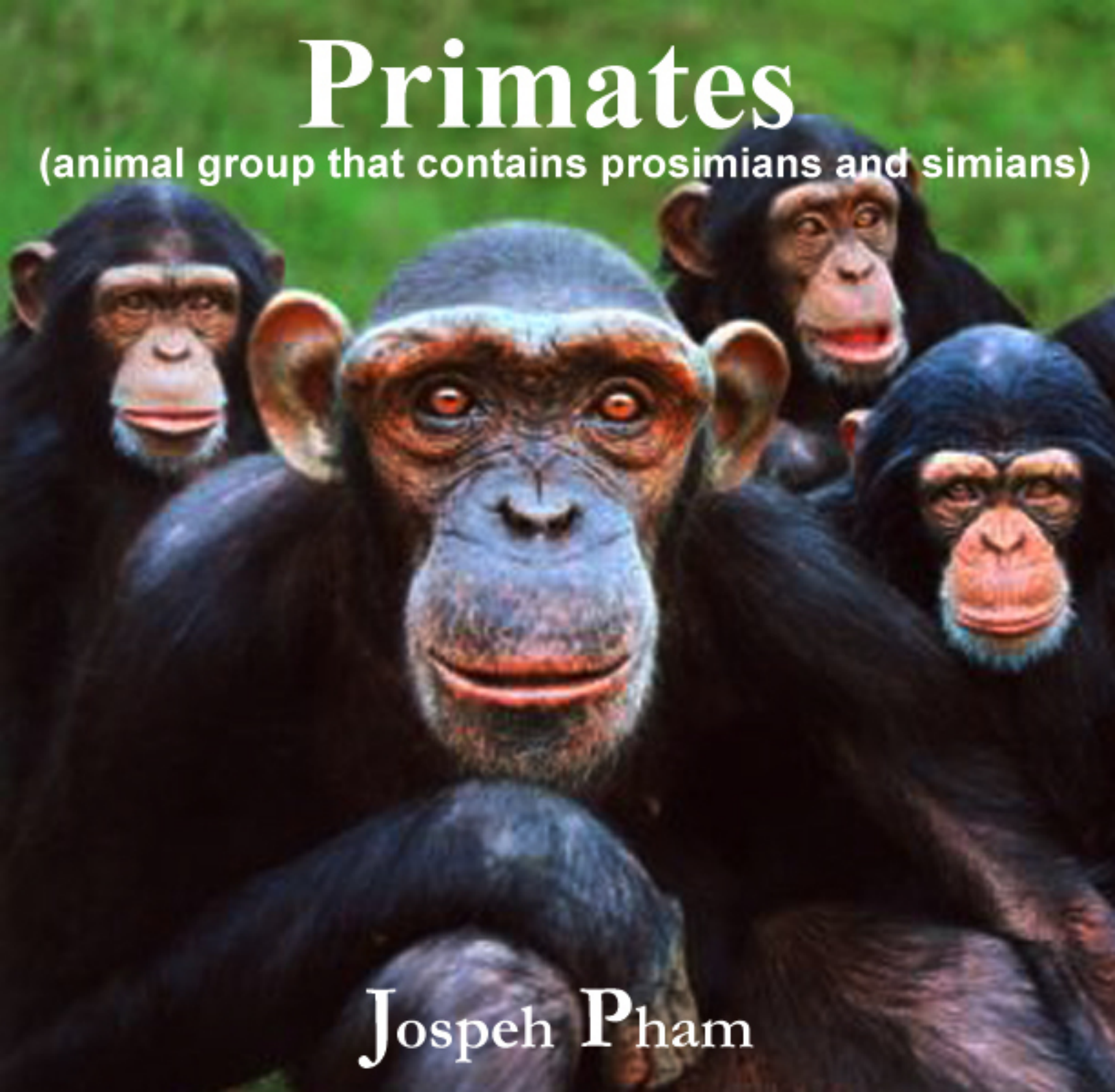
Primates
(animal group that contains prosimians and simians)
Jospeh Pham

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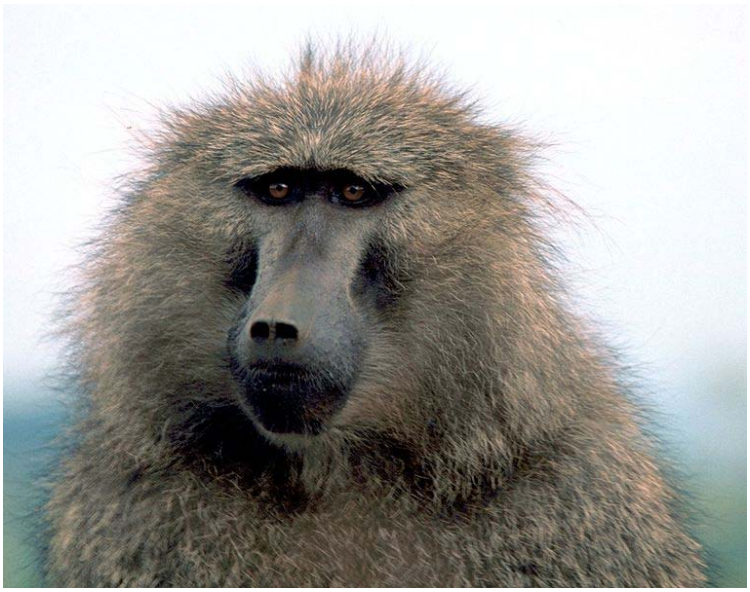
|  | |
| Olive Baboon, *Papio anubis* | |
| **Scientific classification** | |
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Mammalia |
| Infraclass: | Eutheria |
| Superorder: | Euarchontoglires |
| Order: | **Primates**<br>Linnaeus, 1758 |

Range of the non-human primates (green)

A **primate** is a member of the biological order **Primates**, the group that contains prosimians (including lemurs, lorises, galagos and tarsiers) and simians (monkeys and apes). With the exception of humans, who inhabit every continent on Earth, most primates live in tropical or subtropical regions of the Americas, Africa and Asia. Primates range in size from the Madame Berthe's Mouse Lemur, which weighs only 30 grams (1.1 oz) to the Mountain Gorilla weighing 200 kilograms (440 lb). According to fossil evidence, the primitive ancestors of primates may have existed in the late Cretaceous period around 65 million years ago, and the oldest known primate is the Late Paleocene *Plesiadapis*, *c.* 55–58 million years ago. Molecular clock studies suggest that the primate branch may be even older, originating in the mid-Cretaceous period around 85 mya.

The Primates order has traditionally been divided into two main groupings: prosimians and simians. Prosimians have characteristics most like those of the earliest primates, and included the lemurs of Madagascar, lorisiforms and tarsiers. Simians included the monkeys and apes. More recently, taxonomists have created the suborder Strepsirrhini, or curly-nosed primates, to include non-tarsier prosimians and the suborder Haplorrhini, or dry-nosed primates, to include tarsiers and the simians. Simians are divided into two groups: the platyrrhines ("flat nosed") or New World monkeys of South and Central America and the catarrhine (narrow nosed) monkeys of Africa and southeastern Asia. The New World monkeys include the capuchin, howler and squirrel monkeys, and the catarrhines include the Old World monkeys (such as baboons and macaques) and the apes. Humans are the only catarrhines that have spread successfully outside of Africa, South Asia, and East Asia, although fossil evidence shows many species once existed in Europe as well.

Considered generalist mammals, primates exhibit a wide range of characteristics. Some primates (including some great apes and baboons) do not live primarily in trees, but all species possess adaptations for climbing trees. Locomotion techniques used include leaping from tree to tree, walking on two or four limbs, knuckle-walking, and swinging between branches of trees (known as brachiation). Primates are characterized by their large brains, relative to other mammals, as well as an increased reliance on stereoscopic vision at the expense of smell, the dominant sensory system in most mammals. These features are most significant in monkeys and apes, and noticeably less so in lorises and lemurs. Three-color vision has developed in some primates. Most also have opposable thumbs and some have prehensile tails. Many species are sexually dimorphic, which

means males and females have different physical traits, including body mass, canine tooth size, and coloration. Primates have slower rates of development than other similarly sized mammals, and reach maturity later but have longer lifespans. Some species live in solitude, others live in male–female pairs, and others live in groups of up to hundreds of members.

## *Evolutionary history*

The Primates order are a part of the clade Euarchontoglires which is nested within the Eutheria clade of the class Mammalia. Recent molecular genetic research on primates, colugos, and treeshrews has shown that the two species of colugos are more closely related to the primates than the treeshrews, even though the treeshrews were at one time considered primates. These three orders make up the Euarchonta clade. This clade combines with the Glires clade (composed of the Rodentia and Lagomorpha) to form the Euarchontoglires clade. Variously, both Euarchonta and Euarchontoglires are ranked as superorders. Some scientists consider Dermoptera a suborder of Primates and call the "true" primates the suborder Euprimates.

## Evolution

The primate lineage is thought to go back at least 65 mya, even though the oldest known primate from the fossil record is *Plesiadapis* (*c.* 55–58 mya) from the Late Paleocene. Other studies, including molecular clock studies, have estimated the origin of the primate branch to have been in the mid-Cretaceous period, around 85 mya.

In modern cladistic reckonings, the Primates order is monophyletic. The suborder Strepsirrhini, the curly-nosed or "wet-nosed" primates, is generally thought to have split off from the primitive primate line about 63 mya (million years ago), although earlier dates are also supported. The seven strepsirhine families are the five related lemur families and the two remaining families that include the lorisids and the galagos. Older classification schemes wrap the Lepilemuridae into the Lemuridae and the Galagidae into the Lorisidae, yielding a three-two family split instead of the five-two split as presented here. During the Eocene, most of the northern continents were dominated by two groups, the adapiforms and the omomyids. The former is considered a member of Strepsirrhini, but it does not have a toothcomb like modern lemurs; recent analysis has suggested *Darwinius masillae* fits into this grouping. The latter was related closely to tarsiers, monkeys, and apes. It is unclear exactly how these two groups relate to extant primates. Omomyids perished about 30 mya, while Adapids survived until about 10 mya.

Ring-tailed Lemur, a strepsirrhine primate

According to genetic studies, the lemurs of Madagascar diverged from the lorisiforms approximately 75 mya. These studies, as well as chromosomal and molecular evidence, also show that lemurs are more closely related to each other than to other strepsirrhine primates. However, Madagascar split from Africa at 160 mya and from India at 90 mya. For lemurs to be more closely related to each other than other strepsirrhine primates, it is thought that a very small ancestral population came to Madagascar via a single rafting event between 50 and 80 million years ago. Other colonization options have been examined, such as multiple colonizations from Africa and India, but none are supported by the genetic and molecular evidence.

Until recently the Aye-aye has been difficult to place within Strepsirrhini. Theories had been proposed that its family, Daubentoniidae, was either a lemuriform primate (meaning its ancestors split from lemur line more recently than the lemurs and lorises split) or a sister group to all the other strepsirrhines. In 2008, the Aye-aye family (Daubentoniidae) was confirmed to be mostly closely related to the Malagasy lemurs, likely having descended from the same ancestral population that colonized the island.

The suborder Haplorrhini, the simple-nosed or "dry-nosed" primates, is composed of two sister clades. The prosimian tarsiers in family Tarsiidae (monotypic in its own infraorder Tarsiiformes), represent the most primitive division at about 58 mya. The Simiiformes infraorder emerged about 40 mya, and contains the two clades: the parvorder Platyrrhini that developed in South America and contains New World monkeys, and the parvorder Catarrhini that developed in Africa and contains the Old World monkeys, humans and the other apes. A third clade, which included the eosimiids, developed in Asia but went extinct millions of years ago.

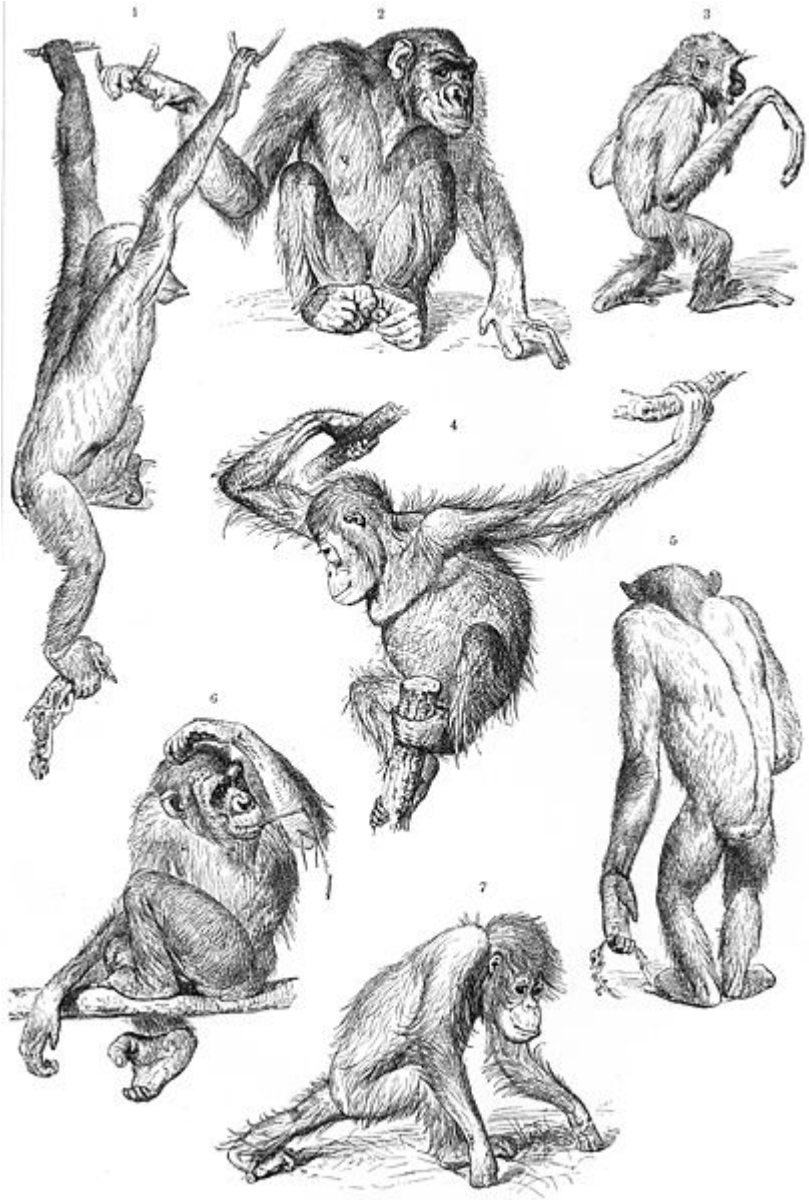
Like the lemurs, the New World monkeys have unclear origins. Molecular sequence studies based on concatenated sequences have yielded wide variations in the estimated date of the divergence between platyrrhines and catarrhines, ranging from 33 to 70 mya, while studies based on mitochondrial sequences suggest a more consistent date of 35 to 43 mya. It has been postulated that there is a single origin for the anthropoids in Africa some migrated and subsequently speciation occurred. It is possible that the anthropoid primates traversed the Atlantic ocean during the Eocene, facilitated by Atlantic Ocean ridges and a lowered sea level, then island-hopped to South America. Once again, a rafting event may explain this transoceanic colonization. Due to continental drift, the young Atlantic Ocean was not nearly as wide as it is today, and research suggests that a small 1 kg (2.2 lb) primate could have survived 13 days on a raft of vegetation. Given estimated current and wind speeds, this would have provided enough time to make the voyage between the continents.

Emperor Tamarin, a New World monkey

Apes and monkeys spread from Africa into Europe and Asia starting in the Miocene. Soon after, the lorises and tarsiers made the same journey. The first hominid fossils were discovered in Northern Africa and date back 5–8 mya. Old World monkeys disappeared from Europe about 1.8 mya. Some molecular and fossil studies generally show that modern humans originated in Africa 100–200 tya (thousand years ago).

Although primates are well studied in comparison to other animal groups, several new species have been recently discovered; genetic tests on some populations have revealed previously unrecognised species. *Primate Taxonomy* listed about 350 species of primates in 2001, the author, Colin Groves, increased that number to 376 for his contribution to the third edition of *Mammal Species of the World* (MSW3). However, MSW3 falls short of current understanding as its collection was completed in 2003; a number of publications have since pushed the number to 424 species, or 658 including subspecies.

## Classification of living primates



A 1927 drawing of chimpanzees, a gibbon (top right) and two orangutans (center and bottom center). The chimp in the upper left is brachiating; the orang at the bottom center is knuckle-walking.

*Homo sapiens*, a member of the order Primates

The following is the listing of the various families of primates:

- **Order Primates**
  - **Suborder Strepsirrhini**: non-tarsier prosimians
    - Infraorder Lemuriformes
      - Family Cheirogaleidae: dwarf lemurs and mouse-lemurs (32 species)
      - Family Daubentoniidae: Aye-aye (1 species)
      - Family Lemuridae: lemurs (22 species)
      - Family Lepilemuridae: sportive lemurs (26 species)
      - Family Indriidae: woolly lemurs and allies (19 species)
    - Infraorder Lorisiformes
      - Family Lorisidae: lorises, pottos and allies (9 species)
      - Family Galagidae: galagos (19 species)
  - **Suborder Haplorrhini**: tarsiers, monkeys and apes
    - Infraorder Tarsiiformes
      - Family Tarsiidae: tarsiers (9 species)
    - Infraorder Simiiformes
      - Parvorder Platyrrhini: New World monkeys
        - Family Callitrichidae: marmosets and tamarins (42 species)

        - Family Cebidae: capuchins and squirrel monkeys (17 species)
        - Family Aotidae: night or owl monkeys (douroucoulis) (10 species)
        - Family Pitheciidae: titis, sakis and uakaris (42 species)
        - Family Atelidae: howler, spider and woolly monkeys (28 species)
    - Parvorder Catarrhini
        - Superfamily Cercopithecoidea
            - Family Cercopithecidae: Old World monkeys (135 species)
        - Superfamily Hominoidea
            - Family Hylobatidae: gibbons or "lesser apes" (13 species)
            - Family Hominidae: great apes, including humans (7 species)

Philippine Tarsier, once considered a prosimian, now predominantly considered a haplorrhine

The order Primates was established by Carl Linnaeus in 1758, in the tenth edition of his book Systema Naturae, for the genera *Homo* (humans), *Simia* (other apes and monkeys), *Lemur* (prosimians) and *Vespertilio* (bats). In the first edition of the same book (1735), he had used the name Anthropomorpha for *Homo*, *Simia* and *Bradypus* (sloths). In 1839, Henri Marie Ducrotay de Blainville, following Linnaeus and imitating his nomenclature, established the orders Secundates (including the suborders Chiroptera, Insectivora and Carnivora), Tertiates (or Glires) and Quaternates (including Gravigrada, Pachydermata and Ruminantia), but these new taxa were not accepted.

Before Anderson and Jones introduced the classification of Strepsirhini and Haplorhini in 1984, (followed by McKenna and Bell's 1997 work *Classification of Mammals: Above the species level*), the Primates were divided into two superfamilies: Prosimii and Anthropoidea. The Prosimii included all of the prosimians: all of Strepsirrhini plus the tarsiers. The Anthropoidea contained all of the simians.

### Hybrids

Primate hybrids usually arise in captivity, but there have also been examples in the wild. Hybridization occurs where two species' range overlap to form hybrid zones; hybrids may be created by humans when animals are placed in zoos or due to environmental pressures such as predation. Intergeneric hybridizations, hybrids of different genera, have also been found in the wild. Although they belong to genera that have been distinct for several million years, interbreeding still occurs between the Gelada and the Hamadryas Baboon.

## *Distinguishing features*

Primates have diversified in arboreal habitats (trees and bushes) and retain many characteristics that are adaptations to this environment. They are distinguished by:

- retention of the collar bone in the pectoral girdle;
- shoulder joints which allow high degrees of movement in all directions;
- five digits on the fore and hind limbs with opposable thumbs and big toes;
- nails on the fingers and toes (in most species);
- a flat nail on the hallux (in all extant species);
- sensitive tactile pads on the ends of the digits;
- orbits encircled in bone;
- a trend towards a reduced snout and flattened face, attributed to a reliance on vision at the expense of olfaction (most notably in haplorrhines, and less so in strepsirrhines);
- a complex visual system with stereoscopic vision, high visual acuity and color vision;
- a brain having a well developed cerebellum with posterior lobe and a Calcarine fissure;
- a large brain in comparison to body size, especially in simians;
- differentiation of an enlarged cerebral cortex;

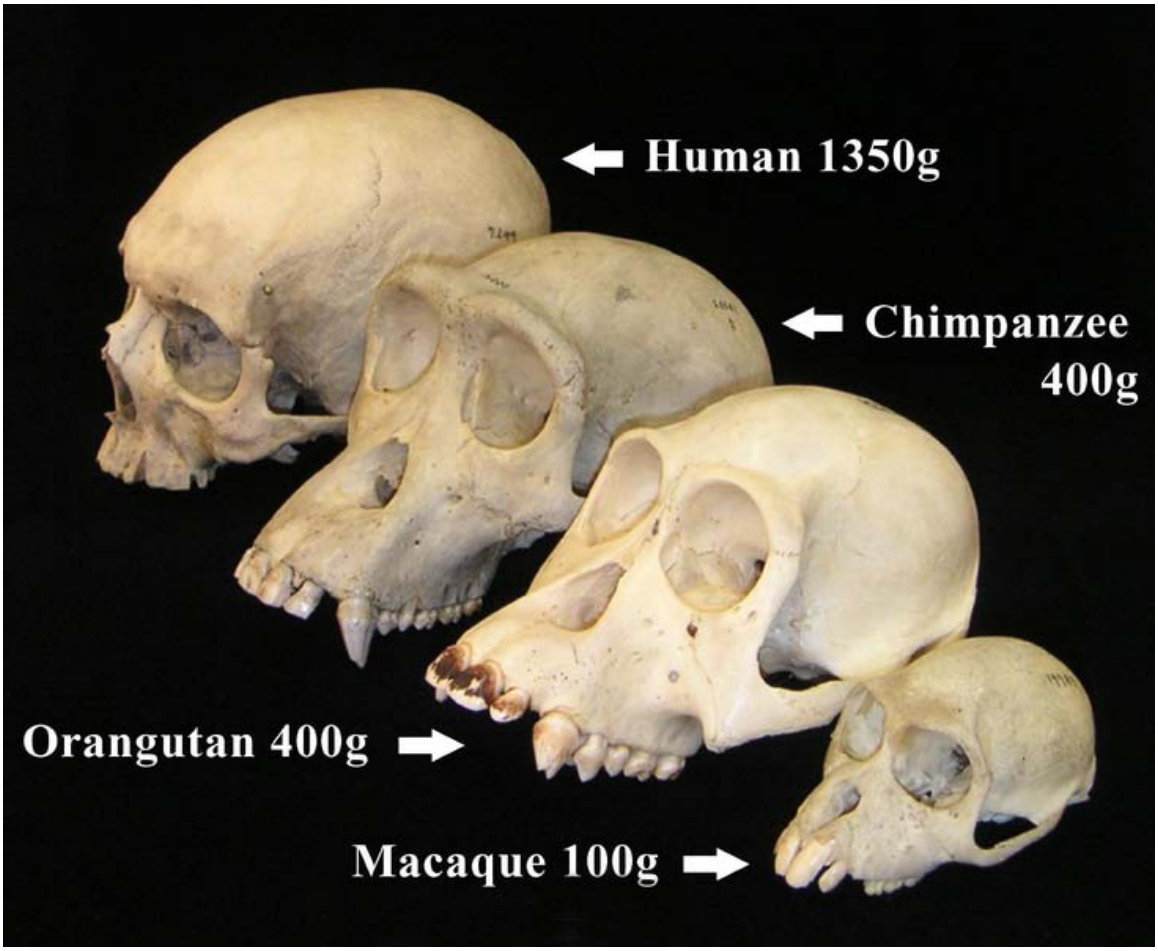
- reduced number of teeth compared to primitive mammals;
- three kinds of teeth;
- a well-developed cecum;
- two pectoral mammary glands;
- typically one young per pregnancy;
- a pendulous penis and scrotal testes;
- a long gestation and developmental period; and
- a trend towards holding the torso upright leading to bipedalism.

Not all primates exhibit these anatomical traits, nor is every trait unique to primates. For example, other mammals have collar bones, three kinds of teeth and a pendulous penis, while spider monkeys have greatly reduced thumbs, ruffed lemurs have six mammary glands and strepsirrhines generally have longer snouts and a strong sense of smell.

In regard to behavior, primates are frequently highly social, with flexible dominance hierarchies. New World species form monogamous pair bonds, and show substantial paternal care of their young, unlike most Old World monkeys.

