ancestral characters. However, both genetic and morphological data suggest that tarsiers are more closely related to monkeys and apes than to prosimians. Thus a purely cladistic classification would place tarsiers in the same **infraorder** (the taxonomic level immediately below suborder) as the monkeys. In fact, many primate taxonomists advocate a taxonomy in which the lemurs and lorises are classified together as **strepsirhines** and the rest of the primates are classified together as **haplorhines**. The more traditional division into prosimians and anthropoids is an example of evolutionary taxonomy in which overall similarity and relatedness are used to classify species.

The Prosimians

The prosimians are divided into three infraorders: Lemuriformes, Lorisiformes, and Tarsiiformes.

The infraorder Lemuriformes includes lemurs, which are found only on Madagascar and the Comoro Islands, off the southeastern coast of Africa. These islands have been separated from Africa for 120 million years. The primitive prosimians who reached Madagascar evolved in total isolation from primates elsewhere in the world, as well as from many of the predators and competitors that primates confront in other places. Faced with a diverse set of available ecological niches, the lemurs underwent a spectacular adaptive radiation. When humans first colonized Madagascar about 2000 years ago, there were approximately 44 species of lemurs, some as small as mouse lemurs and others as big as gorillas. In the next few centuries, all of the larger lemur species became extinct, probably the victims of human hunters. The extant lemurs are mainly small or medium-sized arboreal residents of forested areas; they travel quadrupedally or by jumping in an upright posture from one tree to another, a form of locomotion known as **vertical clinging and leaping**. Activity patterns of lemurs are quite variable: about half are primarily diurnal, others are nocturnal, and some are active during both day and night. One of the most interesting aspects of lemur behavior is that females routinely dominate males. In most lemur species, females are able to supplant males from desirable feeding sites; and in some lemur species, females regularly defeat males in aggressive encounters. Alison Jolly, one of the first observers of

TABLE 5.3 A taxonomy of the living primates. (From R. Martin, 1992, Classification of primates, pp. 20–21 in S. Jones, R. Martin, and D. Pilbeam, The Cambridge Encyclopedia of Human Evolution, Cambridge University Press, Cambridge.)

Suborder	Infraorder	Superfamily	Family	Subfamily
Prosimii (prosimians)	Lemuriformes	Lemuroidea (lemurs)	Cheirogaleidae (dwarf and mouse lemurs)	
			Lemuridae	Lemurinae (true lemurs)
				Lepilemurinae (sportive lemurs)
			Indridae (indris)	
			Daubentoniidae (aye-ayes)	
	Lorisiformes	Lorisoidea (loris group)	Lorisidae	Lorisinae (lorises)
				Galaginae (galagos)
	Tarsiiformes	Tarsioidea	Tarsiidae (tarsiers)	
Anthropoidea (anthropoids)	Platyrrhini	Ceboidea (New World monkeys)	Cebidae	Cebinae (e.g., capuchins)
				Aotinae (e.g., owl monkeys)
				Atelinae (e.g., spider monkeys)
				Alouattinae (howling monkeys)
				Pithecinae (e.g., sakis)
				Callimiconinae (Goeldi's monkeys)
			Callitrichidae (marmosets and tamarins)	
	Catarrhini	Cercopithecoidea (Old World monkeys)	Cercopithecidae	Cercopithecinae (e.g., macaques and vervets)
				Colobinae (e.g., langurs)
		Hominoidea (apes and humans)	Hylobatidae	Hylobatinae (gibbons and siamangs)
			Pongidae	Ponginae (great apes)
			Hominidae	Homininae (humans)

FIGURE 5.6 Galagos are small, arboreal, nocturnal animals who can leap great distances. They are mainly solitary, though residents of neighboring territories sometimes rest together during the day.

FIGURE 5.7 Tarsiers are small, insectivorous primates who live in Asia. Some tarsiers form monogamous pairs.

free-ranging lemurs, noted, "At any time a female may casually supplant any male or irritably cuff him over the nose and take a tamarind pod from his hand." Although such behavior may seem unremarkable in our own liberated times, female dominance is very rare in other primate species.

The infraorder Lorisiformes comprises small, nocturnal, arboreal residents of the forests of Africa and Asia. These animals include two subfamilies with different types of locomotion and activity patterns. Galagos are active and agile, leaping through the trees and running quickly along branches (Figure 5.6). The lorises move with ponderous deliberation, and their wrists and ankles have a specialized network of blood vessels that allows them to remain immobile for long periods of time. These traits may be adaptations that help them avoid detection by predators. Traveling alone, the lorisiforms generally feed on fruit, gum, and insect prey. The lorisiforms leave their dependent offspring in nests built in the hollows of trees or hidden in masses of tangled vegetation. During the day, females sleep, nurse their young, and groom, sometimes in the company of mature offspring or familiar neighbors.

The infraorder Tarsiiformes includes tarsiers, which are enigmatic primates who live in the rain forests of Borneo, Sulawesi, and the Philippines (Figure 5.7). Like many other prosimians, tarsiers are small, nocturnal, and arboreal, and they move by vertical clinging and leaping. Some tarsiers live in monogamous family groups, but many groups have more than one breeding female. Female tarsiers give birth to infants who weigh 25% of their own weight; mothers leave their bulky infants behind in safe hiding places when they forage for insects. Tarsiers are unique among primates because they are the only primates who rely exclusively on animal matter, feeding on insects and small vertebrate prey.

