Primates (Lemurs, Lorises, Tarsiers, Monkeys and Apes)

Introductory article

Online posting date: 15th March 2013

Alfred L Rosenberger, *Brooklyn College, Brooklyn, New York, USA*

Walter C Hartwig, *Touro University College of Osteopathic Medicine, Vallejo, California, USA*

Based in part on the previous version of this eLS article 'Orthologues, Paralogues and Xenologues in Human and Other Genomes' (2008) by Olga Zhaxybayeva, J Peter Gogarten and Lorraine Olendzenski.

The modern primates are a diverse order of mammals that includes lemurs, lorises, tarsiers, monkeys, apes and humans. They are united by a 65 My evolutionary history originally built on an adaptive foundation of tropical arboreality and so they share a collection of traits that are unique among mammals, such as an excellent sense of balance, acute vision, good hand–eye coordination, a large grasping first toe, prehensile feet and hands and a flexible, athletic limb anatomy. Primates also tend to live in relatively large social groups and often have correlatively enlarged brains. They almost always give birth to singletons that grow over a prolonged period, which is advantageous to cognitive development, learning and socialisation. Fossil nonhuman primates have been found on all continents but Australia and Antarctica. Primates have been important elements of tropical and subtropical faunas since mammals rebounded following the mass extinction that also promoted the demise of dinosaurs.

Introduction

Primates are probably the most studied of all mammals, and there is abundant reference information available in the form of books, scientific articles and websites, yet many crucial questions remain unanswered. Primates also enjoy the misfortune of being everywhere threatened with imminent or inevitable extinction by one of their own – humans – which is ironic because as we lose nonhuman primate species and the natural environments in which they evolved, we exhaust the sharpest lenses and sources of information we can bring to bear on our own remote history. Oddly, the affinity that people have for the nonhuman primates is also everywhere evident as humans are inevitably drawn to them because many look and behave so much like us. **See also**: Mammalia

The modern primates (hereafter referring to the nonhuman species) are a diverse order of mammals that includes six major groups: lemurs, lorises, tarsiers, monkeys, apes and humans (Fleagle, 1999). Living primates are concentrated in tropical and subtropical habitats of South America, Africa and Asia and dryer, more open country particularly in Sub-Saharan Africa. In tropical rainforests, primates rank high among the mammalian groups in terms of taxonomic diversity, although they are nowhere near the levels exhibited by the top two groups, rodents and bats. However, few if any extant mammalian orders match the primates in terms of morphological and behavioural variety.

In recent decades, scientists have developed a widely accepted arrangement for classifying the six major living divisions (**Table 1**) according to their phylogenetic, or cladistic, inter-relationships (Szalay and Delson, 1979). But a dual system of concepts and terms is still in use and can cause some confusion, as some scholars also have a preference for traditional terms that are not phylogenetically defined but have historical and, to some extent, functional or adaptive significance. Thus, today we know that the 'monkeys' are not a unified phylogenetic group but are actually comprised of two distinct lineages with separate ancestries and contrasting histories, one evolving isolated in the New World (platyrrhines) and the other in the Old World (cercopithecoids) amongst other primates. Although we call them monkeys, cercopithecoids are more closely related to apes and humans than they are to the platyrrhines; platyrrhines are an offshoot of early anthropoids that arose before cercopithecoids and their ape and human relatives (hominoids) appeared. We also know that the tarsier, a tiny bizarrely adapted, goggle-eyed primate, is more closely related to anthropoid primates than to lemurs and lorises, but many collect tarsiers, lemurs and lorises

eLS subject area: Evolution & Diversity of Life

How to cite:
Rosenberger, Alfred L; and Hartwig, Walter C (March 2013) Primates (Lemurs, Lorises, Tarsiers, Monkeys and Apes). In: eLS. John Wiley & Sons, Ltd: Chichester.
DOI: 10.1002/9780470015902.a0001572.pub3

Table 1 A classification of living primates

Suborder	Infraorder	Superfamily	Family	Subfamily	Genera	Species
Strepsirhini	Lemuriformes	Lemuroidea	Lemuridae		*Lemur*	1
					Eulemur	5
					Hapalemur	3
					Varecia	1
			Cheirogaleidae		*Cheirogaleus*	2
					Microcebus	3
					Mirza	1
					Allocebus	1
					Phaner	1
			Lepilemuridae		*Lepilemur*	7
			Indriidae		*Indri*	1
					Propithecus	3
					Avahi	2
			Daubentoniidae		*Daubentonia*	1
		Lorisoidea	Lorisidae		*Loris*	1
					Perodicticus	1
					Pseudopotto	1
					Arctocebus	1
					Nycticebus	3
			Galagidae		*Galago*	3
					Otolemur	2
					Galagoides	4
					Euoticus	2
Haplorhini	Tarsiiformes	Tarsioidea	Tarsiidae		*Tarsius*	5
	Platyrrhini	Atelidae	Atelidae	Atelinae	*Ateles*	4
					Alouatta	6
					Lagothrix	2
					Brachyteles	1
			Pitheciidae	Pitheciinae	*Pithecia*	5
					Chiropotes	2
					Cacajao	2
				Homunculinae	*Aotus*	8
					Callicebus	11
			Cebidae	Cebinae	*Cebus*	4
					Saimiri	2
				Callitrichinae	*Callithrix*	13
					Cebulla	1
					Callimico	1
					Saguinus	12
					Leontopithecus	4
	Catarrhini	Cercopithecoidea	Cercopithecidae	Cercopithecinae	*Cercopithecus*	20
					Allenopithecus	1
					Miopithecus	1
					Erythrocebus	1
					Chlorocebus	1
					Macaca	19
					Mandrillus	2
					Cercocebus	5
					Lophocebus	2
					Papio	5
					Theropithecus	1
				Colobinae	*Colobus*	4
					Procolobus	1
					Piliocolobus	1

(*continued*)

Table 1 Continued

Suborder	Infraorder	Superfamily	Family	Subfamily	Genera	Species
					Semnopithecus	1
					Kasi	2
					Trachypithecus	7
					Presbytis	7
					Nasalis	1
					Simias	1
					Pygathrix	1
					Rhinopithecus	4
		Hominoidea	Hylobatidae		*Hylobates*	9
			Hominidae	Homininae	*Homo*	1
					Pan	2
					Gorilla	1
				Ponginae	*Pongo*	1

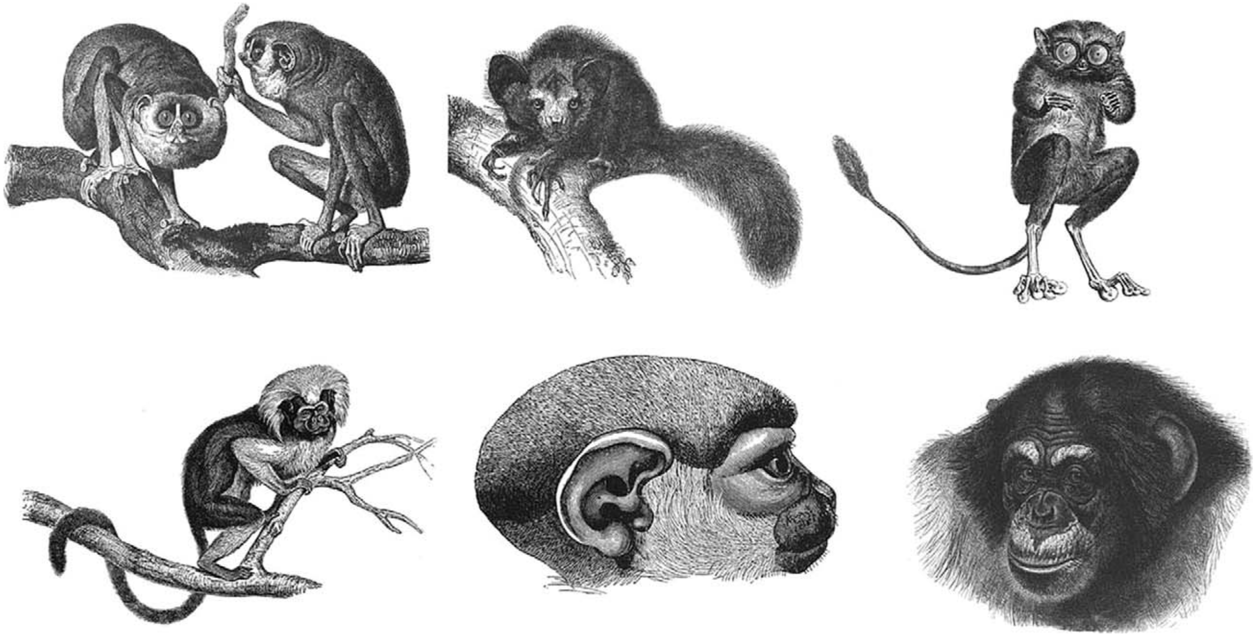

Figure 1 A selection of primate portraits. Clockwise from top left: Slender loris (*Nycticebus*), aye-aye (*Daubentonia*), tarsier (*Tarsius*), chimpanzee (*Pan*), squirrel monkey (*Saimiri*) and tamarin (*Saguinus*). Adapted from Harter (1979).