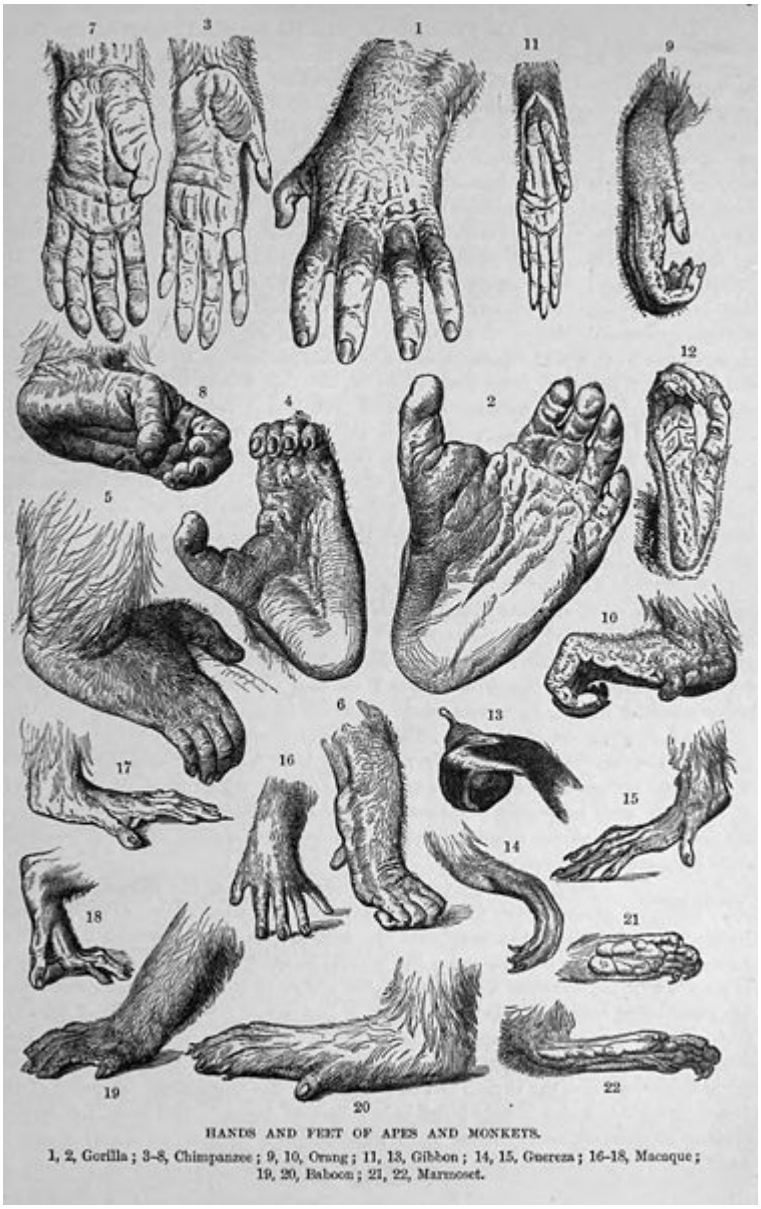
## *Anatomy, physiology, and morphology*

Primates have forward-facing eyes on the front of the skull; binocular vision allows accurate distance perception, useful for the brachiating ancestors of all great apes. There is a bony ridge above the eye sockets; this ridge reinforces weaker bones in the face which are put under strain during chewing. Strepsirrhines have a postorbital bar, a bone which runs around the eye socket, to protect their eyes; in contrast, the higher primates, haplorrhines, have evolved fully enclosed sockets.




Primate crania. The labels indicate mass of brain.

The primate skull has a large domed cranium which is particularly prominent in anthropoids. The cranium protects the large brain, a distinguishing characteristic of this group. The endocranial volume (the volume within the skull) is three times greater in humans than in the greatest non-human primate, reflecting a larger brain size. The mean endocranial volume is 1201 cubic centimeters in humans, 469 $cm^3$ in gorillas, 400 $cm^3$ in chimpanzees and 397 $cm^3$ in orangutans. The primary evolutionary trend of primates has been the elaboration of the brain, in particular the neocortex (a part of the cerebral cortex), which is involved with sensory perception, generation of motor commands, spatial reasoning, conscious thought and, in humans, language. While other mammals rely heavily on their sense of smell, the arboreal life of primates has led to a tactile, visually dominant sensory system, a reduction in the olfactory region of the brain and increasingly complex social behavior.




An 1893 drawing of the hands and feet of primates

Primates generally have five digits on each limb (pentadactyly), with keratin nails on the end of each finger. The bottom sides of the hands and feet have sensitive pads on the fingertips. Most have opposable thumbs, a characteristic primate feature; however, opposing thumbs are not limited to this order (opossums, for example, also have them). Thumbs allow some species to use tools. In primates, the combination of opposing thumbs, short fingernails (rather than claws) and long, inward-closing fingers is a relic of the ancestral practice of gripping branches, and has, in part, allowed some species to develop brachiation (swinging by the arms from tree limb to tree limb) as a significant means of transportation. Prosimians have clawlike nails on the second toe of each foot, called toilet-claws, which they use for grooming.

The primate collar bone is retained as prominent element of the pectoral girdle; this allows the shoulder joint broad mobility. Apes have more mobile shoulder joints and arms due to the dorsal position of the scapula, broad ribcages that are flatter front-to-back, and a shorter, less mobile spine compared to Old World monkeys (with lower vertebrae greatly reduced, resulting in tail loss in some species). Old World monkeys are unlike apes in that most have tails. The only primate family with prehensile tails are the New World Atelids, including the howler, spider and woolly monkeys.

Primates show an evolutionary trend towards a reduced snout. Technically, Old World monkeys are distinguished from New World monkeys by the structure of the nose, and from apes by the arrangement of their teeth. In New World monkeys the nostrils face sideways; in Old World monkeys, they face downwards. There is a considerably varied dental pattern in primates and although some have lost most of their incisors, all retain at least one lower incisor. In most strepsirhines, the lower incisors and canines form a toothcomb, which is used in grooming and sometimes foraging, and the first lower premolar is shaped like a canine. Old World monkeys have eight premolars, compared with twelve in New World monkeys. The Old World species are divided into apes and monkeys depending on the number of cusps on their molars; apes have five, Old World monkeys have four, although humans may have 4 or 5. The main hominid molar cusp (hypocone) evolved in early primate history, while the cusp of the corresponding primitive lower molar (paraconid) was lost. Prosimians are distinguished by their immobilized upper lips, the moist tip of their nose and forward-facing lower front teeth.

The evolution of color vision in primates is unique among most eutherian mammals. While the remote vertebrate ancestors of the primates possessed three color vision (trichromaticism), the nocturnal, warm-blooded, mammalian ancestors lost one of three cones in the retina during the Mesozoic period. Fish, reptiles and birds are therefore trichromatic or tetrachromatic while all mammals, with the exception of some primates and marsupials, are dichromats or monochromats (totally color blind). Nocturnal primates, such as the night monkeys and bush babies, are often monochromatic. Catarrhines are routinely trichromatic due to a gene duplication of the red-green opsin gene at the base of their lineage, 30 to 40 million years ago. Platyrrhines, on the other hand, are trichromatic in a few cases only. Specifically, individual females must be heterozygous for two alleles of the opsin gene (red and green) located on the same locus of the X chromosome. Males, therefore, can only be dichromatic, while females can be either dichromatic or trichromatic. Color vision in strepsirrhines is not as well understood; however, research indicates a range of color vision similar to that found in platyrrhines.

Like catarrhines, Howler monkeys (a family of platyrrhines) show routine trichromatism that has been traced to an evolutionarily recent gene duplication. Howler monkeys are one of the most specialized leaf-eaters of the New World monkeys; fruits are not a major part of their diet, and the type of leaves they prefer to consume (young, nutritive, and digestible) are detectable only by a red-green signal. Field work exploring the dietary preferences of howler monkeys suggests that routine trichromaticism was environmentally selected for.

## Sexual dimorphism

Distinct sexual size dimorphism can be seen between the male Hamadryas Baboons (grey) and the female (brown).

Sexual dimorphism, the variation between individuals of different sex in the same species, is often exhibited in simians, though to a greater degree in Old World species (apes and some monkeys) than New World species. Recent studies involve comparing DNA to examine both the variation in the expression of the dimorphism among primates and the fundamental causes of sexual dimorphism. Primates usually have dimorphism in body mass and canine tooth size along with pelage and skin color. The dimorphism can be attributed to and affected by different factors, including mating system, size, habitat and diet.

Comparative analyses have generated a more complete understanding of the relationship between sexual selection, natural selection, and mating systems in primates. Studies have shown that dimorphism is the product of changes in both male and female traits. Ontogenetic scaling, where relative extension of a common growth trajectory occurs, may give some insight into the relationship between sexual dimorphism and growth patterns. Some evidence from the fossil record suggests that there was convergent evolution of dimorphism, and some extinct hominids probably had greater dimorphism than any living primate.

## Locomotion

Diademed Sifaka, a vertical clinger and leaper, ready to leap to another tree

Primate species move by brachiation, bipedalism, leaping, arboreal and terrestrial quadrupedalism, climbing, knuckle-walking or by a combination of these methods. Several prosimians are primarily vertical clinger and leapers. These include many bushbabies, all indriids (i.e., sifakas, avahis and indris), sportive lemurs, and all tarsiers. Other prosimians are arboreal quadrupeds and climbers. Some are also terrestrial quadrupeds, while some are leapers. Most monkeys are both arboreal and terrestrial quadrupeds and climbers. Gibbons, muriquis and spider monkeys all use brachiation extensively. Woolly monkeys also sometimes brachiate. Orangutans use a similar form of locomotion called quadramanous climbing, in which they use their arms and legs to carry their heavy bodies through the trees. Chimpanzees and gorillas knuckle walk, and can move bipedally for short distances. Although numerous species, such as the Australopithecines and early hominids, have exhibited fully bipedal locomotion, humans are the only extant species with this trait.

## *Behavior*

### Social systems

Richard Wrangham stated that social systems of non-human primates are best classified by the amount of movement by females occurring between groups. He proposed four categories:

- Female transfer systems – females move away from the group in which they were born. Females of a group will not be closely related whereas males will have remained with their natal groups, and this close association may be influential in social behavior. The groups formed are generally quite small. This organization can be seen in chimpanzees, where the males, who are typically related, will cooperate in defense of the group's territory. Among New World Monkeys, spider monkeys and muriquis use this system.

Japanese Macaques bathe together in Jigokudani Hot Spring

- Male transfer systems – while the females remain in their natal groups, the males will emigrate as adolescents. Polygynous and multi-male societies are classed in this category. Group sizes are usually larger. This system is common among the Ring-tailed Lemur, capuchin monkeys and cercopithecine monkeys.

- Monogamous species – a male–female bond, sometimes accompanied by a juvenile offspring. There is shared responsibility of parental care and territorial defense. The offspring leaves the parents' territory during adolescence. Gibbons essentially use this system, although "monogamy" in this context does not necessarily mean absolute sexual fidelity.
- Solitary species – often males who defend territories that include the home ranges of several females. This type of organization is found in the prosimians. Orangutans do not defend their territory but effectively have this organization.

Other systems are known to occur as well. For example, with howler monkeys both the males and females typically transfer from their natal group on reaching sexual maturity, resulting in groups in which neither the males nor females are typically related. Some prosimians, colobine monkeys and callitrichid monkeys use this system.

Chimpanzees are social animals.

Primatologist Jane Goodall, who studied in the Gombe Stream National Park, noted fission-fusion societies in chimpanzees. There is *fission* where the main group splits up to forage during the day, then *fusion* when the group returns at night to sleep as a group. This social structure can also be observed in the Hamadryas Baboon, spider monkeys and the Bonobo. The Gelada has a similar social structure in which many smaller groups come together to form temporary herds of up to 600 monkeys.

These social systems are affected by three main ecological factors: distribution of resources, group size and predation. Within a social group there is a balance between

cooperation and competition. Cooperative behaviors include social grooming (removing skin parasites and cleaning wounds), food sharing, and collective defense against predators or of a territory. Aggressive behaviors often signal competition for availability of food, sleeping sites or mates. Aggression is also used in establishing dominance hierarchies.

## Interspecific associations

Several species of primates are known to associate in the wild. Some of these associations have been extensively studied. In the Tai Forest of Africa several species coordinate anti-predator behavior. These include the Diana Monkey, Campbell's Mona Monkey, Lesser Spot-nosed Monkey, Western Red Colobus, King Colobus and Sooty Mangabey, which coordinate anti-predator alarm calls. Among the predators of these monkeys is the Common Chimpanzee.

The Red-tailed Monkey associates with several species, including the Western Red Colobus, Blue Monkey, Wolf's Mona Monkey, Mantled Guereza, Black Crested Mangabey and Allen's Swamp Monkey. Several of these species are predated on by the Common Chimpanzee.

In South America, squirrel monkeys associate with capuchin monkeys. This may have more to do with foraging benefits to the squirrel monkeys rather than anti-predation benefits.

## Life history

Primates have slower rates of development than other mammals. All non-human primate infants are breastfed by their mothers and rely on them for grooming and transportation. In some species, infants are protected and transported by males in the group, particularly males who may be their fathers. Other relatives of the infant, such as siblings and aunts, may participate in its care as well. Most primate mothers cease ovulation while breastfeeding an infant; once the infant is weaned the mother can reproduce again. This often leads to weaning conflict with infants who attempt to continue breastfeeding.

Primates have a longer juvenile period between weaning and sexual maturity than other mammals of similar size. During the juvenile period, primates are more susceptible than adults to predation and starvation; they gain experience in feeding and avoiding predators during this time  They learn social and fighting skills, often through playing.

Primates, especially females, have longer lifespans than other similarly sized mammals.

## Diet and feeding

Leaf eating Mantled Guereza, a species of black-and-white colobus

Crab-eating Macaques forage and temporarily store food in their cheeks pouches

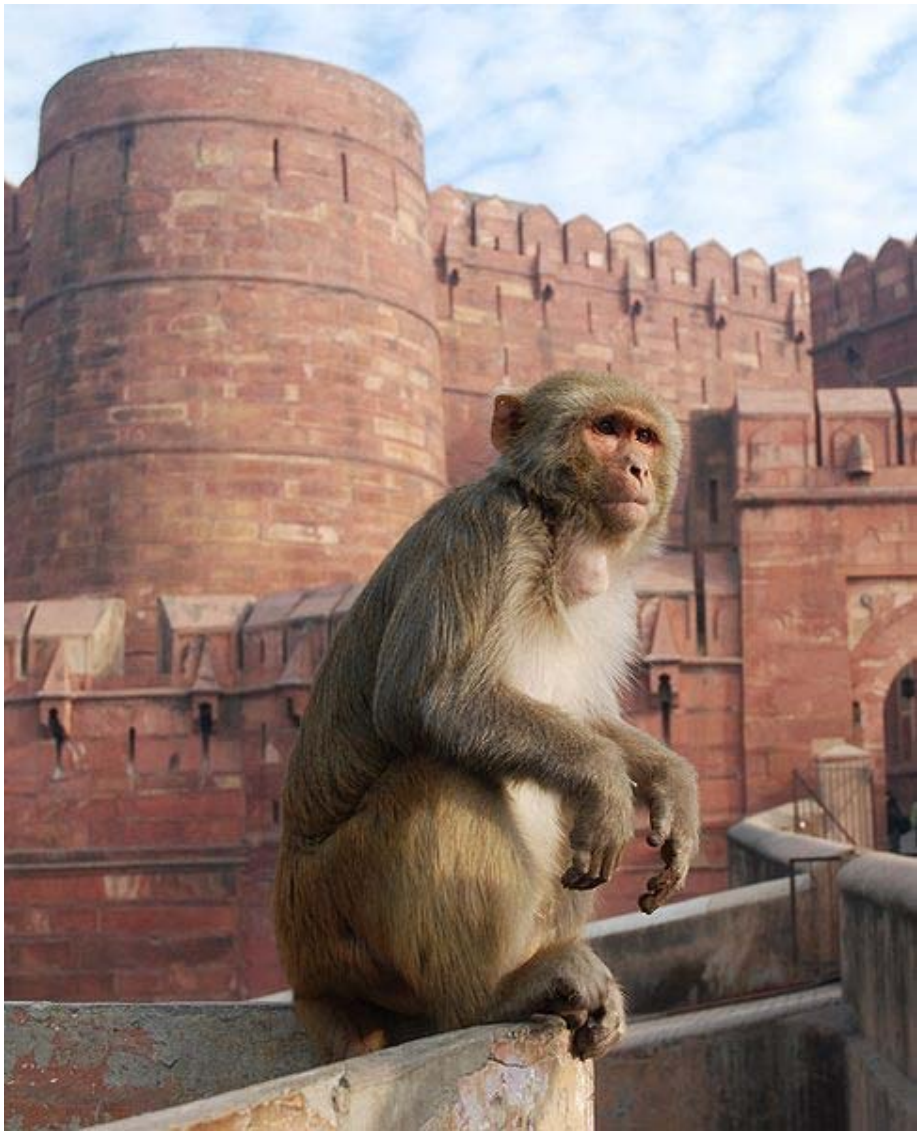
Primates exploit a variety of food sources. It has been said that many characteristics of modern primates, including humans, derive from an early ancestor's practice of taking most of its food from the tropical canopy. Most primates include fruit in their diets to obtain easily digested carbohydrates and lipids for energy. However, they require other foods, such as leaves or insects, for amino acids, vitamins and minerals. Primates in the main suborder Strepsirrhini (non-tarsier prosimians) are able to synthesize vitamin C, while primates of the suborder of Haplorrhini (tarsiers, monkeys and apes) have lost the ability to synthesize vitamin C, and require it in the diet.

Many primates have anatomical specializations that enable them to exploit particular foods, such as fruit, leaves, gum or insects. For example, leaf eaters such as howler monkeys, black-and-white colobuses and sportive lemurs have extended digestive tracts which enable them to absorb nutrients from leaves that can be difficult to digest. Marmosets, which are gum eaters, have strong incisor teeth, enabling them to open tree bark to get to the gum, and claws rather than nails, enabling them to cling to trees while feeding. The Aye-aye combines rodent-like teeth with a long, thin middle finger to fill the same ecological niche as a woodpecker. It taps on trees to find insect larvae, then gnaws holes in the wood and inserts its elongated middle finger to pull the larvae out. Some species have additional specializations. For example, the Grey-cheeked Mangabey has

thick enamel on its teeth, enabling it to open hard fruits and seeds that other monkeys cannot.

The Gelada is the only primate species that feeds primarily on grass. Tarsiers are the only extant obligate carnivorous primates, exclusively eating insects, crustaceans, small vertebrates and snakes (including venomous species). Capuchin monkeys, on the other hand, can exploit many different types of food, including fruit, leaves, flowers, buds, nectar, seeds, insects and other invertebrates, bird eggs, and small vertebrates such as birds, lizards, squirrels and bats. The Common Chimpanzee has a varied diet that includes predation on other primate species, such as the Western Red Colobus monkey.

## *Habitat and distribution*



Rhesus Macaque at Agra Fort, India

Primates evolved from arboreal animals, and many species live most of their lives in trees. Most primate species live in tropical rain forests. The number of primate species within tropical areas has been shown to be positively correlated to the amount of rainfall and the amount of rain forest area. Accounting for 25% to 40% of the fruit-eating animals (by weight) within tropical rainforests, primates play an important ecological role by dispersing seeds of many tree species.

Some species are partially terrestrial, such as baboons and Patas Monkeys, and a few species are fully terrestrial, such as Geladas and Humans. Non-human primates live in a diverse number of forested habitats in the tropical latitudes of Africa, India, Southeast Asia, and South America, including rainforests, mangrove forests, and montane forests. There are some examples of non-human primates that live outside of the tropics; the mountain-dwelling Japanese Macaque lives in the north of Honshū where there is snow-cover eight months of the year; the Barbary Macaque lives in the Atlas Mountains of Algeria and Morocco. Primate habitats span a range of altitudes: the Black Snub-nosed Monkey has been found living in the Hengduan Mountains at altitudes of 4,700 meters (15,400 ft), the Mountain Gorilla can be found at 4,200 meters (13,200 ft) crossing the Virunga Mountains, and the Gelada has been found at elevations of up to 5,000 meters (16,400 ft) in the Ethiopian Highlands. Although most species are generally shy of water, a few are good swimmers and are comfortable in swamps and watery areas, including the Proboscis Monkey, De Brazza's Monkey and Allen's Swamp Monkey, which has developed small webbing between its fingers. Some primates, such as the Rhesus Macaque and gray langurs, can exploit human-modified environments and even live in cities.

## *Interactions with humans*

Close interactions between humans and non-human primates (NHPs) can create pathways for the transmission of zoonotic diseases. Viruses such as *Herpesviridae* (most notably Herpes B Virus), *Poxviridae*, measles, ebola, rabies, the Marburg virus and viral hepatitis can be transmitted to humans; in some cases the viruses produce potentially fatal diseases in both humans and non-human primates.

## Legal and social status

Only humans are recognized as persons and protected in law by the United Nations Universal Declaration of Human Rights. The legal status of NHPs, on the other hand, is the subject of much debate, with organizations such as the Great Ape Project (GAP) campaigning to award at least some of them legal rights. In June 2008, Spain became the first country in the world to recognize the rights of some NHPs when its parliament's cross-party environmental committee urged the country to comply with GAP's recommendations, which are that chimpanzees, bonobos, orangutans, and gorillas not be used for animal experiments.

Capuchin monkeys' manual dexterity is one reason they can assist quadriplegic humans.

Many species of NHP are kept as pets by humans. GAP estimates that around 3,000 NHPs live as exotic pets in the United States, while the Humane Society of the United States puts the figure much higher, at around 15,000. The expanding Chinese middle class has increased demand for NHPs as exotic pets in recent years. Although NHP import for the pet trade was banned in the U.S. in 1975, smuggling still occurs along the United States – Mexico border, with prices ranging from US$3000 for monkeys to $30,000 for apes.

Primates are used as model organisms in laboratories and have been used in space missions. They serve as service animals for disabled humans. Capuchin monkeys can be

trained to assist quadriplegic humans; their intelligence, memory, and manual dexterity make them ideal helpers.

NHPs are kept in zoos around the globe. Historically, zoos were primarily a form of entertainment, but more recently have shifted their focus to conservation, education and research. Many zoos now feature naturalistic exhibits and educational material for the public; in the United States many participate in the Species Survival Plan (SSP), developed by the Association of Zoos and Aquariums (AZA), to maximize genetic diversity through captive breeding. Zoos and other animal welfare supporters generally oppose animal rights initiatives and the GAP's insistence that all NHPs be released from captivity for two primary reasons. First, captive-born primates lack the knowledge and experience to survive in the wild if released. Second, zoos provide living space for primates and other animals threatened with extinction in the wild.

## Role in scientific research

Thousands of non-human primates are used around the world in research because of their psychological and physiological similarity to humans. In particular, the brains and eyes of NHPs more closely parallel human anatomy than those of any other animals. NHPs are commonly used in preclinical trials, neuroscience, ophthalmology studies, and toxicity studies. Rhesus Macaques are often used, as are other Macaques, African green monkeys, chimpanzees, baboons, squirrel monkeys, and marmosets, both wild-caught and purpose-bred. In 2005, GAP reported that 1,280 of the 3,100 NHPs living in captivity in the United States were used for experiments. In 2004, the European Union used around 10,000 NHPs in such experiments; in 2005 in Great Britain, 4,652 experiments were conducted on 3,115 NHPs. Governments of many nations have strict care requirements of NHPs kept in captivity. In the US, federal guidelines extensively regulate aspects of NHP housing, feeding, enrichment, and breeding. European groups such as the European Coalition to End Animal Experiments are seeking a ban on all NHP use in experiments as part of the European Union's review of animal testing legislation.

## Conservation

The International Union for Conservation of Nature (IUCN) lists more than a third of primates as critically endangered or vulnerable. Common threats to primate species include deforestation, forest fragmentation, monkey drives (resulting from primate crop raiding), and primate hunting for use in medicines, as pets, and for food. Large-scale tropical forest clearing is widely regarded as the process that most threatens primates. More than 90% of primate species occur in tropical forests. The main cause of forest loss is clearing for agriculture, although commercial logging, subsistence harvesting of timber, mining, and dam construction contribute to tropical forest depletion too. In Indonesia large areas of lowland forest have been cleared to increase palm oil production, and one analysis of satellite imagery concluded that during 1998 and 1999 there was a loss of 1,000 Sumatran Orangutans per year in the Leuser Ecosystem alone.

Critically endangered Sumatran Orangutan

Primates with a large body size (over 5 kg) have an increased extinction risk due to their increased profitability to poachers compared to smaller primates. They reach sexual maturity later than other animals and have a longer period between births. Populations therefore have a slower recovery time after the loss of members to poaching or the pet trade. Data for some African cities show that half of all protein consumed in urban areas comes from the bushmeat trade. Endangered primates such as guenons and the Drill are hunted at levels that far exceed sustainable levels. This is due to their large body size, ease of transport and profitability per animal. As farming encroaches on forest habitats, primates feed on the crops, causing the farmers large economic losses. Primate crop raiding gives locals a negative impression of primates, hindering conservation efforts.

Madagascar, home to five endemic primate families, has experienced the greatest extinction of the recent past; since human settlement 1,500 years ago, at least eight classes and fifteen species have become extinct due to hunting and habitat destruction. Among the primates wiped out were *Archaeoindris* (a lemur larger than a silverback gorilla) and the families Palaeopropithecidae and Archaeolemuridae.

In Asia, Hinduism, Buddhism, and Islam prohibit eating primate meat; however, primates are still hunted for food. Some smaller traditional religions allow the consumption of primate meat. The pet trade and traditional medicine also increase demand for illegal hunting. The Rhesus Macaque, a model organism, was protected after overtrapping threatened its numbers in the 1960s; the program was so effective that the macaques are now seen as a pest throughout their range.

The critically endangered Cross River Gorilla

In Central and South America forest fragmentation and hunting are the two main problems for primates. Large tracts of forest are now rare in Central America. This increases the amount of forest vulnerable to edge effects such as farmland encroachment, lower levels of humidity and a change in plant life. Movement restriction results in a greater amount of inbreeding, which can cause deleterious effects leading to a population bottleneck, whereby a significant percentage of the population is lost.

There are 21 critically endangered primates, 7 of which have remained on the IUCN's "The World's 25 Most Endangered Primates" list since the year 2000: the Silky Sifaka, Delacour's Langur, the White-headed Langur, the Gray-shanked Douc, the Tonkin Snub-nosed Langur, the Cross River Gorilla and the Sumatran Orangutan. Miss Waldron's Red Colobus was recently declared extinct when no trace of the subspecies could be found from 1993 to 1999. A few hunters have found and killed individuals since then, and the species' prospects remain bleak.