The Anthropoids

The suborder Anthropoidea contains the infraorders Platyrrhini and Catarrhini.

The two infraorders Platyrrhini and Catarrhini are commonly referred to as the New World monkeys and the Old World monkeys and apes, respectively, because platyrrhine monkeys are found in South and Central America, while catarrhine monkeys and apes are found in Africa and Asia. This geographic dichotomy breaks down with humans, however: we are catarrhine primates, but we are spread over the globe.

The infraorder Platyrrhini (New World monkeys) is divided into two families: Callitrichidae and Cebidae.

Although the New World monkeys encompass considerable diversity in size, diet, and social organization, they do share some basic features. All but those in one genus

(*Aotus*) are diurnal, all live in forested areas, and all are mainly arboreal. Most New World monkeys are quadrupedal, moving along the tops of branches and jumping between adjacent trees. Some species in the family Cebidae can suspend themselves by their hands, feet, or tail and can move by swinging by their arms beneath branches.

The family Callitrichidae is composed of the marmosets and tamarins. These species share several morphological features that distinguish them from other anthropoid primate species: they are extremely small, the largest weighing less than 1 kg (2.2 lb); they have claws instead of nails; they have only two molars, while all other monkeys have three; and they frequently give birth to twins and sometimes triplets (Figure 5.8). Marmosets and tamarins are also notable for their domestic arrangements: most species seem to be monogamous, and some may be polyandrous. **Polyandry**, which occurs when two or more males simultaneously form pair-bonds with a single female, is extremely uncommon among mammalian species. In caring for their young, marmoset and tamarin mothers receive a considerable amount of assistance from their mates and older offspring.

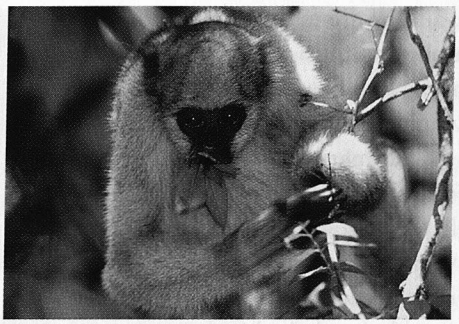
The cebid monkeys are generally larger than the marmosets and tamarins, ranging in size from the 600-g (21-oz) squirrel monkey to the 9.5-kg (21-lb) muriqui (Figure 5.9). Although many people think that all monkeys can swing by their tails, prehensile tails are actually restricted to only the largest species of the Cebidae.

The family Cebidae is divided into six subfamilies that encompass considerable diversity in social organization, feeding behavior, and ecology. The subfamily Alouattinae is composed of several species of howlers, named for the long-distance roars they give in intergroup interactions. Howlers live in small one-male or multimale groups, defend their home ranges, and feed mainly on leaves. The subfamily Atelinae includes spider monkeys and woolly monkeys (Figure 5.9a). These species subsist mainly on fruit and leaves, and they live in multimale, multifemale groups of 15 to 25. Spider monkeys, who rely heavily on ripe fruit, typically break up into small parties for feeding (Figure 5.9b). The subfamily Cebinae includes capuchins and squirrel monkeys. Capuchins are best known to the public as the clever creatures dressed in red caps and jackets who retrieve coins for organ grinders (Figure 5.9c). To primatologists, capuchins are notable in part because they have very large brains in relation to their body size (see Chapter 9). Squirrel monkeys and capuchins live in multimale, multifemale groups of 10 to 50 individuals and forage for fruit, leaves, and insects (Figure 5.9d). The subfamily Aotinae includes the diurnal titi monkey and the only nocturnal anthropoid primate, the owl monkey. The subfamily Callimiconinae is composed of just one species, Goeldi's monkey. Aotinae and Callimiconinae monkeys are small-bodied fruit eaters and live in monogamous groups. Finally, Pithecinae is a subfamily composed of the uakaris and sakis. Uakaris have little hair around their faces, making them look like wizened old men.

FIGURE 5.8 Marmosets are small-bodied South American monkeys who form monogamous or polyandrous social groups. Males and older offspring participate actively in the care of infants.

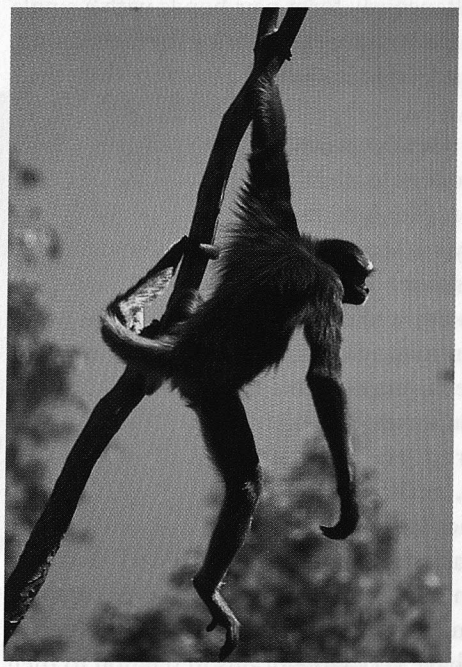
The infraorder Catarrhini contains the monkeys and apes of the Old World and humans.

As a group, the catarrhine primates share a number of anatomical and behavioral features that distinguish them from the New World primates. For example, most Old World monkeys and apes have narrow nostrils that face downward, while New World monkeys have round nostrils. Old World monkeys have two premolars on each side of the upper and lower jaws; New World monkeys have three. Most Old World primates are larger than most New World species, and Old World monkeys and apes occupy a wider range of habitats than New World species do.