into a group called 'prosimians', roughly meaning pre-monkeys. This is a holdover from the eighteenth and nineteenth centuries when the method for classifying reflected judgements as to the 'grade' of evolution attained by species rather than their cladistic affinities, when humans were seen as the epitome of nature and the benchmark for making such judgements. The alternative, modern phylogenetic approach splits the living primates into two groups named after the shape of their nostrils, placing tarsiers and anthropoids in the Haplorhini (simple nosed) and assigning lemurs and lorises to the Strepsirhini (twisted nosed). **See also**: New World Monkeys; Old World Monkeys

The casual observer will often find it easy to identify most primates (**Figure 1**). In the trees, they are the most agile and acrobatic of all nonflying mammals, walking, running, leaping, hanging and swinging through the canopy aided by feet that grasp and mobile shoulders. Many being cat-sized and larger, leaves rustle and branches sway as they locomote, for primates are highly adept – more than any other mammal – in moving through the flexible twigs of the outer canopy. They use their hands as we do to grasp and manipulate with a delicate touch, even when the thumb is not opposable to the index finger. Keen stereoscopic eyesight guides their movement and informs their curiosity. They are furry, often with colourful coats, sometimes with long, luxurious tails. They love fruit. They are rarely solitary but live in groups of varying sizes whose members tend to maintain vocal if not visual contact while foraging. The ground dwellers, which are mostly cercopithecoids and apes, are equally distinctive and recognisable as they have retained all of these bodily traits and magnified others, most notably in areas that suggest high intelligence, intense curiosity and the profoundly complex ways in which interpersonal interactions unfold, so reminiscent of human beings.

Notwithstanding these impressions, technically how to delimit the Order Primates and distinguish it from other mammalian orders has been a matter of intense controversy since the 1960s (Martin, 1990). Ideally, one would wish to rely on a set of universally derived features that are shared by all primates and separates them from other mammals in the same way that, for example, bat wings and rodent gnawing incisors serve to characterise those groups. Powerful diagnostic traits such as these are significant adaptively and also phylogenetically. They indicate that all bats and rodents have their own unique common ancestry and their origins involved entry into unique adaptive zones. But identifying such features among primates turns out not to be simple and the debate has become a line-drawing predicament: Where to place the cut-off between a primate and its closest relatives?

Cladograms (**Figure 2**) are tree-like diagrams designed to illustrate overall genetic relatednes: how close one group is to another (e.g. species A is more closely related to B than to C), but not in terms of actual ancestry and descent (e.g. species X evolved into Y). The lower branches of a cladogram are the early basal members of a radiation, which for primates is a collection of several families known as plesiadapiforms. These are called stem taxonomic groups. They tend to link up to the primate 'super tree' in a linear sequence of branches. But at some point above the stem series, there will be a singular node from which all the living forms and their immediate fossil relatives arise. This constitutes the crown group. A classification predicament, the crown–stem dilemma, often emerges because two perfectly valid classifications can be developed from this model, each with advantages and disadvantages. It is obvious that the crown group, which is called euprimates ('real primates'), must be included in the Order Primates, but what about the plesiadapiforms, the stem primate group? A crown-based classification benefits from a certain coherence. The disadvantage is that this emphasis is somewhat static. By circumscribing the primates based exclusively on living forms, it might lead us to overlook species and anatomies that are actually part of the primate story but are omitted because of an arbitrary decision, for the sole purpose of classification, to simplify the complex patterns generated by evolution. Most pointedly, this approach makes it difficult to reconstruct the sequence by which euprimate characteristics came into being before the pattern was full blown. Emphasising the stem group by including the plesiadapiforms, however, has the advantage of configuring the Order Primates as a monophyletic group that reveals

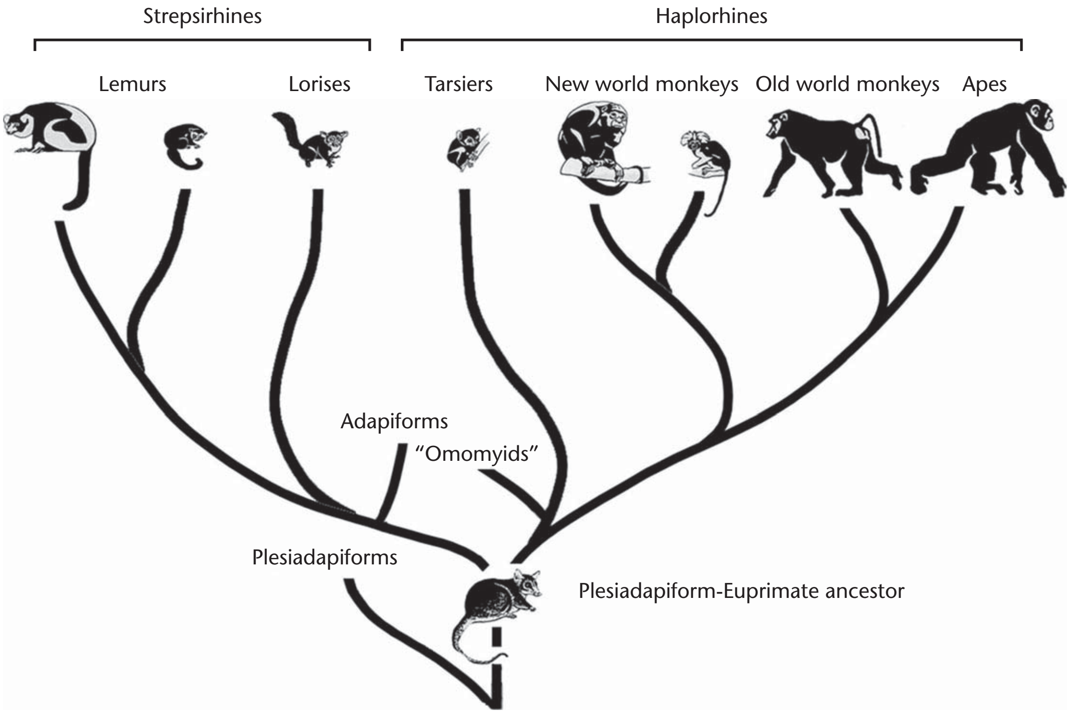

Figure 2 Cladistic relationships of the major primate groups. The strepsirhines and haplorhines are euprimates, distinct from the primate stem group, the plesiadapiforms. Adapiforms are fossil strepsirhines. 'Omomyids' are shown in quotations as the affinities of this group are not well known; some are close tarsier relatives, whereas others may be more basal haplorhines with various affiliations. Adapted from Soligo and Martin (2007). © Elsevier.

the morphological continuity that primates share with other mammalian orders, thus their more remote origins. Its disadvantage is that the order seems less uniform anatomically and adaptively. **See also**: Dermoptera (Flying Lemurs); Mammalia; Molecular Evolution: Introduction; Molecular Phylogeny Reconstruction; Scandentia (Tree Shrews)

