4.03 The Role of Vision in the Origin and Evolution of Primates

C F Ross, University of Chicago, Chicago, IL, USA
R D Martin, The Field Museum, Chicago, IL, USA

Glossary

Anthropoidea — Monophyletic group (clade) consisting of living monkeys, apes, and humans, their last common ancestor, and all fossil taxa more closely related to living anthropoids than other primates.

APA — Arcuate premotor area.

cathemeral — Active during the day and at night.

CMAd and CMAv — Dorsal and ventral cingulate motor areas, located in the cingulated sulcus on the medial aspect of the cerebral hemisphere.

corticospinal tracts — Fiber bundles consisting of axons from cell bodies in the cerebral cortex that connect to motor neurons and interneurons in the spinal cord.

crepuscular — Active in the evening and morning.

diurnal — Active principally or solely during the day.

euprimates or primates of modern aspect — Monophyletic group consisting of Haplorhini, Strepsirrhini, Omomyiformes and Adapiformes. The taxon was erected to distinguish primates of modern aspect from archaic primates, or plesiadapiforms.

frontation — Caudal angle between the nasion–inion chord and the intersection of the midsagittal plane with the orbital plane.

hallux — Big toe, first toe

Haplorhini — Monophyletic group (clade) consisting of Anthropoidea and tarsiers, their last common ancestor, and all fossil taxa more closely related to living haplorhines than to other primates.

MI — Primary motor cortex.

nocturnal — Active principally or solely at night.

orbital convergence — Degree to which orbits face in the same direction, or converge on each other. Convergence is the caudal dihedral angle between the plane of the orbit and the midsagittal plane.

PMv — Ventral premotor area

pollex — Thumb; first, or radial digit

SMA — Supplementary motor area, motor cortex located on the medial aspect of the cerebral hemisphere, dorsal to the cingulate sulcus.

stereopsis — Seeing objects as solid, or three-dimensional.

Strepsirrhini	Monophyletic group (clade) consisting of living lemurs, lorises, and galagos, their last common ancestor, and all fossil taxa more closely related to living strepsirrhines than to other primates.

4.03.1 Introduction

The visual system features prominently in adaptive explanations for the divergence of primates from other mammals and the origin of anthropoid or simian primates from their prosimian ancestors. However, the origin and radiation of primates was associated with modification of a number of other sensory and motor complexes, including the auditory, feeding, and locomotion systems. The integrated nature of these modifications demands that considerations of the role of the visual system in primate evolution include changes in these other systems. Many current explanations for primate origins do not take this integration into account. Here, we consider the role of vision in association with other functional systems. After briefly reviewing the taxonomy of extant primates, we begin by enumerating the features distinguishing primates from other mammals, especially their close relatives. We then review the hypotheses advanced to explain the evolution of these features, evaluating those hypotheses with special reference to the neuroscience literature dealing with the visual system, motor control of hand movements, and eye–hand coordination.

4.03.2 What Is a Primate?

Living primates are classified into three universally accepted groups (Figure 1): Anthropoidea (monkeys, apes, and humans), Tarsiiformes (tarsiers), and Strepsirrhini (Malagasy lemurs together with lorises and galagos) (Martin, 1990; Fleagle, 1999; Hartwig, 2002). (Many publications spell this with one 'r', i.e., Strepsirhini. However, two 'r's are preferable because, although the Zoological Code of Nomenclature does not codify spelling of taxonomic names above the family level, the original spelling of the term was 'Strepsirrhini' (Geoffroy Saint-Hilaire, 1812a) and this is also the correct derivation from the Greek (Jenkins, 1987).) The phylogenetic position of *Tarsius* is controversial, with some researchers placing it as the sister taxon of anthropoids, making a clade Haplorhini (e.g., Cartmill, 1980; Martin, 1990; Kay *et al.*, 1997, 2004; Ross *et al.*, 1998) and others placing it as the sister taxon of strepsirrhines,

making a clade Prosimii (e.g., Eizirik *et al.*, 2001). Many researchers accept Haplorhini as a valid clade, but use the term 'Prosimii' to refer to the paraphyletic group consisting of strepsirrhines and tarsiers. Here we follow the classification of Fleagle (1999).

Living strepsirrhines include the Malagasy primate families united in the Lemuriformes (or Lemuroidea) and the African and Asian strepsirrhines, grouped together in the Lorisiformes (or Lorisoidea). The Lemuriformes includes Cheirogaleidae, Daubentoniidae, Indriidae, Lemuridae, and Lepilemuridae (or Megaladapidae). Lorisiformes includes the African Galagidae, and the African and Asian Lorisidae.

Anthropoids (also known as simians) are divided into two major clades: the Platyrrhini, or New World monkeys; and the Catarrhini, including Old World monkeys, apes, and humans. There is general agreement on the family or subfamily groupings of most of the platyrrhines – Callithrichidae (marmosets and tamarins), Atelinae (spider, woolly, and woolly spider monkeys), Alouattinae (howler monkeys), Pitheciinae (sakis, bearded sakis, and uacaris), Cebinae (including *Cebus* and *Saimiri*), Aotinae (owl or night monkeys), and Callicebinae (titi monkeys) – but the relationships among these groups are debated. The Catarrhini are divided into two major clades, the Cercopithecoidea, including cercopithecines and colobines, and the Hominoidea, including the apes and humans (see The Comparative Biology of Photopigments and Color Vision in Primates, Visual Cortex: Evolution of Maps and Mapping).

It is generally believed that the closest living relatives of primates are scandentians (tree shrews) and dermopterans (flying lemurs), although the phylogenetic relationships of these animals to primates continue to stimulate debate. The hypothesis of a grouping of dermopterans, scandentians, primates, bats, and elephant shrews in a superorder Archonta (Gregory, 1920) is not supported by recent analyses. Bats instead are included with carnivores, ungulates, and whales in a clade Laurasiatheria, while primates group with tree shrews, dermopterans, and the rabbit–rodent clade, Glires, in a larger clade, Euarchontoglires (Springer *et al.*, 1997; O'Brien *et al.*, 1999). Recent molecular trees for mammals either place Scandentia and Dermoptera in a clade that is the sister taxon to primates (Springer *et al.*, 1997; Murphy *et al.*, 1999; Eizirik *et al.*, 2001, 2004) or group Scandentia and Primates in a clade with Dermoptera as the sister taxon (Liu *et al.*, 2001). The long-term robustness of these phylogenetic groupings remains to be seen.
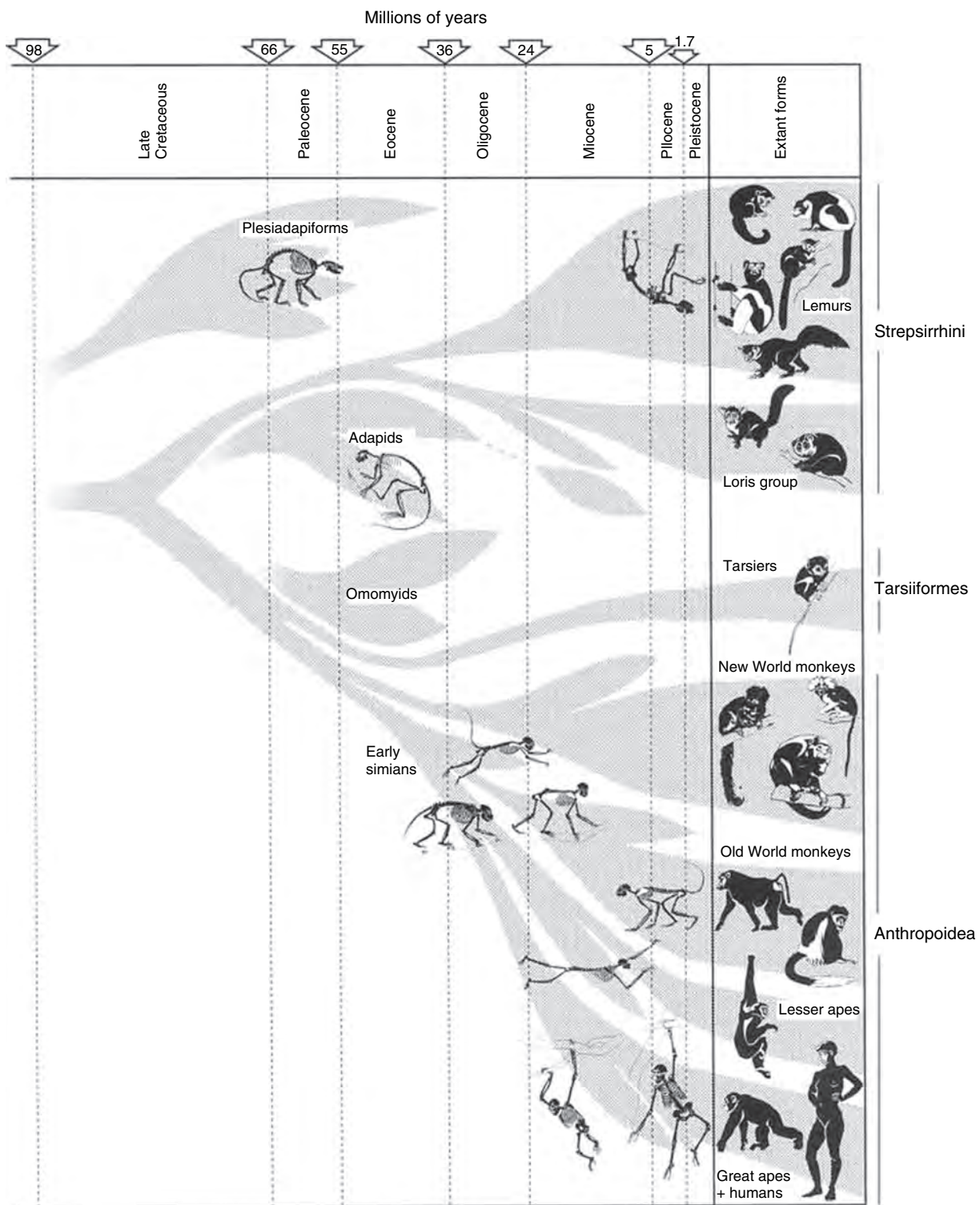
Figure 1 Outline phylogenetic tree of primates (modified from Martin, 1993). The generally accepted groups of living primates are shown on the right. Two groups of fossil primates that appear and radiate in the Eocene – adapids and omomyids – are of uncertain affinities to living primates (Martin, 1993). Plesiadapiforms and their relatives, including carpolestids (Bloch and Boyer, 2002), are also of uncertain affinities to primates. When plesiadapiforms are included in Primates, living primates, omomyids, and adapids are grouped together as Euprimates. Reproduced from Martin, R. D. 1993. Primate origins: Plugging the gaps. *Nature* 363, 223–234, with permission from Nature Publishing Group.