(a)

(b)



(c)

(d)

FIGURE 5.9 Portraits of some cebid monkeys. (a) Muriquis, or woolly spider monkeys, are large-bodied and arboreal. They are extremely peaceful creatures, rarely fighting or competing over access to resources. (b) Spider monkeys rely heavily on ripe fruit and travel in small parties. They have prehensile tails that they can use much like an extra hand or foot. (c) Capuchin monkeys have larger brains in relation to their body sizes than any of the other nonhuman primates. (d) Squirrel monkeys form large multimale, multifemale groups. In the mating season, males gain weight and become "fatted," and then compete actively for access to receptive females. [Photographs courtesy of Sue Boinski (a), Susan Perry (c), and Carlão Limeira (d).]

The catarrhine primates are divided into two superfamilies: Cercopithecoidea (Old World monkeys) and Hominoidea (apes and humans). Cercopithecoidea contains one extant (still living) family, which is further divided into two subfamilies of monkeys: Cercopithecinae and Colobinae.

The superfamily Cercopithecoidea encompasses great diversity in social organization, ecological specializations, and biogeography.

Colobine monkeys are found in the forests of Africa and Asia and are collectively perhaps the most elegant of the primates (Figure 5.10). They have slender bodies, long legs, long tails, and often beautifully colored coats. The black-and-white colobus, for example, has a white ring around its black face, a striking white cape on its black back, and a bushy white tail that flies out behind as it leaps from tree to tree. Colobines are mainly leaf and seed eaters, and most species spend the majority of their time in trees. They have complex stomachs, almost like the chambered stomachs of cows, which allow them to maintain bacterial colonies that facilitate the digestion of cellulose.

(a) (b)

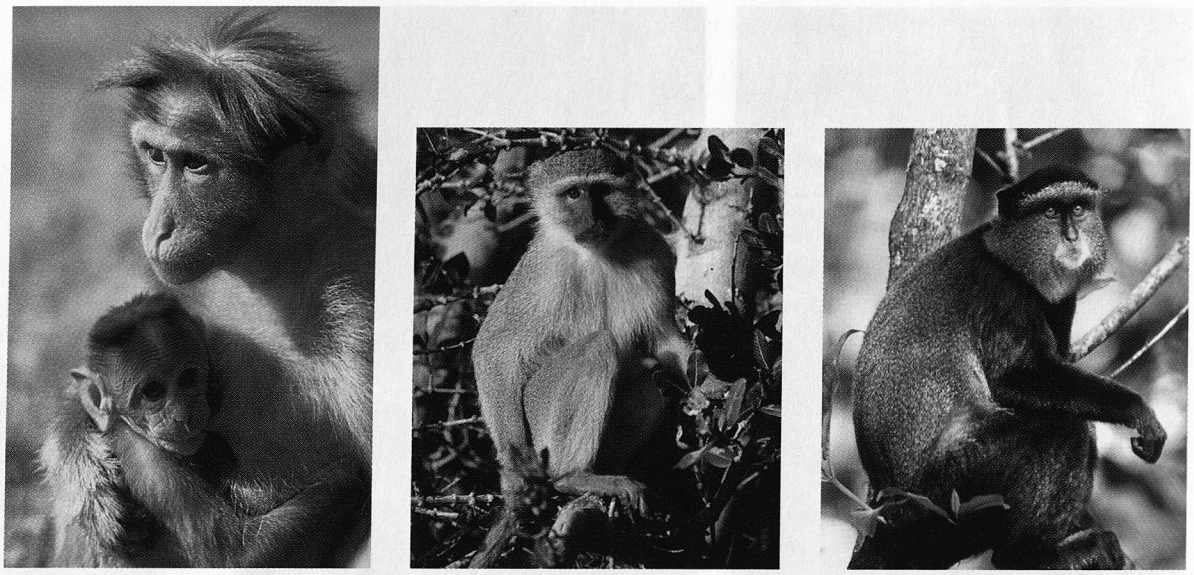
FIGURE 5.10 (a) African colobines, like this black-and-white colobus monkey, are arboreal and feed mainly on leaves. These animals are sometimes hunted for their spectacular coats. (b) Hanuman langurs are native to India and have been the subject of extensive study during the last three decades. In some areas, hanuman langurs form one-male, multifemale groups, and males engage in fierce fights over membership in bisexual groups. In these groups, infanticide often follows when a new male takes over the group. (b, Photograph courtesy of Carola Borries.)

Colobines are most often found in groups composed of one adult male and a number of adult females. As in many other vertebrate taxa, the replacement of resident males in one-male groups is often accompanied by lethal attacks on infants by new males. Infanticide under such circumstances is believed to be favored by selection because it improves the relative reproductive success of infanticidal males. This issue is discussed more fully in Chapter 7.

Most cercopithecine monkeys are found in Africa, though one successful genus (*Macaca*) is widely distributed through Asia and part of Europe (Figure 5.11). The cercopithecines are more variable in size and diet than the colobines are. The social behavior, reproductive behavior, life history, and ecology of a number of cercopithecine species (particularly baboons, macaques, and vervets) have been studied extensively. Cercopithecines typically live in medium or large bisexual (multimale, multifemale) groups. Females typically remain in their **natal groups** (the groups into which they are born) throughout their lives and establish close and enduring relationships with their maternal kin; males leave their natal groups and join new groups when they reach sexual maturity.