Primate Origins

There are several competing models of primate origins (Cartmill, 1993). These views reflect differences in conceptual approach, whether to be guided primarily by contemporary anatomy, fossils or ecology. Since the 1970s, the most popular proposal has been Cartmill's visual predation hypothesis (Cartmill, 1974). It sees the first primates as visually oriented predators with a locomotor skeleton specialised to allow foraging in an arboreal, small-branch setting. It emphasises features associated with the visual system, like the forward-facing eyes also seen among carnivorous mammals. Living primates also have a bony bar that encircles the eyeball laterally (in living strepsirhines) or a partition that backs up the eye posteriorly (in haplorhines), suggesting that vision is important. The visual predation hypothesis has had its own evolution, starting off as a stem-based suggestion and evolving into a crown-based proposal that excludes the plesiadapiforms – which lack these eye-related features – from the order. A second view sees the stem primate breakthrough as a shift in diet followed by a euprimate innovation in locomotion (e.g. Szalay *et al*., 1987). It emphasises the universality of the euprimates' novel foot grasping ability, their widespread, early evolution of long hindlimbs and ankle joints designed for propulsion and stability, and the pervasive blunt-cusped molar teeth, beginning with plesiadapiforms, designed for chewing the enormous variety of fruit (not insects or leaves) found in the canopy, which ultimately become the primate food of choice. It also relies on anatomical details of the ear region that can be used as a touchstone to identify the first primates, but these are not yet explained functionally or developmentally. A third idea focuses on ecology. The angiosperm coevolution hypothesis, elaborated by Sussman (1991), sees the order as an ecological partner involved in contributing to the rise of woody, fruit-bearing trees that began their own success contemporaneously, aided by primates who would eventually serve as major seed dispersers of these plants. Molecular studies have been valuable in trying to pinpoint the time when primates first originated. One recent study (dos Reis *et al*., 2012) suggests that they may be one of the oldest modern orders to appear, at approximately 68–82 Ma, which is before the asteroid impact event that defines the global extinction and faunal turnover at the boundary between the Cretaceous and Palaeocene epochs at 65 My.

How then to explain primate origins? Since the nineteenth century it has been evident that the various orders and adaptive radiations of mammals are each characterised by anatomical specialisations that enable unique access to a type of food got by travelling in a certain way through a particular habitat. The combination of teeth and limbs, particularly the hands and feet (think hooves and clawed paws) that interact directly with the substrate the animals move through, is a large part of what makes a horse an open country, grazing perissodactyl and a tiger a fleet, killing carnivore. It seems indisputable that the universal adaptive zone of primates (excepting a few recent terrestrial offshoots that are clearly secondary) involves tropical arboreality based on a core, frugivorous diet, that is, a body plan that allows manoeuvrability in the trees in order to acquire its most prodigious, easily edible products, fruits. However, starchy and fatty fruit alone, either the pulp or rinds, cannot provide all the nutrients required, so the first primates must also have supplemented their diet with specific additives to provide protein, such as insects or seeds. Among the plesiadapiform subgroups, there are indications that the shift into this adaptive zone was taking place. Their cheek teeth are not the pointy, crested types found among more primitive insect-eating mammals. They are blunt and rounded, typical of frugivores, including predatory seed eaters. Some plesiadapiforms have long manual digits capable of grasping and a divergent, gripping but nonopposable large toe (hallux) tipped with a flat nail (Bloch and Boyer, 2002). The other digits, however, are dressed with claws, as expected. Furthermore, they have small, widely spaced eyes, no postorbital bar and a prodigious snout – one of several characteristics signifying a well developed olfactory system – often finished off anteriorly by a set of large, jutting incisors. All these indicate a smell-oriented foraging mode taking place in the trees, with the face still being used as a beak-like probe to lodge free small adherent food items such as the small fruits and seeds of early angiosperm plants and the occasional insect. None of this means plesiadapiforms were the direct ancestors of primates – most are already too specialised along their own unique trajectories, and cladistic analysis cannot provide that information anyway. But if a broad concept of the order is employed and its stem groups included, it allows reconstructing what the last common ancestor shared by plesiadapiforms and euprimates would have been like and what the transition to euprimates would have involved.

This synthesis is not consistent with the visual predation hypothesis, but it has elements that match the expectations of the other ideas (Rosenberger, 2010a). Reconstructed this way, the plesiadapiform–euprimate common ancestor would have been preadapted to spin off a second major phase of primate evolution leading to the first crown primates, whose anatomy is known rather well from abundant early Eocene fossils. This coincided with a second phase of angiosperm evolution. Their fruits became larger and more colourful, more appetising to primates and highly stimulating to the food chain of a diversifying arboreal fauna that included massive arrays of insects and arthropods. With newly enhanced leaping and visual adaptations, the universal habit of primates widely roaming the forest from fruit tree to fruit tree would have become effective. Evolving relatively flattened nails on the thumb (pollex) and lateral fingers and toes (except for the slightly built grooming claws on the second and/or third toes), along with wide, flat underlying finger bones (Maiolino *et al.*, 2011), suggests the appearance of soft, sensitive fingertips. Gripping without clawed digits may have been an alternative means of preventing slippage during locomotion on supports, and it would have set the stage for developing the enhanced fine motor control and sensitivity of the fingers for manipulating food objects. Thus, in conjunction with newly evolved long, leaping legs, these features made it possible for euprimates to develop acrobatic arboreal locomotion, replacing the more cautious, scampering type of quadrupedalism that characterised the relatively short-legged, claw-based behaviour of plesiadapiforms. Pudgy fingertips are also associated with the grasping locomotion that is required in negotiating the small-branch setting of the canopy periphery where fruit is most abundant, so one can imagine euprimates plotting convenient travel paths through the treetops without much concern for the gaps between branches, their thickness or weight-bearing capacity. During this phase as well, the more frugivorous primates would have probably established a firm role as angiosperm seed dispersers instead of consumers, as the trees themselves began to produce large, attractive pulpy fruits as food in order to have their seeds swallowed (not chewed) and carried away whole to the next feeding site and beyond (Rosenberger, 2010a).

Basics of Design

Among the mix of circumscribed adaptive milieus in the mammalian world that require highly engineered bodies – to list a few, there are gliders, flyers, swimmers, climbers, burrowers, high-speed runners, shambling quadrupeds and upside-down grappling-hook hangers – is one ecological space that can be exploited by the opposite, a relatively unspecialised, functionally versatile anatomy. Primates occupy that niche and it is imprinted in their body plan. Although other orders have modified the extremities by reducing the number of digits, evolving hooved digit tips, fusing the paired long bones of the lower leg and arm or altering the shoulder by eliminating the clavicle, primate skeletons have maintained a compliant design that excels in navigating the extraordinarily varied architecture of the tropical rainforest. The one outstanding, universal (except for humans) departure from primitive mammals that sets primates apart from nearly all other orders is the opposable first toe, of a foot that presents a stunning variety across the order (**Figure 3**). This co-occurs with some form of manual grasping made possible by a variety of anatomical arrangements of the hand to facilitate clutching behaviours, functionally augmented by the touch-sensitive fingertips with nails instead of snagging claws (not so in aye-ayes and callitrichine platyrrhines, two separate reversions to the clawed pattern).

Had primates not evolved those grasping feet, one would be hard pressed to explain why their skeletons are so non-specialised in other areas. With large grasping feet and hands, the answer becomes evident. In the trees, no matter what and where a quadrupedal primate feeds, almost every step cycle requires a foothold and hand placement of out-stretched limbs on a cylindrical, sometimes slippery, angled surface. The substrate may be thick or thin, stout or flexible under body weight. And, not all of these contact points will fall directly in the line of travel or directly below the animal's centre of gravity. The versatile construction of a primate's limbs make them multi-jointed link systems that allow accuracy of reach and swivelling at any angle – backward, forward, to the side, up or down, elbows and knees held close to the body core or cantilevered outwards, travelling below or above a branch, in a quadrupedal stance or clinging vertically or hanging from the tail – to project and position a hand or foot where it is needed and in the proper orientation to manage a grasp.

The absence of long bone, dental and cranial specialisations are the reasons primates are often described as retaining primitive mammalian characteristics, and it partly explains why it has been difficult to arrive at a consensus in diagnosing the order. Even the terrestrial offshoots of this central adaptive theme bear indelible stamps of arboreality. With regard to feeding, primate dentitions are also generalised in structure and quite omnivorous by mammalian standards. They tend to retain a full set of the four tooth groups (incisors, canine, premolars and molars), rarely lose all the teeth from any one group, have not multiplied tooth counts like armadillos, evolved milling cheek teeth like horses, monster canines like sabre-toothed cats or toothless jaws like anteaters. The relatively simple design of primate molars varies mostly by being either pointy- or blunt cusped, with a fairly consistent pattern of ridges built into the occlusal surfaces of uppers and lowers to facilitate mastication. The ridges range from being rather dull to edgy enough to cut a leaf, but they are hardly ever razor sharp. The primate skull is equally simple in comparison with other mammals that may carry horns, elongate tubular snouts or an enormous cyclopean nasal passage over which a trunk is fit. The only obvious, fully unique cranial feature exhibited by a living primate and no other mammal occurs among anthropoids. Their orbits, like ours for we are anthropoids, too, are the only ones that

Figure 3 (a, b) The feet and hands of primates. The diverse morphology of the hands (top row) and feet (bottom row) of primates is an indication of their versatile adaptations to arboreal (and terrestrial) locomotion. (a) Humans are shown in the inset and tree shrews (*Tupaia*), an example of a primitive anatomy lacking a grasping hallux and significant manual prehension, is shown on the top left. Others, from left to right are: Bush baby (*Galago*), Tarsier (*Tarsius*), Slow loris (*Nycticebus*), Indri (*Indri*) and Aye-aye (*Daubentonia*). (b) Chimpanzee (*Pan*), Orangutan (*Pongo*), Siamang (*Hylobates*), Baboon (*Papio*) and Gorilla (*Gorilla*). Reprinted with permission from Biegert (1963). © Wenner-Gren Foundation, Inc.