4.03.3 Early Explanations for Primate Origins

Primates have long been distinguished from other mammals by their grasping hands and feet, various enhancements of the visual system, and their relatively enlarged brains (Geoffroy Saint-Hilaire, 1812a, 1812b; Elliot Smith, 1924). Like many of the explanations to follow, Grafton Elliot Smith's early explanations for primate origins invoked functional benefits of these features in an arboreal habitat, but Elliot Smith also emphasized that changes in primate locomotion and grasping were integrated with changes in the somatic, auditory, and visual sensory systems. In an address to the Anthropological Section of the British Association for the Advancement of Science delivered in 1912 (Elliot Smith, 1924, chapter 1), Elliot Smith identified the neopallium (later termed neocortex) as the most salient feature distinguishing mammalian brains from those of nonmammals. The neopallium of mammals not only receives input from the visual, auditory, tactile, and kinesthetic senses, providing a substrate for merging and associating of the information streaming in from the periphery, but also contains the motor areas that put into effect the decisions made on the basis of these associations. Thus, Elliot Smith saw the neopallium as the organ that made it possible for mammals to learn and adapt to their surroundings.

The adaptability conferred on basal mammals by the neopallium was lost by many descendant lineages when they became specialized for cursorial, flying, aquatic, or burrowing environments. Primates, in contrast, retained their primitive adaptability, plasticity, and flexibility, primarily because they were arboreal. Arboreal mammals, Elliot Smith argued, require a balanced emphasis of the senses, with enhancement of vision, hearing, and touch. The agility of movement required in the trees "necessitates an efficient motor cortex to control and coordinate such actions as an arboreal mode of life demands . . . and also a well-developed muscular sensitivity to enable such acts to be carried out with precision and quickness" (Elliot Smith, 1924, p. 30). This general enhancement of the special senses, as well as the somatic sensory and motor systems used in locomotion, accounted for the general enlargement of the brain characteristic of primates.

Elliot Smith also emphasized the integrated nature of changes in the visual and tactile senses. The integrated nature of the neopallium meant that enhancement of the visual system in primates affected the whole neopallium, not just the visual areas.

The sense of touch also shared in the effects, for tactile impressions and the related kinaesthetic sensibility, the importance of which to an agile tree-living animal is obvious, assist vision in the conscious appreciation of the nature and the various properties of the things seen, and in learning to perform agile actions which are guided by vision Elliot Smith, 1924, p. 32).

This correlated development of visual and tactile senses led to integrated development of improved eye–hand coordination, linking up the tactile, kinesthetic, and visual cortical areas. Thus, for Elliot Smith, primate arboreality was not the only factor responsible for their adaptability, plasticity, and ability to learn, but it also resulted in enhanced development of their visual and grasping abilities, and in the integration and co-evolution of the two systems.

Wood Jones's theory of primate evolution included many of Elliot Smith's conclusions, but he also discussed specific features that are the focus of current explanations for primate origins. Wood Jones (1916) explained forward-facing eyes and postorbital bars as secondary consequences of a shift to arboreality, not specializations for it. He argued that, with progressive adoption of arboreal habits, the hindlimb became specialized for supporting the body weight during climbing, liberating "the fore-limb from any such servile function as supporting the weight of the body: it becomes a free organ full of possibilities," a process Wood Jones referred to as "emancipation of the fore-limb" (Wood Jones, 1916, p. 17). The emancipated forelimb could then take over from the jaws the role of food acquisition, allowing the snout to be reduced in size. As the snout recedes, the orbits are dragged around toward the front of the face, and postorbital ossifications (bar and septum) develop between the orbit and the temporal fossa (Wood Jones, 1916, p. 99). Echoing Elliot Smith, Wood Jones noted that one incidental benefit of the combination of a dextrous forelimb with forward-facing eyes is the ability to simultaneously manipulate and view an object in front of the face, making it advantageous to merge tactile and visual information in the newly expanding cortical association areas created by the expanding brain.

Wood Jones and Elliot Smith's arboreal theory of primate evolution (Howells, 1947) was adopted by Le Gros Clark (1934, 1959) as the explanation for general trends in primate evolution. The sensorimotor integration integral to Wood Jones' and Elliot Smith's theory was embodied in Le Gros Clark's total morphological pattern, "the integrated combination of unitary characters which together make up the complete functional design of a given anatomical structure" (Le Gros Clark, 1959, p. 13). The lack

of specialization and the retention of adaptability were attributed by Le Gros Clark to:

> …an arboreal habitat, a mode of life which among other things demands or encourages prehensile functions of the limbs, a high degree of visual acuity, and the accurate control and coordination of muscular activity by a well-developed brain Le Gros Clark, 1959, p. 43).

Overlapping visual fields and high visual acuity were argued to confer the ability to judge distances necessary for leaping in an arboreal environment. Le Gros Clark also re-emphasized the importance of eye–hand coordination for primate evolution identified by Elliot Smith, arguing that the enhancement of the tactile senses that accompanied the changes to the visual system were related to improved ability for manual manipulation and appreciation of the environment.

4.03.4 Primates in the Fine-Branch Niche

Le Gros Clark's theory of primate evolution was promulgated to the next generation of primatologists and became the received view (Cartmill, 1982). In the 1960s and 1970s, field research on behavior and ecology of nocturnal strepsirrhine primates in Madagascar and West Africa by R. D. Martin and P. Charles-Dominique suggested to them some refinements of the arboreal theory. Their fieldwork revealed similarities between cheirogaleids and galagids in a number of features, including nocturnality, small body size, hindlimb-dominated locomotion utilizing grasping extremities in the fine-branch and creeper niche, and an omnivorous diet including fruit, insects caught with the hands, and gum obtained with the help of the toothcomb (Charles-Dominique and Martin, 1970; Martin, 1972, 1973). They interpreted these commonalities as retentions from the common ancestor of strepsirrhines at least, and possibly primates as a whole, suggesting that occupation of the fine-branch niche might be the adaptive shift that characterized primate origins.

The advantages of the distinctive features of the primate visual system to an occupant of the fine-branch niche were not precisely articulated, although Martin addressed them briefly in 1979:

> Occupation of the "fine branch niche" by a relatively small-bodied ancestral primate would hence explain the emphasis on the grasping foot characteristic throughout the order Primates and at the same time provide a reason for the emphasis on vision and replacement of the primitive prehensile function of the snout by mobile, grasping hands. (Leaping between adjacent fine branches and grasping of small animal prey on nearby supports with the hands would explain the relatively large eyes, the universal possession of a postorbital bar, and the reduction of the snout and anterior teeth among primates.) (Martin, 1979, p. 64).

Martin subsequently argued that forward rotation of the orbits enhances stereoscopic vision that would be advantageous for "[a]ctive locomotion in a network of fine arboreal supports" (Martin, 1990, p. 657). This fine-branch niche hypothesis for primate origins included only very general explanations for the origins of orbital convergence and a postorbital bar in stem primates, made no mention of eye–hand coordination, and emphasized the importance of locomotion in terminal branches over predation or food acquisition (Martin, 1979).

4.03.5 Orbital Convergence, Postorbital Bar, Manual Grasping, and Visual Predation

Cartmill (1970, 1972) took issue with the arboreal theory of primate evolution on the grounds that arboreality alone cannot explain the origins of grasping extremities, convergent orbits, and nails on the digits, because a variety of active, leaping arboreal animals, such as squirrels, lack these features altogether. He argued:

> If the primate evolutionary trends have not been characteristic of other lineages of arboreal mammals, we may conclude that there is something wrong with the arboreal theory in its received form and any explanation of the primate trends must involve a more detailed description of the habitus of the ancestral primate (Cartmill, 1972, pp. 102–103).

Cartmill (1974) noted that many nonprimate animals with forward-facing eyes, such as cats, owls, and hawks, are "visually directed predators," and many nonprimate animals with grasping extremities, such as chameleons and small marsupials, engage in "prolonged and stealthy locomotion on slender terminal branches in pursuit of insects." Cartmill's hypothesis was significant in that it demonstrated that arboreality alone could not explain the evolution of optic convergence and grasping extremities in primates; something more specific was needed. Cartmill invoked adaptation to visual predation in the fine branches of the shrub layer of tropical rainforests to explain both grasping hands and convergent orbits. An integral component of the hypothesis was the importance of eye–hand coordination originally identified by Elliot Smith:

> The prehensile forelimbs necessary for stalking insects along thin branches serve also, among living insectivorous prosimians, as prey-seizing organs analogous to the tongue of a chameleon. The importance to primates of hand–eye coordination, which [Elliot] Smith was the first to stress, can be plausibly traced to an ancestral habitus in which the hand was used for striking prey (Cartmill, 1972, p. 116).