Chapter- 2

# Prehistoric Apes

# Afropithecus

| *Afropithecus*<br>**Fossil range: Miocene** | |
|---|---|
| **Scientific classification** | |
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Mammalia |
| Order: | Primates |
| Superfamily: | Hominoidea |
| Family: | Proconsulidae ? (extinct) |
| Subfamily: | Afropithecinae (extinct) |
| Genus: | ***Afropithecus*** (extinct) |
| Species: | ***A. turkanensis*** |
| **Binomial name** | |
| ***Afropithecus turkanensis***<br>Leakey and Leakey, 1986 | |

***Afropithecus turkanensis***, a new Miocene hominoid, was excavated from a small site near Lake Turkana called Kalodirr in northern Kenya in 1986 and was named by Richard Leakey and Meave Leakey. The estimated age of *Afropithecus* is between 16 and 18 million years old, which was determined with radiometric dating techniques and the geological studies conducted by Broschetto and Brown from the University of Utah. In total there are 46 recovered specimens from Kalodirr relating to *Afropithecus* consisting of cranial, mandible, dentition and post-cranial remains. The type specimen of *Afropithecus turkanensis* is KNM-WK 16999.

## *Morphology*

Leakey and Leakey first described *Afropithecus turkanensis* to be a large hominoid which appeared to have relatively thick enamel. Leakey suggested that *A. turkanensis* shared postcranial features with the species *Prosconsul nyanzae*, which is the best known genus Miocene with literally hundreds of fossils having been found representing almost all skeletal elements, and sharing cranial features with *Aegyptopithecus zeuxis* and dental features with *Heliopithecus leakeyi* which had two weathered molars that indicated a general distinction from known large early catarrhines, and later concluded that *A. turkenensis* was a primitive, arboreal quadruped similar to *P. nyanzae*, and that *A. turkanensis* had primitive facial morphology and derived dental characteristics that would suggest a diet of hard fruits.

### Cranial Morpogology

The type specimen, KNM-WT 16999 is composed of a long distinct snout, the facial skeleton, frontal, much of the coronal structure, most of the sphenoid, and relatively unworn adult dentition; the right orbit (virtually complete), the right zygomatic, the pterygoid, most of the sphenoid and lesser wings, the maxilla and premaxilla, and adult dentition with procumbent incisors. The surface on the right side maxilla and premaxilla along with the enamel on the right molars has been lost over time and has been replaced with calcite crystals, which only provide the general shape and not the details.

From dentition its known that the palate, which is almost completely calcified, of *A. turkanensis* is shallow, long and narrow with tooth rows that converge posteriorly, and it is probable the tooth rows were originally nearly parallel. A. turkanensis had a 6.5mm diastema between its very procumbent second incisor (KNM-WT 16999 had large, broad incisors) and the canine.

The thickness of the enamel on the molars is often reported when fossils are being recorded and used to make comparisons across taxa. The thickness is referred to either as "thin" or "thick" and is commonly assessed as a linear measurement of the enamel on worn or naturally fractured teeth. From enamel testing it has been suggested that *A. turkanensis* is the oldest known thick-enamelled hominoid, which is what would distinguish it from *Kenyapithecus*.

### Post-Cranial Morphology

Post cranial remains such as KNM-WK 16901, includes an associated right fibula (lacking the proximal portion, and is approximately the same size as *Pan troglodytes*; 184 mm), a right proximal third metatarsal, a right fourth metatarsal lacking the head, and an incomplete first metatarsal head.

Other post-cranial remains include: KNM-WK 17016P a large right ulna, and foot or hand bones: KNM-WK 17008, KNM-WK 18395.

# Anoiapithecus

| ***Anoiapithecus*** **Fossil range: 12 Ma Miocene** | |
|---|---|
| **Scientific classification** | |
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Mammalia |
| Order: | Primates |
| Superfamily: | Hominoidea |
| Family: | Dryopithecidae† |
| Genus: | ***Anoiapithecus***† Moyà-Solà et al., 2009 |
| **Species** | |

- †*Anoiapithecus brevirostris*

***Anoiapithecus*** is an extinct genus of ape thought to be closely related to *Dryopithecus*. Both genera lived during the Miocene, approximately 12 million years ago. Fossil specimens named by Salvador Moyà-Solà *Anoiapithecus brevirostris* are known from deposits from Spain.

The discoverers describe *Anoiapithecus brevirostris* as a hominoid (superfamily Hominoidea) in the Dryopithecine tribe. They believe that it has more modern traits then the Kenyapithecines from which Kenyapithecus wickeri from Kenya brings fragmentary information. The African specimens are considered a sister taxon to the hominids, and 2 million year younger European specimens must be from after the time that these two groups split. This means that hominids may have evolved in Europe.

The name comes from the Anoia River region in Catalonia, where the fossil was found. It has been given the nickname *Lluc* (since it is a male individual). The name Lluc is the Catalan form of Luke, which in Latin suggests "light" and this discovery enlighted our early evolution

The modern anatomical features that characterized the family Hominidae visible in Lluc's fossil among others are: unique facial pattern for hominoids, nasal aperture wide at the base, high cheek bone, deep palate.

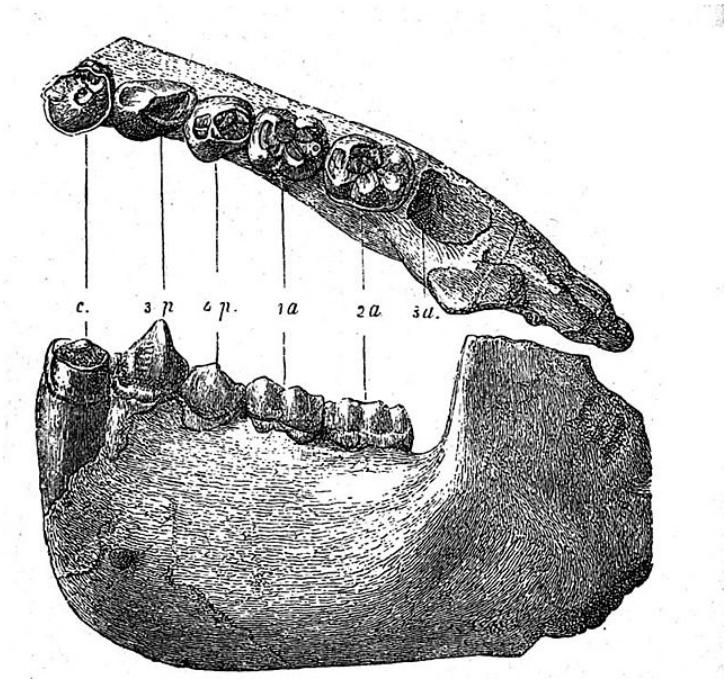
# Bunopithecus sericus

| **Bunopithecus sericus**<br>**Fossil range: Middle Pleistocene** | |
|---|---|
| **Scientific classification** | |
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Mammalia |
| Order: | Primates |
| Family: | Hylobatidae |
| Genus: | ***Bunopithecus***<br>Matthew and Granger, 1923 |
| Species: | ***B. sericus*** |
| **Binomial name** | |
| ***Bunopithecus sericus***<br>Matthew and Granger, 1923 | |

***Bunopithecus sericus*** is an extinct gibbon or gibbon-like primate. Its remains were first discovered in China, but have since been found all over Southern Europe and Asia. It was a frugivore, and, like modern apes, did not have a tail.

Although the two hoolock gibbon species were once included in the ***Bunopithecus*** genus, they have recently been removed and *B. sericus* remains as the only known species of this genus.

# Dryopithecus fontani

| *Dryopithecus fontani*<br>**Fossil range: Miocene** |
|---|
|  |
| Jaw of Dryopithecus fontani |
| **Scientific classification** |
| Kingdom: Animalia |
| Phylum: Chordata |
| Class: Mammalia |
| Order: Primates |
| Superfamily: Hominoidea |
| Family: Dryopithecidae (extinct) |
| Genus: *Dryopithecus* (extinct) |
| Species: ***D. fontani*** |
| **Binomial name** |
| ***Dryopithecus fontani***<br>Lartet, 1856 |

***Dryopithecus fontani*** is an extinct ape that was first discovered in Saint-Gaudens, Haute-Garonne, France, in the 19th century, and was dated to the middle Miocene.

### Morphology

*Dryopithecus fontani* had a dental formula of 2:1:2:3 on both the upper and lower jaw. The incisors of this species were relatively narrow and less spatulate compared to other genera such as Proconsul. The upper molars of this species had a partly developed lingual cingulum. *Dryopithecus fontani* had relatively long upper premolars and relatively broad lower premolars. The lower molars had the Y5 pattern, which is also called the Dryopithecus pattern. The cheek had a thin layer of enamel on them and there were low, rounded cusps. This species had gracile canines and a short premaxilla. The mandible of *Dryopithecus fontani* had an inferior transverse torus but lacked a superior transverse torus. The forelimbs of this species had a reduced olecranon process, a deep humeral trochlea, and the loss of the entepicondylar foramen. *Dryopithecus fontani* had an average body mass of around 35.0 kilograms.

### Range

*Dryopithecus fontani* has been found through the continent of Europe, in locations such as Spain and Hungary.

# Proconsul (primate)

| ***Proconsul*** |
| --- |
| **Fossil range: Miocene (23-17 MYA)** |

*Proconsul* skeleton reconstruction

| **Scientific classification** | |
| --- | --- |
| Kingdom: | Animalia |

| | |
|---|---|
| Phylum: | Chordata |
| Class: | Mammalia |
| Order: | Primates |
| Superfamily: | Hominoidea |
| Family: | † Proconsulidae |
| Subfamily: | **Proconsulinae** |
| Genus: | ***Proconsul*** |

**Species**

- *Proconsul africanus*
- *Proconsul heseloni*
- *Proconsul major*
- *Proconsul nyanzae*

***Proconsul*** is an extinct genus of primates that existed from 23 to 17 million years ago during the Early Miocene epoch. Fossil remains are present in Eastern Africa including Kenya and Uganda. Four species have been classified to date: *P. africanus, P. heseloni, P. major* and *P. nyanzae*. The four species differ mainly in body size. Environmental reconstructions for the Early Miocene *Proconsul* sites are still tentative and range from forested environments to more open, arid grasslands.

They had a mixture of Old World monkey and ape characteristics, so their placement in the ape superfamily Hominoidea is tentative; some scientists place *Proconsul* outside of Hominoidea, before the split of the apes and Old World monkeys.

*Proconsul's* monkey-like features include pronograde postures, indicated by a long flexible back, curved metacarpals, and an above-branch arboreal quadrupedal positional repertoire. The primary feature linking *Proconsul* with extant apes is its lack of a tail; other "ape-like" features include its enhanced grasping capabilities, stabilized elbow joint and facial structure. *Proconsul* was definitely not suspensory like modern apes.

## *Discovery and classification*

*Proconsul nyanzae* fossil, Muséum national d'histoire naturelle, Paris.

*Proconsul heseloni* skull.

The first specimen, a partial jaw discovered in 1909 by a gold prospector at Koru, near Kisumu in western Kenya, was also the oldest fossil hominoid known until recently, and the first fossil mammal ever found in sub-Saharan Africa. The name, Proconsul, was devised by Arthur Hopwood in 1933 and means "before Consul". At the time Consul was being used as a circus name for performing chimpanzees. The Folies Bergère of 1903 in Paris had a popular performing chimpanzee named Consul, and so did the Belle Vue Zoo in Manchester, England, in 1894. On the latter's death in that year Ben Brierley wrote a commemorative poem wondering where the "Missing Link" between chimpanzees and men was.

Hopwood in 1931 had discovered the fossils of three individuals while expeditioning with Louis Leakey in the vicinity of Lake Victoria. The Consul that he selected to use in the name was neither of the ones mentioned above, but another located in the London Zoo. Consul is being used Linnaean-style to symbolize the chimpanzee. Proconsul is therefore "ancestral to the Chimpanzee" in Hopwood's words. He also added africanus as the species name. It was the only one known at the time.

Other fossils discovered later were initially classified as africanus and subsequently reclassified; that is, the total pool of fossils originally considered *africanus* was "split" and the fragments "lumped" with other finds to create a new species. For example, Mary Leakey's famous find of 1948 began as *africanus* and was split from it to be lumped with Thomas Whitworth's finds of 1951 as *heseloni* by Alan Walker in 1993. This process creates some confusion for the public, which is told that *africanus* became *heseloni*. The finds from Koru and Songhor are still considered *africanus*. Four species are still defined even though many fossils have jumped species.

Restoration

The family of **Proconsulidae** was first proposed by Louis Leakey in 1962, eleven years after he and Wilfrid Le Gros Clark had defined *africanus*, *nyanzae* and *major*. It was not immediately accepted but ultimately prevailed.

The history of hominoid classification in the second half of the 20th century is sufficiently complex to warrant a few books itself. Most of the palaeoanthropologists have changed their minds at least once as new fossils have come to light and new observations have made, and will probably continue to do so. The classifications found in the literature of one decade are not generally the same as those of another. For example, in 1987 Peter Andrews and Lawrence Martin, established palaeontologists, took the point of view that Proconsul is not a Hominoid, but is a sister taxon to it.

Chapter- 3

# Prehistoric Monkeys

## Antilles monkey

| Antilles monkeys<br>Fossil range: Miocene-Pleistocene | |
|---|---|
| **Conservation status** | |
| Extinct | |
| **Scientific classification** | |
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Mammalia |
| Order: | Primates |
| Suborder: | Haplorrhini |
| Family: | Pitheciidae |
| Subfamily: | Callicebinae<br>Pocock, 1925 |
| Tribe: | **†Xenotrichini**<br>MacPhee & Horovitz (2004) |
| **Species** | |
| †*Xenothrix mcgregori*<br>†*Paralouatta varonai*<br>†*Paralouatta marianae*<br>†*Antillothrix bernensis* | |

The **Antilles monkeys** (*Xenotrichini*) are a tribe of extinct primates, which lived on the Greater Antilles as recently as the 16th century.

These Caribbean islands no longer contain endemic primates, although the most recently discovered species, the Hispaniola Monkey, was reported to have lived on Hispaniola

until the settlement by the Europeans. The relationship of these species is supported by details in the formation of the skull and the lower jaw, such as a reduction in the number of teeth.

The exact timing and causes of extinction are not well known and their relationship and placement in the parvorder of the New World monkeys is unsure. Originally they were thought to be closely related to the night monkeys, but more recent research as placed them in Callicebinae subfamily, containing the titi monkeys.

So far, four species of Antilles monkeys are known:

- Jamaican Monkey (*Xenothrix mcgregori*), the oldest known type, from Jamaica.
- Cuban Monkeys (*Paralouatta varonai* and *P. marianae*), the largest representatives of this group, from Cuba.
- Hispaniola Monkey (*Antillothrix bernensis*), found in Haiti and the Dominican Republic.

# Biretia

| **Biretia**<br>**Fossil range: Late Eocene** | |
|---|---|
| **Scientific classification** | |
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Mammalia |
| Order: | Primates |
| Suborder: | Haplorrhini |
| Infraorder: | Simiiformes (Anthropoidea) |
| Parvorder: | Catarrhini |
| Family: | †Eosimiidae |
| Genus: | ***†Biretia*** |
| **Species** | |

- *†Biretia piveteaui*
- *†Biretia fayumensis*
- *†Biretia megalopsis*

***Biretia*** is an extinct genus of Old World monkey, of the extinct family Eosimiidae. Fossils are found from Late Eocene strata of Egypt.

The first discovery of *Biretia* was a single tooth at the Bir el Ater site. Aged at approximately 37 mya Original species found was *Biretia piveteaui* found in 1988. Recently however two new species have been classified, *B. fayumensis* and *B. megalopsis* both in 2005. Discovered in Birket Qarun Locality 2 (BQ-2) located about 60 mi south of Cairo in Egypt's Fayum depression. A very small anthropoid it only weighed around 280 to possibly 380 grams. Fragments from the jaw suggest it had had very large eyes in proportion to its body size which would suggest that it was nocturnal. "Biretia is unique among early anthropoids in exhibiting evidence for nocturnality, but derived dental features shared with younger parapithecids draw this genus, and possibly 45-million-year-old Algeripithecus (Strepsirrhini), into a morphologically and behaviorally diverse parapithecoid clade of great antiquity."

The smallest of the species *B. fayumensis* had an estimated weight of 273 g, while the largest of *Biretia*, the *B. megalopsis* had a weight of about 376g. Adaptations of the skull of *B. megalopsis* are easily comparable to the modern *Tarsius* a small, modern Asian primate whose nocturnal insectivorous lifestyle. We infer this possibility of a nocturnal lifestyle from *B. megalopsis'* truncated molar root, which was so in order to made room for the large eye socket typical of a nocturnal primate. The large eye structure and similarity to the modern *Tarsius* also suggests that it has lost its tapetum lucidum. Thus, *B. megalopsis* demonstrates itself as being the oldest known nocturnal primate.

The genus is otherwise known only from a handful of fossil fragments, including a few maxilla fragments and some teeth and teeth fragments from the different species.

Fossil fragments The fossil fragments found for *B. fayumensis*, new species, include a composite of isolated P2 (DPC 21759C), P3(DPC 21249E), P4 (DPC 21371A), M1 (DPC 21250D), and M2 (DPC 21539E. For *B. megalopsis*, new species, maxilla with M1 through M3 (DPC 21358F).

# Hispaniola Monkey

| Hispaniola Monkey<br>Fossil range: Quaternary |
|---|

| Scientific classification | |
|---|---|
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Mammalia |
| Order: | Primates |
| Family: | Pitheciidae |
| Subfamily: | Callicebinae |
| Tribe: | †Xenotrichini |
| Genus: | †***Antillothrix*** |
| Species: | †***A. bernensis*** |

| Binomial name |
|---|
| †***Antillothrix bernensis***<br>Rímoli, 1977 |

| Synonyms |
|---|
| *Saimiri bernensis* |

The **Hispaniola Monkey** (*Antillothrix bernensis*) is an extinct primate found on the island of Hispaniola. The species is thought to have gone extinct around the 16th century. The exact timing and cause of the extinction are unclear, but it is likely related to the settlement of Hispaniola by the Europeans in 1492 after discovery by Christopher Columbus.

At first, the Hispaniola Monkey was thought to be a close relative of the Capuchin monkeys, but later investigation showed that the similarities were due to convergent development.

Horovitz and MacPhee developed the hypothesis, first proposed by MacPhee et al., that all the Antillean monkeys (the others being the two Cuban monkey species of genus *Paralouatta* and *Xenothrix mcgregori* of Jamaica) belonged to a monophyletic group linked most closely with modern Callicebus. They later assigned the Antillean monkeys to the tribe Xenotrichini – the sister group of the tribe Callicebini with extensive anatomical comparisons and by extending their parsimony analysis using PAUP*. They maintained that the monophyly of the Antillean monkeys was still supported in the most parsimonious trees, but in slightly less parsimonious trees, *Aotus* appeared to be linked with *Xenothrix*.

### *Recent Discoveries*

In July 2009, Walter Pickel and Lindsey Pickel (cave divers for the ADM Exploration Foundation) found a *Antillothrix bernensis* skull. The skull, long bones and ribs was recovered by Walter Pickel and Curt Bowen (of the ADM Foundation) in October 2009 under the supervision of the Dominican Republic and Alfred L. Rosenberger (Brooklyn College).

# Jamaican Monkey

| **Jamaican Monkey**<br>**Fossil range: Pleistocene-Holocene** |
|---|
| **Conservation status** |


Extinct (IUCN 3.1)

| **Scientific classification** | |
|---|---|
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Mammalia |
| Order: | Primates |
| Family: | Pitheciidae |
| Subfamily: | Callicebinae |
| Tribe: | †Xenotrichini |
| Genus: | †***Xenothrix*** Williams & Koopman, 1952 |
| Species: | †***X. mcgregori*** |

| **Binomial name** |
|---|
| †***Xenothrix mcgregori*** |

The **Jamaican Monkey** (*Xenothrix mcgregori*) is an extinct species of monkey first uncovered at Long Mile Cave in Jamaica by Harold Anthony in 1919. Anthony is responsible for many species descriptions of Caribbean taxa during this period and his field notes record the discovery of the monkey material:

"January 17 – Spent all day digging in the long mile cave and secured some good bones. The most important find was the lower jaw and femur of a small monkey, found in the

yellow limestone detritus. It was not associated with the human remains but not so far from them that the animal must not be strongly suspected as an introduced species. It was deeper than any of the human bones by at least 10" to 1'…" (reproduced in Williams and Koopman, 1952)

The eventual species description was not completed until 1952 when two graduate students, Ernest Williams and Karl Koopman, found the associated femur and mandibular fragment forgotten in a drawer at the American Museum of Natural History. They remained circumspect in placing this primate taxonomically as it had shared characteristics with a number of platyrrhine taxa.

## Analysis

The small mandible has a dental formula of 2 incisors, 1 canine, 3 premolars and 2 molars – a departure from the vast majority of living platyrrhines, with the notable exception of the callitrichines. It is significantly larger than the living callitrichines, and work by Rosenberger has largely eliminated the possibility that these taxa share a close phylogenetic relationship. Rosenberger suggested that the absence of the third molar in *Xenothrix* was not homologous with this character state in callitrichines. He based his assessment on the length of the molars relative to the molar row, and the inferred retention of hypocones on M1-2, which have been greatly reduced in the marmosets and tamarins. He further suggested that *Xenothrix* shared a close phylogenetic affinity with Callicebus or Aotus. His conclusions were tentative due to the fragmentary nature of the material.

The postcranial remains discovered by Anthony in the 1920's were eventually described by MacPhee and Fleagle who attributed the femur, os coxae, and tibia to the order Primates. MacPhee and Fleagle stated that the primate postcrania bore little resemblance to modern forms, but they interpreted the femur as being indicative of slow climbing. Interestingly, the femur also shares some similarities with *Potos flavus*, the kinkajou. They provisionally accepted Hershkovitz's family Xenotrichidae until further analysis could fully elucidate the relationships of *Xenothrix*.

## Further research

In the 1990s, several expeditions to Jamaican cave sites resulted in the recovery of additional cranial and postcranial material attributed to *Xenothrix*, including a partial lower face containing the palate with left and right P4-M2, most of the maxilla and parts of the sphenoid. This discovery confirmed that the dental formula of this taxon is 2.1.3.2. With the new partial face, Horovitz and MacPhee were able to further develop the hypothesis, first proposed by MacPhee et al., that all the Antillean monkeys (the others being the two Cuban monkey species of genus *Paralouatta* and *Antillothrix bernensis* of Hispaniola) belonged to a monophyletic group linked most closely with modern *Callicebus*.

Rosenberger has objected to this hypothesis and has suggested that *Xenothrix* was a Jamaican owl monkey, thus modifying his earlier view. He based his conclusions on the fairly large orbit size as inferred from the preserved orbital rim, large inferior orbital fissure, and the large I1 alveolus as compared to the I2 alveolus. These characters are shared with *Aotus*. MacPhee and Horovitz tested this alternative phylogeny with extensive anatomical comparisons and by extending their parsimony analysis using PAUP*. They maintained that the monophyly of the Antillean monkeys was still supported in the most parsimonious trees, but in slightly less parsimonious trees, *Aotus* does appear to be linked with *Xenothrix*. MacPhee and Horovitz assigned the Antillean monkeys to the tribe Xenotrichini – the sister group of the tribe Callicebini.

## Chapter- 4

# Tarsier

**Tarsiers**
**Fossil range: 45–0 Ma**
**Late Eocene to Recent**

Philippine Tarsier (*Tarsius syrichta*)

| Scientific classification | |
|---|---|
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Mammalia |
| Order: | Primates |
| Suborder: | Haplorrhini |
| Infraorder: | Tarsiiformes |
| Family: | **Tarsiidae**<br>Gray, 1825 |
| Genus: | ***Tarsius***<br>Storr, 1780 |

| Type species |
|---|
| *Tarsius tarsier*<br>Erxleben, 1777 |

| Species |
|---|

- *Tarsius bancanus*
- *Tarsius dentatus*
- *Tarsius lariang*
- *Tarsius pelengensis*
- *Tarsius pumilus*
- *Tarsius sangirensis*
- *Tarsius syrichta*
- *Tarsius tarsier*
- *Tarsius tumpara*

| Synonyms |
|---|

- *Cephalopachus* Swainson, 1835
- *Hypsicebus* Lesson, 1840
- *Macrotarsus* Link, 1795
- *Rabienus* Gray, 1821

**Tarsiers** are haplorrhine primates of the genus ***Tarsius***, a genus in the family **Tarsiidae**, which is itself the lone extant family within the infraorder Tarsiiformes. Although the group was once more widespread, all the species living today are found in the islands of Southeast Asia.

## *Evolutionary history*

### Fossil record

Fossils of tarsiiform primates are found in Asia, Europe, and North America, and there are disputed fossils from Africa, but extant tarsiers are restricted to several Southeast

Asian islands including the Philippines, Sulawesi, Borneo, and Sumatra. The fossil record indicates that their dentition has not changed much, except in size, in the past 45 million years.

Within the family Tarsiidae, there are two extinct genera, *Xanthorhysis* and *Afrotarsius*. However, the placement of *Afrotarsius* is not certain, and is sometimes listed in its own family, Afrotarsiidae, within the infraorder Tarsiiformes.

Two fossil species of with in the genus *Tarsius* are known from the fossil record. *Tarsius eocaenus* is known from the Middle Eocene in China while *Tarsius thailandicus* lived during the Early Miocene in northwestern Thailand. The genus *Tarsius* has a longer fossil record than any other primate genus, but the assignment of the Eocene and Miocene fossils to the genus is questionable.

## Classification

The phylogenetic position of extant tarsiers within the order Primates has been debated for much of the past century, and tarsiers have alternately been classified with strepsirrhine primates in the suborder Prosimii, or as the sister group to the simians (=Anthropoidea) in the infraorder Haplorrhini. Analysis of SINE insertions, a type of macromutation to the DNA, is argued to offer very persuasive evidence for the monophyly of Haplorrhini, where other lines of evidence, such as DNA sequence data, remain ambiguous. Thus, some systematists argue that the debate is conclusively settled in favor of a monophyletic Haplorrhini. In common with simians, tarsiers have a mutation in the L-gulonolactone oxidase (GULO) gene which confers need for vitamin C in the diet. Since the strepsirrhines do not have this mutation and have retained the ability to make vitamin C, the genetic trait which confers the need for it in the diet would tend to place tarsiers with haplorrhines.

