

1 *Introduction*

The primate order

Primates, members of the Order Primates, are one of many living orders of mammals. A perusal of any major reference book on living mammals (e.g., Nowak 1999) easily demonstrates that the number of primate species is not impressive, when compared to the whole array of living mammals. This is instructive, because, as primates ourselves, we have a natural tendency to overestimate the place of primates in the general scheme of animal life. Humility is sometimes edifying. I will use it to press the case throughout this book that the study of other mammals can illuminate major questions in primate and human evolution.

A simplified classification of living primates is given in Table 1.1. Many alternative classifications exist. Conroy alone (1990: Appendix D) lists four versions. One feature of Table 1.1 is the separation of living primates into the suborders Prosimii (prosimians) and Anthropeidea (anthropoids). The word “anthropoid” was also freely used until the middle of the twentieth century as a synonym for “ape.” Here the term “anthropoid” is used to refer to all higher primates. Some other classifications place the tarsiers with higher primates in a suborder Haplorhini. Because I believe that tarsiers have had a separate evolutionary history for a long time, and have no special connection with higher primates (Chapter 3), I sort the tarsiers with other prosimians. Note that the Family Hominidae in Table 1.1 contains only humans and their fossil ancestors (hominids). Some researchers now use the term “Hominini” (hominins) for this group, because they place both humans and the great apes (pongids) in the Family Hominidae (Chapter 3). I will not use this taxonomy, because I consider that the adaptations of humans and their fossil ancestors are significant enough to warrant a family-level distinction. The African great apes and the orangutan have had separate evolutionary histories, and the orangutan should perhaps be classified in a separate family. However, I retain the traditional taxonomy, because altering it creates a barrier to accessing and understanding over 100 years of technical literature.

At one time, animals now universally placed in other orders, such as bats (Order Chiroptera), colugos (Order Dermoptera), tree shrews (Order

Table 1.1. A simplified classification of living primates

ORDER	PRIMATES									
SUBORDER	PROSIMII					ANTHROPOIDEA				
INFRAORDER	LEMURIFORMES	TARSIFORMES	LORISIFORMES	TARSIIFORMES	PLATYRRHINI	CATARRHINI				
SUPERFAMILY	LEMUROIDEA	DAUBENTONIOIDEA	LORISOIDEA	TARSOIDEA	CEBOIDEA	CERCOPITHECOIDEA	HOMINOIDEA			
FAMILY	Lemuridae; Cheirogaleidae; Megaladapidae; Indridae	Daubentoniidae	Lorisiidae; Galagidae	Tarsiidae	Callitrichidae; Cebidae	Cercopithecidae	Hylobatidae; Pongidae; Hominiidae			
COMMON NAMES	true lemur, dwarf lemur, sportive lemur, indri, sifakas	aye-aye	lorises, pottos, galagos	tarsiers	marmosets, tamarins, cebid monkeys (New World monkeys)	guenons, mangabeys, baboons, macaques, leaf-eating monkeys (Old World monkeys)	gibbons, siamangs, great apes, humans			

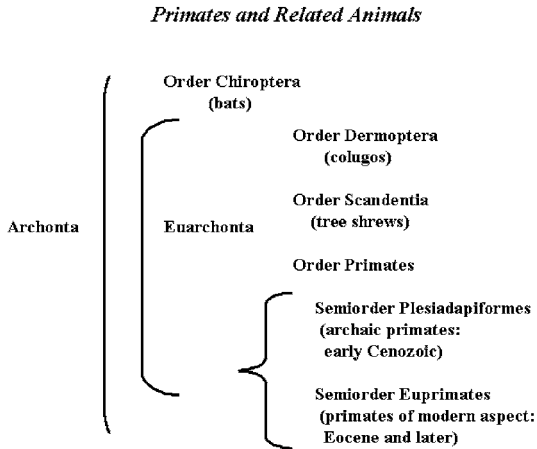


Figure 1.1. Primates are one of several closely related orders of placental mammals placed in the Grandorder Archonta. The order is composed of two subgroups: the extinct plesiadapiforms and the euprimates, primates of anatomically modern aspect that first appear in the Eocene.