Cartmill (1970) formally defined orbit orientation in terms of two variables (convergence and frontation) (Figure 2), which he measured in a wide sample of arboreal mammals. Subsequent morphometric work by Ross (1995), Noble *et al.* (2000), Heesy (2003, 2005), and Ravosa and Savokova (2004) has expanded the available data and the most extensive data set (Heesy, 2003, 2005) is shown in Figure 3. Primates certainly have more convergent orbits than do dermopterans and scandentians, but many other mammals overlap with primates in their degree of orbital convergence, including a number of carnivorans, bats, and marsupials. However, few mammals share the combination of high degrees of frontation and convergence seen in primates, and when allometric factors are taken into account, primates have more convergent orbits for their relative orbit size than other mammals (Noble *et al.*, 2000; Heesy, 2003).

Refinements to Cartmill's visual predation hypothesis were necessary. Pettigrew (cited by Allman, 1977, p. 29; Pettigrew, 1978) and Allman (1977) pointed out that orbital convergence has advantages for nocturnal animals that are not applicable to diurnal animals. The
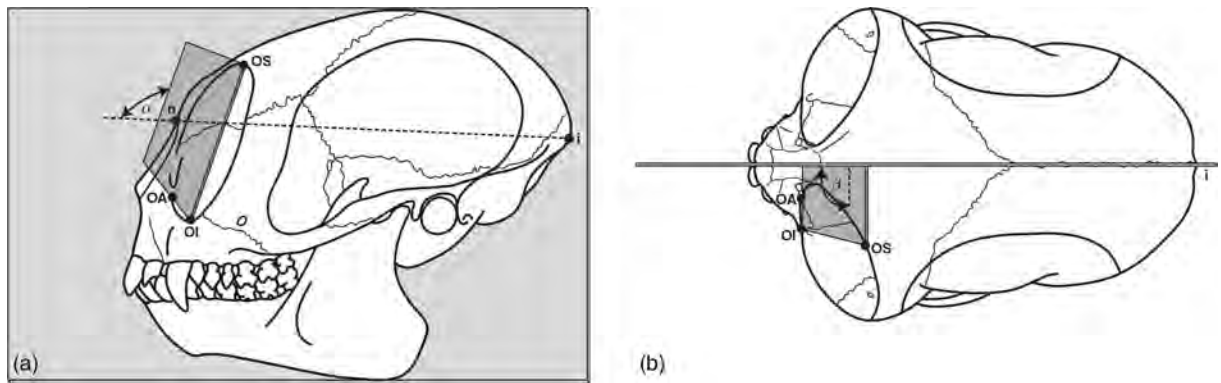

Figure 2   Diagram illustrating definitions of orbital convergence and frontation from Cartmill (1970, 1972) and subsequently used by Ross (1995), Noble *et al.* (2000), Heesy (2003, 2005), and Ravosa and Savakova (2004). The midsagittal plane is lightly shaded, the orbital plane heavily shaded. a, Frontation is the caudal angle between the nasion–inion chord and the intersection of the midsagittal plane with the orbital plane (i.e., $180° - \alpha$). b, Convergence is the caudal dihedral angle between the plane of the orbit and the midsagittal plane (i.e., $180° - \beta$).
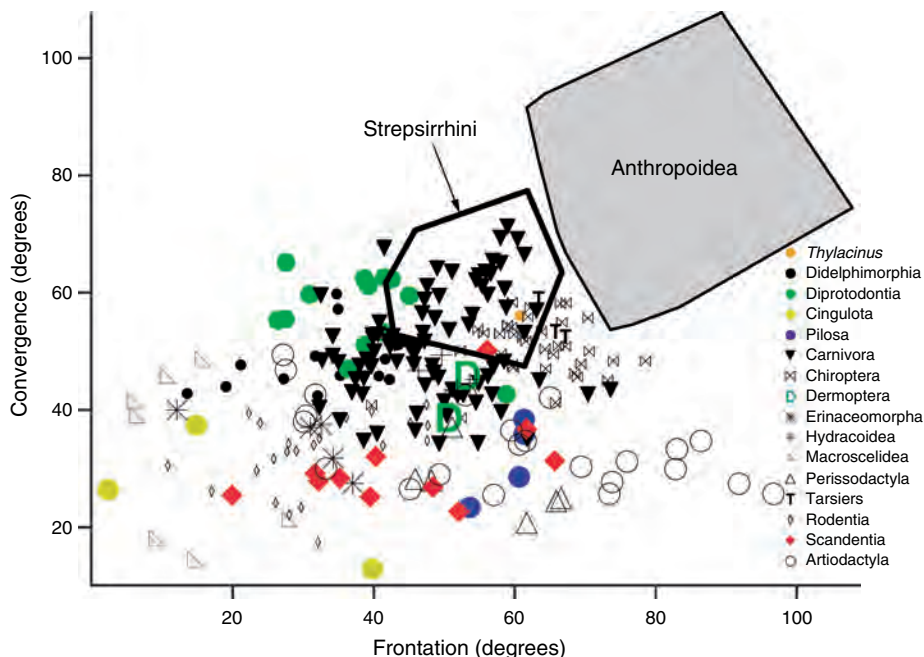

Figure 3   Bivariate plot of orbital convergence angle (degrees) against orbital frontation angle (degrees) in mammals. Individual data points for primates are excluded and replaced by minimum convex polygons (*sensu* Jerison, 1973). Data are from Heesy, C. P. 2005. Function of the mammalian postorbital bar. *J. Morphol.* 264, 363–380.

Allman–Pettigrew model notes that orbital convergence is associated with convergence of the optic axes on the visual axes, a means of improving retinal image quality that is necessary for nocturnal animals but not for diurnal ones. Whereas diurnal animals can ensure high retinal image quality by decreasing pupil diameter, thereby restricting incoming images to the paraxial region of the dioptric apparatus, nocturnal animals must maintain large pupil apertures in order to preserve image brightness. Consequently, nocturnal animals must improve image quality in the area of visual field overlap by optic and orbital convergence. This suggested to Allman (1977) that, if the first primates had high degrees of orbital convergence, they were probably nocturnal (Figure 4).
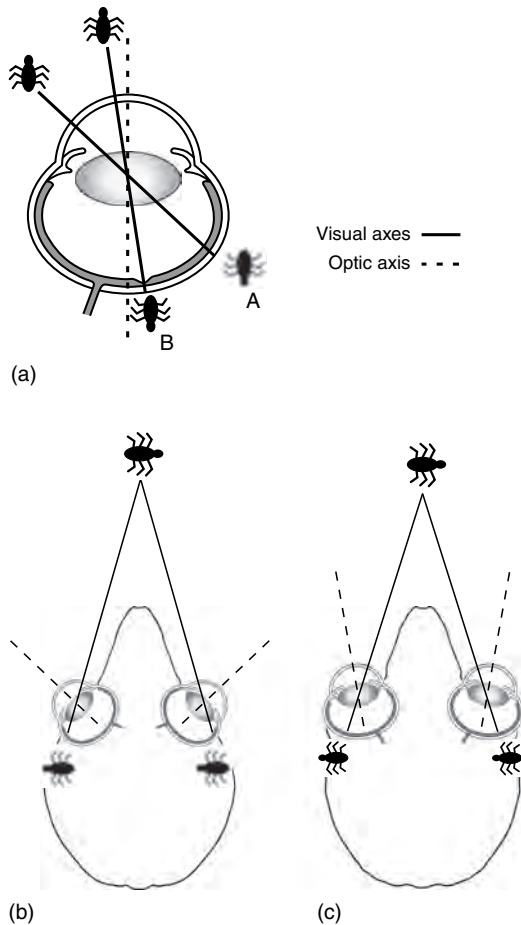

Visual axes ——
Optic axis - - -

Figure 4 Diagrams illustrating functional significance of orbital convergence in nocturnal primates. a, Diagram of eye illustrating the effect of relative orientation of optic and visual axes on image quality. Image quality is best when the visual axis is more closely aligned with the optical axis. b, Diagram of visual and optic axis orientation in an animal with laterally facing orbits. c, Diagram of visual and optic axis orientation in an animal with convergent orbits. The quality of the image of the area in front of the animal is lower in (b) than in (c) because the optic and visual axes are less closely aligned.

4.03.6 The Primate Postorbital Bar

Primates all have postorbital bars which, while not unique to primates, do serve to separate them from their nearest putative fossil relatives, the plesiadapiforms. Cartmill (1970) and Heesy (2003) list a variety of other mammals with postorbital bars and processes. Dermopterans have postorbital processes (i.e., incomplete bars), while tree shrews have complete postorbital bars. Cartmill (1970, 1972) hypothesized that the primate postorbital bar functions to protect the orbital contents against movements originating from the chewing muscles in the temporal fossa. These movements might occur in all chewing animals, but Cartmill hypothesized that they were particularly problematic in animals with convergent orbits. Orbital convergence brings the plane of the orbit out of the plane of the temporal fossa, such that distortions of the postorbital ligament caused by contraction and bulging of the temporal muscles impinge upon the orbital contents (Figure 5).
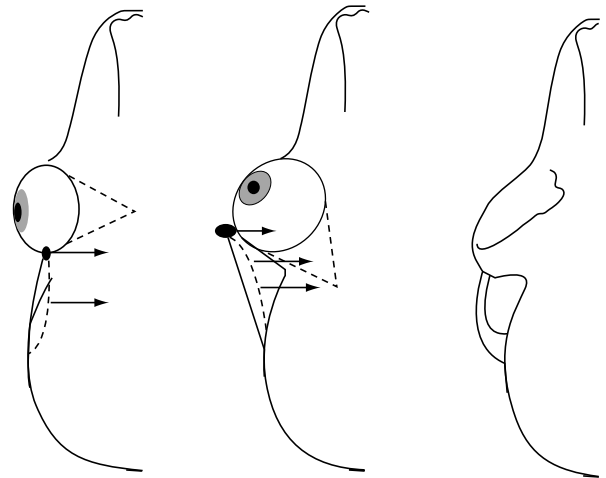

Figure 5 Diagram illustrating the function of the postorbital bar according to Cartmill (1972). In the left figure, the orbit is laterally directed and contractions of the temporalis muscle that pull the temporalis fascia and postorbital ligament medially do not impinge upon the eye (medially directed arrows). In the middle figure, the effects of moderate orbital convergence are illustrated. Convergence of the orbits is achieved by anterolateral displacement of the postorbital ligament. This brings the ligament lateral to the eye so that medial displacement of the ligament moves the eye around. As shown in the right figure, to prevent unwanted eye movements, the ligament is ossified into a postorbital bar to stiffen the lateral orbital wall. Adapted from Heesy, C. P. 2003. The Evolution of Orbit Orientation in Mammals and the Function of the Primate Postorbital Bar. PhD thesis, Stony Brook University, with permission of the author.