At a lower phylogenetic level, it has been indicated that the tarsiers, currently all placed in the genus *Tarsius*, actually should be placed in two (a Sulawesi and a Philippine-Western group) or three separate genera (a Sulawesi, Philippine and Western group). Species level taxonomy is complex, with morphology often being of limited use compared to vocalizations. Several "vocal morphs" may represent undescribed taxa, taxonomically separable from *T. tarsier* (=*spectrum*) (such as Minahasa and a tarsier from the Togian Islands), and many others from Sulawesi and surrounding islands (Shekelle & Leksono 2004). This may also be the case for a number of poorly known isolated Philippine populations (such as the Basilan, Leyte and Dinagat populations of the *T. syrichta* group). Further confusion exists over the validity of certain names. Among others, the widely used *T. dianae* has been shown to be a junior synonym of *T. dentatus*, and comparably *T. spectrum* is now considered a junior synonym of *T. tarsier*.

- Infraorder Tarsiiformes
  - **Family Tarsiidae**: tarsiers
    - **Genus *Tarsius***
      - *T. syrichta* group

        - Western or Horsfield's Tarsier, *Tarsius bancanus*
        - Philippine Tarsier, *Tarsius syrichta*
    - *T. tarsier* group
        - Dian's Tarsier, *Tarsius dentatus*
        - Lariang Tarsier, *Tarsius lariang*
        - Peleng Tarsier, *Tarsius pelengensis*
        - Sangihe Tarsier, *Tarsius sangirensis*
        - Spectral Tarsier, *Tarsius tarsier*
        - Siau Island Tarsier, *Tarsius tumpara*
        - Pygmy Tarsier, *Tarsius pumilus*
        - Wallace's Tarsier, *Tarsius wallacei*

In 2010, Colin Groves and Myron Shekelle suggested splitting the genus *Tarsius* into three genera, the Philippine tarsiers (genus *Carlito*), the western tarsiers (genus *Cephalopachus*), and the eastern tarsiers (genus *Tarsius*). This was based on differences in dentition, eye size, limb and hand length, tail tufts, tail sitting pads, the number of mammae, chromosome count, socioecology, vocalizations, and distribution. Their classification, which includes several newly described species, is as follows:

- Infraorder Tarsiiformes
    - **Family Tarsiidae**: tarsiers
        - **Genus *Carlito***
            - Philippine Tarsier, *Carlito syrichta*
                - *C. s. syrichta*
                - *C. s. fraterculus*
                - *C. s. carbonarius*
        - **Genus *Cephalopachus***
            - Western Tarsier, *Cephalopachus bancanus*
                - *C. b. bancanus*
                - *C. b. natunensis*
                - *C. b. boreanus*
                - *C. b. saltator*
        - **Genus *Tarsius***
            - Dian's Tarsier, *T. dentatus*
            - Lariang Tarsier, *T. lariang*
            - Peleng Tarsier, *T. pelengensis*
            - Sangihe Tarsier, *T. sangirensis*
            - Spectral Tarsier, *T. tarsier*
            - Siau Island Tarsier, *T. tumpara*
            - Pygmy Tarsier, *T. pumilus*
            - *T. wallacei*
            - *T. fuscus*
            - *T.* sp. 1
            - *T.* sp. 2

## *Anatomy and physiology*

Tarsier tree climbing

Tarsiers are small animals with enormous eyes; each eyeball is approximately 16 mm in diameter and is as large as their entire brain. Tarsiers also have very long hind limbs. In fact, their feet have extremely elongated tarsus bones, from which the animals get their name. The head and body range from 10 to 15 cm in length, but the hind limbs are about twice this long (including the feet), and they also have a slender tail from 20 to 25 cm long. Their fingers are also elongated, with the third finger being about the same length as the upper arm. Most of the digits have nails, but the second and third toes of the hind feet bear claws instead, which are used for grooming. Tarsiers have very soft, velvety fur, which is generally buff, beige, or ochre in color.

Unlike other prosimians, tarsiers lack any toothcomb, and their dental formula is also unique: $\frac{2.1.3.3}{1.1.3.3}$

### Vision

All tarsier species are nocturnal in their habits, but like many nocturnal organisms some individuals may show more or less activity during the daytime. Unlike many nocturnal vertebrates, however, tarsiers lack a light-reflecting area (tapetum lucidum) of the eye and have a fovea.

The tarsier's brain is different from other primates in terms of the arrangement of the connections between the two eyes and the lateral geniculate nucleus, which is the main region of the thalamus that receives visual information. The sequence of cellular layers receiving information from the ipsilateral (same side of the head) and contralateral (opposite side of the head) eyes in the lateral geniculate nucleus distinguishes tarsiers from lemurs, lorises, and monkeys, which are all similar in this respect. Some neuroscientists suggested that "this apparent difference distinguishes tarsiers from all other primates, reinforcing the view that they arose in an early, independent line of primate evolution."

## *Behavior*

Tarsiers are the only extant entirely carnivorous primates: they are primarily insectivorous, and catch insects by jumping at them. They are also known to prey on birds, snakes, lizards, and bats. As they jump from tree to tree, tarsiers can even catch birds in motion.

Gestation takes about six months, and tarsiers give birth to single offspring. Young tarsiers are born furred, and with open eyes, and are able to climb within a day of birth. They reach sexual maturity by the end of their second year. Sociality and mating system varies, with tarsiers from Sulawesi living in small family groups, while Philippine and Western tarsiers are reported to sleep and forage alone.

## *Conservation*

Tarsiers have never formed successful breeding colonies in captivity. This may be partly due to their special feeding requirements.

One site on the Philippine island of Bohol is having some success restoring tarsier populations. The Philippine Tarsier Foundation has developed a large semi-wild enclosure that uses lights to attract the nocturnal insects that make up the tarsier's diet.

The 2008 described Siau Island Tarsier is regarded as Critically Endangered and was listed among The World's 25 Most Endangered Primates by Conservation International and the IUCN/SCC Primate Specialist Group in 2008. Malaysian government protects

tarsiers by listing them in the Totally Protected Animals of Sarawak, the Malaysian state in Borneo where they are commonly found.

Chapter- 5

# Eocene Primates

# Anthrasimias

| *Anthrasimias*<br>**Fossil range: 55 Ma** | |
|---|---|
| **Scientific classification** | |
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Mammalia |
| Order: | Primates |
| Suborder: | Haplorrhini |
| Infraorder: | Simiiformes<br>(Anthropoidea) |
| Parvorder: | Catarrhini |
| Family: | †Eosimiidae |
| Genus: | ***†Anthrasimias***<br>Bajpai *et al.*, 2008 |
| Species: | ***†A. gujaratensis***<br>Bajpai *et al.*, 2008 |
| **Binomial name** | |
| ***†Anthrasimias gujaratensis*** | |

***Anthrasimias*** *gujaratensis* was a species of primate first found in Gujarat, India in 2008. *Anthrasimias* is believed to have lived about 55 million years ago, during the early Eocene. Weight 75 grams

*Anthrasimias* is the oldest known member of its family; the next oldest, *Eosimias*, lived about 45 million years ago in China.

# Cantius frugivorus

| *Cantius frugivorus*<br>**Fossil range: Eocene** | |
|---|---|
| **Scientific classification** | |
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Mammalia |
| Order: | Primates |
| Family: | Nothactidae |
| Subfamily: | Nothactinae |
| Genus: | *Cantius* |
| Subgenus: | *Neocantius* |
| Species: | ***C. frugivorus*** |
| **Binomial name** | |
| ***Cantius frugivorus***<br>(Cope, 1875) | |

***Cantius frugivorus*** was a small adapiformes primate that lived in the early Eocene in North America. It is more advanced than the plesiadapiformes.

## Morphology

This species had a dental formula of 2:1:4:3 on both the upper and lower jaw. The incisors are small and vertical in *Cantius frugivorus*, and the canines are prominent. The mandibular symphysis is unfused and this was most likely a diurnal species. *Cantius frugivorus* had an average body mass of around 2.8 kilograms.

## Diet

Based on the dental morphology of *Cantius frugivorus*, it most likely had a frugivorous diet.

## Locomotion

The limb bones of *Cantius frugivorus* suggest it moved by arboreal quadrupedalism and leaping.

# Necrolemur

| *Necrolemur*<br>**Fossil range: Middle Eocene–Late Eocene** |
|---|
|  |
| Restoration |
| **Conservation status** |
| Fossil |
| **Scientific classification** |

| | |
|---|---|
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Mammalia |
| Order: | Primates |
| Suborder: | Haplorrhini |
| Family: | †Omomyidae |
| Genus: | ***†Necrolemur***<br>Filhol, 1873 |

**Species**

- †?*N. antiquus*
- †*N. zitteli*

***Necrolemur*** ("grave lemur") is an extinct genus of primate.

The 25 centimetres (9.8 in) long creature closely resembled a tarsier; it was a nocturnal hunter with very large eyes and ears. *Necrolemur* had sharp teeth, which it probably used to bite through insect armor. Like modern tarsiers, it also possessed long fingers and toes, and a lengthy, balancing, tail. It was also characterised by a short face, a narrow gap between the eyes, a tubular ectotympanic and a relatively large brain.

Fossils of this animal have been found in western Europe.

# Darwinius

| *Darwinius* |
| --- |
| **Fossil range: Eocene, 47 Ma** |

Main slab of the *Darwinius masillae* holotype fossil (specimen PMO 214.214)

| **Scientific classification** | |
| --- | --- |
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Mammalia |
| Order: | Primates |
| Family: | Notharctidae |

| | |
|---|---|
| Subfamily: | Cercamoniinae |
| Genus: | ***Darwinius***<br>Franzen *et al.*, 2009 |
| Species: | ***D. masillae*** |

**Binomial name**

***Darwinius masillae***
Franzen *et al.*, 2009

***Darwinius*** is a genus of Adapiformes, a group of basal primates from the Eocene epoch. Its only known species is *Darwinius masillae*, dated to 47 million years ago (Lutetian stage) based on dating of the fossil site.

The only known fossil, dubbed **Ida**, was discovered in 1983 at the Messel pit. The fossil, divided into a slab and partial counterslab after the amateur excavation and sold separately, was not reassembled until 2007. The fossil is of a juvenile female, approximately 58 cm (23 in) overall length, with the head and body length excluding the tail being about 24 cm (9.4 in). It is estimated that Ida died at about 80–85% of her projected adult body and limb length.

The genus *Darwinius* was named in commemoration of the bicentenary of the birth of Charles Darwin, and the species name *masillae* honors Messel where the specimen was found. The creature appeared superficially similar to a modern lemur.

The authors of the paper describing *Darwinius* classified it as a member of the primate family Notharctidae, subfamily Cercamoniinae, suggesting that it has the status of a significant transitional form (a "link") between the prosimian and simian ("anthropoid") primate lineages. Others have disagreed with this placement.

Concerns have been raised about the claims made about the fossil's relative importance, and the publicising of the fossil before adequate information was available for scrutiny by the academic community.

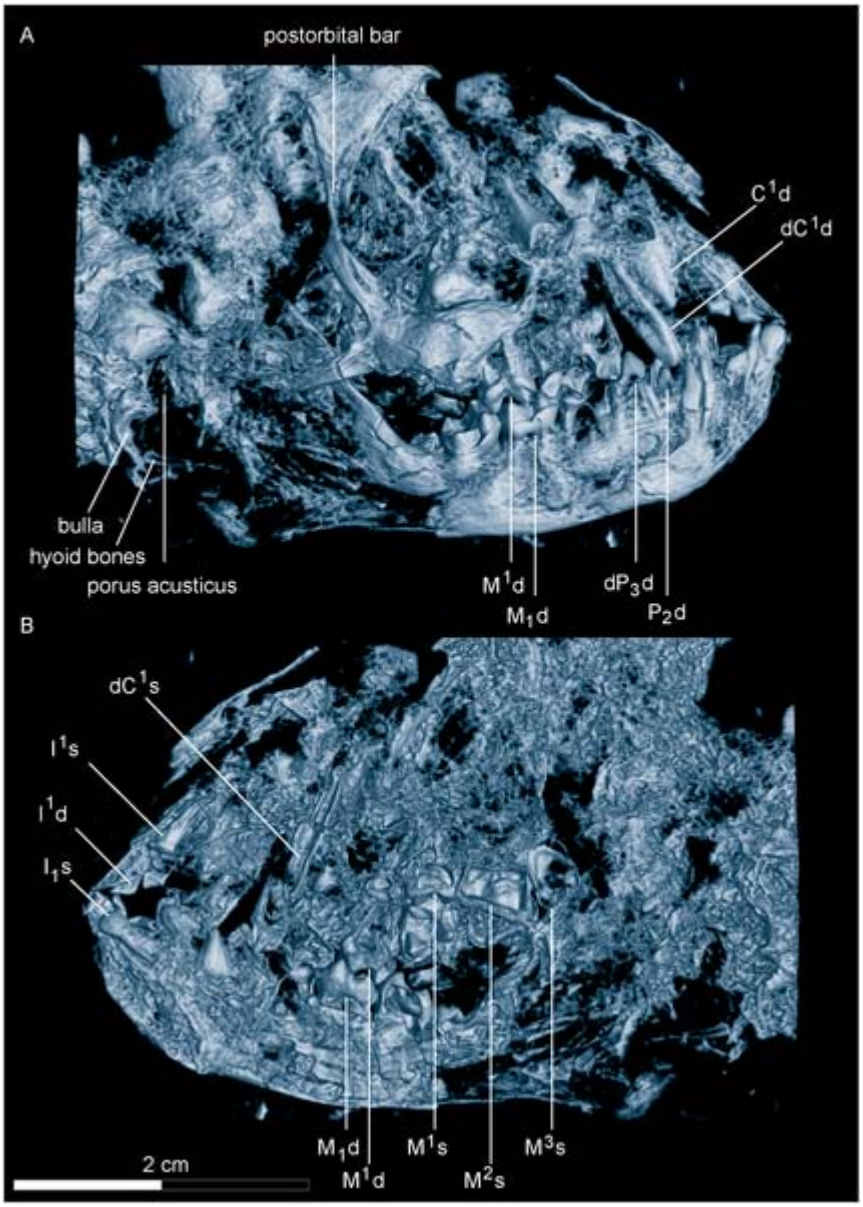
## Taxonomy

Franzen et al. (2009) place the *Darwinius* genus in the Cercamoniinae subfamily of the Notharctidae family within the extinct Adapiformes suborder of early primates.

*Darwinius masillae* is the third primate species to be discovered at the Messel locality that belongs to the cercamoniine adapiforms, in addition to *Europolemur koenigswaldi* and *Europolemur kelleri*. *Darwinius masillae* is similar but not directly related to *Godinotia neglecta* from Geiseltal.

The adapiforms are early primates which are known only from the fossil record, and it is unclear whether they form a suborder proper, or a paraphyletic grouping. They are usually grouped under Strepsirrhini—including Lemurs, Aye-ayes and Lorisiformes—

and as such would not be ancestral to Haplorrhini which includes tarsiers and simians. Simians are usually called anthropoids, and while this name can be confusing, the paper uses the term anthropoids, as does associated publicity material. Simians (anthropoids) include monkeys and apes, which in turn includes humans.




CT image of the skull of *Darwinius*

Franzen et al. in their 2009 paper place *Darwinius* in the "Adapoidea group of early primates representative of early haplorhine diversification". This means that according to these authors, the adapiforms would not be entirely within the Strepsirrhini lineage as hitherto assumed but would qualify as a transitional fossil (a "missing link") between Strepsirrhini and Haplorrhini, and so could be ancestral to humans. They also suggest that tarsiers have been misplaced in the Haplorrhini, and should be considered Strepsirrhini.

To support this view, they show that as many as 6 morphological traits found in "Darwinius" are derived characters present only in the Haplorrhini lineage but absent in the Strepsirrhini lineage, which they interpret as synapomorphies. These include, among others, a cranium with a short rostrum, deep mandibular ramus, loss of all grooming claws. They note "that *Darwinius masillae*, and adapoids contemporary with early tarsioids, could represent a stem group from which later anthropoid primates evolved, but we are not advocating this here, nor do we consider either *Darwinius* or adapoids to be anthropoids."

## Concerns over cladistic analysis

Paleontologists have expressed concern that the cladistic analysis compared only 30 traits, when standard practice is to analyze 200 to 400 traits and to include fossils such as anthropoids from Egypt and the primate genus *Eosimias* which were not included in the analysis. This contrasts with the motive openly stated by the authors, which was to list 30 anatomical and morphological characteristics "commonly used" to distinguish extant strepsirrhine and haplorrhine primates. Paleontologist Richard Kay of Duke University thought the data could have been cherry-picked, and paleontologist Callum Ross of the University of Chicago considered the claim that *Darwinius* should be classified as haplorhine was "unsupportable in light of modern methods of classification." The opinion of Chris Beard, curator of vertebrate paleontology at the Carnegie Museum of Natural History, was that *Darwinius* was not a "missing link" between anthropoids and more primitive primates, but that further study of this remarkably complete specimen would be very informative and could reveal relationships amongst "the earliest and least human-like of all known primates, the Eocene adapiforms." In an interview published on 27 May, Jørn Hurum stated that he had an open mind about the possibility that the fossil might turn out to be a lemur, and that a paper on systematics to be published within about a year would mainly focus on the partial counterslab containing the inner ear and the foot bones.

Most experts hold that the higher primates (simians) evolved from Tarsiidae, branching off the Strepsirrhini before the appearance of the Adapiformes. A smaller group agrees with Franzen et al. that the higher primates descend from Adapiformes (Adapoidea). The view of paleontologist Tim White is that *Darwinius* is unlikely to end the argument.

Philip D. Gingerich states that the seven superfamilies of Primates are commonly associated in the higher taxonomic groupings of suborders Anthropoidea and Prosimii as an alternative to Haplorhini and Strepsirrhini, depending on the position of Adapoidea and Tarsioidea. He puts forward a phylogeny in which the higher primates evolved from *Darwinius*, which he groups with other Adapoidea. He shows the Adapoidea together the Tarsioidea as representing early diversification of the suborder Haplorhini, and shows the Strepsirrhini as having branched off directly from the earliest primates. The Revealing the Link website uses this taxonomic grouping, and states that *Darwinii* is from an early group of primates, just prior to diversification into the anthropoids (monkeys, apes and humans) and the prosimians (lemurs, lorises and tarsiers).

Erik Seiffert and colleagues at Stony Brook University argue that *Darwinius* is on the branch towards the Strepsirrhini, and is not a 'missing link' in the evolution of the Anthropoidea. A phylogenetic analysis of 360 morphological characters in 117 extinct and modern primates places *Darwinius* in a now-extinct group of strepsirrhines, along with a newly discovered 37-million-year-old Egyptian primate, *Afradapis*. Seiffert believes that characteristics that appeared to show a relationship to haplorrhines are due to convergent evolution, and has said that "the PR hype surrounding the *Darwinius* description was very confusing."

## *Type specimen*

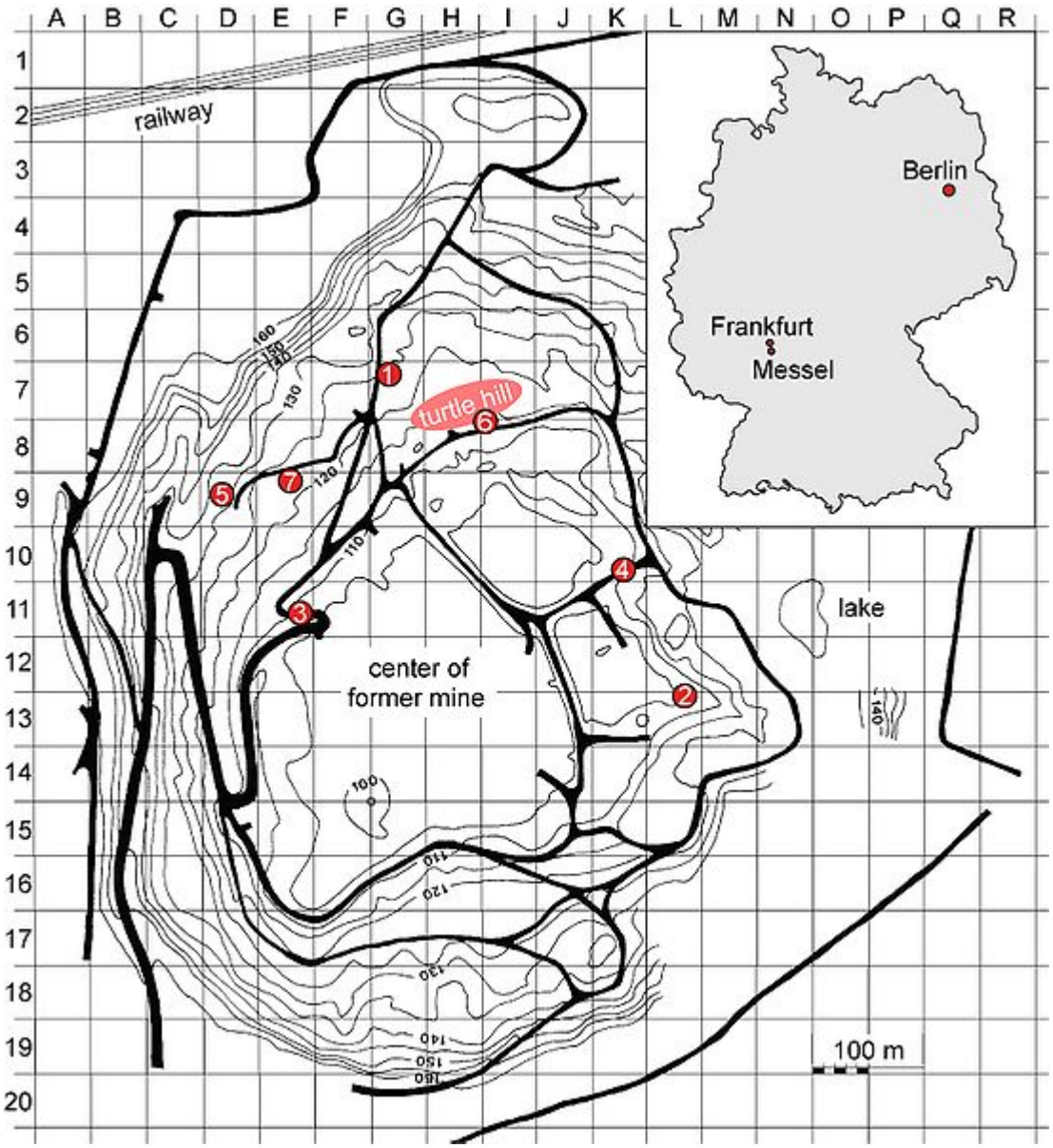

Counter-slab of the *Darwinius masillae* holotype fossil (specimen WDC-MG-210 reversed for comparison). Parts 1 and 2 (enclosed in dashed lines) are genuine; remainder of plate B was fabricated during preparation

The type specimen is a 95%-complete fossil, missing only its left rear leg. It has been named Ida after the daughter of Jørn Hurum, the Norwegian vertebrate paleontologist from the Natural History Museum, University of Oslo, who secured one section of the fossil from an anonymous owner, and led the research. In addition to the bones, remains of Ida's soft tissue and fur outline are present, along with remnants of her last meal of fruit and leaves. The animal is about 58 cm (23 in) from nose to tail, or roughly the size of a small, long-tailed cat.

The lemur-like skeleton of the fossil features primate characteristics of grasping hands with opposable thumbs and nails instead of claws. These would have provided a "precision grip" which, for Ida, was useful for climbing and gathering fruit. Ida also has flexible arms and relatively short limbs. The fossil is missing two anatomical features found in modern lemurs: a grooming claw on the foot and a fused row of teeth, a toothcomb, in the bottom jaw.

Digital reconstructions of Ida's teeth reveal that she has unerupted molars in her jaw, indicating by comparison with modern squirrel monkeys that she was 9–10 months old, and would have reached adulthood at 36 months. The shape of Ida's teeth provides clues as to her diet; jagged molars would have allowed her to slice food, suggesting that she was a leaf and seed eater. This is confirmed by the remarkable preservation of her gut content. Furthermore the lack of a baculum (penis bone) found in all lower primates means that the fossil was from a female. X-rays performed on Ida revealed that her right wrist was healing from a fracture, which may have contributed to her death. The scientists speculate whether she was overcome by carbon dioxide fumes while drinking from the Messel lake. Hampered by her broken wrist, she slipped into unconsciousness, was washed into the lake and sank to the bottom, where unique fossilisation conditions preserved her for 47 million years.