(a)
(b)

have a fully enclosed bony socket enveloping the eyeball. Another likely unique set of features is less obvious but important in aligning the plesiadapiforms with the euprimates. It involves the construction of the middle ear, how some arteries travel through it in bony canals and how its bottom is formed by an outgrowth of the bone that houses the inner ear, called the petrosal (Silcox *et al*., 2007).

Under this flexibility of design, primates came to evolve diverse forms of locomotion and highly varied diets. Their locomotor repertoires, involving above- and below-branch activities, include arboreal (and terrestrial) quadrupedalism, slow climbing, brachiation, vertical clinging and leaping and bipedalism. Dietarily, feeding preferences include a mix of soft- and hard-fruit frugivory, seed eating, folivory, insectivory or animalivory, exudativory and in tarsiers a strictly predaceous diet. No other orders combine such a stunning variety of food types coupled with diverse locomotor styles. And, virtually any primate species will combine almost imperceptibly several of these food types as their daily lives unfold.

The primate body is also noteworthy in presenting a variety of features that have little or nothing to do with locomotion or feeding but reflect self-care, interpersonal, social or mating strategy adaptations. Lemurs, lorises, tarsiers and even a few New World monkeys have grooming claws on one or more pedal digits. This may reflect the widespread importance of fur conditioning and parasite removal, for health and social (which also equates to health) reasons: primates live in a wet world where tiny organisms, some potentially harmful, abound. Living strepsirhines also have a toothcomb for grooming, a combined structure formed by the lower incisors and canines that have been reshaped to work perfectly as a toiletry tool. Other New World monkeys, Old World monkeys and apes have no specific modifications to serve similar purposes. Instead, but these biological roles have clearly been transferred to their all-purpose hands, as any zoogoer will see while watching the intimate attention one baboon gives to another during highly stereotyped grooming episodes. The canine teeth of anthropoid primates vary a great deal in size and shape as an expression of sexual dimorphism, according to how large the social group is and to what extent contest competition occurs among males competing for females. The skulls and jaws of some primates are functionally redesigned to enhance vocalisations as a form of advertisement. This has happened most famously among the New World howler monkeys, where the head is highly modified to accommodate an enormously enlarged voicebox in the neck that produces long-distance, low frequency booming calls that are socially important. Externally, other signalling channels evolved in particular species, like the raised ring tail advertising a stink fight that is underway in a band of lemurs; the red, white and blue hues of the male mandrill's face that indicates social status; the chest patch of skin that is linked to arousal and dominance in male gelada baboons; the sexual swelling of the female chimpanzee that signifies she is in heat; or the cosmetic makeup culture that may be an extrapolation of an evolved system of sexual gestures in human females. **See also**: Adaptation and Natural Selection: Overview; Brain Evolution and Comparative Neuroanatomy; Diversity of Life; Evolution of Ecosystems: Terrestrial; Locomotion; Natural Selection: Introduction

Adaptive Radiations

Primates are organised taxonomically into two broadly distinct, monophyletic groups, the Strepsirhini and Haplorhini (**Table 1**). Living strepsirhines, the lemurs (lemuriforms) and lorises (lorisiforms), are in a sense lip-less. They have a dog-like snout tipped with a bulbous, moist, textured, glandular patch of vertically grooved skin that is continuous with the inner nostrils and also tethered to the gum and palate inside the mouth via a strip that runs through a wide gap situated between the upper incisors. This rhinarium, common among more conservative mammals, reflects a high reliance on the sense of smell and importance of the snout and its whiskers as touch sensors in these largely nocturnal strepsirhines (Muchlinski, 2008). Cranially, it is part of an extensive olfactory system (Smith *et al*., 2007) and dentally it is complemented by low-crowned upper incisors and an unusual arrangement of lower teeth, the toothcomb, a complex that has evolved independently in several orders of mammals. It is made up of six slender, elongate, closely aligned and horizontally oriented teeth, composed of all four incisors and both canines. Given its position in the snout, the tooth comb adds an important olfactory component to the grooming process (Rosenberger and Strasser, 1985). The relatively large eyes of strepsirhines are also nocturnally adapted (Martin, 1990). Their retinas, where the photoreceptors are located, are backed by an additional membrane (tapetum lucidum) whose function is to amplify the limited available night light by mirroring it back to stimulate the photoreceptors a second time. As in lemurs and lorises, this is the optical source of the eyeshine seen in domestic cats and many nocturnal mammals, allowing them to exploit levels of light invisible to the human eye. The strepsirhines are now relatively restricted geographically to suitable Old World habitats of Africa and Asia, but their occurrence in Madagascar is a particularly stunning example of adaptive variety and diversification.

Living haplorhines are the tarsier, New and Old World monkeys, apes and humans. They all have a more human-like configuration of the nose and mouth, although nowhere among them are the lips off-colored, puffy and everted in the typical *Homo sapiens* fashion, a feature that perhaps evolved as a component of courtship behaviour. In haplorhine primates, the nose is separated from the mouth by a hairy flap of skin that is not attached to the gum and is quite well muscled and innervated, thus highly mobile and capable of expression (Smith *et al*., 2007). Haplorhine eyes are also distinctive and designed for high visual acuity rather than low light conditions. They lack the tapetum lucidum, so the retina is not subject to the blurry interference that may result from decoding light originating from two locations, the true source and its reflected position. Furthermore, haplorhine retinas have a concentrated spot (fovea centralis) where receptor cells occur in very high density. This enables them to see fine detail. Their eyes are also set close and forward facing, which improves depth perception in the central field of vision. Even the nocturnal tarsier has these features, which, in conjunction with absurdly enlarged eyeballs – the largest of all mammals relative to body size – are the reasons why it is thought that they evolved from a diurnal haplorhine ancestor but reverted to night living as a specialised predatory strategy. Living haplorhines are more broadly distributed geographically than strepsirhines as they also live in the New World. **See also**: Old World Monkeys

Strepsirhine primates now include only the lemuriforms and lorisiforms, but their fossil record goes as far back as the Eocene, when a very diverse group, the adapiforms, is represented by abundant fossils found in North America, Europe, Asia and Africa. The adapiforms lacked the toothcomb but had other strepsirhine traits. In the absence of this defining characteristic, under the prosimian–anthropoid paradigm the adapiforms were also of particular interest because palaeontologist often considered them to be the most primitive euprimates as well as potential ancestors to anthropoids. Although this view has largely become outmoded under the strepsirhine–haplorhine model of primate evolution, the anatomical reasoning behind the earlier view remains a source of controversy. Thus, the recent discovery of a spectacular 47 My fossil skull and skeleton from Germany, *Darwinius masillae*, which conforms closely to other adapiforms morphologically, was interpreted at first to be a possible anthropoid ancestor (Franzen *et al*., 2009), whereas others regarded it as an adapiform strepsirhine (Williams *et al*., 2009; Maiolino *et al*., 2012) far removed from any haplorhine. Today in Madagascar, lemuriforms are represented by a highly diversified radiation that rivals the platyrrhines. The lorisiforms, which occur on mainland Africa and the Indian subcontinent, evolved into two clades with strongly contrasting insect foraging and locomotor adaptations: galagos are vertical clingers and leapers and the lorises are slow, stealthy quadrupeds.