Scandentia), and elephant shrews (Order Macroscelidea), were often placed in the Order Primates. Supra-ordinal designations such as Archonta and Primatomorpha are still used to link bats, colugos, tree shrews, and primates (Figure 1.1). One factor contributing to the controversy is the taxonomic position of archaic primates: the plesiadapiform primates, extant at the beginning of the Age of Mammals, the Cenozoic. In a number of features, these extinct animals do not resemble modern primates – they have long muzzles, no convergent orbits, no post-orbital bars, small brains, and many species have greatly enlarged incisor teeth, as well as other specializations of the anterior dentition. Cartmill (1972, 1974) first suggested that the plesiadapiforms should be removed from the Order Primates, restricting the order to animals that resemble living primates. Furthermore, when postcranial bones of paromomyid plesiadapiforms appeared to show the existence of a gliding membrane in the hand (Beard 1990), a link seemed to be established between plesiadapiforms and colugos (Order Dermoptera). Colugos are arboreal animals with gliding membranes connecting forelimbs and hindlimbs. Gliding membranes, however, evolve independently in many arboreal mammal groups, and their occurrence in some plesiadapiforms would not be enough to exclude them from the primate order. A recent discovery of a remarkably complete skeleton of *Carpolestes simpsoni*, a 56 my old plesiadapiform primate from Wyoming unmistakably demonstrates that this species had a grasping foot with an opposable, nailed hallux (Bloch & Boyer 2002). The species shares derived anatomical features of the foot with modern primates.¹

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However aberrant the plesiadapiforms were from modern primates, it seems clear that they should be included within the order. Being a primate at the dawn of the Cenozoic was different from being a primate today. The primate adaptive zone was different. The earliest primates were small, arboreal herbivores, and occupied niches later filled more successfully by the rodents.

Another major factor contributing to taxonomic confusion is that, unlike some other mammalian orders, primates possess no keystone feature that unequivocally identifies members of the order. Living species can experience this taxonomic confusion; fossil species, which lack soft tissue traits, and are usually represented only by incomplete dental or skeletal remains, may remain forever in taxonomic limbo, unplaceable even to order. Primate taxonomists experienced two brief spasms of hope when Meissner's corpuscles and the retino-tectal system were identified as keystone traits to identify primates. Meissner's corpuscles are specialized nerve endings embedded deep within the dermis layer of the skin that allow for delicate tactile sensitivity. However, the Virginia opossum, a marsupial mammal, also possesses these corpuscles. They are not therefore unique to primates, and can develop independently through convergent evolution in both marsupial and placental mammals. Similarly, the retino-tectal system of primates, with retinal rearrangement and neural projections that contribute to stereoscopic vision, was once thought to be unique. When fruit bats were discovered to possess the same neural anatomy, at least two major researchers argued that fruit bats were primates. They concomitantly argued that strong, powered flight evolved in mammals during two completely independent events – once among fruit bats (now allied with primates), and once among normal bats (Martin 1986a, Pettigrew 1986). Yet, a flight membrane supported by four fingers did not evolve separately in these two groups. Fruit bats are not primates.

In 1758, Carolus Linnaeus published the tenth edition of *Systema Naturae*, thus initiating binomial nomenclature and a universally recognized taxonomic system for living organisms. This volume becomes the first reference point for formal zoological nomenclature. Since that time, taxonomists have striven to identify traits that differentiate primates from other mammals (Gregory 1910, Simpson 1945, Napier & Napier 1967, 1985, Le Gros Clark 1971, Schwartz *et al.* 1978, Martin 1986b, 1990, MacPhee 1993, Szalay *et al.* 1993, McKenna & Bell 1997).

Accepting that no unique keystone feature exists, how does one diagnose primates? Linnaeus used four traits to define them: “palms which are hands,” four upper incisors, two mammary glands on the chest, and clavicles. Yet, he also included bats in the order. Modern researchers (Napier & Napier 1967, 1985, Le Gros Clark 1971, Schwartz *et al.* 1978, Martin 1986b, 1990), list a dozen features that define living primates, although there are exceptions to many



Figure 1.2. The skeleton of a New World squirrel monkey (*Saimiri oerstedii*), illustrating the generalized nature of the primate postcranium. The scale is in centimeters.

of these traits among living forms. Fossils are often only problematically identified as primates, given the fragmentary nature of fossils, the overwhelming preponderance of teeth, and the loss of most soft tissue information. Recognizing these cautions, the list of defining primate traits follows. These traits exist in euprimates, primates of anatomically modern aspect, that first appear during the Eocene.