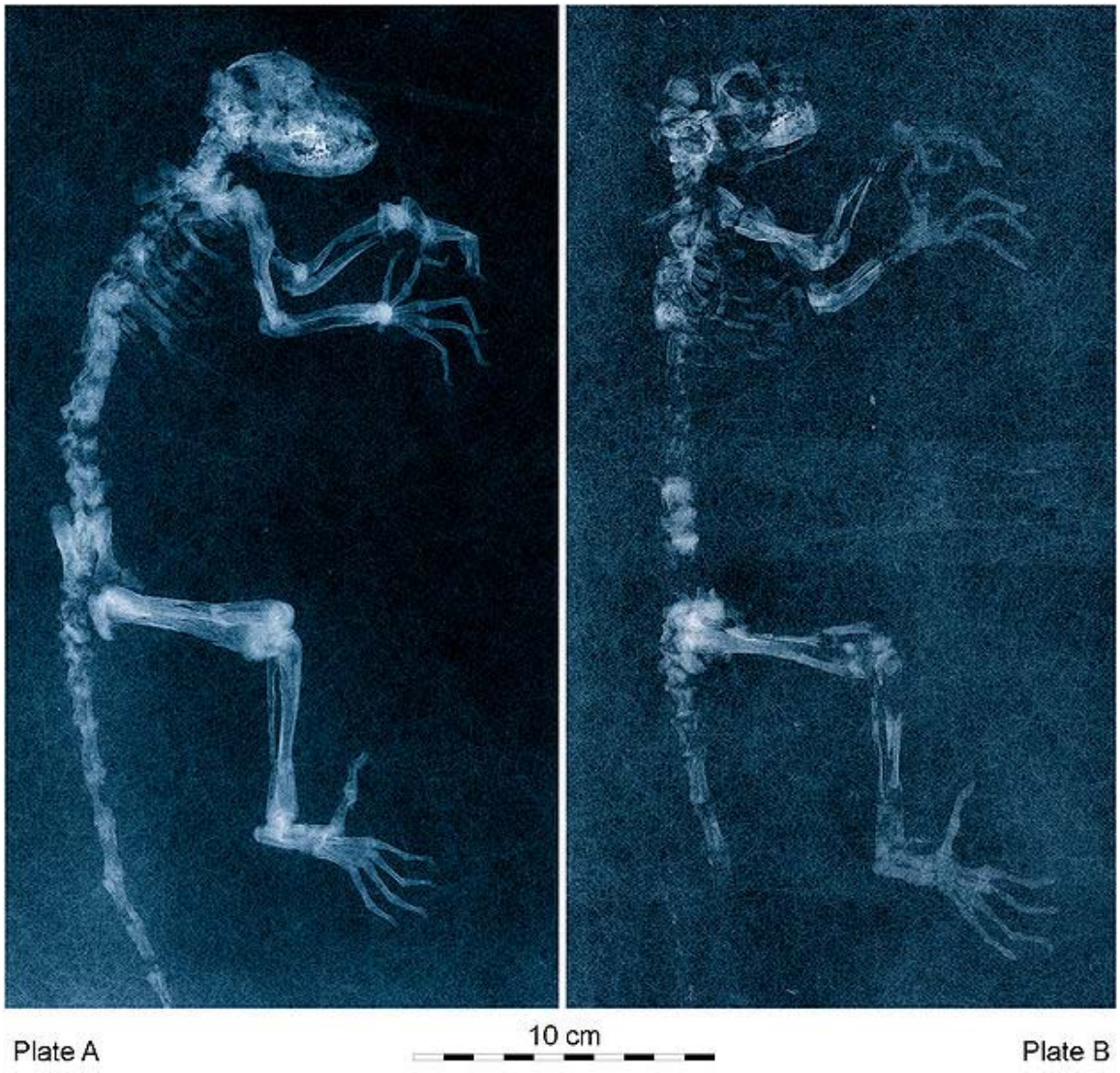
## *Discovery and acquisition*




Map showing where *Darwinius* (6) and other primates have been found in the Messel pit

The events regarding the original unearthing of the fossil are not clear, though some facts are known. It was found at the Messel pit in 1983, a disused shale quarry noted for its astonishing fossil preservation, near the village of Messel, about 35 km (22 mi) southeast of Frankfurt am Main in Germany. The fossil came as a slab and partial counter slab, and was expertly prepared by encasing each slab in resin using the transfer technique necessary to conserve Messel fossils. At some point the slab and counter slab went separate ways. The counter slab was incorporated in a composite of fabricated parts to represent a complete specimen, and arrived at a private Wyoming museum in 1991. Analysis by Jens Franzen of the Natural History Museum of Basel, Switzerland revealed

the mixed actual and faked nature of this slab. A comparison of the two slabs indicates that the forger had access to the whole fossil.




Radiographs of the *Darwinius* holotype fossil, revealing the fabricated parts of the counter-slab

The primary slab remained in Germany, in the possession of a private collector who kept it secret for twenty years before deciding to sell it anonymously via a German fossil dealer. Two German museums turned it down as too expensive, then a year later at the Hamburg Fossil and Mineral Fair in December 2006 the dealer asked Norwegian vertebrate palaeontologist Jørn Hurum, who had done some previous deals, to discuss something privately. The dealer showed Hurum three high resolution colour photographs of the fossil, and told him that the asking price was $1 million. Hurum knew that it was a primate, and according to Tudge's book "was fast concluding that the specimen he was looking at could be one of the holy grails of science — the 'missing link' from the crucial

time period." He asked for time until after Christmas to organise funding to pay for the specimen and ensure that it had been legally collected, had an export permit and would be legitimately available for study. His first choice was the Natural History Museum of Oslo, but it was beyond their means and he began to think of other museums with sponsors available. He persuaded the Oslo museum to make half the funding available, with the remainder to be paid only after X-ray scans proved conclusively that it was not a fake, a process which took several months. He put together a team including leading German experts on the Messel fossils, ensuring international ownership.

After its acquisition it was studied in secret for two years by a team of scientists lead by Hurum; who was joined by primate evolution expert Professor Philip Gingerich of the University of Michigan, and palaeontologists Jens Franzen who had studied the counter slab and Jörg Habersetzer of the Senckenberg Museum's Research Institute.

# Eosimias

| ***Eosimias*** **Fossil range: 45–40 Ma** | |
|---|---|
| **Scientific classification** | |
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Mammalia |
| Order: | Primates |
| Family: | Eosimiidae† |
| Genus: | ***Eosimias***† Beard et al., 1994 |
| **Paleospecies** | |
| *Eosimias sinensis*<br>*Eosimias centennicus*<br>*Eosimias dawsonae* | |

***Eosimias*** was a genus of early primates, first discovered and identified in 1999 from fossils collected in the Shanghuang fissure-fillings of the southern Jiangsu Province, China. It is a part of the family Eosimiidae, which includes three known species: *Eosimias sinensis*, *Eosimias centennicus*, and *Eosimias dawsonae*. It provides us with a glimpse of a primate skeleton similar to that of the common ancestor of the Haplorrhini (including all simians). The name *Eosimias* is designed to mean "dawn monkey", from Greek *eos* "dawn" and Latin *simius* "monkey".

Dating has proven this species lived from 40 to 45 million years ago in the middle Eocene. The *Eosimias* genus is unique because the presence of primitive and derived traits. It provides new insight into the phylogenetic relationships between simians and prosimians (especially the phylogenetic position of the haplorrhine prosimian tarsiers). It

can best be described as a likely tree dweller that relied on a steady diet of insects and nectar. It was probably a nocturnal, solitary creature.

Most eosimiid species are documented by unique or fragmentary specimens. This, as well as the strong belief that simians originated in Africa has made it difficult for many to accept the idea that Asia played a role in early primate evolution. Although some continue to challenge the anthropoid resemblances found in Eosiimidae, there is an extensive amount of anatomical evidence collected over the past decade to substantiate its anthropoid status.

## Eosimias sinensis

***Eosimias sinensis*** (Chinese: 中华曙猿, "dawn monkey of China") was first discovered in China in 1994 by Christopher Beard. It was found in a mountain near Liyang City, Jiangsu province, China. It is the earliest catarrhine that has been discovered.

The species is believed to have lived 45 million years before present, in the Eocene epoch. *E. sinensis* was tiny, as small as the smallest monkey presently, the Pygmy Marmoset (*Cebuella pygmaea*) of South America, and could fit in the palm of a human's hand. Its teeth are considered more primitive than those of early higher primates known from Africa, including *Algeripithecus*. Due to its highly primitive nature, some paleontologists consider *E. sinensis* to be evidence that higher primates may have originated in Asia rather than Africa.

Christopher Beard was the lead member of the team that discovered *Eosimias sinensis* in 1994. Beard recovered a right mandible, cataloged as IVPP V10591, which preserved P4-M2 and roots or alveoli for C1, P2-3, and M3. Although it retains primitive characters such as a small body size (mean estimates range from 67–137 grams (2.4–4.8 oz)) and an unfused mandibular symphysis, it appears to be a primitive simian based on its dental characteristics, including a lower dental formula of 2-1-3-3.

## Eosimias centennicus

*Eosimias centennicus* was found in 1995 while doing fieldwork in the Yuanqu Basin of the southern Shanxi Province in China. Among these recovered fossils is the first complete lower dentition of *Eosimias*, catalogued as IVPP V11000. All anatomical information yielded from these fossils confirms the anthropoid-like traits found in *E. sinensis*. Biostratigraphic evidence also suggests these fossils are younger than *E. sinensis*, which is consistent with the anatomy of eosiimids because the dentition of *E. centennicus* is slightly more derived than that of *E. sinensis*. This species was also found to be a very tiny primate, with mean estimates of body mass ranging from 91 to 179 grams (3.2 to 6.3 oz). *E. sinesis* was originally described on the basis of fragmentary fossils, but with the discovery of *E. centennicus* and a complete lower dentition, *Eosimias* can more definitively be described as an early anthropoid.

## Eosimias dawsonae

*Eosimias dawsonae* is the newest of the *Eosimias* species. It is categorized by the type specimen IVPP V11999, which includes a left dentary fragment and roots of the alveoli. It was collected by Christopher Beard in 1995. Analysis of these remains has led to the conclusion it was the largest of the known species of *Eosimias*, yielding a body mass ranging from 107 to 276 grams (3.8 to 9.7 oz). Stratigraphic evidence also shows *E. dawsonae* is older than *E. centennicus*.

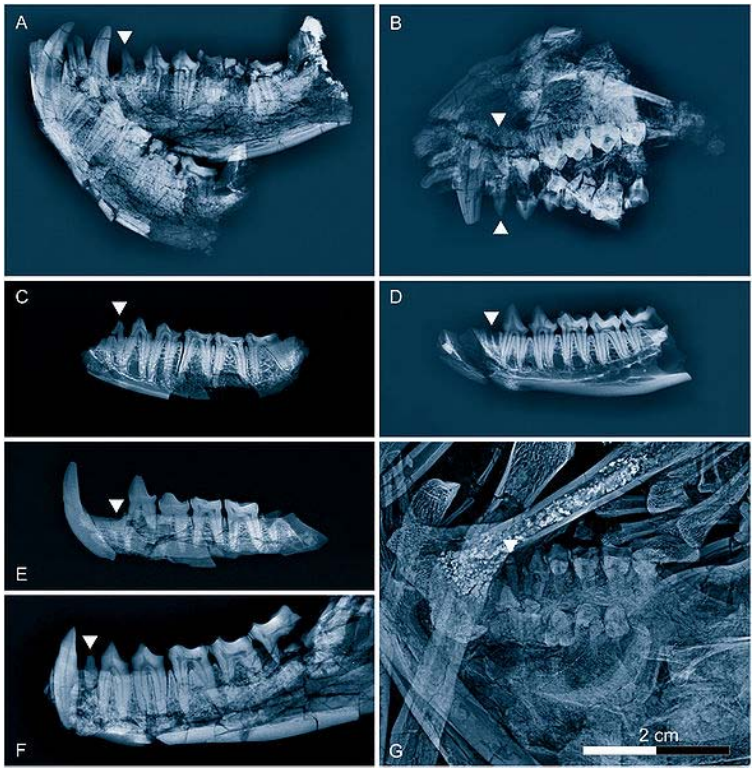
## *Unidentified fossils*

Additionally, an expedition team discovered evidence of a new, small eosiimid from Myanmar in 1999. The new specimen, represented by a right heel bone cataloged as NMMP 23, was found in wash residue in the Pondaung Formation. This specimen is very morphologically similar to the *Eosimias* discovered in the Shanghuang region of China. The best estimate for NMMP 23 includes an overall mean weight of about 111 grams, which places it in the upper-sized end of *Eosimias* fossils discovered. The presence of eosimiid in Myanmar, as well as a high species diversity found in China leads to an apparent conclusion that they had a relatively wide distribution.

## *Eosimias paukkaungensis*

A new species of eosimiid primate, *Eosimias paukkaungensis*, from the latest middle Eocene of Pondaung, central Myanmar, was discovered in the early 2000s. The specimen consists of left and right mandibular fragments preserving only the M3, so that its generic status is provisional. The *E. paukkaungensis* fossil is much larger than homologues of the two *Eosimias* species from China.

# Europolemur

| Europolemur<br>Fossil range: Eocene |
|---|
|  |

Radiographic comparison of middle Eocene primates from Geiseltal in eastern Germany. A to D are fossils of *Europolemur klatti*

| Scientific classification | |
|---|---|
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Mammalia |
| Order: | Primates |
| Family: | Notharctidae |
| Subfamily: | Cercamoniinae |
| Genus: | **Europolemur**<br>Weigelt, 1933 |

**Species (extinct)**

*Europolemur dunaifi*
*Europolemur klatti*
*Europolemur koenigswald*

**Europolemur** was a genus of adapiformes primates that lived in Europe during the Eocene.

## *Europolemur klatti*

***Europolemur klatti*** was an medium to large size adapiformes primate that lived on the continent of Europe from the middle to early Eocene. The most recent relative to this species,appearing to be so from the Geiseltal localities of the DDR, is a recently discovered primate, *Mahgarita stevensi*, whose type specimen is about the size of *Lepilemur leucopus*. This relationship to *M. stevensi* suggests that eastern North America was the possible homeland of lemuriformes with close European phylogenetic ties during the Eocene. Characteristic of most adapines are the reduced or absence of a paraconid and morphology of the paracristid. These and a few other features are synapomorphies that were used to link *E. klatti* with *Leptadapis priscus* and *Microadapis sciureus*, as well as *Smilodectes*.

## *Morphology*

*Europolemur klatti* is part of a group of long-digited fossils, and most likely approximates early euprimate hand proportions. *E. klatti* has a grasping hallux and there is evidence that supports that *E. klatti* may have had nails instead of claws. This insinuates that stabilizing the tips of the digits and hand must have in some way been an important function for them and their lifestyle in their habitat. Relative to the forearm, the hand of *E. klatti* was large which may be related to vertical climbing or posture. The shape of the calcaneus resembles that found in *Smilodectes* and *Notharctus* and *E. klatti* had an average body mass of 1.7 kilograms.

## *Dentition*

In 1995, two isolated upper molars belonging to *E. klatti* were found in an old lake deposit during excavations done by the "Naturhistorisches Museum Mainz/Landessammlung fur Naturkunde Rheinland-Pfalz". The museum determined that the molars (as well as a mandible with nearly complete dentition belonging to another cercamoiines, *Periconodon*) were representative of the first primates from the Middle Eocene Eckfeld maar in Southwest Eifel, Germany ^2. *E. klatti* has a dental formula of $\frac{2.1.3.3}{2.1.3.3}$ (permanent dentition) and a deciduous dentition of $\frac{2.1.4.3}{2.1.4.3}$. One of the most distinguishing characteristics of the genus *Europolemur* is the lack of a metaconule. The dental anatomy of their genus is described in more detail by Franzen as consisting of "upper canines big and pointed; upper molars without postflexus; postprotocrista prominent; no metaconulus; M3 smaller and shorter than M2; P4 much shorter than broad, with a weak parastyle; P4 with a small and unicuspid talonid and a metaconid present to absent; protocristid of M nearly transversely oriented. Protoconid of P3 little higher than that of P4."

## Chapter- 6

# Lemur

| Lemurs |
|---|
|  |
| Ring-tailed Lemur (*Lemur catta*) |

| Scientific classification | |
|---|---|
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Mammalia |
| Order: | Primates |
| Suborder: | Strepsirrhini |

| Families |
|---|
| †Archaeolemuridae |
| Cheirogaleidae |
| Daubentoniidae |
| Indriidae |
| Lemuridae |
| Lepilemuridae |
| †Megaladapidae |

†Palaeopropithecidae

| Diversity |
| --- |
| About 100 living species; |

Range of all lemur species (green)

**Lemurs** are a clade of strepsirrhine primates endemic to the island of Madagascar. They are named after the *lemures* (ghosts or spirits) of Roman mythology due to the ghostly vocalizations, reflective eyes, and the nocturnal habits of some species. Although lemurs often are confused with ancestral primates, the anthropoid primates (monkeys, apes, and humans) did not evolve from them; instead, lemurs merely share morphological and behavioral traits with basal primates. Lemurs arrived in Madagascar around 62 to 65 mya by rafting on mats of vegetation at a time when ocean currents favored oceanic dispersal to the island. Since that time, lemurs have evolved to cope with an extremely seasonal environment and their adaptations give them a level of diversity that rivals that of all other primate groups. Until shortly after humans arrived on the island around 2,000 years ago, there were lemurs as large as a male gorilla. Today, there are nearly 100 species of lemurs, and most of those species have been discovered or promoted to full species status since the 1990s; however, lemur taxonomic classification is controversial and depends on which species concept is used. Even the higher-level taxonomy is disputed, with some experts preferring to place most lemurs within the infraorder **Lemuriformes**, while others prefer Lemuriformes to contain all living strepsirrhines, placing all lemurs in superfamily Lemuroidea and all lorises and galagos in superfamily Lorisoidea.

Ranging in size from 30 g (1.1 oz) to 9 kg (20 lb), lemurs share many common, basal primate traits, such as divergent digits on their hands and feet and nails instead of claws

(in most species). However, their brain-to-body size ratio is smaller than that of anthropoid primates, and among many other traits they share with other strepsirrhine primates, they have a "wet nose" (rhinarium). Lemurs are generally the most social of the strepsirrhine primates and communicate more with scents and vocalizations than with visual signals. Many lemur adaptations are in response to Madagascar's highly seasonal environment. Lemurs have relatively low basal metabolic rates and may exhibit seasonal breeding, dormancy (such as hibernation or torpor), or female social dominance. Most eat a wide variety of fruits and leaves, while some are specialists. Although many share similar diets, different species of lemur share the same forests by differentiating niches.

Lemur research focused on taxonomy and specimen collection during the 18th and 19th centuries. Although field observations trickled in from early explorers, modern studies of lemur ecology and behavior did not begin in earnest until the 1950s and 1960s. Initially hindered by political instability and turmoil on Madagascar during the mid-1970s, field studies resumed in the 1980s and have greatly increased our understanding of these primates. Research facilities like the Duke Lemur Center have provided research opportunities under more controlled settings. Lemurs are important for research because their mix of primitive characteristics and traits shared with anthropoid primates can yield insights on primate and human evolution. However, many lemur species are threatened with extinction due to habitat loss and hunting. Although local traditions generally help protect lemurs and their forests, illegal logging, widespread poverty, and political instability hinder and undermine conservation efforts.

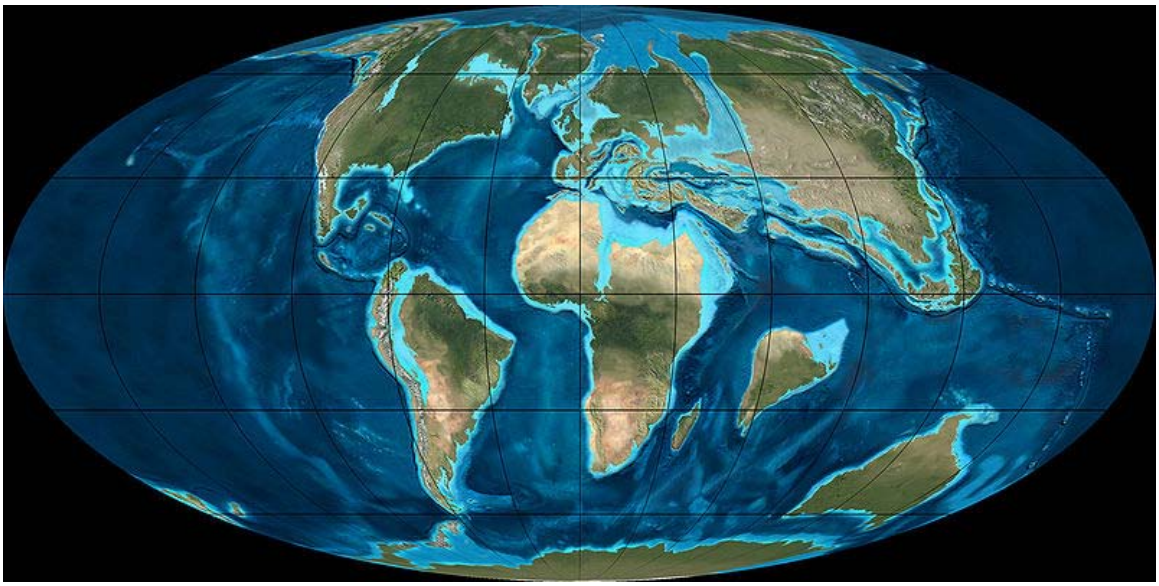
## Etymology

Carl Linnaeus, the founder of modern binomial nomenclature, gave lemurs their name as early as 1754, when he used it in his catalog of the Museum of King Adolf Frederick to describe "*Lemur tardigradus*" (the Red Slender Loris, now known as *Loris tardigradus*). Four years later in *Systema Naturae*, Linnaeus put three species under the genus *Lemur*: *Lemur tardigradus*, *Lemur catta* (the Ring-tailed Lemur), and *Lemur volans* (the Philippine Colugo, now known as *Cynocephalus volans*). Although the term "lemur" was apparently at first used for lorises, it was soon limited to the endemic Malagasy primates, which have been known as "lemurs" ever since. The name derives from the Latin term *lemures*, which refers to specters or ghosts that were exorcised during the Lemuria festival. Linnaeus was familiar with the nocturnal habits and ghost-like appearance of lemurs and lorises, as well as their noiseless movements at night, reflective eyes, and ghostly cries. He may also have known that the some Malagasy people have held legends that lemurs are the souls of their ancestors. Being familiar with the works of Virgil and Ovid and seeing an analogy that fit with his naming scheme, Linnaeus adapted the term "lemur" for these nocturnal primates.

## Evolutionary history

Lemurs are prosimian primates belonging to the suborder Strepsirrhini. Like other strepsirrhine primates, such as lorises, pottos, and galagos, they share ancestral (or plesiomorphic) traits with early primates. In this regard, lemurs are popularly confused

with ancestral primates; however, lemurs did not give rise to monkeys and apes (simians). Instead, they evolved independently in isolation on Madagascar. All modern strepsirrhines including lemurs are traditionally thought to have evolved from primitive primates known as adapiforms during the Eocene (56 to 34 mya) or Paleocene (65 to 56 mya). Adapiforms, however, lack a specialized arrangement of teeth, known as a toothcomb, which nearly all living strepsirrhines possess. A more recent hypothesis is that lemurs descended from lorisiform (loris-like) primates. This is supported by comparative studies of the cytochrome b gene and the presence of the strepsirrhine toothcomb in both groups. Instead of being the direct ancestors of lemurs, the adapiforms may have given rise to both the lemurs and lorisiforms, a split that would be supported by molecular phylogenetic studies. The later split between lemurs and lorises is thought to have occurred approximately 62 to 65 mya according to molecular studies, although other genetic tests and the fossil record in Africa suggest more conservative estimates of 50 to 55 mya for this divergence.



A reconstructed map of the Earth during the Early Paleocene, approximately 65 million years ago, around the time that lemurs first evolved and colonized Madagascar

Once part of the supercontinent Gondwana, the island of Madagascar has been isolated since it broke away from eastern Africa (~160 mya), Antarctica (~80–130 mya), and India (~80–90 mya). Since ancestral lemurs are thought to have originated in Africa around 62 to 65 mya, they would have had to have crossed the Mozambique Channel, a deep channel between Africa and Madagascar with a minimum width of about 560 km (350 mi). In 1915, paleontologist William Diller Matthew noted that the mammalian biodiversity on Madagascar (including lemurs) can only be accounted for by random rafting events, where very small populations rafted from nearby Africa on tangled mats of vegetation, which get flushed out to sea from major rivers. This form of biological dispersal can occur randomly over millions of years. In the 1940s, American paleontologist George Gaylord Simpson coined the term "sweepstakes hypothesis" for such random events. Rafting has since been the most accepted explanation for the lemur

colonization of Madagascar, but until recently this trip was thought to be very unlikely because strong ocean currents flow away from the island. In January 2010, a report demonstrated that around 60 mya both Madagascar and Africa were 1,650 km (1,030 mi) south of their present-day positions, placing them in a different ocean gyre, producing currents that ran counter to what they are today. The ocean currents were shown to be even stronger than today, which would have pushed a raft along faster, shortening the trip to 30 days or less—short enough for a small mammal to survive easily. As the continental plates drifted northward, the currents gradually changed, and by 20 mya the window for oceanic dispersal had closed, effectively isolating the lemurs and the rest of the terrestrial Malagasy fauna from mainland Africa. Isolated on Madagascar with only a limited number of mammalian competitors, the lemurs did not have to compete with other evolving arboreal mammalian groups, such as squirrels. They were also spared from having to compete with monkeys, which evolved later. The intelligence, aggression, and deceptiveness of monkeys gave them an advantage over other primates in exploiting the environment.

## Distribution and diversity

A life restoration of *Babakotia radofilai*, a sloth lemur that became extinct less than two thousand years ago

Lemurs have adapted to fill many open ecological niches since making their way to Madagascar. Their diversity in both behavior and morphology (outward appearance) rivals that of the monkeys and apes found elsewhere in the world. Ranging in size from the 30 g (1.1 oz) Madame Berthe's Mouse Lemur, the world's smallest primate, to the recently extinct 160–200 kg (350–440 lb) *Archaeoindris fontoynonti*, lemurs evolved diverse forms of locomotion, varying levels of social complexity, and unique adaptations to the local climate.

Lemurs lack any shared traits that make them stand out from all other primates. Different types of lemurs have evolved unique combinations of unusual traits to cope with Madagascar's harsh, seasonal climate. These traits can include seasonal fat storage, hypometabolism (including torpor and hibernation), small group sizes, low encephalization (relative brain size), cathemerality (activity both day and night), and strict breeding seasons. Extreme resource limitations and seasonal breeding are also thought to have given rise to three other relatively common lemur traits: female social dominance, sexual monomorphism, and male–male competition for mates involving low levels of agonism, such as sperm competition.