The four distinct extant radiations of haplorhine primates are not equally diverse taxonomically, although this view probably distorts their historical conditions. Tarsiers are now only a single genus, a tiny (60–130 g), leaping, variably monogamous or polygynous (Gursky-Doyen, 2011) and secondarily nocturnal super predator confined to the island archipelagos of Indonesia and the Philippines. During the Eocene, their likely ancestors and close relatives (Gunnell and Rose, 2002), composed of dozens of genera and species nearly all of whom may have been small nocturnal, leaping frugivorous predators, lived throughout the northern continents of Laurasia and probably in Africa as well. Emerging so long ago and having produced such a high level of biodiversity, it is hard to imagine why their numbers are now so depleted taxonomically. In contrast, today's New World monkeys are quite prolific. They range all the way through the tropics of Central and South America, 16 modern genera in all, and are highly diversified adaptively. They may have attained a comparable level of bio and adaptive diversity as early as 20 Ma, even before Amazonia emerged as a dominant neotropical ecosystem.

Old World monkeys are comparable to the platyrrhines in a taxonomic sense but their histories and evolutionary trajectories differ in critical ways: they are a younger lineage and specifically disposed to being terrestrial, hence less varied in locomotion and skeletal anatomy. Their teeth are curiously uniform structurally, although the animals are dietarily flexible, possibly because their molars evolved a simplified, all-purpose occlusal design originally geared to crushing seeds as a critical food resource (Rosenberger *et al*., 2011). As a group, the evolution of cercopithecoids has also been driven by sociality, so anatomical and behavioural features associated with body size and sexual dimorphism, rather than selection for masticatory adaptations, shapes an important amount of the variation seen in the skull, for example. With generalised dentitions, tightly organised social structures, high intelligence and an unspecialised body build, cercopithecoids have become highly successful ecologically and are now a dominant faunal element in terrestrial and arboreal habits of tropical and temperate Africa and Asia, and previously in Europe. They eclipsed the apes, the fourth major haplorhine group, ever since grasslands began to replace contracting forests in the Miocene epoch. Once equally dominant, widespread and biodiverse, modern apes are now a dwindled radiation confined to tropical forests and woodland of Africa and Asia. The great apes, the African chimpanzees and gorillas and the Asian orangutans, are composed of only three genera, all perilously endangered. The lesser apes, the gibbons and siamangs confined to south Asia, are less vulnerable, but their habitats are being destroyed, too. Humans, now a single worldwide population, are classified among these as hominoid primates but are today so fundamentally different in their adaptations that they are rarely compared ecologically to the other apes. In the past, however, it is evident from the fossil record that we too experienced an adaptive radiation that included a handful of African genera during the past 6–7 My.

The success of anthropoids, whose species have replaced strepsirhines and early tarsiiforms as the dominant primates, remains something of a mystery. In a general way it may be attributed to adopting a fully diurnal lifestyle (except for one reversal in the platyrrhine owl monkey). This is tantamount to arriving on a new planet where there are no competitors, for there are no other fruit-eating mammals to contend with during the day if one is a tree-dwelling anthropoid – birds hardly count as ecological competitors. Adapiforms may have been represented by some diurnal lineages as well, but their flimsy anterior teeth and crested molars suggest that they would have been more folivorous than anthropoids if the two competed locally for food resources, or at least less adept than anthropoids at harvesting large fruits when they were in short supply.

But a new planet, almost literally, may indeed have promoted the anthropoids' ecological success. Following the Palaeocene, Eocene climate was very warm, and changing palaeopositions and sea level drops made intercontinental migrations more feasible to curious, clever primates expanding their ranges. Forests quickly spread across temporary land bridges and narrow water gaps into an enormous new tropical landscape that even reached high latitudes now delimited by the Arctic Circle. How quickly arboreal primates might have then circumnavigated the globe is suggested by a study that documented the dispersal of an early Eocene tarsiiform from central China, across Europe and into what is now the American west in: approximately 25 000 years (Smith *et al.*, 2006). Other advantages benefiting anthropoids may relate to a new construction of the skull, which presents a fully partitioned orbit for reasons that are not yet clear, and a reorganisation of the brain, also still to be explained. The benefits of intense sociality and the capacity for cognitive advances should also not be underestimated. Although they did not start out being oversized, anthropoids have evolved large brains several times independently, suggesting an underlying potential that is missing among strepsirhines and tarsiers. Hotly debated is the question of geographic origins: Did anthropoids originate in Africa, Asia or elsewhere? Add to this the question of platyrrhines origins: How did they come to live in South America some 40 Ma, separated from centres of primate evolution in the Laurasian north and from Africa by vast stretches of open ocean? **See also**: New World Monkeys; Old World Monkeys

Ecology and Differentiation

Primates are first and foremost arboreal animals. Their success in the tropics is a function of the global distribution of wet dense forests and the multiple vertical levels of exploitation they provide. No living primate species except for humans is so exclusively adapted to a terrestrial lifestyle that its arboreal ancestry has been almost erased from the locomotor system. The lemurs of Madagascar have radiated into a variety of ecological settings on that island, including bamboo forests, spiny desert and montane forests; recently extinct species were even terrestrial. The compartmentalisation of this adaptive radiation is reflected in the unique specialisations displayed by various species. The sifaka (*Propithecus verreauxi*), for example, is so committed to leaping locomotion that it has difficulty ambling along the ground. The aye-aye (*Daubentonia madagascariensis*), the only primate to subsist on wood-boring grubs, is equipped with an arsenal of novel adaptations designed explicitly for finding, extracting and eating them: mobile, dish antennae-like ears; finger-tapping digits bouncing sound off tree trunks as they trace the echoes of hollowed out burrows; gnawing, ever-growing incisors to chew through wood; elongate, wire-like, clawed grapple hook fingers to scoop them out; blunt molars to crush their soft bodies. Although there are numerous species of lemurs on the island of Madagascar, they are found nowhere in abundance, given the finite nature of island's resources and the inexorable pressure of human presence. Lorises, galagos and tarsiers are also nocturnal arboreal predators but live quite differently from the aye-aye. Galagos, such as the lesser bush babies (*Galago*), occupy a wide variety of habitats including the savannah scrublands of Africa, where they travel by vertical clinging and leaping. The lorises, in contrast, such as the aptly named slow lorises (*Nycticebus*) in Asia, are night creepers that hunt by stealth. They have enlarged eyes, highly mobile limb joints and vise-like, gripping hands and feet that seem never to lose contact as they move in real-time slow motion, sneaking up on prey soundlessly. The East Asian tarsiers are in a class by themselves because they take in no vegetation at all. Their skulls are highly modified to accommodate enormous eyeballs and adjust to novel locomotor requirements. Each eye is as large as the brain itself which makes the head a difficult mass to balance and move. Thus, their locomotor adaptation has been given a category of its own, extreme vertical clinging and leaping (Rosenberger, 2010b). The biomechanics involved in securing these eyeballs in the head while leaping and landing (Rosenberger and Preuschoft, 2013) – thrusting them backward, then pulling them forward due to inertia – has selected for the development of protruding bony flanges around the eye socket and a partial bony wall behind the eye, a trait that resembles the independently evolved anthropoid postorbital wall (Smith *et al.*, 2013).

New World monkeys occupy tropical forest habitats and segregate themselves across genera according to preferences for different vertical zones in the canopy, different food parts and different 'fallback' foods to tide them over the lean seasons. This is facilitated largely by having evolved body size and locomotor variety. The tiny callitrichines (marmosets and tamarins) favour the lower reaches of the canopy and understory to forage for flowers, insects and other fauna, and in the case of the marmosets for tree gums. At the opposite end of the spectrum are the largest of the platyrrhines, the atelids, which prefer the periphery of the high canopy, including emergent trees, to forage for ripe fruits and leaves. They are able to distribute their weight beneath the lighter branches by using their prehensile tail and mobile limbs. Although New World monkeys are found at elevations as high as 3000 m in the Amazon headwaters and as far south as northern Argentina, it is mostly the howler monkeys (*Alouatta*) that venture into more temperate woodlands. New World monkeys are relatively diverse taxonomically and some species are fairly abundant. Habitat destruction, however, threatens many populations, particularly those restricted to the now decimated tropical forest on the Atlantic coast of Brazil, where the lion tamarin (*Leontopithecus*) and muriqui (*Brachyteles*) are close to extinction. **See also**: Conservation of Biodiversity; New World Monkeys

Of all the primate groups, Old World monkeys show the most flexibility for habitat preference. Although many are tropical and arboreal, radiations of Old World monkeys have filled semiterrestrial and marginal habitat niches as well as island and temperate latitude biomes. Japanese macaques (*Macaca fuscata*), for example, range farther to the north and east than any other nonhuman primate does. Old World monkeys have also managed to adapt to the fringes of human habitats, as in the case of baboons along safari trails and langurs living among temple ruins in India. **See also**: Old World Monkeys

Old World monkeys are classified into two major groups, the Cercopithecinae and Colobinae. These separate radiations can be seen as a generalist terrestrial track (cercopithecines) and specialist arborealist track (colobines) based especially on a dietary predilection for leaves in the colobines and locomotor and cheek pouch/food storage adaptations in the cercopithecines. As a result, cercopithecines occupy a wider variety of semiterrestrial and arid habitats in addition to forests. The combination of flexible feeding patterns and relatively open habitats, abetted by psychological and other behavioural conventions geared to troop life, allows cercopithecines to congregate in larger social groups than is typical for other primates. In many ways, the Old World monkeys can be considered the most abundant and 'successful' of the modern primate groups, given their history of opportunistic colonisation, geographic migration and climatic tolerance.