The superfamily Hominoidea includes three families of apes: Hylobatidae (gibbons), Pongidae (orangutans, gorillas, and chimpanzees), and Hominidae (humans).

The hominoids are different from the cercopithecoids in a number of ways. The most readily observed difference between apes and monkeys is that apes lack tails. But there are many other more subtle differences between apes and monkeys. For example, the apes share some derived traits, including broader noses, broader palates, and



(a) (b) (c)

FIGURE 5.11 Some representative cercopithecines: (a) Bonnet macaques are one of several species of macaques that are found throughout Asia and North Africa. Like other macaques, bonnet macaques form multimale, multifemale groups, and females spend their entire lives in their natal (birth) groups. (b) Vervet monkeys are found throughout Africa. Like macaques and baboons, females live among their mothers, daughters, and other maternal kin. Males transfer to nonnatal groups when they reach maturity. Vervets defend their ranges against incursions by members of other groups. (c) Blue monkeys live in one-male, multifemale groups. During the mating season, however, one or more unfamiliar males may join bisexual groups and mate with females. [Photographs courtesy of Kathy West (a) and Marina Cords (c).]

larger brains; and they retain some primitive traits, such as relatively unspecialized molars. In Old World monkeys the prominent anterior and posterior cusps are arranged to form two parallel ridges. In apes, the five cusps on the lower molars are arranged to form a side-turned Y-shaped pattern of ridges (Figure 5.12).

The family Hylobatidae includes lesser apes (gibbons and siamangs), and its living members are now found in Asia. The family Pongidae includes the larger-bodied great apes (orangutans, gorillas, bonobos, and chimpanzees). Humans are traditionally placed in their own family, the Hominidae, but many taxonomists believe that

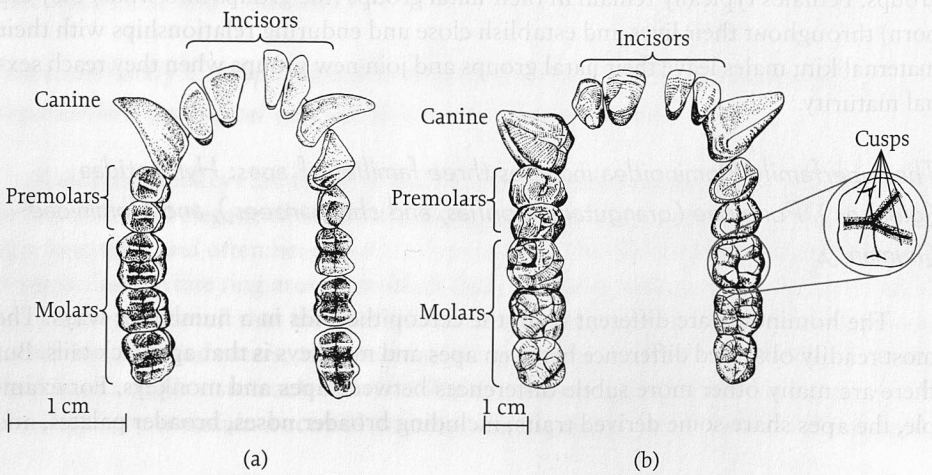


FIGURE 5.12 The upper jaw (left) and lower jaw (right) are shown here for a male colobine (a) and a male gorilla (b). In Old World monkeys, the prominent anterior and posterior cusps of the lower molars form two parallel ridges. In apes, the five cusps of the lower molar form a Y-shaped pattern.

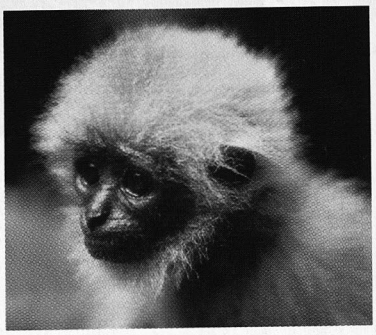
humans belong with the other great apes, in the Pongidae. Orangutans are found in Asia, while chimpanzees, bonobos, and gorillas are restricted to Africa.

The lesser apes are slightly built creatures with extremely long arms in relation to their body size (Figure 5.13). Gibbons and siamangs are strictly arboreal, and they use their long arms to perform spectacular acrobatic feats, moving through the canopy with grace, speed, and agility. Gibbons and siamangs are the only true **brachiators** among the primates, which means they propel themselves by their arms alone and are in free flight between handholds. (To picture this, think about swinging on monkey bars in your elementary school playground.) All of the lesser apes live in monogamous family groups; vigorously defend their **home ranges** (the areas they occupy); and feed on fruit, leaves, flowers, and insects. Siamang males play an active role in caring for young, frequently carrying them during the day; male gibbons are less attentive fathers. In territorial displays, mated pairs of siamangs perform coordinated vocal duets that can be heard over long distances.

Orangutans, now found only on the Southeast Asian islands of Sumatra and Borneo, are among the largest and most solitary species of primates (Figure 5.14). Orangutans have been studied extensively by Biruté Galdikas in Tanjung Puting, Borneo, for more than 20 years. Long-term studies of orangutans have also been conducted at Cabang Panti in Borneo, and at Ketambe and Suaq Balimbing in Sumatra. Orangutans feed primarily on fruit, but they also eat some leaves and bark. Adult females associate mainly with their own infants and immature offspring and do not often meet or interact with other orangutans. Adult males spend the majority of their time alone. A single adult male may defend a home range that encompasses the home ranges of several adult females; other males wander over larger areas and mate opportunistically with receptive females. When resident males encounter these nomads, fierce and noisy encounters may take place.