(1) Primates possess a generalized limb structure, five digits on the extremities, and clavicles (Figure 1.2). These features are lost, reduced, or modified in many other mammal orders. For example, many mammals lose their clavicles, reduce the number of digits, or fuse the lower arm and leg bones together. (2) Primate digits are freely mobile, especially the first digit of the hand (pollex) and foot (hallux). Their extremities are thus capable of grasping. In comparison to other mammals, primate hands, even those of the plesiadapoids, have longer proximal phalanges relative to metacarpal length (Bloch & Boyer 2002: Fig. 5). (3) Flattened nails exist, rather than sharp, compressed claws. All living primates possess at least a nailed hallux. The gripping (volar) surface of each digit ends in a fleshy pad capable of fine tactile sensitivity. Primate hands and feet (and prehensile tail, if it exists) have complex, sculptured patterns on the

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naked skin of the volar surface. These fingerprints (dermatoglyphics) provide friction when objects are grasped, and thus reduce the possibility of slipping. Associated with the dermatoglyphics are Meissner's corpuscles. These are organized nerve endings implanted deep within the naked skin under the dermatoglyphic ridges. Unlike nerve endings in most other mammals, Meissner's corpuscles are not protected by a surrounding membrane, and are therefore more sensitive to pressure or touch.

(4) The primate face is short, because the muzzle is reduced. Some species (e.g., the baboons, drill, and mandrill) secondarily elongate the snout. This secondary elongation is associated with lengthening of the tooth rows. (5) Unlike most mammals, primates rely less on the sense of smell. Snout reduction does not show this, because smell is affected by the size and complexity of the scrolled, paper-thin turbinal bones within the snout. Epithelial tissue that lines the turbinals is involved with both respiration and smell. A reduced emphasis on smell is apparent from the relatively small size of the olfactory bulbs in the primate brain. Furthermore, moist, hairless, glandular tissue at the end of the snout (the rhinarium) is absent in higher primates and tarsiers. Because the rhinarium is important in olfactory sensitivity, its loss highlights primate denigration of the sense of smell. When a rhinarium is present, the upper lip is immobile. A central furrow appears in the skin of the upper lip, indicating the point where the lip is anchored to underlying gum tissue. This furrow is just anterior to a foramen in the bony palate lying between the two upper central incisors. Ducts from this foramen lead back to the vomeronasal organ or Jacobson's organ. The vomeronasal organ is markedly reduced or lost in primates. Vomeronasal neurons are non-olfactory, and are linked to the accessory olfactory bulb of the brain. Vomeronasal signals circumvent higher cognitive centers, and travel to the amygdala and other neural structures that direct emotion and neuroendocrine responses. Hence, this organ underlies a separate sensory modality that allows most mammals to sense pheromones underlying species discrimination and individual recognition, or that prime animals for appropriate sexual behavior (Leinders-Zufall *et al.* 2000, Stowers *et al.* 2002, Luo *et al.* 2003). There is no accessory olfactory bulb in the brain of catarrhine primates, and the vomeronasal organ is clearly vestigial, being represented only by a little pit in the nasal septum. Nevertheless, some researchers have argued that the vomeronasal organ is still functional in catarrhine primates, including humans. The *TRPC2* gene is essential for vomeronasal function in the mouse, and is expressed only in the vomeronasal organ. It was lost in the common ancestor of catarrhine primates at the same time that a gene duplication in the green/red opsin gene took place that allowed the development of trichromatic color vision in catarrhines (Liman & Innan 2003). The *TRPC2* gene is still experiencing selection pressure in *Lemur catta*, a prosimian, but selection pressure on this gene has

been relaxed in several species of New World monkey, including the common marmoset.

Olfactory receptor genes constitute the largest gene family in the human genome, but over 60% of these genes have been silenced, in contrast to the mouse genome, where only 20% of a similarly sized olfactory component have been functionally disrupted. When humans are compared to four other catarrhine species (common chimpanzee, gorilla, orangutan, and rhesus macaque), the human rate of inactivation of olfactory receptor genes is twice as high (Gilad *et al.* 2003). This result indicates a species-specific silencing of olfactory receptor genes in humans that may still be continuing, given the existence of many olfactory receptor genes that are polymorphic for an intact/disrupted coding region. The diminishment of olfaction, and loss or diminishment of vomeronasal signals in primates indicates their reliance on other sensory modalities.