Apes are the most similar primates to humans and the most fragile ecologically. Each ape genus includes at least two 'types', some of which are classified into different species. The chimpanzee, for example, is represented by the common chimp (*Pan troglodytes*) and bonobo (*Pan paniscus*). The gibbons of Southeast Asia (*Hylobates*) include a variety of species, of which one is the distinctive siamang (*Hylobates syndactylus*). Gorillas are a single species (*Gorilla gorilla*), but the mountain gorilla is visually quite distinct from the lowland gorilla. The same applies to Bornean versus Sumatran orangutans (both *Pongo pygmaeus*). All of the apes depend on the integrity of their tropical forest habitats for survival. Two populations, the mountain gorilla and Sumatran orangutan, are perhaps the most narrowly adapted and thus are the most vulnerable to extinction. **See also**: Apes

Apes live in heavily forested habitats that provide them with the abundance of foliage (for gorillas), ripe fruits (for gibbons and orangutans) or mixture of fruits, nuts, leaves and fauna (for chimpanzees). Chimpanzees and gorillas are found along the tropical belt in Africa. Within this range, gorillas are more delimited in the central zone and montane regions of eastern Africa. These large-bodied apes are arbo-terrestrial in habit, employing their own style of quadrupedal locomotion, knuckle-walking, made possible by a suite of anatomical specialisations of the hand, wrist and elbow. The gibbons of peninsular and insular Southeast Asia rarely leave the arboreal sphere. They are superbly adapted to perform the primates' flashiest style of locomotion, ricochetal brachiation. Orangutans are found in two ever-diminishing populations on the islands of Borneo and Sumatra. They forage over extensive ranges of forest and employ a quadrumanous, or four handed, manner of climbing and clambering reminiscent of the relatively tiny lorises. No ape species is abundant in the wild, many are still exploited as bushmeat, and all need aggressive conservation support if they are to survive the twenty-first century. **See also**: Conservation of Populations and Species

Life Histories

Primates are distinguished from other mammals by aspects of their life history strategies, which emphasise learned behaviour, sociality and the reproduction of small numbers of high-quality offspring – usually one per reproductive cycle. Although body size is an important factor that determines rates of growth and maturation, for example, and primates vary considerably in size across the order, mass alone does not explain the patterns which are seen. Gestation lengths range from 60 to 270 days. Weaning takes place from 50 to 1500 days postpartum. The upper end of this span is unusually high and reflects an increase in the capacity of some species to invest heavily in infant development without incurring significant resource or predation losses. Age at sexual maturity ranges from 1 to 9 years (in nonhuman primates), the high end of which is not found in other mammals of comparable body sizes. **See also**: Life History Theory; Reproduction in Mammals: General Overview

Primates give birth to fewer offspring per litter and fewer litters per unit time over the course of a reproductive lifespan, compared with other mammals. This trend is expressed to an extreme degree in the great apes, which reproduce even more slowly than humans do. To survive as a lineage with a life history of reduced reproductive output, primates cannot afford to be a primary, or even secondary, prey species of mammals, reptiles or birds. Without specialised defence mechanisms, such as sharp claws, slashing teeth or large body sizes, primates are at a double disadvantage. They overcome this challenge behaviourally rather than morphologically. In some sense they balance a flexible approach to habitat, food sources and sociality, probably along with relatively acute intelligence and communication skills, to present a more difficult 'capture' target to potential predators. Ironically, these conditions can also make primates very successful predators, even on other primates. Chimpanzees are notorious hunters and consumers of the arboreal, highly social and fiercely protective red colobus monkeys. Humans, of course, have exploited these capacities to the extreme for foraging and sociopolitical purposes, not unlike the smart chimpanzees, where neighbouring troops regularly engage in warfare to acquire females and territory.

Across species, primate groups range in size from a few hundred individuals to some species that are virtually solitary. Male–female relationships also vary from monogamous pair-bonding to harem-level polygamy. As primate groups are studied in the wild for longer and longer periods of time, it becomes evident that the social patterns just mentioned are themselves dynamic and flexible. Perhaps because they tend to be intelligent, primate social organisations can be highly varied even among closely related forms that are not especially divergent in their adaptations or ecology. For example, among apes, the gibbons and siamangs are monogamous, orangutans are solitary, chimpanzees live in multimale/multifemale groups and gorillas establish harems. There is also a broad correlation among primates for group sizes to increase along with relative brain size. **See also**: Reproductive Strategies

Differences in primate life histories influence outcomes such as relative brain size, a physical measurement often used as proxy for cognitive capacity. Primate species with relatively large brains tend to experience longer preadult dependency periods. They tend to belong to species with more complex, intense social interactions and multilevel, hierarchical social groups. Interestingly, growth and development vectors that result in greater neural development vary across the major primate groups. In some cases, a species with a diet heavily dependent on ripe fruits displays a larger relative brain size than that found in a closely related species that depends heavily on nutritionally poor foliage. In other cases, the degree of sociality or even phylogenetic inertia correlates more strongly to maintain relatively unencephalised brains. Regardless of the underlying mechanism for progressive neural growth, primates are rare order of mammals with a demonstrated evolutionary history and interspecific heterogeneity of advanced encephalisation. **See also**: Brain Evolution and Comparative Neuroanatomy

Fossil History

The primate fossil record has been assembled from dedicated field expeditions over more than 150 years from Patagonia to Paris to Pretoria. Some of the geologically young primate fossils from the Dominican Republic have been discovered through a concerted campaign using scuba divers to collect from submerged underwater caverns (**Figure 4**). Others found in Wyoming (**Figure 5**), almost complete skeletons fully articulated, have been locked in ancient blocks of limestone that require months of acid treatment to dissolve. Although such projects have recovered thousands of fossils, the story of primate evolution is known only in bare outline. The record confirms that many generalised anatomical features of living primates extend far back to the early periods of the group's existence. It also confirms that past primate diversity greatly exceeds what is represented today.

The fossil history of the modern euprimate radiations dates to the Eocene epoch, approximately 55 Ma. Plesiadapiform primates existed before that, but their very classification as primates is controversial: some believe that they are arboreally adapted archaic primates that lack merely a few features found among later primates, whereas others feel this disqualifies them from membership in the order. The early success of primates is tied to the massive global spread of wet forests that even reached into high latitudes. This took place during the Eocene 'hot house' phase of the earth history, when sea surface temperatures may have at times reached 35 °C (95 °F) and intercontinental exchanges were favourable across the northern continents and Africa. The Eocene euprimate fossils, placed in the Adapiformes and Tarsiiformes, belong to the same two main branches known today, the strepsirhines and haplorhines. The best-known families belonging to these groups are the Adapidae (sometimes split into Adapidae and Notharctidae) and what is conventionally called Omomyidae (now outmoded, but without replacement),

Figure 4 Diver Cristian Pittaro of the Dominican Republic Speleological Society (DRSS) collects a fossil primate upper jaw (see inset) from a submerged freshwater cave in the Dominican Republic. Photo courtesy of Phillip Lehman (DRSS). © Phillip Lehman.

