WHAT IS A PRIMATE?

There are an estimated 200 to 300 living species of primates. We're not sure how many have existed during the order's evolutionary history of more than 55 million years. Primates range from the very small, such as the mouse lemur of Madagascar, which weighs less than 3 ounces, to the gigantic—Gigantopithecus, an extinct ape from China, Vietnam, and India that may have stood 12 feet tall and weighed over half a ton.

St. George J Mivart (1873) defined Primates (as an order) as "unguiculate, claviculate, placental mammals, with orbits encircled by bone; three kinds of teeth, at least at one time of life; brains always with a posterior lobe and calcarine fissure; the innermost digits of at least one pair of extremities opposable, hallux with a flat nail or none; a well-developed caecum; pendulous penis; testes with scrotum; two pectoral mammae."

Characteristics of Primates

Primates can't be defined by one or even a few traits they share in common because they aren't so specialized. Therefore, primatologists have drawn attention to a group of characteristics that, when taken together, more or less characterize the entire primate order. Still, these are a set of general tendencies that aren't all equally expressed in all primates. In addition, while some of these traits are unique to primates, many others are retained ancestral mammalian characteristics shared with other mammals. The following list is meant to give you a general anatomical and behavioural picture of the primates. In their limbs and locomotion, teeth, diet, senses, brain, and behaviour, primates reflect a common evolutionary history with adaptations to similar environmental challenges, primarily as highly social, arboreal animals.

A. Limbs and Locomotion

1. A **tendency toward an erect posture** (especially in the upper body). All primates show this tendency to some degree, and it's variously associated with sitting, leaping, standing, and, occasionally, bipedal walking.
2. A **generalized limb structure**, which allows most primates to practice numerous forms of locomotion. Various aspects of hip and shoulder anatomy provide primates with a wide range of limb movement and function. Thus, by maintaining a generalized locomotor anatomy, primates aren't restricted to one form of movement, like many other mammals are. Primates also use their limbs for many activities besides locomotion.
3. **Prehensile hands** (and sometimes feet). Many animals can manipulate objects, but not as skilfully as primates. All primates use their hands, and frequently their feet, to grasp and manipulate objects. This ability is variably expressed and is enhanced by several characteristics, including:
    a. **Retention of five digits** on the hands and feet.
    b. An **opposable thumb** and, in most species, a divergent and partially opposable big toe.
    c. **Nails instead of claws**. This characteristic is seen in all primates except some New World monkeys (marmosets and tamarins). All lemurs and lorises also have a claw on one digit.
    d. **Tactile pads** enriched with sensory nerve fibers at the ends of digits. This characteristic enhances the sense of touch.

B. Diet and Teeth

1. **Lack of dietary specialization**. This is typical of most primates, who tend to eat a wide assortment of food items. In general, primates are omnivorous.
2. **A generalized dentition**. Primate teeth aren't specialized for processing only one type of food, a trait related to a general lack of dietary specialization.

C. The senses and the brain.

Primates (diurnal ones in particular) rely heavily on vision and less on the sense of smell, especially when compared with other mammals. This emphasis is reflected in evolutionary changes in the skull, eyes, and brain.

1. **Color vision**. This is a characteristic of all diurnal primates. Nocturnal primates didn't had color vision.
2. **Depth perception**. Primates have stereoscopic vision, or the ability to perceive objects in three dimensions. This is made possible through a variety of mechanisms, including:
    a. **Eyes placed toward the front of the face (not to the sides**). This position provides for overlapping visual fields, or binocular vision.
    b. **Visual information from each eye transmitted to visual centres in both hemispheres of the brain**. In non-primate mammals, most optic nerve fibres cross to the opposite hemisphere through a structure at the base of the brain. In primates, about 40 percent of the fibres remain on the same side, so that both hemispheres receive much of the same information.
    c. **Visual information organized into three-dimensional images by specialized structures in the brain itself**. The capacity for stereoscopic vision depends on each hemisphere of the brain receiving visual information from both eyes and from overlapping visual fields.
3. **Decreased reliance on the sense of smell**. This trend is expressed as an overall reduction in the size of olfactory structures in the brain. Corresponding reduction of the entire olfactory apparatus has also resulted in **decreased size of the snout in most species**. This is related to an increased dependence on vision. Some species, such as baboons, have large muzzles, but this isn't related to olfaction, but rather to the need to accommodate large canine teeth.
4. **Expansion and increased complexity of the brain**. This is a general trend among placental mammals, but it's especially true of primates. In primates, this expansion is most evident in the visual and association areas of the neocortex (portions of the brain where information from different sensory modalities is combined).

D. Maturation, learning, and behaviour

1. **A more efficient means of foetal nourishment, longer periods of gestation, reduced numbers of offspring (with single births the norm), delayed maturation, and extension of the entire life span.**
2. **A greater dependence on flexible, learned behaviour**. This trend is correlated with delayed maturation and subsequently longer periods of infant and adolescent dependency on at least one parent. Because of these trends, parental investment in each offspring is increased; although fewer offspring are born, they receive more intense parental care.
3. **The tendency to live in social groups and the permanent association of adult males with the group**. Except for some nocturnal species, primates tend to associate with other individuals.
4. **The tendency toward diurnal activity patterns**. This is seen in most primates. Lorises, tarsiers, one monkey species, and some lemurs are nocturnal; all the rest (the other monkeys, apes, and humans) are diurnal.

CLARK'S TEN EVOLUTIONARY TREND

Defining primates like other taxonomical groups on the basis of morphological or anatomical characteristics is extremely difficult - Why?

Primates lack distinguishing bodily specializations like other mammalian groups. Primates exhibit amazing variety of forms and grades of organization - Size, Habitat, Behaviour etc. The best and most useful solution to the problem of a definition was devised by one of the foremost primate anatomists, Sir Wilfred E. LeGros Clark.

Though there are ten trends, there are related to three principle areas…
1. Limbs and extremities (1-3)
2. Head- eyes, brain and dentition (trends 4-8)
3. Life cycle-reproduction, growth, and longevity (trends 9 & 10)

These are trends and not characteristics. Hence are not uniformly present, but are expressed to varying degrees among the members of the order. As a rule, except for the first one, these trends are less well developed in the living prosimians and in fossil forms than in the more advanced, modern Higher Primates.

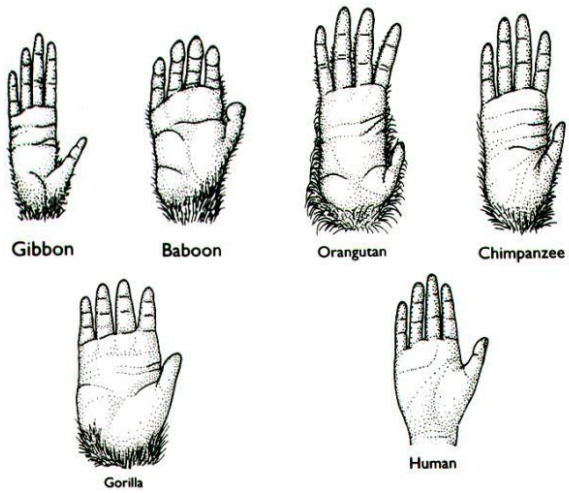
They are all interrelated and adaptive to a mode of life which has been the outstanding factor in primate evolution-the arboreal habitat. Other mammals have taken up arboreal life but none have done it in exactly the same way. Many of man's characteristics are simply refinements of a basic primate pattern that evolved millions of years ago in response to the necessities of arboreal living.

Evolutionary Trends

1. The preservation of a generalized structure of the limbs - like primitive pentadactyly, and the retention of certain elements of the limb skeleton (such as the clavicle) which tend to be reduced or to disappear in some groups of mammals.

2. An enhancement of the free mobility of the digits, especially the thumb and big toe (which are used for grasping purposes).