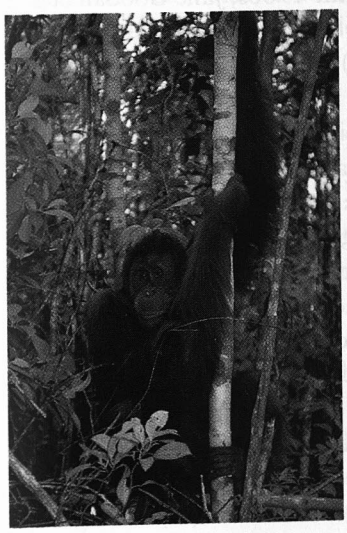
Gorillas, the largest of the apes, existed in splendid isolation from Western science until the middle of the nineteenth century (Figure 5.15). Today, our knowledge of the behavior and ecology of gorillas is based mainly on detailed long-term studies of one subspecies, the mountain gorilla, at the Karisoke Research Center in Rwanda, which was founded by the late Dian Fossey. Mountain gorillas live in small groups that contain one or two adult males and a number of adult females and their young. Each day, mountain gorillas ingest great quantities of various herbs, vines, shrubs, and

(a)



(b)

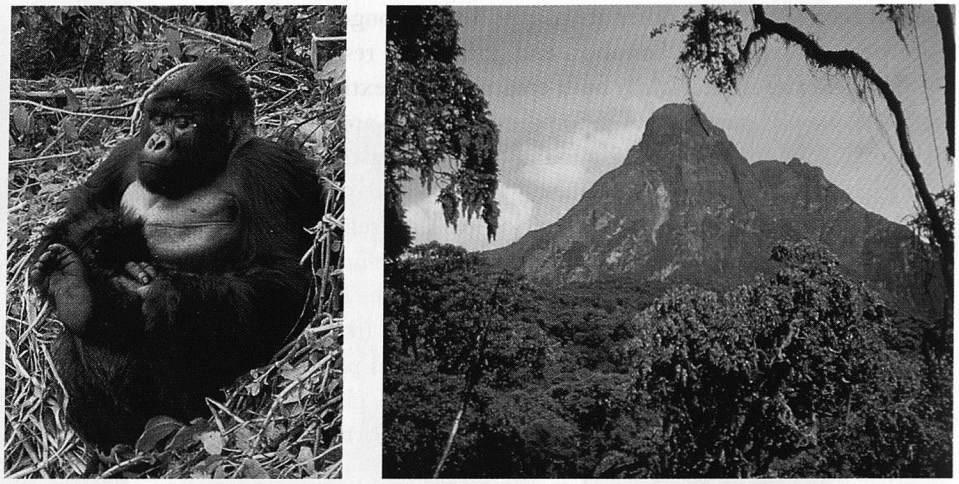
FIGURE 5.13 Gibbons (a) and siamangs (b) live in monogamous groups and actively defend their territories against intruders. They have extremely long arms, which they use to propel themselves from one branch to another as they swing hand over hand through the canopy, a form of locomotion called "brachiation." Siamangs and gibbons are confined to the tropical forests of Asia. Like other residents of tropical forests, their survival is threatened by the rapid destruction of tropical forests. (Photographs courtesy of John Mitani.)



(a)

(b)

FIGURE 5.14 (a) Orangutans are large, ponderous, and mostly solitary creatures. Male orangutans often descend to the ground to travel; lighter females often move through the tree canopy. (b) Today, orangutans are found only on the islands of Borneo and Sumatra, in tropical forests like this one.



(a) (b)

FIGURE 5.15 (a) Gorillas are the largest of the primates. Mountain gorillas usually live in one-male, multifemale groups, but some groups contain more than one adult male. (b) Most behavioral information about gorillas comes from observations of mountain gorillas who live in the Virunga Mountains of central Africa, pictured here. The harsh montane habitat may influence the nature of social organization and social behavior in these animals, and the behavior of gorillas living at lower elevations may differ. (Photographs courtesy of John Mitani.)

bamboo. They eat little fruit because fruiting plants are scarce in their mountainous habitat. Adult male mountain gorillas, called **silverbacks** because the hair on their backs and shoulders turns a striking silver-gray when they mature, play a central role in the structure and cohesion of their social groups. Males sometimes remain in their natal groups to breed, but most males leave their natal groups and acquire females by drawing them away from other males during intergroup encounters. The silverback largely determines the timing of group activity and the direction of travel. As data from newly established field studies of lowland gorilla populations become available, however, we may have reason to revise some elements of this view of gorilla social organization. For example, lowland gorillas seem to eat substantial amounts of fruit, spend more of their time in trees, and form larger and less cohesive social groups than mountain gorillas do.

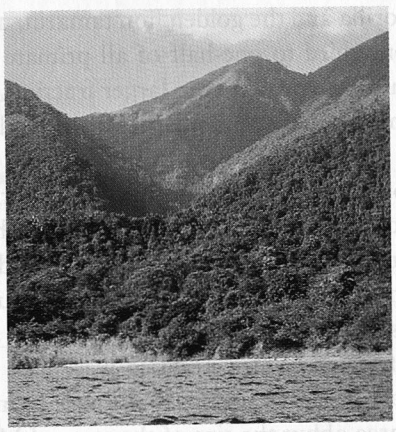
As humankind's closest living relatives, chimpanzees (Figure 5.16a) have played a uniquely important role in the study of human evolution. Whether reasoning by homology or by analogy, researchers have found observations about chimpanzees to be important bases for hypotheses about the behavior of early hominins.