This hypothesis receives support from recent comparative morphometric analyses of orbit orientation in nonprimate mammals. Increased orbital frontation (roughly equivalent to verticality) in animals with moderate degrees of orbital convergence also causes the orbital and temporal planes to diverge, necessitating evolution of a postorbital bar (Noble *et al.*, 2000; Ravosa and Savokova, 2004). Heesy (2003, 2005) showed that the degree of postorbital ossification across a wide range of mammals is correlated with the degree to which the planes of the orbital aperture and of the temporal fossa diverge, regardless of whether that divergence is caused by increased orbital convergence, frontation, or displacement (Figure 6). This suggests that the evolution of the postorbital bar in primates represents an instantiation of a general principle identified by Cartmill that applies across all mammals: when the orbit and temporal fossa are not coplanar, movements in the temporal fossa are more likely to disturb the orbital contents and some kind of postorbital ossification is necessary to insulate the orbit.

The precise source, magnitude, and nature of the eye movements originating in the temporal fossa are unknown. Lemme *et al.* (2005) measured deformation in the postorbital ligament of pigs during stimulation of the temporalis and masseter muscles, and during mastication. They found that deformation of the ligament was primarily caused by contraction of the ipsilateral superficial masseter. In nonanthropoid primates, the chewing muscles, including the superficial masseter, are recruited much more vigorously on the working side than the balancing side, producing higher bone strain magnitudes on the postorbital bar of the working side than that of the balancing side (Ravosa *et al.*, 2000). Together, these results suggest that any disturbances suffered by the eyes during chewing would be asymmetrical. It might be difficult to offset or tolerate this asymmetry (Ravosa *et al.*, 2000), although this would depend on the nature of the movements. If the eyes were primarily protruded, the resulting diplopia would be less than if the eyes were abducted or adducted. Heesy *et al.* (2006) measured eye movements in anesthetized cats and galagos during stimulation of the masticatory muscles and found varying amounts of protrusion and abduction. Whether these movements occur in awake, chewing primates has not been established.
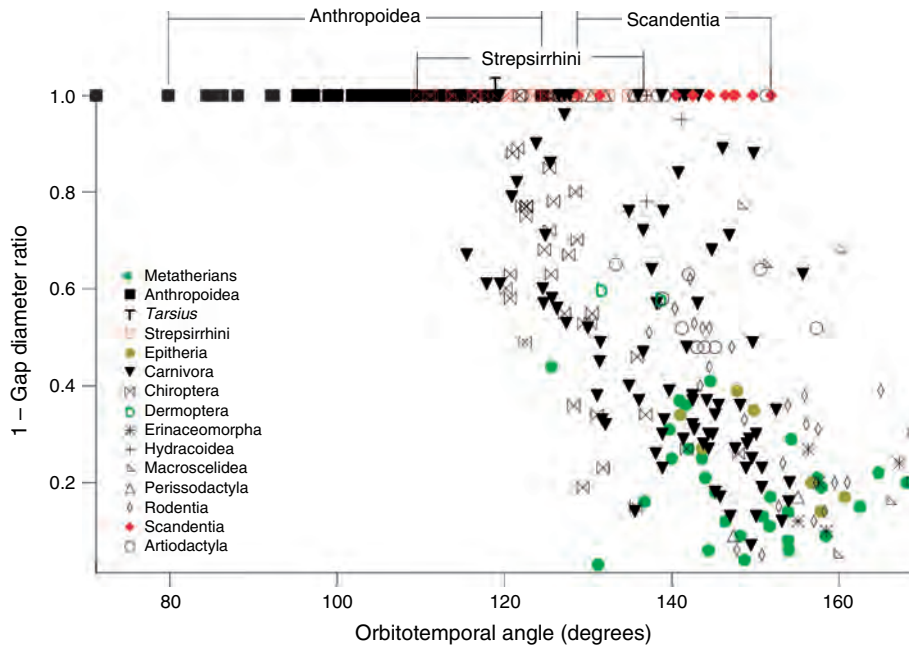

Figure 6   Bivariate plot of 1− postorbital gap:orbit diameter ratio against orbitotemporal angle. The gap:diameter ratio is the distance between the tips of the postorbital processes divided by orbit diameter. This value is subtracted from 1.0 so that animals with longer processes or bars are higher on the y-axis. Animals with values of 1.0 at least have complete postorbital bars. Orbitotemporal angle is the dihedral angle between the plane of the orbit and the plane of the temporal fossa. This angle quantifies the internal angle between the plane of the orbit and the plane of the temporal fossa. This plot shows that as the orbit becomes less coplanar with the temporal fossa (i.e., as the orbitotemporal angle decreases), the length of the gap between the postorbital processes decreases. Only animals with postorbital bars can have orbital planes that are strongly divergent from the plane of the temporal fossa. Note that only animals with postorbital septa (i.e., tarsiers and anthropoids) have extreme values of orbitotemporal angle. The data are from Heesy, C. P. 2005. Function of the mammalian postorbital bar. *J. Morphol.* 264, 363–380.

4.03.7 Criticisms of the Nocturnal Visual Predation Hypothesis

The visual predation hypothesis was the most widely accepted explanation of primate origins until counter-arguments began to appear in the 1990s. Critiques of the nocturnal visual predation (NVP) hypothesis can be grouped into three categories of argument: that the ancestral primates were not nocturnal; that the predatory adaptations of the ancestral primates were not visual; and that the visual adaptations of the ancestral primates were not predatory.

4.03.7.1 Ancestral Primates Were Not Nocturnal

Several researchers have argued against the NVP hypothesis on the grounds that basal primates were not nocturnal. Tan and Li's (1999; Li, 000) hypothesis that the ancestral primates were trichromatic and diurnal is unparsimonious in the context of a more comprehensive analysis of the data (Heesy and Ross, 2001). More recently, Ni *et al.* (2004) reported the discovery of a skull of the basal omomyiform primate *Teilhardina asiatica* from the earliest Eocene deposits of the Lingcha Formation, China (Figure 7). On the basis of the relative orbit size of this specimen, Ni *et al.* suggested that *T. asiatica* was diurnal. The use of relative orbit size as an indicator of activity pattern in fossil primates was pioneered by Walker (1967), but fully developed by Kay and Cartmill (1977; Kay and Kirk, 2000). This work showed that, in living primates with skull lengths below approximately 75 mm, nocturnal species generally have larger orbits than diurnal species. This separation of nocturnal and diurnal species in relative orbit size makes it possible to discriminate activity pattern in fossil species by plotting orbit size against body size to see whether the fossil resembles living nocturnal or diurnal primates. Applying this technique to interpret the activity pattern of the tiny *T. asiatica* necessitates extrapolation below the range of skull lengths exhibited by living primates. Ni and colleagues used a least-squares regression model to estimate the orbit dimensions of nocturnal and diurnal taxa at the skull length of *T. asiatica*, and argued that the relative orbit size of *T. asiatica* suggests that it was diurnal. Optimizing activity pattern onto a phylogenetic tree of primates and their relatives, Ni *et al.* reconstructed diurnality at the stem primate node, hence calling the NVP hypothesis into question.

Ni *et al.*'s analysis suffers from the difficulty of extrapolating the relationship between relative orbit size and activity pattern below the body size range of living primates (Martin and Ross, 2005). The
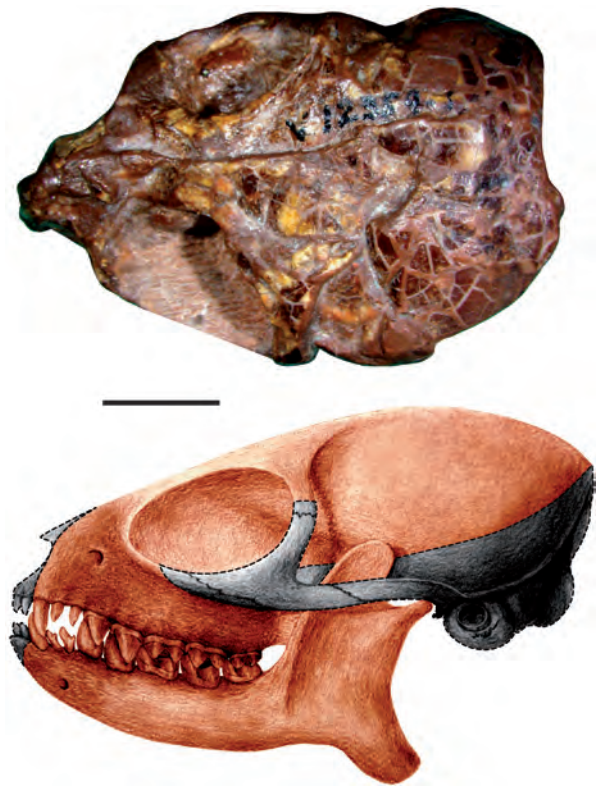

Figure 7 Skull of *T. asiatica* in dorsal and reconstructed lateral view; (IVVP V12357), earliest Eocene Lingcha Formation, Hengyang Basin, China (Ni *et al.*, 2004). Scale bar: 5 mm. Reproduced from Ni, X., Wang, Y., Hu, Y., and Li, C. (2004). A euprimate skull from the early Eocene of China. *Nature* 427, 65–68, with permission from Nature Publishing Group.

relationship between eye size and body size in mammals has been claimed to be nonlinear, such that eye size declines rapidly at body sizes below the range of extant primates (Ross, 2000; Kiltie, 2000; Martin and Ross, 2005). In Figure 8, corneal diameter of the eye is plotted against head-and-body length in mammals. The line that best fits the data is a fourth-degree polynomial, and a quadratic explains the data better than a linear least-squares line, but none of these lines is significantly different from any others, making it difficult to determine what kind of regression line should be used at small body sizes. This calls into question the hypothesis that *T. asiatica* was diurnal and raises the thorny issue of how to reconstruct activity pattern in fossil primates at body sizes below those of extant forms.