3. The replacement of sharp compressed claws by flattened nails, associated with the development of highly sensitive tactile pads on the digits.



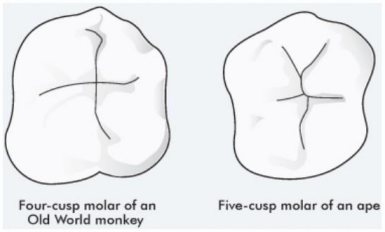
4. The progressive abbreviation of the snout or muzzle.

5. The elaboration and perfection of the visual apparatus with the development to varying degrees of binocular vision.

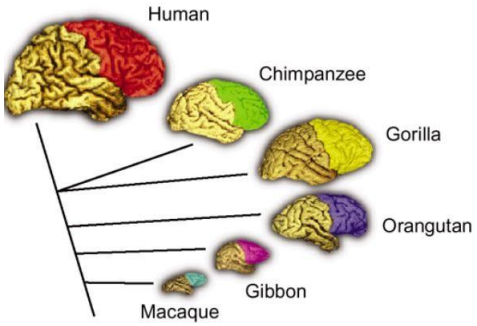
6. Reduction of the apparatus of smell.

7. The loss of certain elements of the primitive mammalian dentition (3:1:4:3), and the preservation of a simple cusp pattern of the molar teeth.

Old World monkeys have four cusps and apes and humans have five. It would seem that the increased number of cusps would be for a specialized diet of more plant material.



8. Progressive expansion and elaboration of the brain, affecting predominantly the cerebral cortex and its dependencies.



9. Progressive and increasingly efficient development of those gestational processes concerned with the nourishment of the foetus before birth.

10. Prolongation of postnatal life periods.

Comparative Data on Growth & Development			
Species	**Gestation**	**Age at sexual maturity**	**Length of growth period**
Rhesus Monkey	5 ½ months	2-3 years	7-8 years
Chimpanzee	7 ½ months	8-9 years	11-12 years
Man	9 months	13-15 years	20-21 years

PRIMATE ADAPTATIONS

In this section, we consider how primate anatomical traits evolved as adaptations to environmental circumstances. It's important to remember that the phrase "environmental circumstances" refers to several interrelated variables, including climate, diet, habitat (woodland, grassland, forest, and so on), and predation.

Evolutionary Factors

Traditionally, the group of characteristics shared by primates has been explained as the result of an adaptation to arboreal living. While other mammals were adapting to various ground dwelling lifestyles and marine environments, the primates found their adaptive niche in the trees. A number of other mammals were also adapting to arboreal living, but though many of them nested in the trees, they continued to forage for food on the ground. Throughout the course of evolution, the primates increasingly found food (leaves, seeds, fruits, nuts, insects, and small mammals) in the trees themselves. Over time, this dietary shift enhanced a general **trend toward omnivory**, and this trend in turn **led to the retention of the generalized dentition that's typical of most primates.**

Increased reliance on vision, coupled with grasping hands and feet, are also adaptations to an arboreal lifestyle. In a complex, three-dimensional environment with uncertain footholds, acute color vision with depth perception is, for obvious reasons, extremely beneficial.

An alternative to this traditional arboreal hypothesis is based on the fact that animals such as squirrels and raccoons are also arboreal, yet they haven't evolved primate-like adaptations such as prehensile hands or forward facing eyes. But visual predators, such as cats and owls, do have forward-facing eyes, and this fact may provide insight into an additional factor that could have shaped primate evolution. **Forward-facing eyes (which facilitate binocular vision), grasping hands and feet, and the presence of nails instead of claws may not have come about solely as adaptive advantages** in a purely arboreal setting. **They may also have been the hallmarks of an arboreal visual predator**. So it's possible that early primates may first have adapted to shrubby forest undergrowth and the lowest tiers of the forest canopy, where they hunted insects and other small prey (Cartmill, 1972, 1992). In fact, many smaller primates occupy just such an econiche today.

In a **third scenario**, basic primate traits developed along with another major evolutionary occurrence, the appearance and diversification of flowering plants that began around 140 mya (Sussman, 1991). Flowering plants provide numerous resources for primates, including nectar, seeds, and fruits. Because visual predation isn't common among primates, forward facing eyes, grasping hands and feet, omnivory, and color vision may have arisen in response to the demand for fine visual and tactile discrimination, necessary for feeding on small food items such as fruits, berries, and seeds among branches and stems (Dominy and Lucas, 2001).

These hypotheses aren't mutually exclusive. The complex of primate characteristics might well have originated in non-arboreal settings. These traits could also have been adaptive when evolving flowering plants opened up new econiches. But at some point, probably as a result of these and even other factors, primates did take to the trees, and that's where most of them still live today.

What Makes Primates Good at Living in Trees?

Primates show a series of behavioral and anatomical tendencies that make them especially good at living in trees.

CHARACTERISTIC	FEATURES
Versatile skeletal structure emphasizing mobility and flexibility	Separation of bones in articular joints associated with mobility: clavicle; radius and ulna; wrist; opposable thumb; opposable big toe in many primates Five functionally distinct vertebrae types: cervical, thoracic, lumbar, sacral, coccygeal
Enhanced sense of touch	Dermal ridges at ends of fingers and toes; nails instead of claws
Enhanced sense of vision	Convergence of eyes; color vision

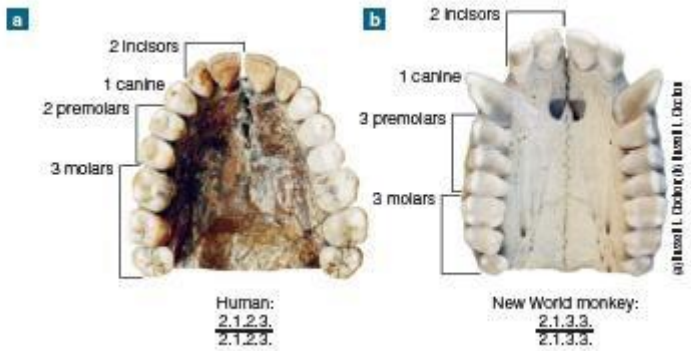
Geographical Distribution and Habitats

With just a couple of exceptions, nonhuman primates **are found in tropical or semitropical areas of the New and Old Worlds**. In the New World, these areas include southern Mexico, Central America, and parts of South America. Old World primates are found in Africa, India, Southeast Asia (including numerous islands), and Japan. Even though most nonhuman primates are arboreal and live in forest or woodland habitats, some Old World monkeys (for example, baboons) spend much of the day on the ground. The same is true for the African apes (gorillas, chimpanzees, and bonobos). Nevertheless, all nonhuman primates spend some time in the trees, especially when sleeping.

Diet and Teeth

Omnivory is one example of the overall lack of specialization in primates. Although all primates tend to favour some food items over others, most eat a combination of fruit, nuts, seeds, leaves, other plant materials, and insects. Many also get animal protein from birds, amphibians, and small mammals, including other primates. Others have become more specialized and mostly eat leaves. Such a wide array of choices is highly adaptive, even in fairly predictable environments. Like nearly all other mammals, almost all primates have four kinds of teeth: incisors and canines for biting and cutting, and premolars and molars for chewing and grinding. Biologists use what's called a dental formula to describe the number of each type of tooth that typifies a species. A dental formula indicates the number of each tooth type in each quadrant of the mouth. For example, all Old World anthropoids (monkeys, apes and humans) have two incisors, one canine, two premolars, and three molars on each side of the midline in both the upper and lower jaws, for a total of 32 teeth. This is represented by the following dental formula:

2.1.2.3 (upper)
2.1.2.3 (lower)



(a) The human maxilla illustrates a dental formula characteristic of all Old World monkeys, apes, and humans. (b) The New World monkey (*Cebus*) maxilla shows the dental formula that is typical of most New World monkeys. (Not to scale, the monkey maxilla is actually much smaller than the human maxilla.)