Before the arrival of humans roughly 1500 to 2000 years ago, lemurs were found all across the island. However, early settlers quickly converted the forests to rice paddies and grassland through slash-and-burn agriculture (known locally as *tavy*), restricting lemurs to approximately 10% of the island's area, ~60,000 $km^2$ (23,000 sq mi). Today, the diversity and complexity of lemur communities increases with floral diversity and precipitation and is highest in the rainforests of the east coast, where precipitation and floral diversity are also at their highest. Despite their adaptations for weathering extreme adversity, habitat destruction and hunting have resulted in lemur populations declining sharply, and their diversity has diminished, with the recent extinction of at least 17 species in eight genera, known collectively as the subfossil lemurs. Most of the approximately 100 species and subspecies of lemur are either threatened or endangered. Unless trends change, extinctions are likely to continue.

Until recently, giant lemurs existed on Madagascar. Now represented only by recent or subfossil remains, they were modern forms that were once part of the rich lemur diversity that has evolved in isolation. Some of their adaptations were unlike those seen in their living relatives. All 17 extinct lemurs were larger than the extant (living) forms, some weighing as much as 200 kg (440 lb), and are thought to have been active during the day. Not only were they unlike the living lemurs in both size and appearance, they also filled ecological niches that either no longer exist or are now left unoccupied. Large parts of Madagascar, which are now devoid of forests and lemurs, once hosted diverse primate communities that included more than 20 lemur species covering the full range of lemur sizes.

## Taxonomic classification and phylogeny

From a taxonomic standpoint, the term "lemur" originally referred to the genus *Lemur*, which currently contains only the Ring-tailed Lemur. The term is now used in the colloquial sense in reference to all Malagasy primates.

Lemur taxonomy is controversial, and not all experts agree, particularly with the recent increase in the number of recognized species. According to Russell Mittermeier, the president of Conservation International (CI), taxonomist Colin Groves, and others, there are nearly 100 recognized species or subspecies of extant (or living) lemur, divided into five families and 15 genera. Because genetic data indicates that the recently extinct subfossil lemurs were closely related to living lemurs, an additional three families, eight genera, and 17 species can be included in the total. In contrast, other experts have labeled this as taxonomic inflation, instead preferring a total closer to 50 species.

The classification of lemurs within the suborder Strepsirrhini is equally controversial, although the most experts agree on the same phylogenetic tree. In one taxonomy published by Colin Groves, the Aye-aye was placed in its own infraorder, Chiromyiformes, while the rest of the lemurs were placed in Lemuriformes. In another taxonomy, Lemuriformes contains all living strepsirrhines in two superfamilies, Lemuroidea for all lemurs and Lorisoidea for lorises and galagos.

The Sahamalaza Sportive Lemur (*Lepilemur sahamalazensis*) was identified as a distinct species in 2006.

Lemur taxonomy has changed significantly since the first taxonomic classification of lemurs by Carl Linnaeus in 1758. One of the greatest challenges has been the classification of the Aye-aye, which has been a topic of debate up until very recently. Until Richard Owen published a definitive anatomical study in 1866, early naturalists were uncertain whether the Aye-aye (genus *Daubentonia*) was a primate, rodent, or marsupial. However, the placement of the Aye-aye within the order Primates remained problematic until very recently. Based on its anatomy, researchers have found support for classifying the genus *Daubentonia* as a specialized indriid, a sister group to all strepsirrhines, and as an indeterminate taxon within the order Primates. Molecular tests have now shown Daubentoniidae is basal to all Lemuriformes, and in 2008, Russell

Mittermeier, Colin Groves, and others ignored addressing higher-level taxonomy by defining lemurs as monophyletic and containing five living families, including Daubentoniidae.

Relationships among lemur families have also proven to be problematic and have yet to be definitively resolved. To further complicate the issue, several Paleogene fossil primates from outside Madagascar, such as *Bugtilemur*, have been classified as lemurs. However, scientific consensus does not accept these assignments based on genetic evidence, and therefore it is generally accepted that the Malagasy primates are monophyletic. Another area of contention is the relationship between the sportive lemurs and the extinct koala lemurs (Megaladapidae). Formerly grouped in the same family due to similarities in dentition, they are no longer considered to be closely related due to genetic studies.

More taxonomic changes have occurred at the genus level, although these revisions have proven more conclusive, often supported by genetic and molecular analysis. The most noticeable revisions included the gradual split of a broadly defined genus *Lemur* into separate genera for the Ring-tailed Lemur, ruffed lemurs, and brown lemurs due to a host of morphological differences.

Due to several taxonomic revisions by Russell Mittermeier, Colin Groves, and others, the number of recognized lemur species has grown from 33 species and subspecies in 1994 to approximately 100 in 2008. With continuing cytogenetic and molecular genetic research, as well as ongoing field studies, particularly with cryptic species such as mouse lemurs, the number of recognized lemur species is likely to keep growing. However, the rapid increase in the number of recognized species has had its critics among taxonomists and lemur researchers. Since classifications ultimately depend on the species concept used, conservationists often favor definitions that result in the splitting of genetically distinct populations into separate species to gain added environmental protection. Others favor a more thorough analysis.

## *Anatomy and physiology*

Lemurs vary greatly in size. They include the smallest primates in the world and, until recently, also included some of the largest. They currently range in size from about 30 g (1.1 oz) for Madame Berthe's Mouse Lemur (*Microcebus berthae*) up to 7–9 kg (15–20 lb) for the Indri (*Indri indri*) and Diademed Sifaka (*Propithecus diadema*). When recently extinct species are considered, the size range extended up to that of a gorilla at 160–200 kg (350–440 lb) for *Archaeoindris fontoynonti*.

Close-up of a ruffed lemur's foot, showing the toilet-claw on the second toe and nails on all other toes

Like all primates, lemurs have five divergent digits with nails (in most cases) on their hands and feet. Most lemurs possess a laterally compressed, elongated nail, called a toilet-claw, on the second toe and use it for scratching and grooming. In addition to the toilet-claw, lemurs share a variety of other traits with other strepsirrhine primates, which include a rhinarium (or "wet nose"); a fully functional vomeronasal organ, which detects pheromones; a postorbital bar and the lack of postorbital closure (a wall of thin bone behind the eye); orbits (bony sockets that enclose the eye) that are not fully facing forward; left and right mandible (lower jaw) bones that are not fully fused; and a small brain-to-body mass ratio.

Additional traits shared with other prosimian primates (strepsirrhine primates and tarsiers) include a bicornuate (two-horned) uterus and epitheliochorial placentation. Because their thumbs are only pseudo-opposable, making their movement less independent of the other fingers, their hands are less than perfect at grasping and manipulating objects. On their feet, they have a widely abducted hallux (first toe) which

facilitates the grasping of tree limbs. A common misconception is that lemurs have a prehensile tail, a trait found only in New World monkeys, particularly atelids, among primates. Lemurs also rely heavily on their sense of smell, a trait shared with most other mammals and primitive primates, but not with the visually oriented higher primates.

Lemurs are a diverse group of primates in terms of morphology and physiology. Some lemurs, such as the sportive lemurs and indriids, have longer hind limbs than forelimbs, making them excellent leapers. Indriids also have a specialized digestive system for folivory, exhibiting enlarged salivary glands, a spacious stomach, and an elongated caecum (lower gut) that facilitates fermentation. The Hairy-eared Dwarf Lemur (*Allocebus trichotis*) reportedly has a very long tongue, allowing it to feed on nectar. Likewise, the Red-bellied Lemur (*Eulemur rubriventer*) has a feathery brush-shaped tongue, also uniquely adapted to feed on nectar and pollen. The Aye-aye has evolved some traits that are unique among primates, making it stand out among the lemurs. Such traits include continuously growing, rodent-like front teeth for gnawing through wood and hard seeds; a highly mobile, filiform (filament-shaped) middle finger for extracting food from tiny holes; large, bat-like ears for detecting hollow spaces within trees; and use of self-generated acoustical cues to forage.

Lemurs are unusual since they have great variability in their social structure, yet generally lack sexual dimorphism in size and canine tooth morphology. However, some species tend towards having larger females, and two species of true lemur (genus *Eulemur*), the Gray-headed Lemur (*E. albocollaris*) and the Red Lemur (*E. rufus*), exhibit size differences in canine teeth. True lemurs show sexual dichromatism (sexual differences in fur coloration), but the difference between the genders varies from strikingly obvious, as in the Black Lemur (*E. macaco*), to nearly imperceptible in the case of the Common Brown Lemur (*E. fulvus*).

Crypsis, or the inability of humans to visually distinguish between two or more distinct species, has recently been discovered among lemurs, particularly within the sportive lemurs (*Lepilemur*) and mouse lemurs (*Microcebus*). With sportive lemurs, subspecies were traditionally defined based on slight morphological differences, but new genetic evidence has supported giving full species status to these regional populations. In the case of mouse lemurs, the Gray Mouse Lemur (*M. murinus*), Golden-brown Mouse Lemur (*M. ravelobensis*), and Goodman's Mouse Lemur (*M. lehilahytsara*) were considered the same species until recently, when genetic tests identified them as cryptic species.

## Dentition

Lemur deciduous and permanent dentitions

| Family | Deciduous dental formula | Permanent dental formula |
|---|---|---|
| Cheirogaleidae, Lemuridae | $\frac{2.1.3}{2.1.3} \times 2 = 24$ | $\frac{2.1.3.3}{2.1.3.3} \times 2 = 36$ |
| Lepilemuridae | $\frac{2.1.3}{2.1.3} \times 2 = 24$ | $\frac{0.1.3.3}{2.1.3.3} \times 2 = 32$ |
| †Archaeolemuridae | $\frac{2.1.3}{2.0.3} \times 2 = 22$ | $\frac{2.1.3.3}{1.1.3.3} \times 2 = 34$ |

| | | |
|---|---|---|
| †Megaladapidae | $\frac{1.1.3}{2.1.3} \times 2 = 22$ | $\frac{0.1.3.3}{2.1.3.3} \times 2 = 32$ |
| Indriidae, †Palaeopropithecidae | $\frac{2.1.2}{2.1.3} \times 2 = 22$ | $\frac{2.1.2.3}{2.0.2.3} \times 2 = 30$ |
| Daubentoniidae | $\frac{1.1.2}{1.1.2} \times 2 = 16$ | $\frac{1.0.1.3}{1.0.0.3} \times 2 = 18$ |

The lemur dentition is heterodont (having multiple tooth morphologies) and derives from an ancestral primate permanent dentition of $\frac{2.1.3.3}{2.1.3.3}$. Indriids, sportive lemurs, the Aye-aye, and the extinct sloth lemurs, monkey lemurs, and koala lemurs have reduced dentitions, having lost incisors, canines, or premolars. The ancestral deciduous dentition is $\frac{2.1.3}{2.1.3}$, but young indriids, Aye-ayes, koala lemurs, sloth lemurs, and probably monkey lemurs have fewer deciduous teeth.

There are also noticeable differences in dental morphology and tooth topography between lemurs. Indri, for instance, have teeth that are perfectly adapted for shearing leaves and crushing seeds. In the toothcomb of most lemurs, the bottom incisors and canine teeth are procumbent (face forward rather than up) and finely spaced, thus providing a tool for either grooming or feeding. For instance, Indri use their toothcomb not only for grooming, but also to pry out the large seeds from the tough exocarp of *Beilschmiedia* fruits, while fork-marked lemurs use their relatively long toothcomb to cut through tree bark to induce the flow of tree sap. Only the Aye-aye, the extinct Giant Aye-aye, and the largest of the extinct giant sloth lemurs lack a functional strepsirrhine toothcomb. In the case of the Aye-aye, the morphology of the deciduous incisors, which are lost shortly after birth, indicate that its ancestors had a toothcomb. These milk teeth are lost shortly after birth and are replaced by open-rooted, continually growing (hypselodont) incisors.

A six-tooth version of the strepsirrhine toothcomb in a Ring-tailed Lemur, with canine-like premolars behind it

The toothcomb in lemurs normally consists of six teeth (four incisors and two canines), although indriids, monkey lemurs, and some sloth lemurs only have a four-tooth toothcomb due to the loss of either a canine or an incisor. Because the lower canine is either included in the toothcomb or lost, the lower dentition can be difficult to read, especially since the first premolar (P2) is often shaped like a canine (caniniform) to fill the canine's role. In folivorous (leaf-eating) lemurs, except for indriids, the upper incisors are greatly reduced or absent. Used together with the toothcomb on the mandible (lower jaw), this complex is reminiscent of an ungulate browsing pad.

Lemurs are unusual among primates for their rapid dental development, particularly among the largest species. For example, indriids have relatively slow body growth but extremely fast tooth formation and eruption. By contrast, anthropoid primates exhibit slower dental development with increased size and slower morphological development. Lemurs are also dentally precocious at birth, and have their full permanent dentition at weaning.

Lemurs generally have thin tooth enamel compared to anthropoid primates. This may result in extra wear and breakage to the anterior (front) teeth due to heavy use in grooming, feeding, and fighting. Little other dental health information is available for lemurs, except that wild Ring-tailed Lemurs at Berenty Private Reserve occasionally exhibit abscessed maxillary canines (seen as open wounds on the muzzle) and tooth decay, possibly due to the consumption of non-native foods.

## Senses

The sense of smell, or olfaction, is highly important to lemurs and is frequently used in communication. Lemurs have long snouts (compared to the short snouts of haplorrhines) that are traditionally thought to position the nose for better sifting of smells, although long snouts do not necessarily translate into high olfactory acuity since its not the relative size of the nasal cavity that correlates with smell, but the density of olfactory receptors. Instead, the long snouts may facilitate better chewing.

Lemurs generally have a wet nose, or rhinarium, as well as a longer snout than anthropoid primates.

The wet nose, or rhinarium, is a trait shared with other strepsirrhines and many other mammals, but not with haplorrhine primates. Although it is claimed to enhance the sense of smell, it is actually a touch-based sense organ that connects with a well-developed

vomeronasal organ (VNO). Since pheromones are usually large, non-volatile molecules, the rhinarium is used to touch a scent-marked object and transfer the pheromone molecules down the philtrum (the nasal mid-line cleft) to the VNO via the nasopalatine ducts that travel through the incisive foramen of the hard palate.

To communicate with smell, which is useful at night, lemurs will scent mark with urine as well as scent glands located on the wrists, inside elbow, genital regions, or the neck. The scrotal skin of most male lemurs has scent glands. Ruffed lemurs (genus *Varecia*) and male sifakas have a gland at the base of their neck, while the Greater Bamboo Lemur (*Prolemur simus*) and the Ring-tailed Lemur have glands inside the upper arms near the axilla. Male Ring-tailed Lemurs also have scent glands on the inside of their forearms, adjacent to a thorn-like spur, which they use to gouge, and simultaneously, scent-mark tree branches. They will also wipe their tails between their forearms and then engage in "stink fights" by waving their tail as their opponents.

Lemurs (and strepsirrhines in general) are considered to be less visually oriented than the higher primates, since they rely so heavily on their sense of smell and pheromone detection. The fovea on the retina; which yields higher visual acuity, is not well-developed. The postorbital septum (or bony closure behind the eye) in haplorrhine primates is thought to stabilize the eye slightly, allowing for the evolution of the fovea. With only a postorbital bar, lemurs have been unable to develop a fovea. Therefore, regardless of their activity pattern (nocturnal, cathemeral, or diurnal), lemurs exhibit low visual acuity and high retinal summation. Lemurs can see a wider visual field, however, than anthropoid primates due to a slight difference in the angle between the eyes, as shown in the following table:

**Optical angles and visual fields**

| | Angle between eyes | Binocular field | Combined field (binocular + periphery) |
|---|---|---|---|
| **Lemurs** | 10–15° | 114–130° | 250–280° |
| **Anthropoid primates** | 0° | 140–160° | 180–190° |

Although they lack a fovea, some diurnal lemurs have a cone-rich, although less clustered, area centralis. This area centralis has a high rod-to-cone cell ratio in many diurnal species studied thus far, whereas diurnal anthropoids have no rod cells in their

fovea. Once again, this suggests lower visual acuity in lemurs than in anthropoids. Furthermore, the rod-to-cone cell ratio can be variable even among diurnal species. For instance, Verreaux's Sifaka (*Propithecus verreauxi*) and the Indri (*Indri indri*) have only a few large cones scattered along their predominantly rod-dominated retina. The eyes of the Ring-tailed Lemur contain one cone to five rods. Nocturnal lemurs such as mouse lemurs and dwarf lemurs, on the other hand, have retinas made up entirely of rod cells.

Since cone cells make color vision possible, the high prevalence of rod cells in lemur eyes suggest they have not evolved color vision. The most studied lemur, the Ring-tailed Lemur, has been shown to have blue-yellow vision, but lacks the ability to distinguish red and green hues. Due to polymorphism in opsin genes, which code for color receptivity, trichromatic vision may rarely occur in females of a few lemur species, such as Coquerel's Sifaka (*Propithecus coquereli*) and the Red Ruffed Lemur (*Varecia rubra*). Most lemurs, therefore, are either monochromats or dichromats.

Aye-ayes exhibit eyeshine because they have a reflective layer of tissue in the eye, called a tapetum lucidum.

Most lemurs have retained the tapetum lucidum, a reflective layer of tissue in the eye, which is found in many vertebrates. This trait is absent in haplorrhine primates, and its presence further limits the visual acuity in lemurs. The strepsirrhine choroidal tapetum is unique among mammals because it is made up of crystalline riboflavin, and the resulting optical scattering is what limits visual acuity. Although the tapetum is considered to be

ubiquitous in lemurs, there appear to be exceptions among true lemurs, such as the Black Lemur and the Common Brown Lemur, as well as the ruffed lemurs. Since the riboflavins in the tapetum have a tendency to dissolve and vanish when processed for histological investigation, however, the exceptions are still debatable.

### Metabolism

Lemurs have low basal metabolic rates (BMR), which helps them to conserve energy during the dry season, when water and food are scarce. They can optimize their energy use by lowering their metabolic rate to 20% below the values predicted for mammals of similar body mass. The Red-tailed Sportive Lemur (*Lepilemur ruficaudatus*), for instance, reportedly has one of the lowest metabolic rates among mammals. Its low metabolic rate may be linked to its generally folivorous diet and relatively small body mass. Lemurs exhibit behavioral adaptations to complement this trait, including sunning behaviors, hunched sitting, group huddling, and nest sharing, in order to reduce heat loss and conserve energy. Dwarf lemurs and mouse lemurs exhibit seasonal cycles of dormancy to conserve energy. Before dry season, they will accumulate fat in white adipose tissue located at the base of the tail and hind legs, doubling their weight. At the end of the dry season, their body mass may fall to half of what it was prior to the dry season. Lemurs that do not experience states of dormancy are also able to shut down aspects of their metabolism for energy conservation.

## *Behavior*

Lemur behavior is as variable as lemur morphology. Differences in diet, social systems, activity patterns, locomotion, communication, predator avoidance tactics, breeding systems, and intelligence levels help define lemur taxa and set individual species apart from the rest. Although trends frequently distinguish the smaller, nocturnal lemurs from the larger, diurnal lemurs, there are often exceptions that help exemplify the unique and diverse nature of these Malagasy primates.

## Diet

Mouse lemurs primarily eat fruit, although their diet also includes insects.

Lemur diets are highly variable and demonstrate a high degree of plasticity, although general trends suggest that the smallest species primarily consume fruit and insects (omnivory), while the larger species are more herbivorous, consuming mostly plant material. As with all primates, hungry lemurs might eat anything that is edible, whether or not the item is one of their preferred foods. For instance, the Ring-tailed Lemur eats insects and small vertebrates when necessary and as a result it is commonly viewed as an opportunistic omnivore. Coquerel's Giant Mouse Lemur (*Mirza coquereli*) is mostly frugivorous, but will consume insect secretions during the dry season.

A common assumption in mammalogy is that small mammals cannot subsist entirely on plant material and must have a high-calorie diet in order to survive. As a result, it was thought that the diet of tiny primates must be high in protein-containing insects (insectivory). Research has shown, however, that mouse lemurs, the smallest living primates, consume more fruit than insects, contradicting the popular hypothesis.

Plant material makes up the majority of most lemur diets. Members of at least 109 of all known plant families in Madagascar (55%) are exploited by lemurs. Since lemurs are primarily arboreal, most of these exploited species are woody plants, including trees, shrubs, or lianas. Only the Ring-tailed Lemur, the bamboo lemurs (genus *Hapalemur*), and the Black-and-white Ruffed Lemur (*Varecia variegata*) are known to consume herbs. While Madagascar is rich in fern diversity, these plants are rarely eaten by lemurs. One

possible reason for this is that ferns lack flowers, fruits, and seeds—common food items in lemur diets. They also occur close to the ground, while lemurs spend most of their time in the trees. Lastly, ferns have an unpleasant taste due to the high content of tannins in their fronds. Likewise, mangroves appear to be rarely exploited by lemurs due to their high tannin content. Some lemurs appear to have evolved responses against common plant defenses, however, such as tannins and alkaloids. The Golden Bamboo Lemur (*Hapalemur aureus*), for instance, eats giant bamboo (*Cathariostachys madagascariensis*), which contains high levels of cyanide. This lemur can consume twelve times the typically lethal dose for most mammals on a daily basis; the physiological mechanisms that protect it from cyanide poisoning are unknown. At the Duke Lemur Center (DLC) in the United States, lemurs that roam the outdoor enclosures have been observed eating poison ivy (*Taxicodendron radicans*), yet have shown no ill effects.

Up to 95% of the Greater Bamboo Lemur's diet consists of bamboo.

Many of the larger lemur species consume leaves (folivory), particularly the indriids. However, some smaller lemurs such as sportive lemurs (genus *Lepilemur*) and woolly lemurs (genus *Avahi*) also primarily eat leaves, making them the smallest primates that do so. The smallest of the lemurs generally do not eat much leaf matter. Collectively, lemurs have been documented consuming leaves from at least 82 native plant families and 15 alien plant families. Lemurs tend to be selective in their consumption of the part of the leaf or shoot as well as its age. Often, young leaves are preferred over mature leaves.

Many lemurs that eat leaves tend to do so during times of fruit scarcity, sometimes suffering weight loss as a result. Most lemur species, including most of the smallest lemurs and excluding some of the indriids, predominantly eat fruit (frugivory) when available. Collectively, lemurs have been documented consuming fruit from at least 86 native plant families and 15 alien plant families. As with most tropical fruit eaters, the lemur diet is dominated by fruit from *Ficus* (fig) species. In many anthropoid primates, fruit is a primary source of vitamin C, but unlike anthropoid primates, lemurs (and all strepsirrhines) can synthesize their own vitamin C. Historically, captive lemur diets high in vitamin C-rich fruits have been thought to cause hemosiderosis, a type of iron overload disorder, since vitamin C increases iron absorption. Although lemurs in captivity have been shown to be prone to hemosiderosis, the frequency of the disease varies across institutions and may depend on the diet, husbandry protocols, and genetic stock. Assumptions about the problem need to be tested separately for each species. The Ring-tailed Lemur, for instance, seems to be less prone to the disorder than other lemur species.

Only eight species of lemur are known to be seed predators (granivores), but this may be under-reported since most observations only report fruit consumption and do not investigate whether the seeds are consumed as well. These lemurs include some indriids, such as the Diademed Sifaka (*Propithecus diedema*), the Golden-crowned Sifaka (*Propithecus tattersalli*), the Indri, and the Aye-aye. The Aye-aye, which specializes in structurally defended resources, can chew through *Canarium* seeds, which are harder than the seeds that New World monkeys are known to break open. At least 36 genera from 23 families of plants are targeted by lemur seed predators.

Inflorescences (clusters of flowers) of at least 60 plant families are eaten by lemurs ranging in size from the tiny mouse lemurs to the relatively large ruffed lemurs. If the flowers are not exploited, sometimes the nectar is consumed (nectarivory) along with the pollen (palynivory). At least 24 native species from 17 plant families are targeted for nectar or pollen consumption.

Bark and plant exudates such as tree sap are consumed by a few lemur species. The exploitation of exudates has been reported in 18 plant species and only in the dry regions in the south and west of Madagascar. Only the Masoala Fork-marked Lemur (*Phaner furcifer*) and Coquerel's Giant Mouse Lemur regularly consume tree sap. Bark has never been reported as an important food item in lemur diets, but at least four species eat it: the Aye-aye, the Red-tailed Sportive Lemur (*Lepilemur ruficaudatus*), the Common Brown Lemur (*Eulemur fulvus*), and Verreaux's Sifaka (*Propithecus verreauxi*). Most bark

feeding is directly linked to exudate feeding, except for the Aye-aye's bark feeding on *Afzelia bijuga* (genus *Afzelia*) at Nosy Mangabe in the northeast.

Soil consumption (geophagy) has also been reported and likely helps with digestion, provides minerals and salts, and helps absorb toxins. Sifakas have been observed eating soil from termite mounds, possibly adding beneficial intestinal flora to aid the digestion of cellulose from their folivorous diet.

## Social systems

Lemurs are social and live in groups that usually include less than 15 individuals. Observed social organization patterns include "solitary but social", "fission-fusion", "pair bonds", and "multi-male group". Nocturnal lemurs are mostly solitary but social, foraging alone at night but often nesting in groups during the day. The degree of socialization varies by species, gender, location, and season. In many nocturnal species, for instance, the females, along with their young, will share nests with other females and possibly one male, whose larger home range happens to overlap one or more female nesting groups. In sportive lemurs and fork-marked lemurs, one or two females may share a home range, possibly with a male. In addition to sharing nests, they will also interact vocally or physically with their range-mate while they forage at night. Diurnal lemurs exhibit many of the social systems seen in monkeys and apes, living in relatively permanent and cohesive social groups. Multi-male groups are the most common, just as they are in most anthropoid primates. True lemurs utilize this social system, often living in groups of ten or less. Ruffed lemurs have been shown to live in fission-fusion societies, and Indri forms pair bonds.