Detailed knowledge of chimpanzee behavior and ecology comes from a number of long-term studies conducted at sites across Africa. In the 1960s, Jane Goodall began her well-known study of chimpanzees at the Gombe Stream National Park on the shores of Lake Tanganyika in Tanzania (Figure 5.16b). About the same time, a second study was initiated by Toshisada Nishida at a site in the Mahale Mountains not far from Gombe. These studies are now moving into their fourth decade. Other important study sites have been established at Boussou, Guinea; in the Taï Forest of the Ivory Coast; and at two sites in the Kibale Forest of Uganda: Kanyawara and Ngogo.

Bonobos (Figure 5.16c), another member of the genus *Pan*, live in inaccessible places and are much less well studied than common chimpanzees. Important field studies on bonobos have been conducted at two sites in the Democratic Republic of the Congo (formerly Zaire): Wamba and Lomako. Field studies of bonobos have been disrupted by civil conflicts that have ravaged central Africa over the last two decades.

Chimpanzees and bonobos form large multimale, multifemale communities. These communities differ from the social groups formed by most other species of primates in two important ways. First, female chimpanzees usually disperse from their natal groups when they reach sexual maturity, while males remain in their natal groups

(a)



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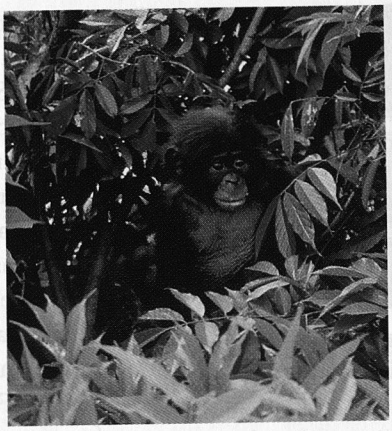

(c)

FIGURE 5.16 (a) Chimpanzees live in multimale, multifemale social groups. In this species, males form the core of the social group and remain in their natal groups for life. Many researchers believe that chimpanzees are our closest living relatives. (b) Like other apes, chimpanzees are found mainly in forests like this area on the shores of Lake Tanganyika in Tanzania. However, chimpanzees sometimes range into more open areas as well. (c) Bonobos are members of the same genus as chimpanzees and are similar in many ways. Bonobos are sometimes called "pygmy chimpanzees," but this is a misnomer because bonobos and chimpanzees are about the same size. This infant bonobo is sitting in a patch of terrestial herbaceous vegetation, one of the staples of the bonobo's diet. (b, c, Photographs courtesy of John Mitani.)

throughout their lives. Second, the members of chimpanzee communities are rarely found together in a unified group. Instead, they split up into smaller parties that vary in size and composition from day to day. In chimpanzees, the strongest social bonds among adults are formed among males, while bonobo females form stronger bonds with one another and with their adult sons than males do. Chimpanzees modify natural objects for use as tools in the wild. At several sites, chimpanzees strip twigs and poke them into termite mounds and ant nests to extract insects, a much-prized delicacy. In the Taï Forest, chimpanzees crack hard-shelled nuts using one stone as a hammer and a heavy, flat stone or a protruding root as an anvil. At Gombe, chimpanzees wad leaves in their mouths and then dip these "sponges" into crevices to soak up water. New data also reveal tool use by wild orangutans, but chimpanzee tool use is more diverse and better studied.

PRIMATE CONSERVATION

Many species of primates are endangered by (1) habitat destruction, (2) hunting, or (3) live capture for trade and export.

Sadly, no introduction to the primate order would be complete without acknowledgment that the prospects for the continued survival of many primate species are grim. Today, nearly 100 primate species are considered to be endangered or critically endangered, and are in real danger of extinction. Already, primate conservation biologists believe that one subspecies, Miss Waldron's red colobus, has become extinct. The populations of some of the most gravely endangered species, such as the

FIGURE 5.17 Many populations of primates are in danger of extinction. This is a free-ranging member of a subspecies of squirrel monkeys that may number only 200 in the wild.

mountain gorilla and the golden lion tamarin, number only in the hundreds. In Africa and Asia, one-third to one-half of all primate species are endangered, and in some parts of South America an even larger fraction of species are at risk (Figure 5.17). At least two-thirds of the lemur species in Madagascar are in immediate danger of extinction.

As arboreal residents of the tropics, most primate populations are directly affected by the rapid and widespread destruction of the world's forests. Primate ecologists Colin Chapman of the University of Florida and Carlos Peres of the University of East Anglia recently reviewed the conservation status of the world's primate populations. Their analysis is quite sobering. Between 1980 and 1995, approximately 10% of the forests in Africa and Latin America were lost, and 6% of the forests of Asia disappeared (Figure 5.18). Countries that house primates are losing about 125,000 km^2 of forest—an area about the size of the state of Mississippi—*every year*.

The destruction of tropical forests is the product of economic and demographic pressures acting on governments and local residents. Many developing countries have huge foreign debts that must be repaid. The need to raise funds to pay off these debts generates intense pressure for timber harvesting and more intensive agricultural activity. Each year, 5 million to 6 million hectares of forest is logged, seriously disrupting the lives of the animals that live in them. (A hectare is a square measuring 100 m on a side, or about 2.5 acres.)