Primate Dental Formulae

The major primate groups are distinguished dentally by the number of incisors, canines, premolars, and molars.

	UPPER	LOWER
Tarsiers	2.1.3.3	1.1.3.3
Lemurs	2.1.3.3	2.1.3.3 (although there is much variation with lemurs)
Lorises	2.1.3.3	2.1.3.3
New World Monkeys	2.1.3.2 *or* 2.1.3.3	2.1.3.2 *or* 2.1.3.3
Old World Monkeys	2.1.2.3	2.1.2.3
Great Apes and Humans	2.1.2.3	2.1.2.3

This formula differs from that of the New World monkeys in that there's one less premolar. The overall lack of dietary specialization in primates is reflected in the lack of specialization in the size and shape of the teeth, because tooth shape and size are directly related to diet. For example, carnivores typically have premolars and molars with high, pointed cusps adapted for tearing meat; but herbivores, such as cattle and horses, have premolars and molars with broad, flat surfaces suited to chewing tough grasses and other plant materials. Most primates have premolars and molars with low, rounded cusps, a pattern that enables them to process most types of foods. So, throughout their evolutionary history, the primates have developed a dentition adapted to a varied diet, and the capacity to exploit many foods has contributed to their overall success during the last 50 million years.

What Gives Primates Their Dietary Flexibility?

Primates display a broad range of dietary adaptations. Although prosimians' and anthropoids' teeth have evolved specializations, such as the tooth comb in lemurs, the overall retention of a nonspecialized, primitive dentition reflects the order's diverse diet.

PRIMITIVE CHARACTERISTIC	FEATURE
Multiple tooth types	Incisors, canine, premolars, molars
Reduced number of teeth	Fewer premolars and molars

Locomotion

Almost all primates are, at least to some degree, quadrupedal, whether they're entirely arboreal or spend some time on the ground. However, most primates use more than one form of locomotion, and they're able to do this because of their generalized anatomy.

Vertical clinging and leaping, another form of locomotion, is characteristic of some lemurs and tarsiers. As the term implies, vertical clingers and leapers support themselves vertically by grasping onto trunks of trees or other large plants while their knees and ankles are tightly flexed. By forcefully extending their long hind limbs, they can spring powerfully away either forward or backward.

Brachiation, or arm swinging, is a suspensory form of locomotion and the body moves by being alternatively suspended by one arm or the other.

(a) Skeleton of a vertical clinger and leaper

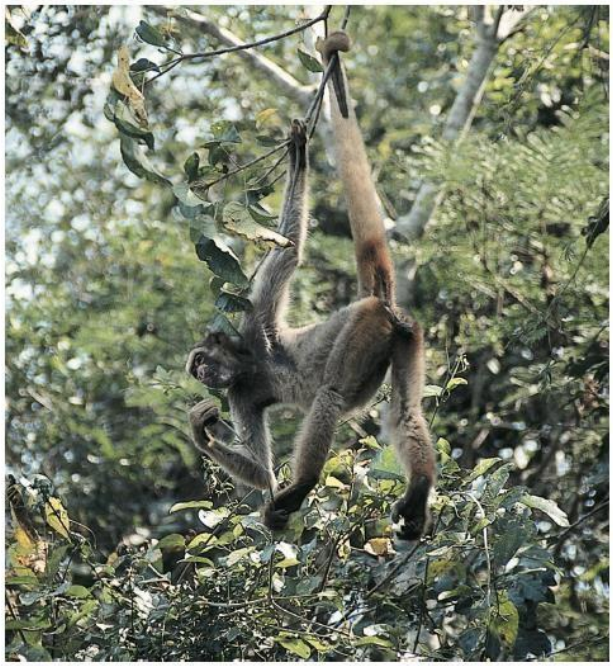
Indri

(b) Skeleton of a brachiator

Gibbon

(You may have brachiated as a child on "monkey bars" in playgrounds.) Because of anatomical modifications at the shoulder joint, apes and humans are capable of true brachiation. However, only the small gibbons and siamangs of Southeast Asia use this form of locomotion almost exclusively. Brachiation is seen in species characterized by arms longer than legs, a short, stable lower back, long curved fingers, and shortened thumbs. As these traits are seen in all the apes, it's believed that although none of the great apes (orangutans, gorillas, bonobos, and chimpanzees) habitually brachiates today, they probably inherited these characteristics from brachiating or climbing ancestors.

Some New World monkeys, such as spider monkeys and muriquis, are called semibrachiators, since they practice a combination of leaping and some arm swinging. Also, some New World monkeys enhance arm swinging by using a **prehensile tail**, which in effect serves as an extra hand. It's important to mention that no Old World monkeys have prehensile tails.

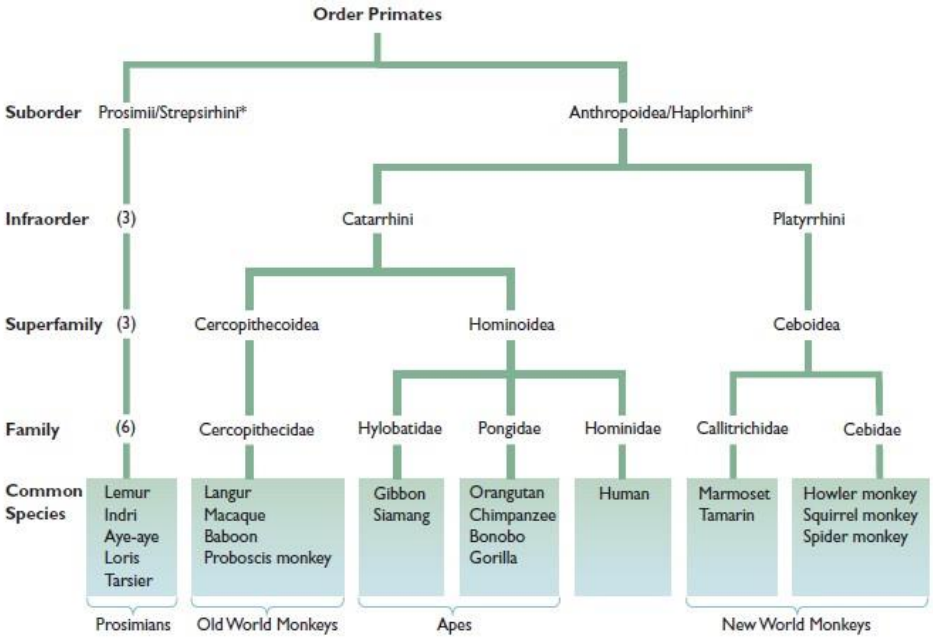


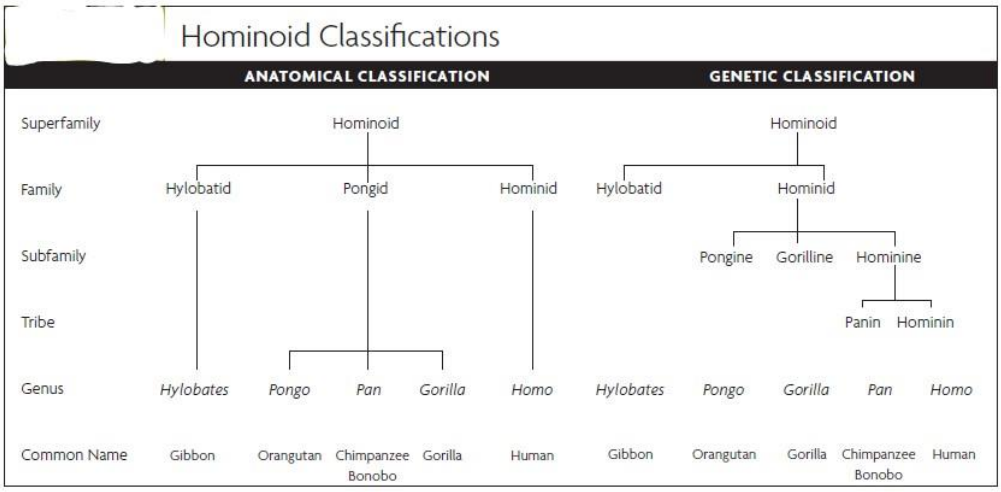
Northern woolly spider monkey, a platyrrhine primate from Brazil. Note the prehensile tail with the bare strip of skin on the inner surface to enhance its grasping ability. Note also the typical platyrrhine nose (see also Figure 7.6 *bottom left*).