(6) Primates emphasize vision. The eyeballs or orbits are increasingly more convergent, or rotated towards the same plane. In addition, nearly all primates exhibit frontality, because the plane of both orbits is oriented towards the front of the head, rather than facing downward or upward. Orbital convergence and frontality allow stereoscopic vision to occur. Yet, stereoscopic vision is finally achieved only when the brain integrates information from the overlapping visual fields of both eyes. Allman (1982) discovered what at first appeared to be a unique primate neural specialization: besides the systematic representation of the visual field of the opposite eye in each optic tectum, found in other mammals, one-half of each visual field also projects to the opposite optic tectum. This necessitates a re-organization of both the retina and the visual system projecting from the retina back to the brain (the retino-tectal system). The system was later found to exist in fruit bats. This neural anatomy underlies specialization for stereoscopic vision. Areas of the brain devoted to processing of visual information are relatively enlarged in primates, in comparison to other mammals. As an additional visual specialization, diurnal primates (i.e., some diurnal prosimians and all anthropoids except the secondarily nocturnal owl monkey genus *Aotus*) develop color vision. All normal Old World higher primates have trichromatic color vision. Diurnal New World higher primates have an autosomal color gene and one X-linked color gene. Only the New World howler monkeys (genus *Alouatta*) have two X-linked color genes. However, several New World monkey genera have allele variations at the single X-linked color gene locus, which would enable some females to possess trichromatic color vision (Boissinot *et al.* 1998). The relatively small size of the cornea in higher primates also underlies greater visual acuity in these animals (Kirk 2004). (7) There is some bony separation between the primate orbit and the temporalis muscle immediately posterior to the orbit. This separation may be either a bar or a septum of bone (Cachel 1979a).

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(8) The auditory region (the bulla) of the primate basicranium is derived from the petrosal bone (Van Valen 1965, MacPhee *et al.* 1983). Evidence from the developing fetus is generally needed to perceive details of bulla formation. Plesiadapiform evidence can be equivocal. CT scans of the paromomyid plesiadapiform primate *Ignacius graybullianus* shows that the bulla is formed from the entotympanic bone, yet it also has a bony tube for branches of the internal carotid artery and nerves, a trait found in tree-shrews and euprimates. The internal carotid nerves in *Ignacius* are laterally positioned, which is a euprimate trait (Silcox 2003). (9) Unlike most mammals, the molar teeth of primates have a relatively simple occlusal surface pattern. There are no complicated crests or enamel folds. However, even the first primate genus, *Purgatorius*, from the early Paleocene (65.5–61.7 mya), has quadrangular molars with low rounded cusps that resemble the teeth of condylarths, very generalized contemporary herbivores. Some researchers therefore suggest that the first primates were herbivores/frugivores (Van Valen & Sloan 1965, Szalay 1968). This would signify a basic shift away from the insectivory found in ancestral mammals.

(10) Placental tissues are increasingly elaborated in primates, developing a more intimate contact between maternal and fetal blood supply. (11) When primates are compared to other mammals of the same body size, fetal and post-natal life periods are relatively extended. (12) The primate brain, especially the neocortex, is large relative to body size. Note, however, the contrary evidence discussed in Chapter 8.

The most essential primate criteria appear to involve locomotion. This has resulted in a long series of publications about the fundamental nature of primate locomotion. Gregory (1920) argued that a deep-seated functional dichotomy exists between the primate forelimb and hindlimb – the hands explore and manipulate, while the feet grasp arboreal supports, powerfully anchor animals in an arboreal setting, and drive animals forward (Figure 1.3). Napier and Walker (1967) argued that the first primates engaged in vertical clinging and leaping, a form of arboreal locomotion in which the legs thrust animals forward in great leaps from one vertical support to another, while the trunk is orthograde (held upright). During rest, the trunk is orthograde, and the abdomen is pressed against a vertical arboreal support. Cartmill (1972, 1974) argued that the first primates were arboreal animals specialized for slow, cautious movement along small-diameter supports in the terminal branches of trees or in dense brush or secondary vegetation. Both hands and feet exerted a powerful grasp, but the hands could also thrust out quickly to capture agile insect prey.