Dwarf lemurs are solitary but social, foraging alone but often sleeping in groups.

Some lemurs exhibit female philopatry, where females stay within their natal range and the males migrate upon reaching maturity, and in other species both sexes will migrate. In some cases, female philopatry may help explain the evolution of female-bonded multi-male groups, such as those of the Ring-tailed Lemur, Milne-Edwards' Sifaka (*Propithecus edwardsi*), and the Verreaux's Sifaka. Their ancestors may have been more solitary, with females that lived in mother-daughter pairs (or dyads). Over time, these dyads may have allied themselves with other neighboring mother-daughter dyads in order to defend more distributed resources in a wide home range. If this is true, then multi-male groups in lemurs may differ fundamentally in their internal structure from those in catarrhine primates (Old World monkeys and apes).

The presence of female social dominance sets lemurs apart from most other primates and mammals; in most primate societies, males are dominant unless females band together to form coalitions that displace them. However, many *Eulemur* species are exceptions and the Greater Bamboo Lemur (*Prolemur simus*) does not exhibit female dominance. When females are dominant within a group, the way they maintain dominance varies. Ring-tailed Lemur males act submissively with or without signs of female aggression. Male Crowned Lemurs (*Eulemur coronatus*), on the other hand, will only act submissively when females act aggressively towards them. Female aggression is often associated with, but not limited to, feeding.

There have been many hypotheses that have attempted to explain why lemurs exhibit female social dominance while other primates with similar social structures do not, but no consensus has been reached after decades of research. The dominant view in the literature states that female dominance is an advantageous trait given the high costs of reproduction and the scarcity of resources available. Indeed, female dominance has been shown to be linked to increased maternal investment. However, when reproductive costs and extreme seasonality of resources were compared across primates, other primates demonstrated male dominance under conditions that were similar to or more challenging than those faced by lemurs. In 2008, a new hypothesis revised this model using simple game theory. It was argued that when two individuals were equally matched in fighting capacity, the one with the most need would win the conflict since it would have the most to lose. Consequently, the female, with higher resource needs for pregnancy, lactation, and maternal care, was more likely to win in resource conflicts with equally sized males. This, however, assumed monomorphism between sexes. The following year, a new hypothesis was proposed to explain monomorphism, stating that because most female lemurs are only sexually receptive for a day or two each year, males can utilize a more passive form of mate guarding: copulatory plugs, which block the female reproductive tract, preventing other males from successfully mating with her, and thus reducing the need for aggression and the evolutionary drive for sexual dimorphism.

Social grooming serves many functions for social lemurs.

In general, levels of agonism (or aggression) tend to correlate with relative canine height. The Ring-tailed Lemur has long, sharp upper canine teeth in both sexes, and it also exhibits high levels of agonism. The Indri, on the other hand, has smaller canines and exhibits lower levels of aggression. When neighboring groups of the same species defend their territories, the conflict can take the form of ritualized defense. In sifakas, these ritualized combats involve staring, growling, scent-marking, and leaping to occupy certain sections of the tree. The Indri defends its home range with ritualized "singing" battles.

Like other primates, lemurs groom socially (allogroom) to ease tensions and solidify relationships. They groom in greeting, when waking up, when settling in for sleep, between mother and infant, in juvenile relations, and for sexual advances. Unlike anthropoid primates, who part the fur with the hands and pick out particles with the fingers or mouth, lemurs groom with their tongue and scraping with their toothcomb. Despite the differences in technique, lemurs groom with the same frequency and for the same reasons as anthropoids.

## Activity patterns

The biological rhythm can vary from nocturnal in smaller lemurs to diurnal in most larger lemurs. Diurnality is not seen in any other prosimian. Cathemerality, where an animal is active sporadically both day and night, occurs among some of the larger lemurs. Few if any other primates exhibit this sort of activity cycle, either regularly or irregularly under changing environmental conditions. The most heavily studied cathemeral lemurs are the true lemurs. Although the Mongoose Lemur (*E. mongoz*) is the best-documented

example, every species in the genus studied has shown some degree of cathemeral behavior, although night activity is often restricted by light availability and moon periodicity. This type of behavior was first documented in the 1960s in true lemur species as well as other Lemuridae species, such as ruffed lemurs and bamboo lemurs. Initially described as "crepuscular" (active at dawn and dusk), anthropologist Ian Tattersall stimulated additional research and coined the new term "cathemeral", although many non-anthropologists prefer the terms "circadian" or "diel".

In order to conserve energy and water in their highly seasonal environment, mouse lemurs and dwarf lemurs exhibit seasonal behavioral cycles of dormancy where the metabolic rate and body temperature are lowered. They are the only primates known to do so. They accumulate fat reserves in their hind legs and the base of their tail before the dry winter season, when food and water are scarce, and can exhibit daily and prolonged torpor during the dry season. Daily torpor constitutes less than 24 hours of dormancy, whereas prolonged torpor averages two weeks in duration and signals hibernation. Mouse lemurs have been observed experiencing torpor that lasts for several consecutive days, but dwarf lemurs are known to hibernate for six to eight months every year, particularly on the west coast of Madagascar.

Dwarf lemurs are the only primates known to hibernate for extended periods. Unlike other hibernating mammals from temperate regions, which have to awaken regularly for a few days, dwarf lemurs experience five months of continuous deep hibernation (May through September). Before and after this deep hibernation, there are two months (April and October) of transition, where they will forage on a limited basis to reduce demands on their fat reserves. Unlike any other hibernating mammal, the body temperature of hibernating dwarf lemurs will fluctuate with the ambient temperature rather than remaining low and stable.

Other lemurs that do not exhibit dormancy conserve energy by selecting thermoregulated microhabitats (such as tree holes), sharing nests, and reducing exposed body surfaces, such as by hunched sitting and group huddling. Also, the Ring-tailed Lemur, ruffed lemurs, and sifakas are commonly seen sunning, thus using solar radiation to warm their bodies instead of metabolic heat.

## Locomotion

Sifakas are specially adapted to vertical clinging and leaping, so they must hop sideways to move on the ground.

Locomotor behavior in lemurs, both living and extinct, is highly varied and its diversity exceeds that of anthropoids. Locomotor postures and behaviors have included vertical clinging and leaping (including saltatory behavior), seen in indriids and bamboo lemurs; slow (loris-like) arboreal quadrupedal locomotion, once exhibited by *Mesopropithecus*; fast arboreal quadrupedal locomotion, seen in true lemurs and ruffed lemurs; partially terrestrial quadrupedal locomotion, seen in the Ring-tailed Lemur; highly terrestrial quadrupedal locomotion, once exhibited by monkey lemurs such as *Hadropithecus*; and sloth-like suspensory locomotion, once exhibited by many of the sloth lemurs, such as *Palaeopropithecus*. The Lac Alaotra Gentle Lemur (*Hapalemur alaotrensis*) has even

been reported to be a good swimmer. Sometimes these locomotor types are lumped together into two main groups of lemurs, the vertical clingers and leapers and the arboreal (and occasionally terrestrial) quadrupeds.

The jumping prowess of the indriids have been well documented and are popular among ecotourists visiting Madagascar. Using their long, powerful back legs, they catapult themselves into the air and land in an upright posture on a nearby tree, with both hands and feet tightly gripping the trunk. Indriids can leap up to 10 m (33 ft) rapidly from tree trunk to tree trunk, an ability referred to as "ricochetal leaping". Verreaux's Sifaka (*Propithecus verreauxi*) manages to do this in the spiny forests of southern Madagascar. It is unknown how it avoids impaling its palms on the thorn-covered trunks of large plants such as *Alluaudia*. When distances between trees are too great, sifakas will descend to the ground and cross distances more than 100 m (330 ft) by standing upright and hopping sideways with the arms held to the side and waving up and down from chest to head height, presumably for balance. This is sometimes described as a "dance-hop".

## Communication

Lemur communication can be transmitted through sound, sight, and smell (olfaction). The Ring-tailed Lemur, for instance, uses complex though highly stereotyped behaviors such as scent-marking and vocalizations. Visual signals are probably the least used by lemurs, since they lack many of the muscles used in common primate facial expressions. Given their poor vision, whole-body postures are probably more noticeable. However, the Ring-tailed Lemur has demonstrated distinct facial expressions including a threat stare, pulled back lips for submission, and pulled back ears along with flared nostrils during scent-marking. This species has also been observed using yawns as threats. Their ringed tails also communicate distance, warn off neighboring troops, and help locate troop members. Sifakas are known to exhibit an open-mouth play face as well as a submissive teeth-baring grimace used in agonistic interactions.

Lemurs communicate by scent-marking their territory.

Olfaction is particularly important to lemurs, except for the Indri, which lacks most common lemur scent glands and has a greatly reduced olfactory region in the brain.) Olfaction can communicate information about age, sex, reproductive status, as well as demarcate the boundaries of a territory. It is most useful for communication between animals that rarely encounter each other. Small, nocturnal lemurs mark their territories with urine, while the larger, diurnal species use scent glands located on various parts of their anatomy. The Ring-tailed Lemur engages in "stink fights" by rubbing its tail across scent glands on its wrists, and then flicking its tail at other male opponents. Some lemurs defecate in specific areas, otherwise known as latrine behavior. Although many animals exhibit this behavior, it is a rare trait among primates. Latrine behavior can represent territorial marking and aid in interspecies signaling.

Compared to other mammals, primates in general are very vocal, and lemurs are no exception. Some lemur species have extensive vocal repertoires, including the Ring-tailed Lemur and ruffed lemurs. Some of the most common calls among lemurs are predator alarm calls. Lemurs not only respond to alarm calls of their own species, but also alarm calls of other species and those of non-predatory birds. The Ring-tailed Lemur and a few other species have different calls and reactions to specific types of predators. With mating

calls, it has been shown that mouse lemurs that cannot be discerned visually respond more strongly to the calls of their own species, particularly when exposed to the calls of other mouse lemurs that they would encounter normally within their home range. Lemur calls can also be very loud and carry long distances. Ruffed lemurs use several loud calls that can be heard up to 1 km (0.62 mi) away on a clear, calm day. The loudest lemur is the Indri, whose calls can be heard up to 2 km (1.2 mi) or more and thus communicate more effectively the territorial boundaries over its 34 to 40 hectares (0.13 to 0.15 sq mi) home range. Both ruffed lemurs and the Indri exhibit contagious calling, where one individual or group starts a loud call and others within the area join in. The song of the Indri can last 45 seconds to more than 3 minutes and tends to coordinate to form a stable duet comparable to that of gibbons.

Tactile communication (touch) is mostly used by lemurs in the form of grooming, although the Ring-tailed Lemur also clumps together to sleep (in an order determined by rank), reaches out and touches adjacent members, and cuffs other members. Reaching out and touching another individual in this species has been shown to be a submissive behavior, done by younger or submissive animals towards older and more dominant members of the troop. Allogrooming, however, appears to occur more frequently between higher ranking individuals, a shared trait with other primate species. Unlike anthropoid primates, lemur grooming seems to be more intimate and mutual, often directly reciprocated. Anthropoids, on the other hand, use allogrooming to manage agonistic interactions. The Ring-tailed Lemur is known to be very tactile, spending between 5 and 11% of its time grooming.

## Predator avoidance

All lemurs experience some predation pressure. Common defenses against predation include the use of alarm calls and predator mobbing, mostly among diurnal lemurs. The leaping abilities of lemurs may have evolved for predator avoidance rather than for travel, according to a study in kinematics. Nocturnal lemurs are difficult to see and track at night and decrease their visibility by foraging alone. They also try to avoid predators by using concealing sleeping locations, such as nests, tree holes, or dense vegetation, and alternating between multiple sleeping locations. Even torpor and hibernation states among cheirogaleids may be partly due to high levels of predation. Infants are protected while foraging by either leaving them in the nest or by stashing them in a hidden location, where the infant remains immobile in the absence of the parent.

Diurnal lemurs are visible during the day, so many live in groups, where the increased number of eyes and ears helps aid in predator detection. Diurnal lemurs use and respond to alarm calls, even those of other lemur species and non-predatory birds. The Ring-tailed Lemur has different calls and reactions to different classes of predators, such as predatory birds, mammals, or snakes. Some lemurs, such as the Indri, use crypsis to camouflage themselves. They are often heard but difficult to see in the trees due to the dappled light, earning them the reputation of being "ghosts of the forest".

## Reproduction

Except for the Aye-aye and the Lac Alaotra Gentle Lemur, lemurs are seasonal breeders with very short mating and birth seasons influenced by the highly seasonal availability of resources in their environment. Mating seasons usually last less than three weeks each year, with the female vagina opening up only during a few hours or days of her most receptive time of estrus. These narrow windows for reproduction and resource availability appear to relate to their short gestation periods, rapid maturation, and low basal metabolic rates, as well as the high energy costs of reproduction for females. This may also relate to the relatively high mortality rate among adult females and the higher proportion of adult males in some lemur populations—both unusual traits among primates. In both the Aye-aye and Lac Alaotra Gentle Lemur, birth (parturition) occurs over a six-month period.

Lemurs time their mating and birth seasons so that all weaning periods are synchronized to match the time of highest food availability. Weaning occurs either before or shortly after the eruption of the first permanent molars in lemurs. Mouse lemurs are able to fit their entire breeding cycle into the wet season, whereas larger lemurs, such as sifakas, must lactate for two months during the dry season. Infant survival in some species, such as Milne-Edwards' Sifaka, has been shown to be directly impacted by both environmental conditions and the rank, age, and health of the mother. The breeding season is also affected by geographical location. For example, mouse lemurs give birth between September and October in their native habitat in the southern hemisphere, but from May through June in the captive settings in the northern hemisphere.

Woolly lemurs are nocturnal and typically give birth to one offspring, which they carry with them while foraging.

Scent factors heavily into lemur reproduction. Scent-marking activity escalates during the mating season. Pheromones may coordinate reproductive timing for females coming into estrus. Mating can be either monogamous or promiscuous for both males and females, and mating can include individuals from outside the group. Monogamous lemurs include the Red-bellied Lemur (*Eulemur rubriventer*) and the Mongoose Lemur (*Eulemur mongoz*), although the Mongoose Lemur has been observed mating outside of its pair bond. Monogamy is most common among nocturnal species, although some exhibit scramble competition, sexual suppression of subordinates, or competitions between males that avoid direct fighting. In mouse lemurs, males utilize sperm plugs, developed enlarged testes during the mating season, and develop size dimorphism (likely due to the

enlarged testes). These indicate a mating system known as scramble competition polygyny, where males cannot defend females or the resources that might attract them.

The gestation period varies within lemurs, ranging from 9 weeks in mouse lemurs and 9–10 weeks in dwarf lemurs to 18–24 weeks in other lemurs. The smaller, nocturnal lemurs, such as mouse lemurs, giant mouse lemurs, and dwarf lemurs, usually give birth to more than one infant, whereas the larger, nocturnal lemurs, such as fork-marked lemurs, sportive lemurs, and the Aye-aye usually have one offspring. Dwarf and mouse lemurs have up to four offspring, but both average only two. Ruffed lemurs are the only large, diurnal lemurs to consistently give birth to two or three offspring. All other lemurs have single births. Multiple births in lemurs are normally fraternal, and are known to occur in every five to six births in species such as the Ring-tailed Lemur and some *Eulemur*.

After the offspring are born, lemurs either carry them around or stash them while foraging. When transported, the infants either cling to the mother's fur or are carried in the mouth by the scruff. In some species, such as bamboo lemurs, infants are carried by mouth until they are able to cling to their mother's fur. Species that park their offspring include nocturnal species (e.g. mouse lemurs, sportive lemurs, and dwarf lemurs), bamboo lemurs, and ruffed lemurs. In the case of the ruffed lemurs, the young are altricial and the mothers build nests for them, much like the smaller, nocturnal lemur species. Woolly lemurs are unusual for nocturnal lemurs because they live in cohesive family groups and carry their single offspring with them rather than parking them. Alloparenting (multiple or group parenting) has been reported in all lemur families except the sportive lemurs and Aye-aye. Allonursing is also known to occur in several lemur groups. Even males have been observed caring for infants in species such as the Red-bellied Lemur, Mongoose Lemur, Eastern Lesser Bamboo Lemur, Silky Sifaka, Fat-tailed Dwarf Lemur, and ruffed lemurs.

Yet another trait that sets most lemurs apart from anthropoid primates is their long lifespan together with their high infant mortality. Many lemurs, including the Ring-tailed Lemur, have adapted to a highly seasonal environment, which has affected their birthrate, maturation, and twinning rate (r-selection). This helps them to recover rapidly from a population crash. In captivity, lemurs can live twice as long as they do in the wild, benefiting from consistent nutrition that meets their dietary requirements, medical advancements, and improved understanding of their housing requirements. In 1960, it was thought that lemurs could live between 23 and 25 years. We now know that the larger species can live for more than 30 years without showing signs of aging (senescence) and still be capable of reproduction.

## Cognitive abilities and tool use

Lemurs have traditionally been regarded as being less intelligent than anthropoid primates, with monkeys and apes often described as having more cunning, guile, and deceptiveness. Many lemur species, such as sifakas and the Ring-tailed Lemur, have scored lower on tests designed for monkeys while performing as well as monkeys on other tests. These comparisons may not be fair since lemurs prefer to manipulate objects

with their mouths (rather than their hands) and only take interest in objects when in captivity. Tool use has not been witnessed by lemurs in the wild, although in captivity the Common Brown Lemur and the Ring-tailed Lemur have been demonstrated to be able to understand and use tools.

A few lemurs have been noted to have relatively large brains. The extinct *Hadropithecus* was as large as a large male baboon and had a comparably sized brain, giving it the largest brain size relative to body size among all prosimians. The Aye-aye also has a large brain-to-body ratio, which may indicate a higher level of intelligence. However, despite having a built-in tool in the form of its thin, elongated middle finger, which it uses to fish for insect grubs, the Aye-aye has tested poorly in the use of extraneous tools.

## *Ecology*

Madagascar not only contains two radically different climatic zones, the rainforests of the east and the dry regions of the west, but also swings from extended drought to cyclone-generated floods. These climatic and geographical challenges, along with poor soils, low plant productivity, wide ranges of ecosystem complexity, and a lack of regularly fruiting trees (such as fig trees) have driven the evolution of lemurs' immense morphological and behavioral diversity. Their survival has required the ability to endure the persistent extremes, not yearly averages.

The Fossa (above) and the Madagascar Harrier-hawk (below) are predators of many lemur species.

Lemurs have either presently or formerly filled the ecological niches normally occupied by monkeys, squirrels, woodpeckers, and grazing ungulates. With the diversity of adaptations for specific ecological niches, habitat selections among lemur families and some genera are often very distinct, thus minimizing competition. In nocturnal lemurs from the more seasonal forests in the west, up to five species can coexist during the wet season due to high food abundance. However, to endure the extreme dry season, three of the five species utilize different dietary patterns and their underlying physiological traits to allow them to coexist: fork-marked lemurs feed on tree gum, sportive lemurs feed on leaves, and giant mouse lemurs sometimes feed on insect secretions. The other two species, the Gray Mouse Lemur and the Fat-tailed Dwarf Lemur (*Cheirogaleus medius*), avoid competition through reduced activity. The Gray Mouse Lemur uses bouts of torpor, while the Fat-tailed Dwarf Lemur hibernates completely. Similarly, on the east coast entire genera focus on specific food to avoid too much niche overlap. True lemurs and ruffed lemurs are frugivorous, indriids are folivorous, and bamboo lemurs specialize in bamboo and other grasses. Once again, seasonal dietary differences as well as subtle differences in substrate preferences, forest strata used, activity cycle, and social organization enable lemur species to coexist, although this time the species are more closely related and have similar niches. A classic example involves resource partitioning between three species of bamboo lemur that live in close proximity in small forested

areas: the Golden Bamboo Lemur, the Greater Bamboo Lemur, and the Eastern Lesser Bamboo Lemur (*Hapalemur griseus*). Each utilizes either different species of bamboo, different parts of the plant, or different layers in the forest. Nutrient and toxin content (such as cyanide) help regulate food selection, though seasonal food preferences are also known to play a role.

Dietary regimes of lemurs include folivory, frugivory, and omnivory, with some being highly adaptable while others specialize on foods such as plant exudates (tree gum) and bamboo. In some cases, lemur feeding patterns directly benefit the native plant life. When lemurs exploit nectar, they may act as pollinators as long as the functional parts of the flower are not damaged. In fact, several unrelated Malagasy flowering plants demonstrate lemur-specific pollination traits, and studies indicate that some diurnal species, such as the Red-bellied Lemur and the ruffed lemurs, act as major pollinators. Two examples of plant species that rely on lemurs for pollination include Traveller's Palm (*Ravenala madagascariensis*) and a species of legume-like liana, *Strongylodon cravieniae*. Seed dispersal is another service lemurs provide. After passing through the lemur gut, tree and vine seeds exhibit lower mortality and germinate faster. Latrine behavior exhibited by some lemurs may help improve soil quality and facilitate seed dispersal. Because of their importance in maintaining a healthy forest, frugivorous lemurs may qualify as keystone mutualists.

All lemurs, particularly the smaller species, are affected by predation and they are important prey items for predators. Humans are the most significant predator of diurnal lemurs, despite taboos that occasionally forbid the hunting and eating of certain lemur species. Other predators include native euplerids, such as the Fossa, feral cats, domestic dogs, snakes, diurnal birds of prey, owls, and crocodiles. Extinct giant eagles, including one or two species from the genus *Aquila* and the giant Malagasy Crowned Eagle (*Stephanoaetus mahery*), as well as the Giant Fossa (*Cryptoprocta spelea*), previously also preyed on lemurs, perhaps including the giant subfossil lemurs or their subadult offspring. The existence of these extinct giants suggests that predator-prey interactions involving lemurs were more complex than they are today. Today, predator size only restricts owls to the smaller lemurs, usually 100 g (3.5 oz) or less, while the larger lemurs fall victim to the larger diurnal birds of prey, such as the Madagascar Harrier-hawk (*Polyboroides radiatus*) and the Madagascar Buzzard (*Buteo brachypterus*).

## *Research*

Similarities that lemurs share with anthropoid primates, such as diet and social organization, along with their own unique traits, have made lemurs the most heavily studied of all mammal groups on Madagascar. Research often focuses on the link between ecology and social organization, but also on their behavior and morphophysiology (the study of anatomy in relation to function). Studies of their life-history traits, behavior and ecology help understanding of primate evolution, since they are thought to share similarities with ancestral primates.

Lemurs have been the focus of monographic series, action plans, field guides, and classic works in ethology. However, few species have been thoroughly studied to date, and most research has been preliminary and restricted to a single locality. Only recently have numerous scientific papers been published to explain the basic aspects of behavior and ecology of poorly known species. Field studies have given insights on population dynamics and evolutionary ecology of most genera and many species. Long-term research focused on identified individuals is in its infancy and has only been started for a few populations. However, learning opportunities are dwindling as habitat destruction and other factors threaten the existence of lemur populations across the island.


Berenty Private Reserve in southern Madagascar is both a popular tourist destination and research location. Alison Jolly began her research here in 1962.

Lemurs are mentioned in sailors' voyage logs as far back as 1608 and in 1658 that at least seven lemur species were described in detail by the French merchant, Étienne de Flacourt, who may also have been the only westerner to see and chronicle the existence of a giant (now extinct) lemur, which he called the *tretretretre*. Around 1703 merchants and sailors began bringing lemurs back to Europe, at which time James Petiver, an apothecary in London, described and illustrated the Mongoose Lemur. Starting in 1751, the London illustrator George Edwards began describing and illustrating some lemur species, of which a few were included in various editions of *Systema Naturae* by Carl Linnaeus. In the 1760s and 1770s, French naturalists Georges-Louis Leclerc, Comte de Buffon and Louis-Jean-Marie Daubenton began describing the anatomy of several lemur species. The first traveling naturalist to comment on lemurs was Philibert Commerçon in 1771, although it was Pierre Sonnerat who recorded a greater variety of lemur species during his travels.

During the 19th century, there was an explosion of new lemur descriptions and names, which later took decades to sort out. During this time, professional collectors gathered specimens for museums, menageries, and cabinets. Some of the major collectors were Johannes Hildebrandt and Charles Immanuel Forsyth Major. From these collections, as well as increasing observations of lemurs in their natural habitats, museum systematists including Albert Günther and John Edward Gray continued to contribute new names for new lemur species. However, the most notable contributions from this century includes the work of Alfred Grandidier, a naturalist and explorer who devoted himself to the study of Madagascar's natural history and local people. With the help of Alphonse Milne-Edwards, most of the diurnal lemurs were illustrated at this time. However, lemur taxonomic nomenclature took its modern form in the 1920s and 1930s, being standardized by Ernst Schwarz in 1931.

Although lemur taxonomy had developed, it was not until the 1950s and 1960s that the in-situ (or on-site) study of lemur behavior and ecology began to blossom. Jean-Jacques Petter and Arlette Petter-Rousseaux toured Madagascar in 1956 and 1957, surveying many of its lemur species and making important observations about their social groupings and reproduction. In 1960, the year of Madagascar's independence, David Attenborough introduced lemurs to the West with a commercial film. Under the guidance of John Buettner-Janusch, who founded the Duke Lemur Center in 1966, Alison Jolly traveled to Madagascar in 1962 to study the diet and social behavior of the Ring-tailed Lemur and Verreaux's Sifaka at Berenty Private Reserve. The Petters and Jolly spawned a new era of interest in lemur ecology and behavior and were shortly followed by anthropologists such as Alison Richard, Robert Sussman, Ian Tattersall, and many others. Following the political turmoil of the mid-1970s and Madagascar's revolution, field studies resumed in the 1980s, thanks in part to the renewed involvement of the Duke Lemur Center under the direction of Elwyn Simons and the conservation efforts of Patricia Wright. In the decades that followed, huge strides have been made in lemur studies and many new species have been discovered.