Forests are also cleared for agricultural activities. Rapid increases in the population of underdeveloped countries in the tropics have created intense demand for addi-

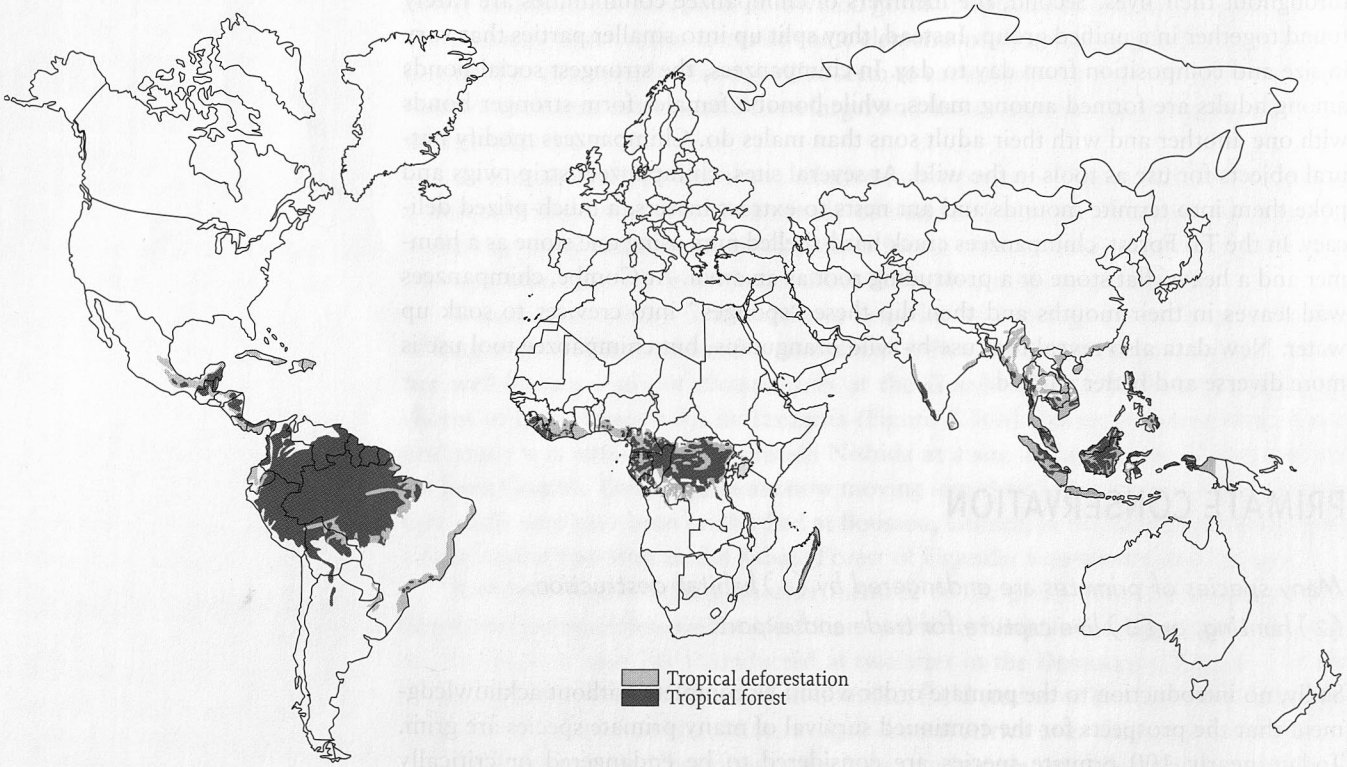

FIGURE 5.18 This map shows the major locations of tropical forest and the areas that have become deforested (90% of the canopy cover has been lost). Deforestation is a major threat to primates because many primate species live in tropical forests.

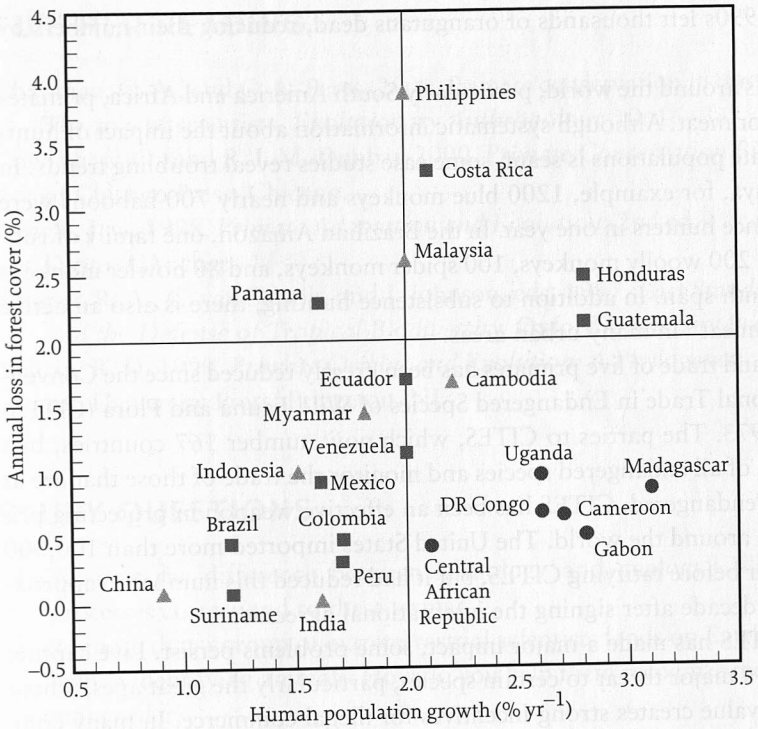

FIGURE 5.19 The destruction of tropical forests is often related to population pressures. Here, data on deforestation and human population growth are plotted for some of the countries that harbor free-ranging primate populations. Countries that have high rates of population growth have the highest rates of deforestation.

tional agricultural land (Figure 5.19). In West Africa, Asia, and South America, for example, vast expanses of forests have been cleared to accommodate the demands of subsistence farmers trying to feed their families, as well as the needs of large-scale agricultural projects (Figure 5.20). In Central and South America, massive areas have been cleared for large cattle ranches.