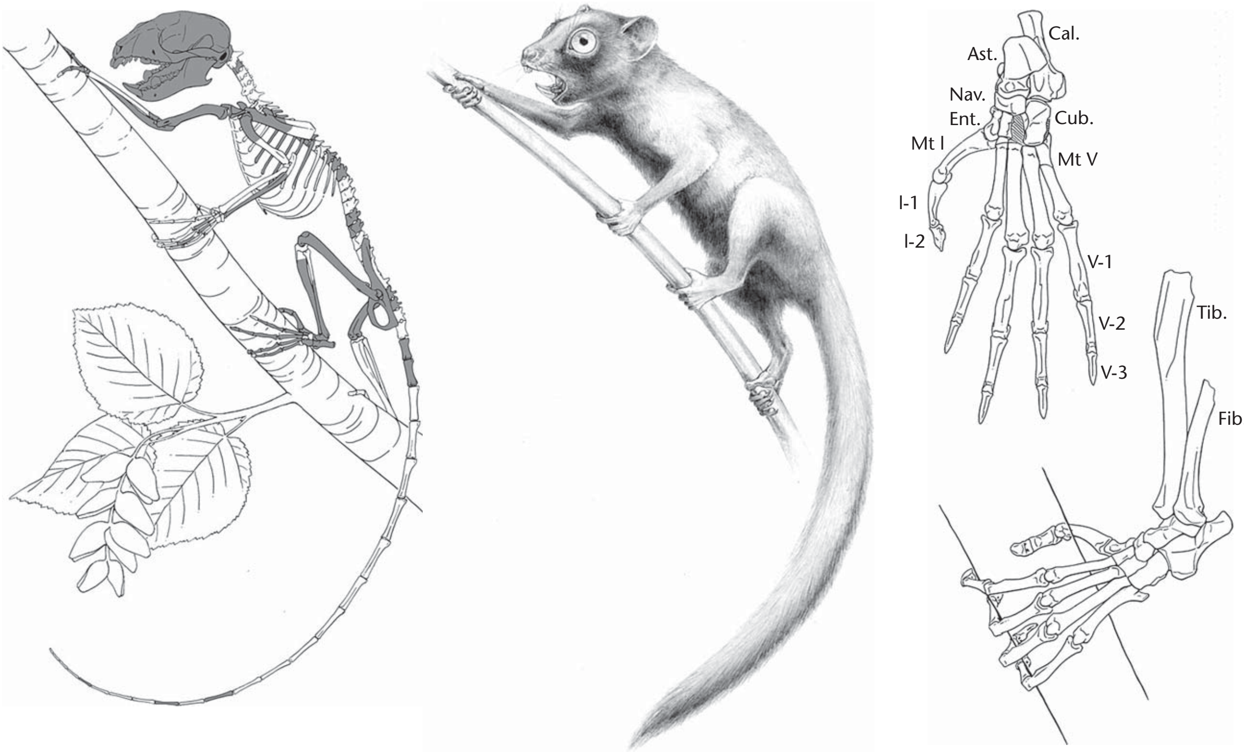

Figure 5 Reconstructions of a well preserved, articulated specimen of a plesiadapiform primate, *Carpolestes simpsoni*, approximately 55 My old, illustrating its primitive arboreal locomotor body plan and skull. Shaded bones were recovered. The foot skeleton on the right was capable of inward rotation to provide a flexible stance on variable substrates. It has a grasping, nailed hallux, whereas other toes are clawed. Adapted from Bloch and Boyer (2002). © American Association for the Advancement of Science.

respectively. Specimens of both may be quite abundant at many localities. **See also**: Diversity of Life through Time; Fossil Record; Fossils and Fossilization

Because traditional images of primates were for a long time those of monkeys and apes, the ancestry of haplorhine primates, which includes the unmonkey-like tarsiers as well, early became a primary study topic in primatology. All haplorhines are firmly linked by many characteristics of soft anatomy but, frustrating to palaeontology, only the few that are bony can become fossilised. Many aspects of haplorhine evolution are well rendered by the Eocene fossil record, but the manner in which these tarsiiforms are related to modern tarsiers, on the one hand, and to the anthropoids, on the other, is controversial. This argument is one of the great challenges of meshing theories concerning the origins and early evolution of monkeys, apes and humans. **See also**: Human Evolution: Overview

The study of anthropoid origins has been advanced greatly in the past 30 years by numerous discoveries from the Fayum badlands south of Cairo that have produced abundant late Eocene and early Oligocene primates (Seiffert *et al.*, 2010). The most primitive of these tend to resemble some platyrrhines, just as theory predicts, and not catarrhines, which are quite advanced anthropoids. These 30–40 My old fossils have yielded a large number and variety of forest-dwelling anthropoids belonging to a stem radiation that may be involved in platyrrhine ancestry and also the later catarrhines. Eocene localities in China and Southeast Asia have also contributed fossils to a lively debate on anthropoid origins, notably the eosimiids, first found in the 1990s, and, beginning decades ago, the amphipithecids (Beard, 2002). These fossils, still mostly represented by teeth, range from being very small to medium-sized as primates go, but it remains to be seen whether or not they turn out to be anthropoids at all. Many believe the amphipithecids are more likely to be early strepsirhines, most usefully compared with the adapids (notharctines) that are known from Western Europe and North America. The Chinese and Myanmar eosimiids (Takai *et al.*, 2005) have very primitive teeth. They are also no better than being long-shot candidates for first anthropoid, but they do prove that early haplorhine primates were present in the Asian Eocene in addition to their long-known prolific occurrences in Western Europe and North America at that time.

The New World monkey fossil record has accumulated in three or four distinct temporal and geographic zones (Rosenberger *et al.*, 2009). The earliest fossils, from the late Oligocene and early Miocene, are found in Bolivia, Chile and Argentina, largely outside of the geographic range of their living relatives. None of them offer any clues to the biogeographic puzzle surrounding platyrrhine origins: Did the first ones come from North America or Africa? The second zone of fossils includes numerous genera found at the middle Miocene age La Venta locality in Colombia. Many of the fossils from this locality closely resemble living species and indicate the expansive radiation of modern platyrrhines goes as far back as 13 My. These fossils indicate that an impressive number of modern platyrrhine monkeys lineages are long lived, spanning well more than 10 My and perhaps as many as 20 million, which is consistent with molecular estimates. The third and fourth zones in the New World monkey fossil record sample Caribbean islands and a Pleistocene megafaunal phase in Brazil that conforms with the evidence of mammalian ‘gigantism’ known from several continents at this time. Two impressively large (Halenar, 2011) fossil genera (*Caipora* and *Protopithecus*) from east-central Brazil indicate that the evolving New World monkeys experienced the same kind of body size increase and adaptive specialisation that peaked – or was artificially terminated by extirpation – among the Pleistocene subfossil lemurs of Madagascar and the Pleistocene Old World monkeys and apes. The Caribbean animals, found on Cuba, Hispaniola and Jamaica, intriguingly suggest an initial early origin for this group as well, probably via overwater dispersal from South America during the Miocene (Cooke *et al*., 2011). **See also**: New World Monkeys

The fossil record of Old World monkeys mirrors the recency and robustness of the modern radiation. The earliest specimens are rare and date to the Miocene epoch in Africa, at which time hominoids dominated Old World primate biodiversity. Few other Old World monkeys have been found in the rest of the Miocene anywhere in Africa or Eurasia until an explosion of taxa appears in Pliocene deposits ranging from the tip of South Africa to Europe and insular Southeast Asia. **See also**: Old World Monkeys

The fossil record of apes emerges in the early Miocene of Africa with a diversity of body sizes and taxa that greatly exceeds that of the moderns. Relationships among these early hominoids are difficult to determine because they present anatomical patterns for which there are no living analogues. Very shortly after their emergence in Africa, hominoids appeared in Europe and Asia, but this proliferation lasted only until the end of the Miocene epoch. Fossil apes disappeared entirely from Europe at this time and persisted in Asia only as the modern gibbons and orangutans and as a peculiar gigantic ape of the Pleistocene (*Gigantopithecus*) that was contemporaneous with *Homo erectus*. **See also**: Apes

The intense interest in human origins has resulted in many new findings in recent years. This includes the discovery of new genera and species and also the recovery of wonderfully complete remains. One of the most exciting is a 6-foot-tall skeleton of a subadult male from Kenya that is classified as either *H. erectus* or *Homo ergaster* (Walker and Leakey, 1993). Others being brought to light lived in South Africa at approximately 1.9 Ma, *Australopithecus sediba* (Berger *et al*., 2010). A remarkable series of fossils belonging to *Homo*, the earliest of their kind from Eurasia at approximately 1.8 My old, has been found in Dmanisi, Georgia (Gabunia *et al*., 2000). Most intriguing of all, but still poorly known, is a somewhat damaged but fairly complete skull from Chad, in north central Africa, named *Sahelanthropus tchadensis* (Brunet *et al*., 2002). Although very ape-like in appearance, some consider this to be the oldest hominin, at more than 6 My, which possibly places the specimen close to the time of origin of the human lineage.