Lastly, all the apes, to varying degrees, have arms that are longer than legs, and some (gorillas, bonobos, and chimpanzees) practice a special form of quadrupedalism called **knuckle walking**. Because their arms are so long relative to their legs, they support the weight of their upper body on the back surfaces of their bent fingers.

Chimpanzee knuckle walking. Note how the weight of the upper body is supported on the knuckles and not on the palm of the hand.

PRIMATE TAXONOMY





insights & advances

A ROSE BY ANY OTHER NAME: HOMININS VERSUS HOMINIDS

The traditional classification system of the hominoids—humans, the great apes, and the lesser apes—is based on morphological characteristics. In this traditional system, the superfamily Hominoidea contains three families: Hominidae, Pongidae, and Hylobatidae (Figure A Part [a]). In this view, the Hominidae, or hominids, are humans and our extinct ancestors; the Pongidae includes the African and Asian great apes; and the Hylobatidae are the lesser apes (gibbons and siamangs). This system reflects how startlingly different we bipeds are from our closest quadrupedal relatives. However, genetic distances suggest a slightly different classification system. Recall from Chapter 9 that genetically humans and chimpanzees are more closely related to one another than either is to the gorilla. Therefore, humans and chimps should be grouped together, despite their morphological differences. And both African apes are more closely related to humans than either is to orangutans.

In the new classification system that reflects these genetic distances (Figure A Part [b]) the superfamily Hominoidea contains two families: Hominidae and Hylobatidae. The Hominidae now includes humans and our extinct ancestors as well as the great apes and their ancestors. Within the family Hominidae are two subfamilies that separate African apes including ourselves (Homininae) from the orangutans (Ponginae) because of our genetic differences. And within the subfamily Homininae, humans and our ancestors are in the tribe Hominini, or hominins for short. In this book we use the molecular classification system and call humans and our exclusive ancestors *hominins* because this is the way that most of the recent literature is constructed. But you should be aware that earlier literature and some current papers use the term *hominids*. So always be sure to check your definitions!

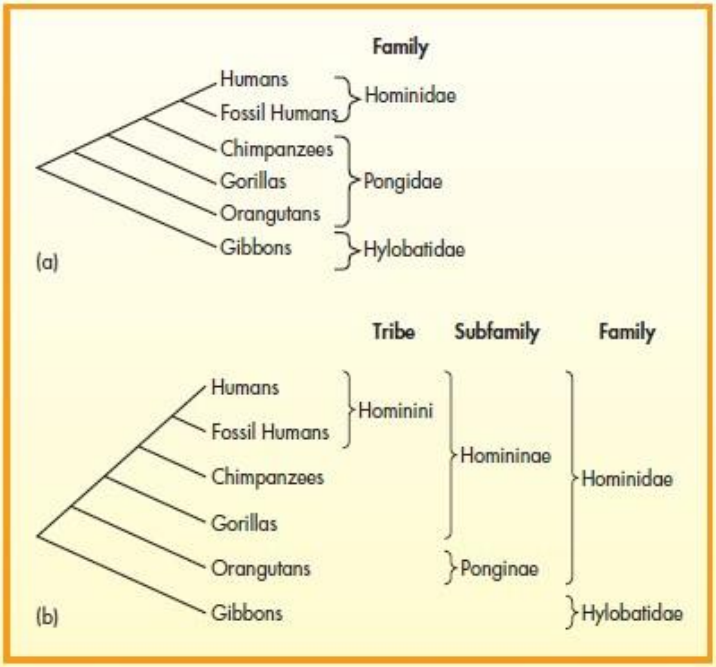


FIGURE A Taxonomic classification of hominids versus hominins. (a) A traditional classification system recognizes only humans and our fossil ancestors in the family Hominidae, which we refer to as hominids. (b) A classification system that reflects molecular relationships groups African great apes and humans together at the subfamily level in the Homininae and humans and our ancestors in the tribe Hominini or hominins.

Prosimians

The order Primates is traditionally divided into two major suborders, Prosimii and Anthropoidea. **Prosimians ("pre-apes")** represent the most primitive primates, that is, those that most closely resemble the earliest primates. At first widespread, prosimians were pushed into marginal areas as newer, more adaptively generalized primates evolved. Some modern prosimians live on the mainlands

of Africa, India, and Southeast Asia and on the isolated islands of Southeast Asia, but the **majority inhabit the island of Madagascar.**

The forty or so living species of prosimians exhibit a number of differences from the general primate pattern. About half of the prosimian species are nocturnal and so lack color vision. They **have large eyes that can gather more light**, as well as **better than average senses of smell and hearing**. To aid their olfactory sense, they have **a protruding snout** with a large smell receptor area (the mucous membranes within the nose) and **a moist, naked outer nose** (like that of a dog or cat) to help pick up the molecules that make up olfactory signals. Prosimians do have **the stereoscopic vision** characteristic of primates, because they need to judge distances in bushes and trees, and their threedimensional vision helps them catch insects, a favourite food of many prosimian species.

Prosimians have prehensile hands and feet, but the opposability of their thumbs is limited. Many can only touch the thumb with the other four digits together; their digits don't move independently. Some prosimians have claws instead of the typical primate nails on a couple of fingers or toes. These are known as grooming claws and are used both for that purpose and to help acquire food. A few species of lemurs from Madagascar give birth to twins or even triplets on a regular basis. Transporting the infants through the trees, however, is no problem because an adult male or an older sibling often helps the mother carry and care for her infants. At other times, the infants are kept in a nest.

A particularly interesting primate is the tarsier of Southeast Asia. Weighing just 4 to 5 ounces, this little insect eater has powerful hind limbs for jumping, enlarged fingertips and toetips for added friction, and the ability to turn its head 180 degrees in either direction, like an owl. Its name comes from its elongated ankle (or tarsal) bones, which make its legs look as if they bend too many times. Because of its flat face, upright posture when clinging to trunks and branches, lack of the moist, naked nose of other prosimians, and some recent genetic comparisons, some authorities suggest placing the tarsier in the second primate suborder, Anthropoidea.

Two prosimians. The slender loris of India and Sri Lanka (left) has the large eyes and moist, naked nose characteristic of this suborder. Note also the prehensile hands and feet and the grooming claw on one toe of the foot at the top of the picture (see arrow). The crowned lemur of Madagascar (right) displays a posture that is typical of the locomotor pattern called *vertical clinging and leaping*. All the Madagascar primates are endangered.

Philippine tarsier. Note the huge eyes (each eyeball is as big as the entire brain) for nocturnal vision, the enlarged fingertips and toetips, and the powerfully built legs with elongated ankles.

Anthropoids

The anthropoid ("humanlike") primates include monkeys, apes, and humans. Suborder Anthropoidea is further divided into two infraorders, Platyrrhini and Catarrhini. This division is based on a geographic separation of early primates into a Western Hemisphere (or New World) group and an Eastern Hemisphere (or Old World) group. All the New World platyrrhine primates are monkeys. The Old World catarrhine primates comprise monkeys, apes, and humans. Despite the fact that humans now inhabit the entire globe, we first evolved in the Old World, in Africa.