In the last two decades, a new threat to the forests of the world has emerged: wildfire. Major fires have destroyed massive tracts of forest in Southeast Asia and South America. Ecologists believe that natural fires in tropical forests are relatively rare, and that these devastating fires are the product of human activity. In Indonesia, massive

FIGURE 5.20 This forest, on the border of the Lomas Barbudal Biological Reserve, a national park in Costa Rica, has just been logged. In many countries, cultivation of all the land surrounding nature reserves and national parks has created forest islands. Although primates may be protected within these reserves, their isolation threatens their long-term survival. The elimination of surrounding forest corridors restricts the movement of migrating animals and limits the size and genetic diversity of local primate populations. (Photograph by Colin Chapman.)

fires in the late 1990s left thousands of orangutans dead, reducing their numbers by nearly a third.

In many areas around the world, particularly South America and Africa, primates are also hunted for meat. Although systematic information about the impact of hunting on wild primate populations is scant, some case studies reveal troubling trends. In one forest in Kenya, for example, 1200 blue monkeys and nearly 700 baboons were killed by subsistence hunters in one year. In the Brazilian Amazon, one family of rubber tappers killed 200 woolly monkeys, 100 spider monkeys, and 80 howler monkeys during an 18-month span. In addition to subsistence hunting, there is also an active market for "bushmeat" in many urban areas.

The capture and trade of live primates has been greatly reduced since the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) was drafted in 1973. The parties to CITES, which now number 167 countries, ban commercial trade of all endangered species and monitor the trade of those that are at risk of becoming endangered. CITES has been an effective weapon in protecting primate populations around the world. The United States imported more than 100,000 primates each year before ratifying CITES, but it had reduced this number to approximately 13,000 a decade after signing the international agreement.

Although CITES has made a major impact, some problems persist. Live capture for trade remains a major threat to certain species, particularly the great apes, whose high commercial value creates strong incentives for illegal commerce. In many communities, young primates are kept as pets (Figure 5.21). For each animal taken into captivity, many other animals are put at risk because hunters cannot obtain young primates without capturing their mothers, who are usually killed in the process. In addition, many prospective pets die after capture, from injuries suffered during capture and transport or from poor housing conditions and inappropriate diets while in captivity.

Efforts to save endangered primate populations have met with some success.

Although much remains to be done, conservation efforts have significantly improved the survival prospects of a number of primate species. These efforts have helped preserve muriquis and golden lion tamarins in Brazil and golden bamboo lemurs in Madagascar. But there is no room for complacency. Promising efforts to save orangutans in Indonesia and mountain gorillas in Rwanda have been seriously impeded by regional political struggles and armed conflict, putting the apes' habitats and their lives in serious jeopardy. A number of different strategies to conserve forest habitats and preserve animal populations are on the table. These include land-for-debt swaps in which foreign debts are forgiven in exchange for commitments to conserve natural habitats, to develop ecotourism projects, and to promote sustainable development of forest resources. But as conservationists study these solutions and try to implement them, the problems facing the world's primates become more pressing. More and more forests disappear each year, and many primates are lost, perhaps forever.

FIGURE 5.21 These two colobine monkeys were captured by poachers for the pet trade. The animals were then confiscated by the Uganda Wildlife Authority and taken to a local zoo. (Photograph by Colin Chapman.)

FURTHER READING

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STUDY QUESTIONS

1. What is the difference between homology and analogy? What evolutionary processes correspond to these terms?
2. Suppose that a group of extraterrestrial scientists lands on Earth and enlists your help in identifying animals. How do you help them recognize members of the primate order?
3. What kinds of habitats do most primates occupy? What are the features of this kind of environment?
4. Outline the taxonomy of the living primates to the superfamily level. Identify the geographic regions the animals inhabit, as well as their major features.
5. What primitive characteristics do modern prosimians retain?
6. In many ways, the superfamily Lemuroidea comprises a more diverse group than other primate superfamilies do. Why is this?
7. What genera are included in the family Pongidae? Briefly describe the social organization and geographic range of each of these genera.
8. Why are contemporary primate species threatened? In other words, what are the major hazards facing them today?
9. How can we balance the needs and rights of people living in developing nations with the needs of the primates who live around them?
10. Local peoples have been living alongside monkeys and other animals in tropical forests for thousands of years. If this is the case, then why do we face the present conservation crisis? What has changed?

KEY TERMS

viviparity
diurnal
nocturnal
conspecifics
sexual dimorphism
binocular vision
stereoscopic vision
prosimian
anthropoid
infraorder
strepsirhines
haplorhines
vertical clinging and leaping
ployandry
natal groups
brachiators
home ranges
silverbacks

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