Various lines of evidence point to a nocturnal origin for basal euprimates (reviewed by Ross *et al.*, 2006). Charles-Dominique and Martin (1970) argued that the ancestral primate was probably nocturnal because nocturnality characterizes galagids, cheirogaleids, and lorisids, and these animals are probably the most primitive members of their respective lineages. Later, Martin (1973)
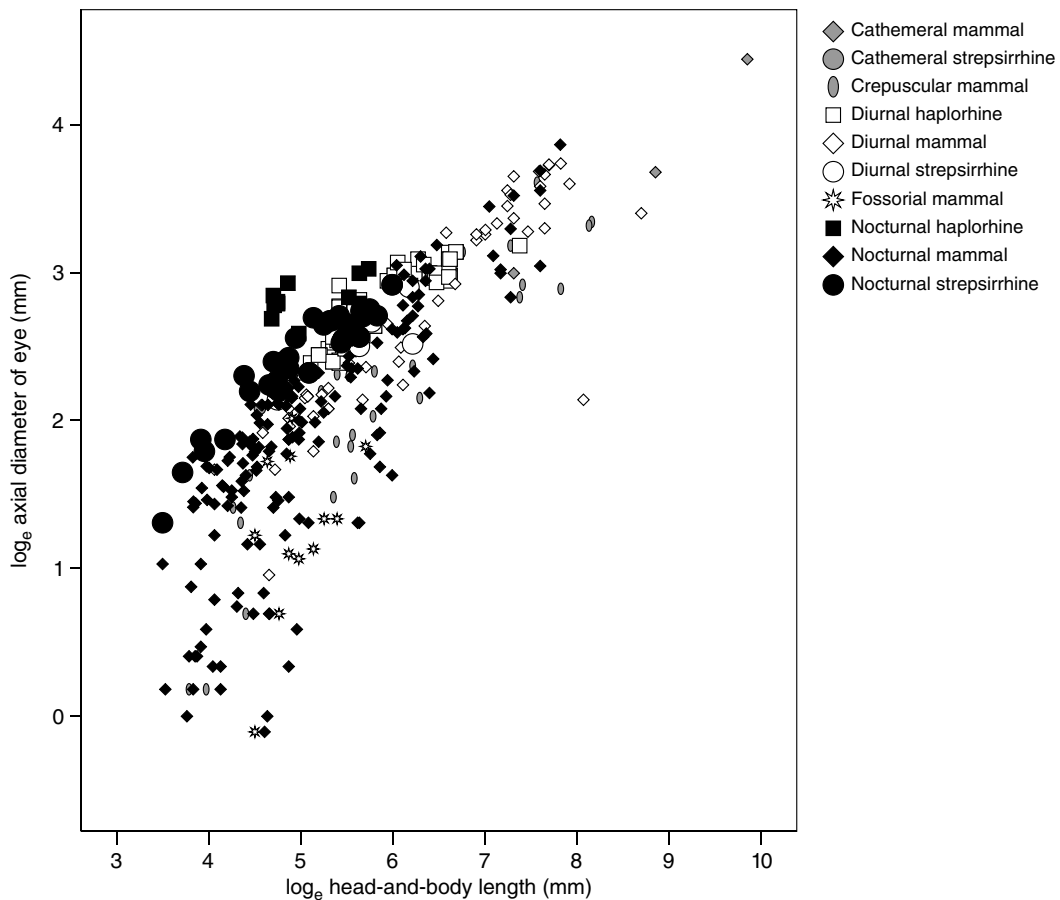
Figure 8 Plot of axial diameter of the eye against head-and-body length in mammals. Data from Ritland, S. 1982. The Allometry of the Vertebrate Eye. Unpublished PhD dissertation, Department of Biology, University of Chicago and Ross (unpublished data).

bolstered this argument by pointing out that the presence of the tapetum found in diurnal lemurids is best explained as a primitive retention from a last common ancestor of strepsirrhines that was nocturnal. Ross (2000) hypothesized that the earliest primates also probably possessed a tapetum. Explicitly cladistic reconstructions of the evolution of activity pattern in primates and their relatives corroborate the hypothesis that nocturnality characterized the first euprimates (Heesy and Ross, 2001). The possibility that certain early primates were extremely small, even around 10 g in size (Gebo *et al.*, 2000; Gebo, 2004), also suggests that these animals were nocturnal, as most living mammals in this size range are nocturnal. The possibility that basal primates were smaller than any living primates is not universally accepted, but some of them certainly were. It is therefore important to ask what the visual systems of such animals would have been like. Most extant mammals in this size range are olfactory-dominated animals. What kind of eye could a 10 g primate have carried and how would its brain organization have been affected

(Kaas, 2000)? Theoretical investigations of such issues, combined with future fossil discoveries, promise to provide important clues as to the visual adaptations of early primates.

4.03.7.2 Predatory Adaptations of the Ancestral Primates Were Not Visual

The most common criticism of the NVP hypothesis is that primates use nonvisual senses to locate prey (Rasmussen, 1990; Sussman, 1991; Crompton, 1995). Sussman (1991) reviewed relevant data, pointing out that *Galagoides demidoff* and *Tarsius* can localize prey using hearing (Charles-Dominique, 1977; Niemitz, 1979), whereas lorises localize prey with olfaction. However, as has been noted previously, the fact that primates use nonvisual senses to localize prey does not necessarily mean that their visual sense is not important for prey localization (Dominy *et al.*, 2004; Ross *et al.*, 2005). Both galagos and lorises have been reported to use visual cues to localize moving prey (Charles-Dominique, 1977, p. 39; Schulze and Meier, 1995).

Moreover, it is also clear that, among extant mammals, increases in sound-localization acuity are associated both with increases in width of the binocular visual field and with narrowing of the field of highest visual acuity (Heffner and Heffner, 1985, 1992): animals with the highest auditory acuity also have large binocular visual fields and narrow fields of high-acuity vision. These data led Heffner and Heffner to suggest that the function of sound localizing is "directing the attention of other senses toward the sound-producing object" (Heffner and Heffner, 1992, p. 711). Primates notably have increased sound-localizing ability, increased binocular field width, and narrow fields of high visual acuity, and the work of Heffner and Heffner suggests that these features are interrelated. It cannot therefore be argued that use of auditory information for prey localization falsifies the hypothesis that visual cues are used as well (Sussman, 1991; Crompton, 1995). On the contrary, it suggests that if early primates were indeed nocturnal visual predators, they were probably auditory predators as well, and vice versa.

4.03.7.3 Visual Adaptations of Ancestral Primates Were Not Predatory

The most important criticism of the NVP hypothesis proposes alternate explanations for the origins of the high degrees of orbital convergence characteristic of primates. Two alternate reasons for orbital convergence have been suggested: localizing small fruits in terminal branches and locomotion in the fine-branch niche.

Sussman (1991) agreed with Cartmill that the divergent hallux and pollex and flattened nails are grasping organs, noting:

> It is generally agreed that these adaptations would have allowed Eocene prosimians far greater access to fruits and flowers, as well as plant-visiting insects, making them much more efficient at locomoting and foraging in the small terminal branches of bushes and trees than were the plesiadapoids (Sussman, 1991, p. 219).

But Sussman went on to suggest that the evolution of orbital and optic convergence is not explained either by locomotion or by predation on small insects, which he saw as being captured using hearing and olfaction. Instead, Sussman notes that fruit bats also appear to have convergent orbits, like primates, and implicitly suggests that in primates this might be related in some way to eye–hand coordination:

> these nocturnal animals [i.e., fruit bats and primates] were feeding on and manipulating items of very small size (e.g., fruits, flowers and insects), at very close range, and under low light conditions. This might require acute powers of discrimination and precise coordination (Sussman, 1991, p. 219).

Rasmussen's (1990) study of the feeding and locomotor behavior of *Caluromys* led him to suggest that there might be elements of truth to both Cartmill's and Sussman's models. He suggested that the stem primates were lured out onto the terminal branches by:

> ...fruit and flowers with associated coevolving insect faunas ...Once up into the swaying terminal branches, those individuals that could best meet their arthropod requirements by visual predation probably had a selective advantage over those whose visual, locomotor and manual coordination abilities were less suited for such a complex task (Rasmussen, 1990, p. 274).

Thus, Rasmussen argues that early primates were lured out into the terminal branches for the reasons advocated by Sussman, but the visual specializations were adaptations for the NVP suggested by Cartmill.

Crompton (1995) argued that stereopsis in the fine-branch niche "cannot readily be ascribed to the need to detect cryptic, immobile insects, since they are not the typical prey" (Crompton, 1995, p. 25). Instead, in a modified version of the fine-branch niche hypothesis, Crompton argued that foraging, leaping, and climbing among the dense supports of the fine-branch niche would benefit from stereopsis and grasping hands because this environment:

> ...provides a visually complex, confusing background against which to distinguish a variety of mobile and immobile targets, both dietary items (fruit, as well as insects) and locomotor substrates (Crompton, 1995, p. 25).

In the end, Crompton invoked a multifactorial explanation for the origins of the orbital convergence.

> Orbital frontality is more likely to have first appeared as a consequence of the more general benefit that accrues, for a small-bodied primate similar to *Microcebus*, in the fine branch niche. This is provision of scotopic acuity and depth perception for the location of diverse targets, fruit and branches as well as insects in a complexly shaded environment (Crompton, 1995, p. 26).