Several features distinguish New World from Old World primates. The most obvious is the nose. Platyrrhine means "broad-nosed," and the noses of the Central and South American monkeys have widely spaced nostrils separated by a broad septum. By comparison, catarrhine is translated "hooknosed." The typical Old World nose has closely spaced nostrils that face downward. Just look in the mirror. New World and Old World anthropoids also have different dental formulas, that is, the number of each type of tooth in each quadrant of the mouth. Old World anthropoids have two incisors, one canine, two premolars (bicuspids), and three molars. This is written as **2123**. Some of the New World anthropoids have four additional premolars written as **2133**.

Because New World monkeys are almost entirely arboreal, they have evolved long limbs, and some have clawlike nails. Several species also have evolved prehensile tails and thus effectively have fi ve grasping limbs. No Old World monkey evolved this adaptation. Finally, two groups of platyrrhines, the marmosets and tamarins, normally give birth to twins.

The Old World primates are divided into two super-families. The monkeys of Europe (now limited to Gibraltar), Africa, and Asia make up superfamily Cercopithecoidea. Apes and humans are in superfamily Hominoidea, which is further divided into three families. There are 100 or more species of cercopithecoids. They have the nasal shape and tooth number of all Old World primates, and most have tails. Males tend to be larger than females, a trait not common in New World species. Also unlike the platyrrhines, the Old World monkeys have fully opposable thumbs. The monkeys of the Eastern Hemisphere seem more adaptively flexible than those of the New World. At home in the trees, many cercopithecoids are equally comfortable on the ground. They live everywhere from the deserts of Africa and the Middle East to the mountains of northern Japan.

Superfamily Hominoidea contains the larger, tailless primates. The hominoids—the apes and humans—are generally larger than the monkeys and have larger brains, both relatively and absolutely. Their brains also have larger neocortexes, meaning that the hominoids are more intelligent. Finally, a series of traits make the hominoids good suspensory climbers and hangers; they are adapted to an arboreal environment through the ability to climb and hang from branches with their arms. The traits behind this ability are a flexible shoulder joint, a more posterior shoulder blade than in monkeys, and a stronger collarbone (clavicle) for added support. Although modern humans do not display the ability to climb or hang using the arms as often or as well as the apes, we still possess it, as demonstrated by gymnasts on the high bar or rings.

Family Hylobatidae includes the gibbons and siamangs of Southeast Asia and Malaysia. Sometimes referred to as lesser apes, they are noted for their brachiating mode of locomotion. They also have an unusual social organization for primates. Male and female hylobatids form a monogamous pair, though not neccessarily a permanent one. There are four species collectively known as the great apes: the orangutan of Southeast Asia and the gorilla (possibly two species), chimpanzee, and bonobo of Africa (all traditionally in family Pongidae).

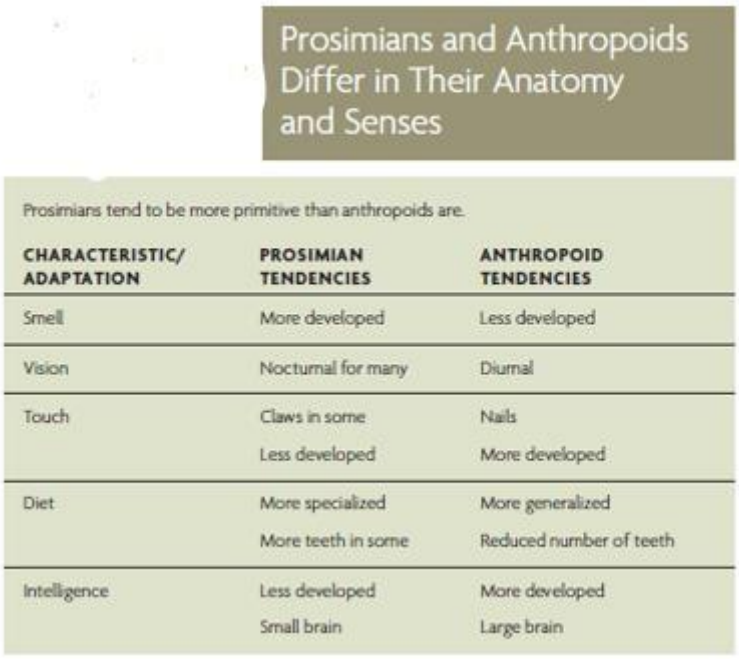
The great apes are large (a male gorilla in the wild may weigh 450 pounds), with heavy, powerful jaws used for eating a wide range of fruits, nuts, and vegetables. Chimps and bonobos also eat meat on occasion. The apes are quadrupeds, although chimps, gorillas, and especially bonobos are fairly good at upright walking for short distances. Orangutans are solitary, but the other apes live in social groups marked by some degree of dominance but otherwise with fairly loose organization and changeable group membership.

The apes have relatively large brains; a large chimp may have a brain half the size of the smallest modern human brain. Apes are intelligent. They have, for example, an intimate knowledge of a large number of food sources, many of which ripen seasonally or grow in limited areas.

Some chimpanzees can make simple tools; the best known is their termite “fishing stick,” a modified twig or blade of grass they insert into a hole in a termite mound and wiggle around to stimulate an attack by the insects. The termites cling to the “invader,” and the chimps draw out a tasty meal. Other chimps have been seen using rocks to break open hard-shelled nuts. Chimps are also known to cooperatively hunt small animals, including other primates, and meat is the one food source that chimps will share with one another. And in 2007 it was reported that some chimps in Senegal had been seen sharpening sticks with their teeth to use as spears for stabbing and extracting galagos (also called bush babies, small nocturnal primates) from their daytime holes in trees.

Finally, apes have a large repertoire of calls, facial expressions, and body gestures with which they communicate information, mostly about emotional states. Although this form of communication is nothing like human language, some individuals from all the great ape species have been taught to use nonvocal versions of human languages, most notably American Sign Language (Ameslan), developed for the hearing impaired. It is said by some researchers that with this skill they can communicate at the level of a 4- or 5-yearold human.

One branch within superfamily Hominoidea is family Hominidae. This includes all living and extinct species of habitually bipedal primates.



Prosimians and Anthropoids Differ in Their Anatomy and Senses

Prosimians tend to be more primitive than anthropoids are.

CHARACTERISTIC/ ADAPTATION	PROSIMIAN TENDENCIES	ANTHROPOID TENDENCIES
Smell	More developed	Less developed
Vision	Nocturnal for many	Diurnal
Touch	Claws in some Less developed	Nails More developed
Diet	More specialized More teeth in some	More generalized Reduced number of teeth
Intelligence	Less developed Small brain	More developed Large brain

OLD WORLD MONKEY VS NEW WORLD MONKEY

Approximately 85 percent of all primates are monkeys. Primatologists estimate that there are about 195 species, but it's impossible to give precise numbers because the taxonomic status of some monkeys remains in doubt, and previously unknown species are still being discovered. Monkeys are divided into two groups separated by geographical area (New World and Old World), as well as at least 40 million years of separate evolutionary history.

New World Monkeys The approximately 70 New World monkey species can be found in a wide range of environments throughout most forested areas in southern Mexico and Central and South America. They exhibit considerable variation in size, diet, and ecological adaptations. In size, they vary from the tiny marmosets and tamarins that weigh only about 12 ounces to the 20-pound howler monkeys. New World monkeys are almost exclusively arboreal, and some never come to the ground.

In addition to being the smallest of all monkeys, marmosets and tamarins have several other distinguishing features. They have claws instead of nails, and unlike other primates, they usually give birth to twins instead of one infant. They live in social groups usually composed of a mated pair, or a female and two adult males, and their offspring. This type of mating pattern is rare among mammals, and marmosets and tamarins are among the few primate species in which males are extensively involved in infant care.