References

Beard KC (2002) Basal anthropoids. In: Hartwig WC (ed.) *The Primate Fossil Record*, pp. 133–149. Cambridge, UK: Cambridge University Press.

Berger LR, de Ruiter DJ, Churchill SE *et al*. (2010) *Australopithecus sediba*: a new species of *Homo*-like australopith from South Africa. *Science* **328**(5975): 195–204.

Biegert J (1963) The evaluation of characteristics of the skull, hands and feet for primate taxonomy. In: Washburn SL (ed.) *Classification and Human Evolution*, pp. 116–145. Chicago: Aldine Publishing.

Bloch JI and Boyer DM (2002) Grasping primate origins. *Science* **298**: 1606–1610.

Brunet M, Guy F, Pilbeam D *et al*. (2002) A new hominid from the upper Miocene of Chad, central Africa. *Nature* **418**: 145–151.

Cartmill M (1974) Rethinking primate origins. *Science* **184**: 43.

Cartmill M (1993) New views on primate origins. *Evolutionary Anthropology* **1**: 105–111.

Cooke SB, Rosenberger AL and Turvey S (2011) An extinct monkey from Haiti and the origins of the Greater Antillean primates. *Proceedings of the National Academy of Sciences* **108**(7): 2699–2704.

Fleagle JG (1999) *Primate Adaptation and Evolution*. San Diego: Academic Press.

Franzen JL, Gingerich PD, Habersetzer J *et al*. (2009) Complete primate skeleton from the middle Eocene of Messel in Germany: morphology and paleobiology. *PLoS One* **4**(e5723): 1–27.

Gabunia L, Vekua A, Swisher CC III *et al*. (2000) Earliest Pleistocene hominid cranial remains from Dmanisi, Republic of Georgia: taxonomy, geological setting, and age. *Science* **288**: 1019–1025.

Gunnell GF and Rose KD (2002) Tarsiiformes: evolutionary history and adaptation. In: Hartwig WC (ed.) *The Primate Fossil Record*, pp. 45–82. Cambridge: Cambridge University Press.

Gursky-Doyen S (2011) The tarsiidae, In: Bearder S, Campbell C, Fuentes A, MacKinnon K and Panger M (eds) *Primates in Perspective*, pp. 79–90. Oxford: Oxford University Press.

Halenar LB (2011) Reconstructing the locomotor repertoire of *Protopithecus brasiliensis* I: body size. *Anatomical Record* **294**: 2048–2063.

Harter JA (1979) *Copyright-Free Illustrations of Mammals, Birds, Fish, Insects, etc. A Pictorial Archive from Nineteenth-Century Sources*. Mineola: Dover Publications.

Maiolino S, Boyer DM and Rosenberger AL (2011) Morphological correlates of the grooming claw in distal phalanges of platyrrhines and other primates: a preliminary study. *Anatomical Record* **294**: 1975–1990.

Maiolino S, Boyer DM, Bloch JI, Gilbert CC and Groenke J (2012) Evidence for a grooming claw in a North American adapiform primate: implications for anthropoid origins. *PLoS One* **7**(1): e29135. doi:10.1371/journal.pone.0029135.

Martin RD (1990) *Primate Origins and Evolution: a Phylogenetic Reconstruction*. London: Chapman and Hall.

Muchlinski MN (2008) The infraorbital foramen, infraorbital nerve, and maxillary mechanoreception: implications of interpreting the paleoecology of fossil mammals based on infraorbital foramen size. *Anatomical Record* **291**: 1221–1226.

dos Reis M, Inoue J, Hasegawa M *et al*. (2012) Phylogenomic datasets provide both precision and accuracy in estimating the timescale of placental mammal phylogeny. *Proceedings Royal Society B* **279**: 3491–3500.

Rosenberger AL (2010b) The skull of *Tarsius*: functional morphology, eyeballs, and the non-pursuit predatory lifestyle. *International Journal of Primatology* **31**(4): 1032–1054.

Rosenberger AL, Halenar LB and Cooke SB (2011) The making of platyrrhine semi-folivores: models for the evolution of folivory in primates. *Anatomical Record* **294**: 2112–2130.

Rosenberger AL and Preuschoft H (2013) Evolutionary morphology, cranial biomechanics and the origins of tarsiers and anthropoids. *Palaeobiodiversity and Palaeoenvironments* **92**: 76–85.

Rosenberger AL and Strasser ME (1985) Toothcomb origins: support for the grooming hypothesis. *Primates* **26**: 76–85.

Rosenberger AL, Tejedor MF, Cooke SB, Halenar LB and Pekkar S (2009) Platyrrhine ecophylogenetics, past and present. In: Garber P, Estrada A, Bicca-Marques JC, Heymann EW and Strier KB *et al*. (eds) *South American Primates: Comparative Perspectives in the Study of Behavior, Ecology and Conservation*, pp. 69–112. New York: Springer.

Rosenberger AL (2010a) Adaptive profile versus adaptive specialization: fossils and gummivory in primate evolution. In: Burrows AM and Nash L (eds) *The Evolution of Exudativory in Primates*, pp. 273–296. New York: Springer.

Seiffert ER, Simons EL, Fleagle JG and Godinot M (2010) Paleogene anthropoids. In: Werdelin L and Sanders WJ (eds) *Cenozoic Mammals of Africa*, pp. 369–391. Berkeley: University of California Press.

Silcox MT, Sargis EJ, Bloch JI and Boyer DM (2007) Primate origins and supraordinal relationships: morphological evidence. In: Henke W and Tattersall I (eds) *Handbook of Paleoanthropology, Vol. 2: Primate Evolution and Human Origins*, pp. 831–859. Heidelberg, Germany: Springer-Verlag.

Smith T, Rose KD and Gingerich PD (2006) Rapid Asia–Europe–North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene–Eocene Thermal Maximum. *Proceedings of the National Academy of Sciences* **103**(30): 11223–11227.

Smith TD, Deleon VB, Rosenberger AL (2013) At birth, tarsiers lack a postorbital bar or septum: evidence for homoplasy of the haplorhine lateral orbital mosaic. *The Anatomical Record* **296**(3): 365–377.

Smith TD, Rossie JB and Bhatnagar KB (2007) Evolution of the nose and nasal skeleton in primates. *Evolutionary Anthropology* **16**: 132–146.

Soligo C and Martin RD (2007) The first primates: a reply to Silcox *et al*. (2007). *Journal of Human Evolution* **53**: 325–328.

Sussman RW (1991) Primate origins and the evolution of angiosperms. *American Journal of Primatology* **23**: 209–223.

Szalay FS and Delson E (1979) *Evolutionary history of the Primates*. New York: Academic Press.

Szalay FS, Rosenberger AL and Dagosto M (1987) Diagnosis and differentiation of the Order Primates. *Yearbook Physical Anthropology* **30**: 75–105.

Takai M, Sein C, Tsubamoto T *et al*. (2005) New eosimiid from the latest middle Eocene in Pondaung, central Myanmar. *Anthropological Science* **113**: 17–25.

Walker A and Leakey R (1993) *The Nariokotome Homo erectus Skeleton*. Cambridge: Harvard University Press.

Williams BA, Kay RF, Kirk EC and Ross CF (2009) *Darwinius masillae* is a strepsirhine – A reply to Franzen *et al*. (2009). *Journal Human Evolution* **59**(5): 567–573.

Further Reading

Dolhinow PA and Fuentes AG (eds) (1999) *The Nonhuman Primates*. Mountain View, CA: Mayfield.

Fleagle JG and Kay RF (1994) *Anthropoid Origins*. New York: Plenum Press.

Hartwig WC (ed.) (2002) *The Primate Fossil Record*. Cambridge: Cambridge University Press.

McGrew WC, Marchant LF and Nishida T (1996) *Great Ape Societies*. Cambridge: Cambridge University Press.

Norconk MA, Rosenberger AL and Garber PA (eds) (1996) *Adaptive Radiations of Neotropical Primates*. New York: Plenum Press.

Rosenberger AL (1992) Evolution of feeding niches in New World monkeys. *American Journal of Physical Anthropology* **88**: 545–562.

Rowe N (1996) *A Pictorial Guide to the Living Primates*. New York: Pogonias Press.