The importance of the grasping hand for Crompton lies not only in climbing and manipulation of food, but also in securing a safe landing after short leaps. Once again, eye–hand coordination is implicit in Crompton's argument, although the relevance of this coordination for landing after a leap is not clear.

Thus, the adaptive significance of the distinctive features of the primate visual system is debated. Cartmill (1972, 1974) and Rasmussen (1990) agree that orbital convergence facilitates NVP on insects, captured with the hands in the fine-branch milieu; Sussman (1991) argues that orbital convergence is linked to manipulating small fruits, flowers, and insects under low light levels; Martin (1990) links orbital convergence to locomotion in a fine-branch niche, and Crompton (1995) invokes both

feeding on small food objects and locomotion to explain the evolution of orbital convergence.

These debates over the ecological significance of increased orbital convergence stimulated additional comparative morphometric research on orbit orientation in mammals. Heesy (2003) measured orbit orientation in a large sample of metatherian and eutherian mammals, and found strong effects of locomotor substrate, activity pattern, and diet on orbital orientation. Orbital convergence and frontation are higher in arboreal taxa than terrestrial or aerial taxa, and frontation and verticality are higher in faunivorous and omnivorous taxa than in opportunistic and nonpredatory animals. When these analyses were performed on eutherians exclusive of primates, nocturnal and cathemeral/crepuscular animals were found to have more convergent orbits than diurnal animals, and faunivorous taxa to have more convergent orbits than nonpredators. When all possible categories of locomotor substrate, activity pattern, and diet were considered, arboreal, nocturnal faunivores were ranked as having the highest degrees of orbital convergence. Heesy's analyses suggest that, across a wide range of mammals, nocturnal, arboreal faunivores tend to have more convergent orbits than other ecological categories. In a similar study, Ravosa and Savakova (2004) showed that, when allometric factors are taken into account, pteropodid bats do not have orbits that are as convergent as those of primates, negating one of Sussman's criticisms of the NVP hypothesis. Moreover, felid carnivorans (which are predominantly nocturnal) have primate-like degrees of orbital convergence, while nocturnal visual predatory tree shrews (*Ptilocercus*) and nocturnal procyonid carnivorans have more convergent orbits than diurnal predatory close relatives.

Both of these studies (Heesy, 2003; Ravosa and Savakova, 2004) corroborate the NVP hypothesis, but neither study explicitly evaluates the hypothesis relative to the fine-branch niche locomotion hypothesis. Ravosa and Savokova show that felids – NVPs not living in the fine-branch niche – have primate-like levels of orbital convergence, suggesting that NVP is sufficient to produce orbital convergence, but they do not exclude the possibility that fine-branch living also would produce this effect, even in the absence of NVP. Similar issues emerged from Lemelin's (1999) comparison of hand morphology in didelphid marsupials and primates. Although he confirmed that locomotion on fine terminal branches is associated with convergent similarities in hand and foot anatomy and proportions in marsupials and primates, the animals concerned also fed on small fruits and insects in the terminal branches. This makes it difficult to factor out the relative importance of feeding versus locomotion and of insectivory versus frugivory for hand and foot morphology.

To demonstrate that NVP is necessary and sufficient to explain orbital convergence and the unique hand morphology of primates, but fine branch locomotion or fruit feeding are not, NVPs living in the fine-branch niche need to be compared with non-NVPs living in the fine-branch niche. Variation in degrees of predation, hand morphology, and orbital convergence within primates provides one source of appropriate comparisons. Lemelin (1996, p. 173) reports preliminary results of analyses that demonstrated "significant and positive covariation between amount of insectivory, selection to catch styles, and relative lengths of the digits among closely related prosimians."

4.03.8 Comparative Neuroscience

In parallel with these developments in primatology, comparative neuroscience has revealed a series of distinctive features of the primate nervous system, which, judging by their common occurrence in most primates, can be hypothesized to have evolved along the primate stem lineage, after the divergence of any sister group, such as tree shrews and dermopterans.

4.03.8.1 Visual System

The high degree of orbital convergence characteristic of primates increases the size of the binocular field (Ross 2000; Heesy, 2004) and improves the potential and actual quality of the image falling on the central retina. These changes make it worthwhile increasing relative eye size to increase image size (Ross *et al.*, 2006), increase the density of photoreceptors and ganglion cells in the central retina to increase sampling frequency, and increase representation of the central retina in the visual structures of the brain (Allman, 1977). Barton (2004) has shown that, while controlling for body size, increases in relative orbital convergence are associated with increases in the relative volume of the lateral geniculate nucleus, relative area of the primary visual cortex, and relative neocortex size in general. Barton also shows that these increases are primarily attributable to increases in parvocellular rather than magnocellular pathways, suggesting that they reflect adaptations for improved fine-grained stereopsis, rather than increased sensitivity to movement. He suggests that:

> . . .the increase in visual brain size in primates with more convergent orbits might reflect enhancements of stereo-acuity and vergence-control mechanisms specifically related to the visually guided grasping and close-range manipulation of food items (Barton, 2004, p. 10115).

Barton's analysis treats variation in the visual system within primates, not across mammals, as a whole, so caution must be exercised when extending the results back into the primate stem lineage. To the extent that such extrapolation is valid, many of the changes to the visual system that occurred in the primate stem lineage can be hypothesized to have been not only integrated with each other, but also associated with improvements in fine-grained stereopsis and visual acuity in the center of the visual field. However, it is important to remember that the visual systems of stem primates were also characterized by an array of changes related to other functions, including improved sensitivity to movement, and improved ability to locate movements and sounds in space. Primates exhibit extensive projections from each retina to its ipsilateral lateral geniculate nucleus and superior colliculus, and both the visual cortex and superior colliculus contain representations of only the contralateral visual field. The superior colliculus provides the substrate for the visuomotor response, in which the eyes are directed to novel objects entering the visual field (Schiller and Stryker, 1972) and the unique arrangement of the projections to the superior colliculus in primates removes ambiguity regarding the position of those objects (Allman, 1999). As noted above, increased overlap of the visual fields across mammals is also associated with increased ability of the auditory system to localize sounds in space, suggesting that such abilities also characterized basal primates (Heffner and Heffner, 1982, 1992; Heffner, 2004). Primates are characterized by expansion and multiplication of their extrastriate visual areas, including not only areas that process information on fine-grained stereopsis and acuity (the ventral information stream in temporal cortex), but also areas such as the middle temporal (MT) area devoted to analysis of movement in the contralateral visual field (see reviews in Allman, 1977, 1999; Allman and McGuinness, 1988; Kaas, 2002). Thus, there is evidence that the basal primate visual system was modified not only to enhance fine-grained stereopsis (Barton, 2004), but also to improve the ability to detect and localize sources of movement and sound in the visual field. These latter attributes would be of particular benefit to NVPs, but of little obvious use for finding fruits and berries.

4.03.8.2 Hand Motor Control

In vertebrates, control of voluntary limb movements is mediated by descending pathways from the brain to the motor neurons in the spinal cord. All vertebrates possess reticulospinal, rubrospinal, tectospinal, and various other pathways from the brain to the spinal cord (Nudo and Masterson, 1988), but corticospinal tracts (CSTs) are found only in mammals. Simian primates and carnivores have larger CSTs than other mammals (Phillips and Porter, 1977; Figure 9), and the lateral CST of primates is unusual in both the degree to which it penetrates to caudal spinal cord segments and in the directness of its connections with motor neurons of the muscles of the distal extremities (Phillips and Porter, 1977; Heffner and Masterson, 1983). Across mammals and within primates, increased CST penetration down the spinal cord and increasingly ventral termination of CST connections within the cord are correlated with progressive increases in the degree of digital dexterity (Heffner and Masterson, 1975). This suggests that the emergence of these features in basal primates was associated with increased manual digital dexterity. Extant primates use their hands for many things, including grasping branches during locomotion, acquiring food, and social grooming (Bishop, 1964). Precisely which of these functions originally demanded enhanced dexterity is not immediately obvious from the anatomical data.

One question arising from these data is why there is a relationship between manual digital dexterity and CST penetration beyond those cervical spinal cord segments that supply the muscles of the forelimb (Heffner and Masterson, 1975). The answer to this conundrum may lie in a Wood Jonesian emancipation of the forelimb accompanying increased coordination of the hindlimbs and forelimbs. One benefit of this is illustrated in Figure 10, a photograph of a *Mirza coquereli* cantilevering from a
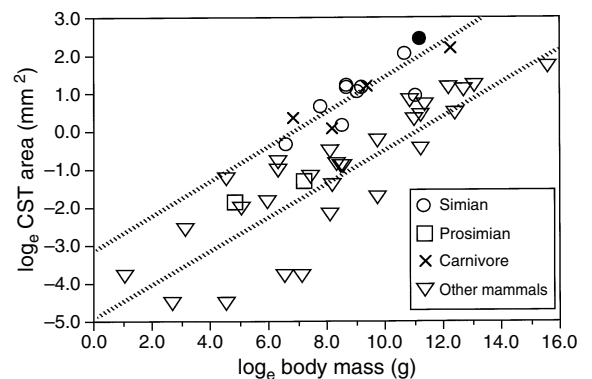
Figure 9 Bivariate plot of the natural log of CST area against the natural log of body mass in mammals. The least-squares regression lines for simian primates and for rodents are shown. Humans are shown by the solid circle. Simian primates have larger CSTs than other mammals, a feature in which they resemble carnivores. Data from Heffner, R. and Masterton, B. 1975. Variation in form of the pyramidal tract and its relationship to digital dexterity. *Brain Behav. Evol.* 12, 161–200.