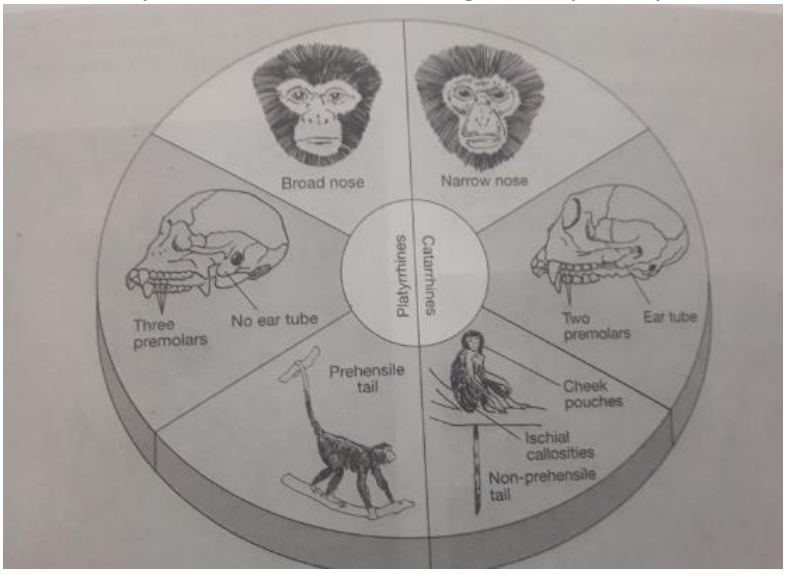
New World monkeys rely on a combination of fruits and leaves supplemented to varying degrees with insects. Most are quadrupedal; but some, such as spider monkeys are, semi-brachiators. Howlers, muriquis, and spider monkeys also have prehensile tails that are used not only in locomotion but also for hanging from branches. Socially, most New World monkeys live in groups composed of both sexes and all age categories. Some (such as titis) form monogamous pairs and live with their subadult offspring.

Old World Monkeys Old World monkeys are the most widely distributed of all living primates. They're found throughout sub-Saharan Africa and southern Asia, ranging from tropical jungle habitats to semi-arid desert and even to seasonally snow-covered areas in northern Japan.

Most Old World monkeys are arboreal, but some (such as baboons) spend a great deal of time on the ground and return to the trees for the night. They have areas of hardened skin on the buttocks called ischial callosities that serve as sitting pads, making it possible to sit and sleep on tree branches for hours at a time.

Many Old World monkey species exhibit pronounced sexual dimorphism. This is especially true of the more terrestrial species (such as baboons) in which males may be almost twice the size of females. Females of several species (especially baboons and some macaques) have pronounced cyclical changes of the external genitalia. These changes, which include swelling and redness, are associated with **estrus**, a hormonally initiated period of sexual receptivity in female nonhuman mammals correlated with ovulation. They serve as visual cues to males that females are sexually receptive.

Old World monkeys live in a few different kinds of social groups. Colobines tend to live in small groups, with only one or two adult males. Savanna baboons and most macaque species are found in large social units comprising several adults of both sexes and offspring of all ages. Monogamous pairing isn't common in Old World monkeys, but it's seen in a few langurs and possibly one or two guenon species.



Character	**New world (platyrrhine)**	**Old World(catarrhines)**
Size	Small-medium	Medium – large
Nose	Flat nose with nostrils on the side	Sharp and narrow nostril downwards
Tail	prehensile	Non- prehensile due to butt padd
Vision	Dichromatic	Trichromatic
Dentition	12 premolars- 2133	8 premolars-2123
Butt	No buttpads	Present
Habitat	Tree top	Arboreal and terrestrial
Thumb	Not opposable	Opposable (sometimes in both)
Pairing	Most of them are monogamous with male contributing to child care	Less monogamous
Ear lobe	Not present	Present

Cheek pouches	Absent	Present
Palate	Short	Long
Basic cranial axis	Long	Short
Kidney	Contains 4-5 pyramid	Single pyramid
Stomach	Simple	Complex
Nails	Claws	Flat nails
Distribution	South and central America	Africa, Asia, Europe
Species	Sakis, squirrel monkey, Titi monkey	Baboons and langurs

PRIMATE BEHAVIOUR

Some Factors That Influence Social Structure

1) **Body Size**
2) **Basal Metabolic Rate (BMR)**
3) **Diet**
4) **Distribution of Resources**
5) **Predation**
6) **Life Histories**
7) **Activity Patterns- whether diurnal or nocturnal**
8) **Human Activities**

PRIMATE SOCIAL BEHAVIOUR

DOMINANCE

Many primate societies are organized into dominance hierarchies, which impose a certain degree of order by establishing parameters of individual behaviour. Although aggression is frequently used to increase an animal's status, dominance hierarchies usually reduce the amount of actual physical violence. Not only are lower-ranking animals unlikely to attack or even threaten a higher-ranking one, but dominant animals are usually able to exert control simply by making a threatening gesture. Individual rank or status can be measured by access to resources, including food items and mating partners.

Dominant animals (alpha males and females) are given priority by others, and they rarely give way in confrontations. Many primatologists think that the primary benefit of dominance is the increased reproductive success of high ranking animals. This is true in many cases, but there's good evidence that lower-ranking males also successfully mate. High-ranking females also have higher reproductive success because they have greater access to food than subordinate females. Therefore, they obtain more energy for the production and care of offspring.

An individual's position in the hierarchy isn't permanent. Instead, it changes throughout life. It's influenced by many factors, including sex, age, level of aggression, amount of time spent in the group, intelligence, perhaps motivation, and sometimes the mother's social position (particularly true of macaques). In species organized into groups containing a number of females associated with one or several adult males, the males are generally dominant to females. Within such groups, males and females have separate hierarchies, although very high-ranking females can dominate the

lowestranking males, particularly young ones. But there are exceptions to this pattern of male dominance. In many lemur species, females are the dominant sex.

All primates learn their position in the hierarchy. From birth, an infant is carried by its mother, and it observes how she responds to every member of the group. Just as importantly, it sees how others react to her. Dominance and subordination are indicated by gestures and behaviours, some of which are universal throughout the primate order (including humans), and this gestural repertoire is part of every youngster's learning experience.

Young primates also acquire social rank through play with age peers, and as they spend more time with play groups, their social interactions widen. Competition and rough and tumble play allow them to learn the strengths and weaknesses of peers, and they carry this knowledge with them throughout their lives.

COMMUNICATION

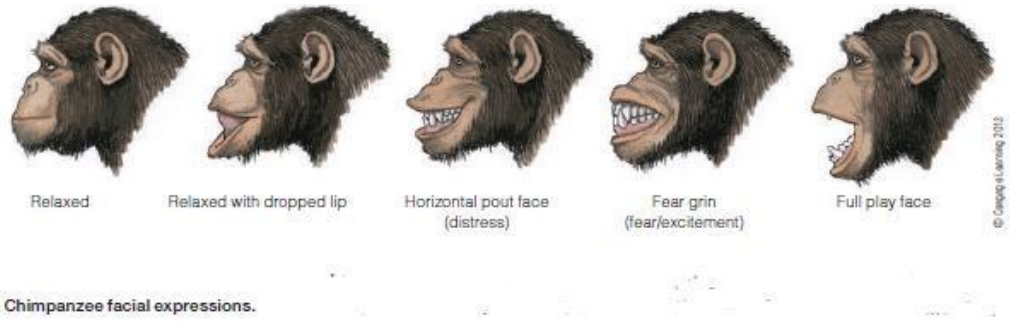
Communication is universal among animals and includes scents and unintentional, autonomic responses, as well as behaviours that convey meaning. Such attributes as body posture provide information about an animal's emotional state.