Ex situ research (or off-site research) is also popular among researchers looking to answer questions that are difficult to test in the field. For example, efforts to sequence the genome of the Gray Mouse Lemur will help researchers understand which genetic traits set primates apart from other mammals and will ultimately help understand what genomic traits set humans apart from other primates. One of the foremost lemur research facilities is the Duke Lemur Center (DLC) in Durham, North Carolina. It maintains the largest captive lemur population outside of Madagascar, which it maintains for non-invasive research and captive breeding. Many important research projects have been carried out there, including studies of lemur vocalizations, basic locomotor research, the kinematics of bipedalism, the effects of social complexity transitive reasoning, and cognition studies involving a lemur's ability to organize and retrieve sequences from memory. Other facilities, such as the Lemur Conservation Foundation, located near Myakka City, Florida, have also hosted research projects, such as one that looked at lemurs' ability to preferentially select tools based on functional qualities.

***Conservation status***

Lemurs in the spiny forests of Madagascar are threatened by deforestation for the creation of farmland and pasture (above) as well as firewood and charcoal production (below) for cooking fuel.

Lemurs are threatened by a host of environmental problems, including deforestation, hunting for bushmeat, live capture for the exotic pet trade, and climate change. As of 2005, the International Union for Conservation of Nature (IUCN) listed 16% of all lemur species as Critically Endangered, 23% as Endangered, 25% as Vulnerable, 28% as "Data Deficient", and only 8% as Least Concern. Over the next five years, at least 28 species were newly identified, none of which have had their conservation status assessed. Many are likely to be considered threatened since the new lemur species that have been described recently are typically confined to small regions. Given the rate of continued habitat destruction, undiscovered species could go extinct before being identified. Since the arrival of humans on the island approximately 2000 years ago, all endemic Malagasy vertebrates over 10 kg (22 lb) have disappeared, including 17 species, 8 genera, and 3

families of lemurs. The IUCN Species Survival Commission (IUCN/SSC), the International Primatological Society (IPS), and Conservation International (CI) have included as many as five lemurs in their biennial "Top 25 Most Endangered Primates". The 2008–2010 list includes the Greater Bamboo Lemur, Gray-headed Lemur (*Eulemur cinereiceps*), Blue-eyed Black Lemur (*Eulemur flavifrons*), Northern Sportive Lemur (*Lepilemur septentrionalis*), and Silky Sifaka.

Madagascar is one of the poorest countries in the world, with a high population growth rate of 2.5% per year and nearly 70% of the population living in poverty. The country is also burdened with high levels of debt and limited resources. These socioeconomic issues have complicated conservation efforts, even though the island of Madagascar has been recognized by IUCN/SSC as a critical primate region for over 20 years. Due to its relatively small land area—587,045 $km^2$ (226,659 sq mi)—compared to other high-priority biodiversity regions and its high levels of endemism, the country is considered one of the world's most important biodiversity hotspots, with lemur conservation being a high priority. Despite the added emphasis for conservation, there is no indication that the extinctions that began with the arrival of humans have come to an end.

## Threats in the wild

The greatest concern facing lemur populations is habitat destruction and degradation. Deforestation takes the form of local subsistence use, such as slash and burn agriculture (referred to as *tavy* in Malagasy), the creation of pasture for cattle through burning, and legal and illegal gathering of wood for firewood or charcoal production; commercial mining; and the illegal logging of precious hardwoods for foreign markets. After centuries of unsustainable use, as well as rapidly escalating forest destruction since 1950, less than 60,000 $km^2$ (23,000 sq mi) or 10% of Madagascar's land area remains forested. Only 17,000 $km^2$ (6,600 sq mi) or 3% of the island's land area is protected and due to dire economic conditions and political instability, most of the protected areas are ineffectively managed and defended. Some protected areas were set aside because they were naturally protected by their remote, isolated location, often on steep cliffs. Other areas, such as the dry forests and spiny forests of the west and south, receive little protection and are in serious danger of being destroyed.

Some species may be in risk of extinction even without complete deforestation, such as ruffed lemurs, which are very sensitive to habitat disturbance. If large fruit trees are removed, the forest may sustain fewer individuals of a species and their reproductive success may be affected for years. Small populations may be able to persist in isolated forest fragments for 20 to 40 years due to long generation times, but in the long term, such populations may not be viable. Small, isolated populations also risk extirpation by natural disasters and disease outbreaks (epizootics). Two diseases that are lethal to lemurs and could severely impact isolated lemur populations are toxoplasmosis, which is spread by feral cats, and the herpes simplex virus carried by humans.

Lemurs, such as this White-fronted Brown Lemur, are killed for bushmeat in Madagascar.

Climate change and weather-related natural disasters also threaten lemur survival. For the last 1000 years, western and highland regions have been growing significantly drier, but in the past few decades, severe drought has become much more frequent. There are indications that deforestation and forest fragmentation are accelerating this gradual desiccation. The effects of drought are even felt in the rainforests. As annual rainfall decreases, the larger trees that make up the high canopy suffer increased mortality, failure to fruit, and decreased production of new leaves, which folivorous lemurs prefer. Cyclones can defoliate an area, knock down canopy trees, and create landslides and flooding. This can leave lemur populations without fruit or leaves until the following spring, requiring them to subsist on crisis foods, such as epiphytes.

Lemurs are hunted for food by the local Malagasy, either for local subsistence or to supply a luxury meat market in the larger cities. Most rural Malagasy do not understand what "endangered" means, nor do they know that hunting lemurs is illegal or that lemurs are found only in Madagascar. Many Malagasy have taboo, or *fady*, about hunting and eating lemurs, but this does not prevent hunting in many regions. Even though hunting has been a threat to lemur populations in the past, it has recently become a more serious threat as socioeconomic conditions deteriorate. Economic hardships have caused people to move around the country in search of employment, leading local traditions to break down. Drought and famine can also relax the *fady* that protect lemurs. Larger species, such as sifakas and ruffed lemurs, are common targets, but smaller species are also hunted or accidentally caught in snares intended for larger prey. Experienced, organized hunting parties using firearms, slings and blowguns can kill as many as eight to twenty lemurs in one trip. Organized hunting parties and lemur traps can be found in both non-protected areas and remote corners of protected areas. National parks and other protected areas are not adequately protected by law enforcement agencies. Often, there are too few park rangers to cover a large area, and sometimes terrain within the park is too rugged to check regularly.

Although not as significant as deforestation and hunting, some lemurs, such as Crowned Lemurs and other species that have successfully been kept in captivity, are occasionally kept as exotic pets by Malagasy people. Bamboo lemurs are also kept as pets, although they only survive for up to two months. Live capture for the exotic pet trade in wealthier countries is not normally considered a threat due to strict regulations controlling their export.

## Conservation efforts

Rosewood is logged illegally from national parks, such as Marojejy.

Lemurs have drawn much attention to Madagascar and its endangered species. In this capacity, they act as flagship species, the most notable of which is the Ring-tailed Lemur, which is considered an icon of the country. The presence of lemurs in national parks helps drive ecotourism, which especially helps local communities living in the vicinity of the national parks, since it offers employment opportunities and the community receives half of the park entrance fees. In the case of Ranomafana National Park, job opportunities and other revenue from long-term research can rival that of ecotourism.

Starting in 1927, the Malagasy government has declared all lemurs as "protected" by establishing protected areas that are now classified under three categories: National Parks (Parcs Nationaux), Strict Nature Reserves (Réserves Naturelles Intégrales), and Special Reserves (Réserves Spéciales). There are currently 18 national parks, 5 strict nature reserves, and 22 special reserves, as well as several other small private reserves, such as Berenty Reserve and Sainte Luce Private Reserve, both near Fort Dauphin. All protected areas, excluding the private reserves, comprise approximately 3% of the land surface of Madagascar and are managed by Madagascar National Parks, formerly known as l'Association Nationale pour la Gestion des Aires Protégées (ANGAP), as well as other non-governmental organizations (NGOs), including Conservation International (CI), the Wildlife Conservation Society (WCS), and the World Wide Fund for Nature (WWF).

Most lemur species are covered by this network of protected areas, and a few species can be found in multiple parks or reserves.

Conservation is also facilitated by the Madagascar Fauna Group (MFG), an association of nearly 40 zoos and related organizations, including the Duke Lemur Center, the Durrell Wildlife Conservation Trust, and the Saint Louis Zoological Park. This international NGO supports Madagascar's Parc Ivoloina, helps protect Betampona Reserve and other protected areas, and promotes field research, breeding programs, conservation planning, and education in zoos. One of their major projects involved the release of captive Black-and-white Ruffed Lemurs, designed to help restock the dwindling population within Betampona Reserve.

Rice paddies have gradually replaced lemur habitat, particularly in the central part of the island.

Habitat corridors are needed for linking these protected areas so that small populations are not isolated. In September 2003 in Durban, South Africa, Madagascar's former president Marc Ravalomanana promised to triple the size of the island's protected areas in five years. This became known as the "Durban Vision". In June 2007, the World Heritage Committee included a sizable portion of Madagascar's eastern rainforests as a new UNESCO World Heritage Site.

Debt relief may help Madagascar protect its biodiversity. With the political crisis in 2009, illegal logging has proliferated and now threatens rainforests in the northeast, including its lemur inhabitants and the ecotourism that the local communities rely upon.

Captive lemur populations are maintained outside of Madagascar in many zoos, although the diversity of species is limited. Sikafas, for instance, do not survive well in captivity,

so few facilities have them. The largest captive lemur population can be found at the Duke Lemur Center (DLC), whose mission includes non-invasive research, conservation (e.g. captive breeding), and public education.

## Chapter- 7

# Ape

| Apes<br>Fossil range: Late Oligocene - Recent | |
|---|---|
|  | |
| Lar Gibbon (*Hylobates lar*) | |
| **Scientific classification** | |
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Mammalia |
| Subclass: | Theria |
| Infraclass: | Eutheria |
| Order: | Primates |
| Suborder: | Haplorrhini |
| Infraorder: | Simiiformes |
| Parvorder: | Catarrhini |
| Superfamily: | **Hominoidea** |

Gray, 1825

| Families |
| --- |
| Hylobatidae |
| Hominidae |
| †Proconsulidae |
| †Dryopithecidae |
| †Oreopithecidae |
| †Pliopithecidae |

Under the current classification system there are two families of **hominoids**:

- the family Hylobatidae consists of 4 genera and 14 species of gibbon, including the Lar Gibbon and the Siamang, collectively known as the lesser apes.
- the family Hominidae consisting of chimpanzees, gorillas, humans and orangutans collectively known as the great apes.

A few other primates, such as the Barbary Ape, have the word *ape* in their common names (usually to indicate lack of a tail), but they are not regarded as true apes.

Except for gorillas and humans, all true apes are agile climbers of trees. Their diet is best described as omnivorous, their diet consisting of fruit, including grass seeds, and in most cases other animals, either hunted or scavenged, along with anything else available and easily digested. They are native to Africa and Asia, although humans have spread to all parts of the world.

Most nonhuman ape species are rare or endangered. The chief threat to most of the endangered species is loss of tropical rainforest habitat, though some populations are further imperiled by hunting for bushmeat.

## *Historical and modern terminology*

"Ape", from Old English *apa*, is possibly an onomatopoetic imitation of animal chatter. The term has a history of rather imprecise usage. Its earliest meaning was a tailless (and therefore exceptionally human-like) non-human primate, but as zoological knowledge developed, it became clear that taillessness occurred in a number of different and otherwise unrelated species.

The original usage of "ape" in English might have referred to the baboon, an African monkey. Two tailless species of macaque are commonly named as apes, the Barbary ape of North Africa (introduced into Gibraltar), *Macaca sylvanus*, and the Sulawesi black ape or Celebes crested macaque, *M. nigra*.

Until a few decades ago, humans were thought to be distinctly set apart from the other apes (even from the other great apes), so much so that most people still do not think of the term "apes" to include humans at all. However, it is not considered accurate by many biologists to think of apes in a biological sense without considering humans to be

included. The terms "non-human apes" or "non-human great apes" is used with increasing frequency to show the monophyletic relationship of humans to the other apes while yet talking only about the non-human species.

A group of apes may be referred to as a *troop* or a *shrewdness*.

## *Biology*

The gibbon family, Hylobatidae, is composed of fifteen medium-sized species. Their major distinction is their long arms, which they use to brachiate through the trees. As an evolutionary adaptation to this arboreal lifestyle, their wrists are ball and socket joints. The largest of the gibbons, the Siamang, weighs up to 14 kg (31 lb). In comparison, the smallest great ape is the Common Chimpanzee at a modest 40 to 65 kg (88 to 143 lb).

The great ape family was previously referred to as Pongidae, and humans (and fossil hominids) were omitted from it, but there is no biological case for doing this. This definition is still used by many anthropologists and by lay people; however, it makes Pongidae paraphyletic, whereas most taxonomists nowadays encourage monophyletic groups. Chimpanzees, gorillas, humans and orangutans are all more closely related to one another than any of these four genera are to the gibbons. However, the term "hominid" is still used with the specific meaning of extinct animals more closely related to humans than the other great apes (for example, australopithecines), even though "hominin" is now correct in that usage. It is now usual to use even finer divisions, such as subfamilies and tribes to distinguish which hominoids are being discussed. Current evidence implies that humans share a common, extinct, ancestor with the chimpanzee line, from which we separated more recently than the gorilla line.

Both great apes and lesser apes fall within Catarrhini, which also includes the Old World monkeys of Africa and Eurasia. Within this group, both families of apes can be distinguished from these monkeys by the number of cusps on their molars (apes have five—the "Y-5" molar pattern, Old World monkeys have only four in a bilophodont pattern). Apes have more mobile shoulder joints and arms due to the dorsal position of the scapula, broad ribcages that are flatter front-to-back, and a shorter, less mobile spine compared to Old World monkeys (with caudal vertebrae greatly reduced, resulting in tail loss in some species). These are all anatomical adaptations to vertical hanging and swinging locomotion (brachiation) in the apes, as well as better balance in a bipedal pose. All living members of the Hylobatidae and Hominidae are tailless, and humans can therefore accurately be referred to as bipedal apes. However, there are also primates in other families that lack tails, and at least one (the Pig-Tailed Langur) that has been known to walk significant distances bipedally. The front skull is characterised by its sinuses, fusion of the frontal bone and post-orbital constriction.

Although the hominoid fossil record is far from complete, and the evidence is often fragmentary, there is enough to give a good outline of the evolutionary history of humans. The time of the split between humans and living apes used to be thought to have occurred 15 to 20 million years ago, or even up to 30 or 40 million years ago. Some apes

occurring within that time period, such as *Ramapithecus*, used to be considered as hominins, and possible ancestors of humans. Later fossil finds indicated that *Ramapithecus* was more closely related to the orangutan, and new biochemical evidence indicated that the last common ancestor of humans and other hominins occurred between 5 and 10 million years ago, and probably in the lower end of that range.

## *History of hominoid taxonomy*

The history of hominoid taxonomy is somewhat confusing and complex. The names of subgroups have changed their meaning over time as new evidence, from fossil discoveries and comparisons of anatomy and DNA sequences, has changed understanding of the relationships between hominoids. The story of the hominoid taxonomy is one of gradual demotion of humans from a special position in the taxonomy to being one branch among many. It also illustrates the growing influence of cladistics (the science of classifying living things by strict descent) on taxonomy.

As of 2006, there are eight extant genera of hominoids. They are the four great ape genera (*Homo* (humans), *Pan* (chimpanzees and bonobos), *Gorilla*, and *Pongo* (orangutans)), and the four genera of gibbons (*Hylobates*, *Hoolock*, *Nomascus*, and *Symphalangus*). (The genus for the hoolock gibbons was recently changed from *Bunopithecus* to *Hoolock*.)

In 1758, Carolus Linnaeus, relying on second- or third-hand accounts, placed a second species in *Homo* along with *H. sapiens*: *Homo troglodytes* ("cave-dwelling man"). It is not clear to which animal this name refers, as Linnaeus had no specimen to refer to, hence no precise description. Linnaeus named the orangutan *Simia satyrus* ("satyr monkey"). He placed the three genera *Homo*, *Simia* and *Lemur* in the order of Primates.

The *troglodytes* name was used for the chimpanzee by Blumenbach in 1775 but moved to the genus *Simia*. The orangutan was moved to the genus *Pongo* in 1799 by Lacépède.

Linnaeus's inclusion of humans in the primates with monkeys and apes was troubling for people who denied a close relationship between humans and the rest of the animal kingdom. Linnaeus's Lutheran Archbishop had accused him of "impiety." In a letter to Johann Georg Gmelin dated 25 February 1747, Linnaeus wrote:

> It is not pleasing to me that I must place humans among the primates, but man is intimately familiar with himself. Let's not quibble over words. It will be the same to me whatever name is applied. But I desperately seek from you and from the whole world a general difference between men and simians from the principles of Natural History. I certainly know of none. If only someone might tell me one! If I called man a simian or vice versa I would bring together all the theologians against me. Perhaps I ought to, in accordance with the law of Natural History.

Accordingly, Johann Friedrich Blumenbach in the first edition of his *Manual of Natural History* (1779), proposed that the primates be divided into the Quadrumana (four-handed,

i.e. apes and monkeys) and Bimana (two-handed, i.e. humans). This distinction was taken up by other naturalists, most notably Georges Cuvier. Some elevated the distinction to the level of order.

However, the many affinities between humans and other primates — and especially the great apes — made it clear that the distinction made no scientific sense. Charles Darwin wrote, in *The Descent of Man*:

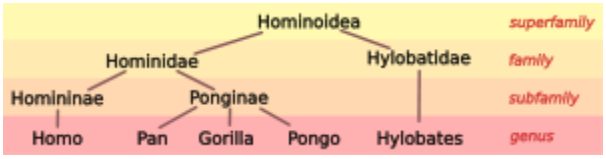
> The greater number of naturalists who have taken into consideration the whole structure of man, including his mental faculties, have followed Blumenbach and Cuvier, and have placed man in a separate Order, under the title of the Bimana, and therefore on an equality with the orders of the Quadrumana, Carnivora, etc. Recently many of our best naturalists have recurred to the view first propounded by Linnaeus, so remarkable for his sagacity, and have placed man in the same Order with the Quadrumana, under the title of the Primates. The justice of this conclusion will be admitted: for in the first place, we must bear in mind the comparative insignificance for classification of the great development of the brain in man, and that the strongly marked differences between the skulls of man and the Quadrumana (lately insisted upon by Bischoff, Aeby, and others) apparently follow from their differently developed brains. In the second place, we must remember that nearly all the other and more important differences between man and the Quadrumana are manifestly adaptive in their nature, and relate chiefly to the erect position of man; such as the structure of his hand, foot, and pelvis, the curvature of his spine, and the position of his head.

## Changes in taxonomy

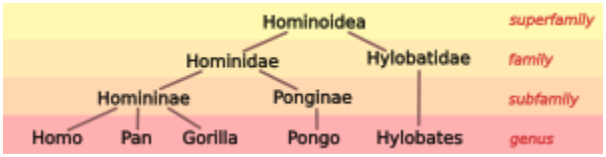
Until about 1960, the hominoids were usually divided into two families: humans and their extinct relatives in Hominidae, the other apes in Pongidae.


The 1960s saw the application of techniques from molecular biology to primate taxonomy. Goodman used his 1964 immunological study of serum proteins to propose a division of the hominoids into three families, with the non-human great apes in Pongidae and the lesser apes (gibbons) in Hylobatidae. The trichotomy of hominoid families, however, prompted scientists to ask which family speciated first from the common hominoid ancestor.

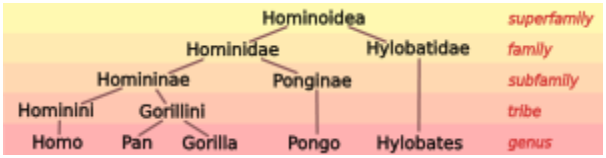
Within the superfamily Hominoidea, gibbons are the outgroup: this means that the rest of the hominoids are more closely related to each other than any of them are to gibbons. This led to the placing of the other great apes into the family Hominidae along with humans, by demoting the Pongidae to a subfamily; the Hominidae family now contained the subfamilies Homininae and Ponginae. Again, the three-way split in Ponginae led scientists to ask which of the three genera is least related to the others.



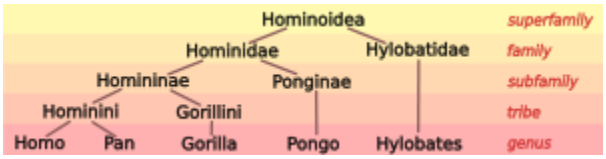

Investigation showed orangutans to be the outgroup, but comparing humans to all three other hominid genera showed that African apes (chimpanzees and gorillas) and humans are more closely related to each other than any of them are to orangutans. This led to the placing of the African apes in the subfamily Homininae, forming another three-way split. This classification was first proposed by M. Goodman in 1974.



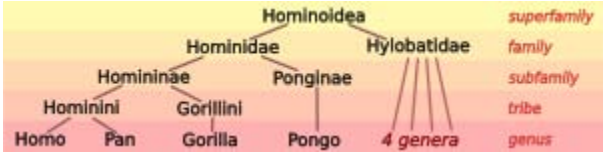

To try to resolve the hominine trichotomy, some authors proposed the division of the subfamily Homininae into the tribes Gorillini (African apes) and Hominini (humans).




However, DNA comparisons provide convincing evidence that within the subfamily Homininae, gorillas are the outgroup. This suggests that chimpanzees should be in Hominini along with humans. This classification was first proposed (though one rank lower) by M. Goodman et al. in 1990.




Later DNA comparisons split the gibbon genus *Hylobates* into four genera: *Hylobates*, *Hoolock*, *Nomascus*, and *Symphalangus*.



## *Classification and evolution*

As discussed above, hominoid taxonomy has undergone several changes. Genetic analysis shows that apes diverged from the Old World monkeys between 29 million and 34.5 million years ago. The lesser and greater apes split about 18 mya, and the hominid splits happened 14 mya (*Pongo*), 7 mya (*Gorilla*), and 3-5 mya (*Homo* & *Pan*).

Listed are the families and genera of apes; also listed are the extant species.

- **Superfamily Hominoidea**
  - Family Hylobatidae: gibbons
    - Genus *Hylobates*
      - Lar Gibbon or White-handed Gibbon, *H. lar*
      - Agile Gibbon or Black-handed Gibbon, *H. agilis*
      - Müller's Bornean Gibbon, *H. muelleri*
      - Silvery Gibbon, *H. moloch*
      - Pileated Gibbon or Capped Gibbon, *H. pileatus*
      - Kloss's Gibbon or Mentawai Gibbon or Bilou, *H. klossii*
    - Genus *Hoolock*
      - Western Hoolock Gibbon, *H. hoolock*
      - Eastern Hoolock Gibbon, *H. leuconedys*
    - Genus *Symphalangus*
      - Siamang, *S. syndactylus*
    - Genus *Nomascus*
      - Black Crested Gibbon, *N. concolor*
      - Eastern Black Crested Gibbon, *N. nasutus*
      - Hainan Gibbon, *N. hainanus*
      - Southern White-cheeked Gibbon *N. siki*
      - White-cheeked Crested Gibbon, *N. leucogenys*
      - Yellow-cheeked Gibbon, *N. gabriellae*
  - Family Hominidae: great apes
    - Genus *Pongo*: orangutans
      - Bornean Orangutan, *P. pygmaeus*
      - Sumatran Orangutan, *P. abelii*
    - Genus *Gorilla*: gorillas
      - Western Gorilla, *G. gorilla*
      - Eastern Gorilla, *G. beringei*
    - Genus *Homo*: humans
      - Human, *H. sapiens*
    - Genus *Pan*: chimpanzees
      - Common Chimpanzee, *P. troglodytes*
      - Bonobo, *P. paniscus*
      - Bili Ape, newly discovered, no taxonomy

## *Behaviour and cognition*

Although there had been earlier studies, the scientific investigation of behaviour and cognition in non-human apes expanded enormously during the latter half of the twentieth century. Major studies of behaviour in the field were completed on the three better-known great apes, for example by Jane Goodall, Dian Fossey and Birute Galdikas (field work on gibbons and the Bonobo is still relatively underdeveloped). These studies have shown that in their natural environments, the different apes show sharply varying social structure: gibbons are monogamous, territorial pair-bonders, orangutans are solitary, gorillas live in small troops with a single adult male leader, while chimpanzees live in larger troops with Bonobos exhibiting promiscuous sexual behaviour. Their diets also vary; gorillas are foliovores while the others are all primarily frugivores, although the Common Chimpanzee does some hunting for meat. Foraging behaviour is correspondingly variable.

All the apes are generally thought of as highly intelligent, and scientific study has broadly confirmed that they perform outstandingly well on a wide range of cognitive tests - though again there is relatively little data on gibbon cognition. The early studies by Wolfgang Köhler demonstrated exceptional problem-solving abilities in chimpanzees, which Köhler attributed to insight. The use of tools has been repeatedly demonstrated; more recently, the manufacture of tools has been documented, both in the wild and in laboratory tests. Imitation is much more easily demonstrated in great apes than in other primate species. Almost all the studies in animal language acquisition have been completed with great apes, and though there is continuing dispute as to whether they demonstrate real language abilities, there is no doubt that they involve significant feats of learning. Chimpanzees in different parts of Africa have developed tools that are used in food acquisition, demonstrating a form of animal culture.

## *Cultural aspects of non-human apes*

Often, non-human apes are said to be the result of a curse—a Jewish folktale claims that one of the races who built the Tower of Babel became apes as punishment, while Muslim lore says that the Jews of Eilat became non-human apes as punishment for fishing on the Sabbath. Some sects of Christianity have folklore that claims that these apes are a symbol of lust and were created by Satan in response to God's creation of humans. It is uncertain whether any of these references are to any specific apes. All of these concepts date from a period when neither the distinction between apes and monkeys, nor the fact that humans are apes, was widely understood, if understood at all.