Figure 10 *M. coquereli* adopting a cantilever posture. Image of Coquerel's dwarf Lemur, *M. coquereli*, Kirindy Forest, Madagascar, © Manfred Eberle, www.phocus.org.

vertical branch to grasp something out of the air. Various prosimians (cheirogaleids, galagos, and tarsiers) have been reported to manually acquire flying prey while holding onto branches with their feet (Crompton and Andau, 1986; Gebo, 1987; Martin, 1990). We hypothesize that extension of the CST down to lumbar and sacral spinal cord segments provides the anatomical connections necessary for arboreal mammals to coordinate a secure hold on the substrate with their hindlimbs or tail while they use their hands for catching insects, harvesting fruits, or other tasks requiring manual dexterity.

Another distinctive aspect of the primate corticomotor (CM), system is the degree of multiplication of premotor areas in frontal cortex. Macaques, for example, exhibit at least six separate premotor areas that project not only into primary motor cortex (MI), but also give origin to corticospinal neurons. In the three areas in which this has been studied, these corticospinal neurons include CM fibers that run directly from the cortex to the motor neurons in the ventral horn of the cervical and lumbar regions of the spinal cord (Dum and Strick, 2002). Five of the six premotor areas have distinct projections to both upper and lower cervical spinal cord segments. Three of these areas (supplementary motor area (SMA), dorsal cingulate motor areas (CMAd), ventral cingulate motor areas (CMAv)) project to lower cervical spinal cord segments, specifically to the intermediate zone and ventral horn, the latter of which contains the motor neuron cell bodies for the hand muscles. Each premotor area receives inputs from a different combination of posterior parietal and prefrontal cortical areas, "each participates in distinct loops with the basal ganglia and cerebellum" (Dum and Strick, 2002, p. 681), and each projects in parallel to the spinal cord. Just as

the multiplicity of prestriate visual areas serves as the substrate for a multiplicity of diverse visual functions, so each of these multiple premotor areas is argued to be "a functionally distinct efferent system that differentially generates and/or controls specific aspects of motor behavior" (Dum and Strick, 2002, p. 677). The anatomical and physiological relationships between these areas and the control of hand movements suggests that the increased dexterity characteristic of primates is related to the multiplication and increased functional diversity of these cortical premotor areas.

Nudo and Masterson (1990b) showed that the size of CST cortex is highly correlated with body mass, brain mass, and the area of the neocortex, with the strongest relationship between CST cortex area and overall neocortex area. After they factored out the effect of increased cortex size, they found primates to show a constant proportion of CST cortex to overall cortex area, while raccoons show relative increases in CST cortex compared to other carnivorans. They attributed the enlargement of the CST cortex in primates to overall neocortical enlargement. Whatever the mechanism of enlargement, the size of the cortical areas giving rise to CSTs increases along the lineages leading to humans and raccoons from basal mammals in parallel with their dexterity (Nudo and Masterson, 1990b).

4.03.8.3 Eye–Hand Coordination

Elliot Smith noted that eye–hand coordination is an important component of the basal primate adaptations, but most explanations for primate origins in the literature have neglected to emphasize this basal attribute. Recent studies in comparative neuroscience have revealed distinctive anatomical features of the primate brain that are involved in mediating this coordination.

Although nonprimate mammals have premotor areas that give origin to CSTs, primates are unique in having CSTs arise from a distinct subregion of ventral premotor cortex not found in other mammals: region C of Nudo and Masterson (1990a) or the arcuate premotor area (APA) of Dum and Strick (2002). Allman (1999) synonymized region C with the ventral premotor region, PMv, but region C in macaques at least is only the rostral part of PMv lying within the posterior bank of the inferior limb of the arcuate sulcus. Regardless of terminology, primates are unique in possessing areas PMv and APA/region C, both of which appear to be important in the control of visually guided reaching and grasping movements (i.e., eye–hand coordination).

APA is unusual among the six premotor areas discussed above in that it exhibits very dense and numerous connections to the hand representation in MI, and to upper cervical segments supplying the muscles crossing the shoulder and elbow joints, but does not project to lower cervical spinal cord segments where hand motor neurons are located. Nevertheless, stimulation of this area commonly elicits movements of the fingers and thumb, but less commonly movements of more proximal joints, such as the wrist, elbow, and shoulder (Martino and Strick, 1987; Dum and Strick, 1991; He et al., 1993). Dum and Strick (2002, p. 681) suggested that APA/region C "is primarily involved with control of distal forelimb movements" and the anatomical data presented above suggest that this control involves coordination of the movements in joints of the upper arm as well.

Preuss (1993) reviewed the evidence available at that time that PMv plays "a role in visually guided reaching and prehension." The work of Rizzolati et al. had revealed that neurons in PMv respond not only to tactile stimuli applied to the hands and face, but also to visual stimuli, especially to stimuli within reaching distance. Neurons in this region are active, "specifically during purposive, prehensive movements of the face and forelimbs" (Preuss, 1993). Preuss argued that integrated use of the mouth and the hand may have been important components of early primate feeding adaptations, whether for visually guided manual predation on insects as suggested by Cartmill (1970) or "visually guided grasping and manipulating fruits and flowers" as advocated by Rasmussen and Sussman (Preuss, 1993, p. 355). Preuss' hypothesis receives support from more recent observations that when PMv caudal to the inferior limb of the arcuate sulcus – close to the origin of the CST – is stimulated, coordinated movement of the hand to the mouth is elicited, accompanied by opening of the mouth (Graziano et al., 2002a). This suggests an important role for PMv in visually guided movements of the arm and hand during feeding. However, PMv also functions in the integration of tactile, auditory, and visual information in the control of arm movements (Graziano and Gandhi, 2000; Graziano et al., 1999, 2002a, 2002b). Graziano's work has revealed a polysensory zone that integrates visual, auditory, and tactile information into the planning of hand movements in space (Graziano et al., 1999; Graziano and Gandhi, 2000). Integration of visual, auditory, and tactile information is plausibly related to capturing flying or moving prey, whereas auditory information is not obviously necessary for coordination of movements associated with locomotion or grasping fruits.

Improved sensorimotor coordination in control of primate hand movements is also indicated by expansion and elaboration of somatosensory areas (ventral somatosensory area (VS), the parietal rostral area (PR), and the retroinsular area (Ri)) and areas in the posterior parietal cortex that are important for visual and visuomotor processing (Wu et al., 2000; Kaas, 2004). The latter areas connect forward into the array of new premotor areas in the frontal lobe, including the multiple premotor areas controlling hand and digit movements (e.g., PMv, SMA). Stimulation of the rostral half of posterior parietal cortex in Otolemur (Stepniewska et al., 2005) and macaques (Their and Andersen, 1998; Cooke and Graziano, 2003) elicits complex movements that "seem to be components of ethologically meaningful behavioral patterns such as feeding and defense" (Stepniewska et al., 2005, p. 4882). To the extent that these attributes and connections of PMv characterized stem primates, PMv was probably an important component of a neural system adapted not only for foraging for small fruits and berries, but also for NVP. Unfortunately, the available data do not allow definitive statements as to the original function of PMv. Graziano's research was carried out on macaques, and it is not clear to what extent nocturnal primates such as galagos and lorises possess a polysensory zone in PMv. Moreover, although the origin of PMv may have been more important for mediating eye–hand coordination used in feeding than in locomotion, the other premotor areas distinctive of primates (Kaas, 2004) may well have had locomotor-related functions originally, and the precise order in which they arose cannot currently be discerned. Indeed, it may be that the neurological adaptations associated with eye–hand coordination are either interchangeable with or so extremely similar for both NVP and fine-branch locomotion as to make it impossible to discriminate between these competing hypotheses regarding primate origins. However, both scenarios imply that improved eye–hand coordination was a fundamental adaptation in basal primates.

4.03.9 Locomotor System

As reviewed above, it was F. Wood Jones who suggested that specialization of the hindlimb for supporting body weight during climbing emancipated the forelimb from supportive functions, freeing it for specialization to perform other tasks. Several attributes of the primate locomotor system suggest that Wood Jones' hypothesis contains some nuggets of truth. The feet of primates are adapted for grasping as part of a distinctive grasp-leaping

pattern of locomotion (Szalay and Dagosto, 1988). Changes to the joint between the first metatarsal and the entocunieform allow the hallux (big toe) to be held in an abducted position, divergent from the rest of the digits, and to be stable under high forces during grasping. The proximal end of the first metatarsal manifests a robust process that not only buttresses the enotcunieform joint but also provides a hypertrophied area of attachment for the powerful peroneus longus muscle that plantarflexes and everts the foot at the ankle. The primate upper ankle joint is adapted for stability across an enhanced range of flexion and extension, as would be encountered during leaping, and the tarsal elements are elongated to enhance the length of the hindlimb, facilitating a more powerful leap (Martin, 1979). The lower ankle joint evinces adaptations for increased inversion and eversion of the foot necessary during climbing (Dagosto, 1988).

All digits of primates typically bear nails, rather than claws, although some species have re-evolved claw-like nails. Callitrichids and *Daubentonia* have claws on all digits except the hallux, and prosimians have a toilet claw on one pedal digit. The skin of the distal digits is expanded into pads sporting cutaneous ridges for increasing friction on arboreal supports. These ridges are also associated with Meissner's corpuscles for enhanced tactile sensitivity (Martin, 1986). The phalanges of the hands and feet are lengthened relative to the metapodials to improve grasping abilities on fine branches, an adaptation evolved convergently with didelphid marsupials (Lemellin, 1999).