Olfactory: The odours of pheromones secreted by the scent glands in various areas of the body eg armpit, along forearm or near the base of tail are generally used for sexual interaction. In many species the males smell the anoperineal region of the female or even examine her vagina to monitor her reproductive status. At height of estrus there may be several males following one female. Other than sexual attraction, many primates use scent markings to establish territories, as alarm mechanisms and in aggressive encounters.

Many intentional behaviours also serve as communication. In primates, these include a wide variety of **gestures, facial expressions, and vocalizations** some of which we humans share. Among many primates an **intense stare indicates a mild threat**; and indeed, we humans find prolonged eye contact with strangers very uncomfortable.

Other threat gestures include a **quick yawn to expose canine teeth** (baboons, macaques); **bobbing back and forth in a crouched position** (patas monkeys); **and branch shaking** (many monkey species). High ranking baboons mount the hindquarters of subordinates to express dominance. **Mounting** may also serve to defuse potentially tense situations by indicating something like, "It's okay, I accept your apology.

A **wide variety of facial expressions** indicating emotional state is seen in chimpanzees and, especially, in bonobos. These include the well-known play face (also seen in several other primate and nonprimate species), associated with play behaviour, and the fear grin to indicate fear and submission.



Chimpanzee facial expressions.

Not surprisingly, **vocalizations** play a major role in primate communication. Some, such as the bark of a baboon that has just spotted a leopard, are unintentional startled reactions. Others, such as the chimpanzee food grunt, are heard only in specific contexts; in this case in the presence of food. These vocalizations, whether deliberate or not, inform others of the possible presence of predators or food.

Primates (and other animals) also communicate through **displays**, which are more complicated, frequently elaborate combinations of behaviours. For example, the exaggerated courtship dances of many male birds, often enhanced by colorful plumage, are displays. Chest slapping and tearing vegetation are common gorilla threat displays.

All nonhuman animals use various body postures, vocalizations, and facial expressions to transmit information. But the array of communicative devices is much richer among nonhuman primates, even though they don't use language the way humans do. Communication is important, because it's what makes social living possible. Through submissive gestures, aggression is reduced and physical violence is less likely. Likewise, friendly intentions and relationships are reinforced through physical contact and grooming. Indeed, we humans can see ourselves in other primates most clearly in their use of nonverbal communication, particularly because some of their gestures and facial expressions carry the same meaning as ours do.

AGGRESSIVE INTERACTIONS

Within primate societies, there is an interplay between aggressive behaviours, which can lead to group disruption, and affiliative behaviours, which promote group cohesion. Conflict within a group frequently develops out of competition for resources, including mating partners or food. Instead of actual attacks or fighting, most intragroup aggression occurs in the form of various signals and displays, frequently within the context of a dominance hierarchy. The majority of tense situations are resolved through various submissive and appeasement behaviours.

But conflicts aren't always resolved peacefully; in fact, they can have serious and even fatal consequences. For example, high-ranking female macaques frequently intimidate, harass, and even attack lower-ranking females to keep them away from food. Dominant females consistently chase subordinates away from food and have even been observed taking food from their mouths. Eventually, these actions can cause weight loss and poor nutrition in low-ranking females. These, in turn, can reduce the reproductive success of these females because they're less able to rear offspring to maturity simply because they don't get enough to eat (Silk et al., 2003).

Competition between males for mates frequently results in injury and even death. In species that have a distinct breeding season, such as New World squirrel monkeys, conflict between males is most common during that time.

Between groups, aggression is often used to **protect resources or territories**. Primate groups are associated with a home range where they remain permanently.

AFFILIATION AND ALTRUISM

To minimize actual violence, promote group cohesion, and defuse potentially dangerous situations, there are many behaviours that reinforce bonds between individuals and enhance group stability. Common affiliative behaviours include reconciliation, consolation, and simple amicable interactions between friends and relatives. Most such behaviours involve various forms of physical contact such as touching, hand-holding, hugging, and among chimpanzees, kissing. In fact, physical contact is one of the most important factors in primate development and it's crucial in promoting peaceful relationships and reinforcing bonds in many primate social groups.

Grooming is one of the most important affiliative behaviours in many primate species. Although grooming occurs in other animal species, social grooming is mostly a primate activity, and it plays an important role in day to- day life. Because grooming involves using the fingers to pick through the fur of another individual (or one's own) to remove insects, dirt, and other materials, it serves hygienic functions. But it's also an immensely pleasurable activity that members of some species, especially chimpanzees, engage in for long periods of time. Grooming occurs in a variety of contexts. Mothers groom infants; males groom sexually receptive females; subordinate animals groom dominant ones, sometimes to gain favour; and friends groom friends. In general, grooming is comforting. It restores peaceful relationships after conflict, and provides reassurance during tense situations. In short, grooming reinforces social bonds and consequently helps strengthen and maintain a group's structure.

Conflict resolution through reconciliation is another important aspect of primate social behaviour. Following a conflict, chimpanzee opponents frequently move, within minutes, to reconcile (de Waal, 1982). Reconciliation takes many forms, including hugging, kissing, and grooming. In addition, bonobos are unique in their use of sex to promote group cohesion, restore peace after conflicts, and relieve tension within the group (de Waal, 1987, 1989).

Altruism is behaviour that benefits another while involving some risk or sacrifice to the performer. Altruism, cooperation, and assistance are fairly common in many primate species, and altruistic acts sometimes contain elements of what might be interpreted as empathy. The most fundamental of altruistic behaviours, the protection of dependent offspring, is ubiquitous among mammals and birds, and in the majority of species, altruistic acts are confined to this context. However, chimpanzees routinely come to the aid of relatives and friends; female langurs join forces to protect infants from infanticidal males; and male baboons protect infants and cooperate to chase predators.

PRIMATE REPRODUCTIVE STRATEGIES: MALES' DIFFER FROM FEMALES'

Because reproduction makes very different demands on males and females in terms of energy expenditure and time investment, each sex has a different set of reproductive strategies and interests.

Males' primary strategy is to physically compete for access to reproductively mature females, resulting in a strong degree of natural selection in males for both large bodies and large canines. This form of natural selection is called **sexual selection.** Another male strategy is **infanticide,** the killing of a nursing infant, primarily by a foreign male who has driven the single male out of a one-male, multifemale group. The American primatologist Sarah Blaffer Hardy has hypothesized that the new male kills the nursing infant so that its mother stops lactating, resumes ovulation, and becomes sexually receptive to him. As a result, the new male enhances his reproductive fitness, largely at the expense of the previous male.

Primates are among the most K-selected of mammals. By this we mean that individuals produce only a few young, in whom they invest a tremendous amount of parental care. Contrast this pattern with

r-selected species, where individuals produce large numbers of offspring but invest little or no energy in parental care. Good examples of r selected species include insects, most fishes, and, among mammals, mice and rabbits. Considering the degree of care required by young, dependent primate offspring, it's clear that enormous investment by at least one parent is necessary, and in a majority of species, the mother carries most of the burden, certainly before, but also after birth. Primates are completely helpless at birth. They develop slowly and, consequently, they're exposed to expanded learning opportunities within a social environment.

Female primates spend almost all their adult lives either pregnant, lactating, and/or caring for offspring, and the resulting metabolic demands are enormous. A pregnant or lactating female, although perhaps only half the size of her male counterpart, may require about the same number of calories per day. Given these physiological costs, and the fact that her reproductive potential is limited by lengthy intervals between births, a female's best strategy is to maximize the amount of resources available to her and her offspring.

Males, however, face a different set of challenges. Having little investment in the rearing of offspring and the continuous production of sperm, it's to the male's advantage to secure as many mates and produce as many offspring as possible.