A major functional distinction between hindlimbs and forelimbs was established at the beginnings of the primate order (Gregory 1920). The hindlimbs are used principally for weight support and propulsion, and the forelimbs are used principally for reaching and grasping. It seems clear that even the most ancient



Figure 1.3. A squirrel monkey (*Saimiri oerstedii*) actively searching for insect prey in Corcovado National Park, Costa Rica. The hands are used to unroll furred leaves where insects are hiding. The feet strongly grasp arboreal supports.

members of the primate order have specializations for arboreal climbing, especially for powerful grasping with the foot (Gregory 1920, Szalay & Dagosto 1988, Bloch & Boyer 2002).² The early appearance of a nailed hallux signals climbing in small branches. The origins of primate locomotor traits for specialized movement in small branches is confirmed by the independent, convergent evolution of some of these specializations in a living New World arboreal marsupial, the woolly opossum (*Caluromys philander*) of South America. This species moves agilely through fine terminal branches using quadrupedal grasping, short leaps, bridging, and suspensory behaviors. And, under experimental laboratory conditions, the woolly opossum demonstrates three primate-like locomotor features. It uses the diagonal couplets gait; its arm position at hand touchdown is greater than 90 degrees relative to the horizontal axis of the body; and its forelimbs receive less peak substrate reaction forces than its hindlimbs (Schmitt & Lemelin 2002).

Allometry needs to be taken into account before assessing function (Alexander 1985). Allometric analysis of mammals across a size range from shrews to elephants reveals that primates have relatively long limb bones, and an

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especially long femur (Alexander *et al.* 1979). The muscles of the thigh and foot are also relatively large in primates (Alexander *et al.* 1981). The relatively large size of the hindlimb prefigures its dominance in primate locomotion. In addition, the primate center of gravity is more caudal than in other mammals; the hindlimbs therefore carry more body weight (Reynolds 1981, 1985a, 1985b). In addition, primates have a much longer stride length than other mammalian quadrupeds. This is principally caused by large angular excursions (Reynolds 1983).³ Unlike the vast majority of mammals, primates utilize a sequence of diagonal couplets during quadrupedal locomotion – the foot contacts the substrate before the hand on the opposite side of the body (Hildebrand 1985). This strange primate gait is caused by two factors: the more caudal position of the center of gravity, and the use of the hindlimb to supply not only the principal accelerating force during each stride, but also the principal braking force (Hildebrand 1985). In other mammals, the center of gravity is cranially located, and the forelimb provides the major braking force. Thus, a suite of features characterizes primate locomotion: grasping foot, early appearance of a nailed hallux, caudal center of gravity, long femur, large hindlimb muscles, hindlimb dominance in carrying body weight, diagonal couplets gait, and hindlimb dominance during both maximal braking and acceleration. Taken all together, these features imply a fundamental primate adaptation to arboreal travel in areas where supports are small, discontinuous, flexible, and mobile. The feet grasp and hold strongly, while the hands reach out for different supports, and the center of gravity of the moving body is transferred to the opposite side.

What else can be inferred about the fundamental primate adaptive zone? The occlusal surface of the molars implies a dietary shift toward herbivory/frugivory in even the earliest primates (Van Valen & Sloan 1965, Szalay 1968). Neuro-anatomical specializations for vision and orbital convergence and frontality signal an early reliance on vision. At the same time, olfaction is downplayed, as confirmed by the reduction of the olfactory bulbs, eventual loss of the rhinarium, and reduction or loss of the vomeronasal organ. Cartmill (1972, 1974) attributed visual specializations to the fact that the first primates were visually oriented predators focusing upon solitary, agile insects. He removed the plesiadapiform primates from the order when making this argument for origins, because they lack cranial specializations for visual predation. Including plesiadapiform primates in the order signifies a dietary shift away from insectivory towards herbivory/frugivory in the earliest primates. And, of course, the earliest primates were arboreal animals adapted for moving among small branches, which is associated with a grasping foot and the early appearance of a nailed hallux. Study of locomotion in living primates documents a more caudal center of gravity, hindlimb dominance in carrying body weight, hindlimb ascendancy