INFANTICIDE AS REPRODUCTIVE STRATEGY

One way males may increase their chances of reproducing is to kill infants fathered by other males. This explanation was first offered in an early study of Hanuman langurs in India (Hardy, 1977). Hanuman langurs typically live in groups composed of one adult male, several females, and their offspring. Other males without mates form "bachelor" groups that frequently forage within sight of one-male–multi-female units. These peripheral males occasionally attack and defeat a reproductive male and drive him from his group.

The application of DNA technology to a long-unanswered question has provided strong evidence suggesting that infanticide may indeed give males an increased chance of fathering offspring. Moreover, this study provides another example of how hypotheses are further tested as new technologies are developed.

CONCEPT CHECK

Male and Female Reproductive Strategies

Reproductive strategies differ in male and female primates. Males compete for mates, but females both compete for resources and invest time and energy in care of offspring.

SEX	REPRODUCTIVE STRATEGY AND OUTCOME
Males	*Behavior:* Physical competition for access to females *Outcome:* Selection for large body size and for large canines; selection for loud vocalization ability in some territorial primates
	Behavior: Sometime killing of nursing young (infanticide) *Outcome:* Suppressed lactation, resumption of ovulation, and receptiveness to new male partner
Females	*Behavior:* Acquisition of resources for raising young, usually in competition with other females *Outcome:* Higher-ranked females provide more resources than low-ranked females do.

PRIMATE RESIDENCE PATTERNS

Individual primate species combine different patterns, and their social groups are strongly influenced by factors such as food availability, environment, and competition. Although it is thus exceedingly difficult to fully understand primate social behaviour, primatologists have identified six main types of primate residence patterns.

1. **One-male, multifemale**. This harem like organization consists of one reproductive-age male, several mature females, and the immature offspring. The society is **polygynous,** meaning that the one male has more than one partner. Some howler monkeys, some langurs, and some Old World monkeys, such as gelada baboons, practice this social system.

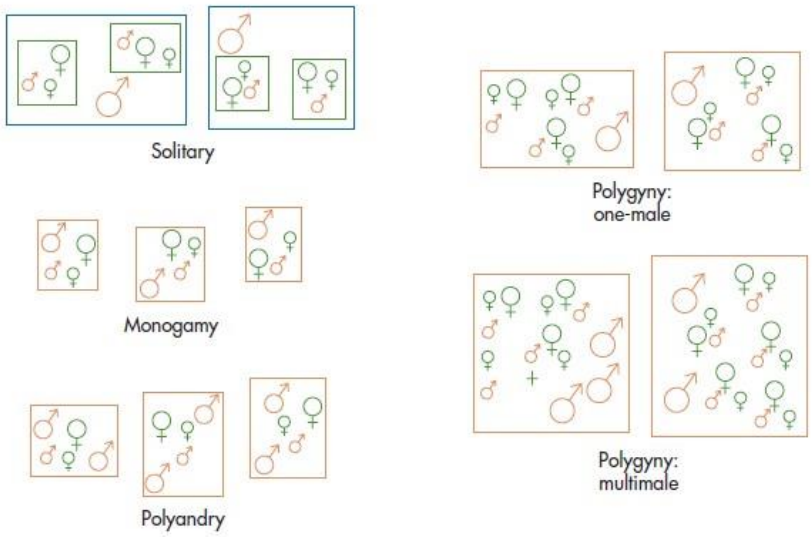
2. **One-female, multimale**. This group consists of one reproductive-age female, several mature males, and the immature offspring. The society is **polyandrous,** meaning that the one female mates with nonpolygynous males. The males often cooperate with the females in parenting activities. Only some New World monkeys practice this social system, and only rarely.

3. **Multimale, multifemale**. This group consists of many adults, male and female, and the offspring. Both sexes mate promiscuously. Competition for mates tends to be relatively low, especially among males. Many Old World monkeys, a few New World monkeys, and chimpanzees fit in this category.

4. **All-male**. In some species, such as baboons, males form at least temporary groups, typically before joining or forming groups that include males and females. All-male groups commonly exist together with multimale, multifemale groups.

5. **One-male, one-female.** This group consists of an adult male, an adult female, and their immature offspring. Mating is typically **monogamous,** so each partners' reproductive success is tied to that of the other, and the male invests a relatively large amount of time and energy in the young (e.g., through protection and food acquisition). Gibbons, siamangs, a couple of ceboids (owl monkeys and marmosets), and several species of prosimians practice this form of society.

6. **Solitary**. Solitary primates go it alone—rarely are individuals seen with others. Interaction between adult males and adult females occurs only for sexual activity. Only orangutans and a few prosimians are solitary. An orangutan male has greater reproductive success if he maintains a territory with areas traversed by two or more females. Orangutan sexual dimorphism is predictably quite high—adult males are twice the size of adult females and have large canines, large cheek pads, and very loud calls over long distances. Males that have been relatively unsuccessful at competing for access to females tend to be more solitary than more successful males.



A taxonomy of primate social systems. Larger symbols indicate adults. (Adapted from Strier 1994)

PRIMATE CULTURAL BEHAVIOUR

Undeniably, most aspects of culture are uniquely human, and we should be cautious when we try to interpret nonhuman animal behaviour. But, because humans are products of the same evolutionary forces that have produced other species, we can be expected to exhibit some of the same behavioural patterns seen in other primates. Because of increased brain size and learning capacities, humans express many characteristics to a greater degree, and culture is one of those characteristics

Cultural behaviour is learned. In other words, it's not genetically determined, although the capacity to learn is genetically influenced. Like young nonhuman primates, human children also acquire a tremendous amount of knowledge through observation rather than instruction. By watching their mothers and other members of their group, nonhuman primate infants learn about food items, appropriate behaviours, and how to use and modify objects to achieve certain ends. In turn, their own offspring will observe their activities.

Primates without a warm, social relationship with a mother or other individual donot appear to develop appropriate patterns of social interaction. In a series of classic experiments with rhesus monkeys, Harry Harlow investigated the effects of maternal neglect and isolation on offspring. He found that due to isolation some monkeys are unable to lead normal social lives. They develop aberrant sexual activities, may eve become juvenile delinquents.

The earliest reported example of cultural behaviour concerned a study group of Japanese macaques on Koshima Island, Japan. In 1952, Japanese researchers began feeding the macaques sweet potatoes. The following year, a young female started washing her potatoes in a freshwater stream before eating them. Within 3 years, several monkeys were washing their potatoes, though instead of using the stream, they were taking their potatoes to the ocean nearby. Maybe they liked the salt!

A study of orangutans listed 19 behaviours that showed sufficient regional variation to be classed as "very likely cultural variants" (van Schaik et al., 2003). Four of these were differences in how nests were used or built. Other behaviours that varied included the use of branches to swat insects and pressing leaves or hands to the mouth to amplify sounds.

"Termite fishing" is a common behaviour among many chimpanzee groups. Chimpanzees routinely insert twigs and grass blades into termite mounds. The termites seize the twig and, unfortunately for them, they become a light snack once the chimpanzee pulls the twig out of the mound. Chimpanzees also modify some of their stems by stripping the leaves, or breaking them until they're the right length. In effect, this is making a tool, and chimpanzees have been seen making these tools even before the termite mound is in sight. The modification of natural objects for use as tools has several implications for nonhuman primate intelligence.

First, the chimpanzees are involved in an activity that prepares them for a future task at a somewhat distant location, and this implies planning and forethought.

Second, attention to the shape and size of the raw material indicates that chimpanzees have a preconceived idea of what the finished product needs to be in order to be useful. To produce a tool, even a simple one, based on a concept is an extremely complex behaviour that, as we now know, is not the exclusive domain of humans.

This female capuchin must use most of her strength to smash a pine nut with a heavy stone, especially when carrying her infant on her back. Meanwhile, by watching her, the infant is learning the nut-smashing technique.

A female western lowland gorilla using a "wading stick" (in her right hand) for support.