Primate locomotor gaits are also distinctive (Martin, 1990; Schmitt, 2003). Primates typically employ diagonal sequence gaits in which the footfall of the forefoot always follows the contralateral hindfoot, ensuring a secure grasp of the substrate with the hindfeet before moving the forefoot (Cartmill *et al.*, 2002). Primates also walk with a compliant gait, characterized by more elbow flexion, less vertical displacement of the center of mass, and longer stride lengths than other mammals. These traits are hypothesized to have arisen as adaptations to locomotion on small compliant branches (Cartmill *et al.*, 2002; Schmitt and Lemelin, 2002). Convergent evolution of diagonal sequence gaits in the arboreal woolly possum, *Caluromys*, corroborates the hypothesized link between this trait and locomotion on fine supports (Lemelin *et al.*, 2003). Primates also have greater peak reaction forces at their hindlimbs than their forelimbs and they display a more protracted forelimb at touchdown than other mammals (Larson *et al.*, 2001). Convergent evolution of this complex of features

in the arboreal kinkajou (*Potos flavus*), a carnivore that also possesses a prehensile tail, provides support for Wood Jones' suggestion that the forelimb function becomes more diverse when the hindlimbs bear the majority of the body weight. Kinkajous not only support more of their body weight with their hindlimbs than their forelimbs, and exhibit highly protracted forelimbs at touchdown, resembling primates (Larson *et al.*, 2001), but they also possess CM connections to the ventral horn of the spinal cord, and relatively dextrous forelimbs (Petras, 1969).

4.03.10 The Fossil Record of Primate Origins

Although it may not be possible to determine from studies of extant primates alone whether the visual and grasping adaptations of early primates originally functioned as adaptations for locomotion or for feeding on insects and small fruits in light-limited environments (Allman, 1977; Pettigrew, 1978; Martin, 1990; Cartmill, 1982; Crompton, 1995), more direct evidence from the fossil record can provide insight.

The lineage leading to extant primates is traditionally thought to have diverged from other mammals close to the Cretaceous/Tertiary boundary. The first members of this primate lineage were long thought to be the plesiadapiforms, a radiation of fossil mammals that thrived in the Paleocene and Early Eocene of the northern continents. The traditional interpretation is that plesiadapiforms, or archaic primates, gave rise to a single stem lineage for euprimates, which quickly divided into two lineages, the omomyiforms and adapiforms, which appear in northern continents at the beginning of the Eocene (*c.* 55 Mya). Compared with plesiadapiforms, these latter two clades manifest closer anatomical similarities and phyletic affinities with extant primates and are grouped with them as Euprimates. In the 1980s and 1990s, many researchers excluded plesidapiforms from Primates because they are not adaptively similar to euprimates, and because cladistic analyses identified at least some plesiadapiforms as basal dermopterans (Beard, 1990; Kay *et al.*, 1992). Recent fossil discoveries and reinterpretation of old fossils have called into question the possibility of dermopteran relationships for plesiadapiforms and have once again identified them as the fossil group most closely allied with euprimates, placing them even closer to extant primates than tree shrews (Silcox, 2001; Bloch and Boyer, 2002).

The best-preserved plesiadapiform skull, that of the paromomyid, *Ignacius graybullianus*, is illustrative of plesiadapiform skulls in general (Figure 11). The braincase is relatively small and the orbits are small, superiorly facing, and completely confluent with the temporal fossa. The infraorbital foramen, like that of *Palaechthon* (Kay and Cartmill, 1977), is relatively large, suggestive of the importance of the vibrissae in detecting prey (Kay *et al.*, 1992). Skulls of *Plesiadapis* are similar, suggesting that the pronounced visual adaptations of euprimates were not shared by plesadapiforms. In contrast, postcranial fossils of many plesiadapiforms display a range of adaptations for arboreality (Szalay and Dagosto, 1988). Recently, a grasping foot with a nail on the hallux was reported from the carpolestid plesiadapiform *Carpolestes,* a putative close relative of primates (Bloch and Boyer, 2002). If *Carpolestes* is indeed representative of the stem lineage of euprimates, it suggests that the manual and pedal grasping abilities of primates evolved prior to their visual specializations, potentially supporting Rasmussen's hypothesis that early primates originally ventured into the small terminal branches in search of small fruits and only subsequently developed the visual adaptations characteristic of living primates (Bloch and Boyer, 2002).

Figure 11   Skull of *I. graybullianus* in dorsal, rostral, and ventral (stereopair) view. Scale bar: 1 cm. Images courtesy of R. F. Kay.

Although *Carpolestes* may have resembled the antecedents of the ancestral primates in some respects, several problems dictate caution in basing interpretations on a direct reading of the fossil record. First, the fossil record is notoriously incomplete. Tavaré *et al.* (2002) have estimated that less than 7% of the species in the primate crown clade have been recovered such that major gaps are present. Hence, even when fossil evidence of extinct species of primates and their relatives is available, these species can be separated from events of interest by significant lengths of time, diminishing their relevance as direct indicators (Ross *et al.*, 2002). These issues are particularly relevant to *Carpolestes*. Statistical analysis of the primate fossil record suggests that the branching points for the origins of extant primates are significantly older than the earliest known fossil representatives currently available. Tavaré *et al.* (2002) estimated the age of primates to be approximately 82 Mya, whereas *Carpolestes* lived at the very end of the Paleocene (*c.* 56 Mya), 26 Mya later. This problem is compounded by the phylogenetic position of *Carpolestes*, which Bloch *et al.* (2001) have argued is nested deep within the carpolestids, removing the species morphologically as well as temporally from developments in the origin of primates. Indeed, from a temporal and phylogenetic perspective, the relevance of *Carpolestes* to questions surrounding primate origins is comparable (at best) to the relevance of living gibbons for hypotheses surrounding human origins. Future fossil discoveries will be needed to address these issues more directly.

4.03.11 Conclusions

The origin of primates of modern aspect was associated with the evolution of a suite of changes to the visual system in concert with changes in other functional systems. We contend that understanding the role of vision in primate origins and evolution requires an understanding of the integration between these systems. Changes to the visual system producing increased sensitivity to low light levels, improved fine-grained stereopsis, and increased visual acuity and motion sensitivity were accompanied by improved abilities to localize sounds or movements in space, increased dexterity, and changes to the somatosensory and somatic motor systems that provided for improved control of visually guided reaching and grasping movements. These changes were accompanied by modifications in gait and musculoskeletal anatomy of the hands and feet related to arboreal

locomotion, including leaping and grasping on fine-branch supports. These changes were manifest not only in the musculoskeletal periphery, but also throughout the central nervous system, including the origins and terminations of the CSTs, the premotor areas controlling limb movements, the visual cortex, and the primary and secondary sensorimotor areas.

References

Allman, J. 1977. Evolution of the visual system in the early primates. In: Progress in Psychobiology and Physiological Psychology (eds. J. M. Sprague and A. N. Epstein), vol. 7, pp. 1–53. Academic Press.

Allman, J. M. 1999. Evolving Brains. W. H. Freeman.

Allman, J. M. and McGuinness, E. 1988. Primate visual cortex. In: Comparative Primate Biology (eds. H. Steklis and J. Erwin), pp. 279–326. Wiley.

Barton, R. A. 2004. Binocularity and brain evolution in primates. Proc. Natl. Acad. Sci. USA 101, 10113–10115.

Beard, K. C. 1990. Gliding behavior and palaeoecology of the alleged primate family Paromomyidae (Mammalia, Dermoptera). Nature 345, 340–341.

Bishop, A. 1964. Use of the hand in lower primates. In: Evolutionary and Genetic Biology of Primates (ed. J. Buettner-Janusch), pp. 133–225. Academic Press.

Bloch, J. I. and Boyer, D. M. 2002. Grasping primate origins. Science 298, 1606–1610.

Bloch, J. I., Fisher, D. C., Rose, K. D., and Gingerich, P. D. 2001. Stratocladistic analysis of Paleocene Carpolestidae (Mammalia, Plesiadapiformes) with description of a new late Tiffanian genus. J. Vertebrate Paleontol. 21, 119–131.

Cartmill, M. 1970. The Orbits of Arboreal Mammals: A Reassessment of the Arboreal Theory of Primate Evolution. Unpublished PhD dissertation, University of Chicago.

Cartmill, M. 1972. Arboreal adaptations and the origin of the order Primates. In: The Functional and Evolutionary Biology of Primates (ed. R. Tuttle), pp. 97–122. Aldine.

Cartmill, M. 1974. Rethinking primate origins. Science 184, 436–443.

Cartmill, M. 1980. Morphology, function and evolution of the anthropoid postorbital septum. In: Evolutionary Biology of the New World Monkeys and Continental Drift (eds. R. L. Ciochon and A. B. Chiarelli), pp. 243–274. Plenum.

Cartmill, M. 1982. Basic primatology and primate evolution. In: A History of American Physical Anthropology, 1930–1980 (ed. F. Spencer), pp. 147–186. Academic Press.

Cartmill, M., Lemelin, P., and Schmitt, D. 2002. Support polygons and symmetrical gaits in mammals. Zool. J. Linnaean Soc. 136, 401–420.

Charles-Dominique, P. 1977. Ecology and Behavior of Nocturnal Primates. Columbia University Press.

Charles-Dominique, P. and Martin, R. D. 1970. Evolution of lorises and lemurs. Nature 227, 257–260.

Cooke, D. F. and Graziano, M. S. A. 2003. Defensive movements evoked by air puff in monkeys. J. Neurophysiol. 90, 3317–3329.

Crompton, R. H. 1995. 'Visual predation', habitat structure, and the ancestral primate niche. In: Creatures of the Dark: The Nocturnal Prosimians (eds. L. Alterman, G. A. Doyle, and M. K. Izard), pp. 11–30. Plenum.

Crompton, R. H. and Andau, P. M. 1986. Locomotion and habitat utilization in free-ranging Tarsius bancanus: A preliminary report. Primates 27, 337–355.

Dagosto, M. 1988. Implications of postcranial evidence for the origin of euprimates. J. Hum. Evol. 17, 35–56.

Dominy, N. J., Ross, C. F., and Smith, T. D. 2004. Evolution of the special senses in primates: Past, present, and future. Anat. Rec. 281, 1078–1082.

Dum, R. P. and Strick, P. L. 1991. The origin of corticospinal projections from the premotor areas in the frontal lobe. J. Neurosci. 11, 667–689.

Dum, R. P. and Strick, P. L. 2002. Motor areas in the frontal lobe of the primate. Physiol. Behav. 77, 677–682.

Eizirik, E., Murphy, W. J., and O'Brien, S. J. 2001. Molecular dating and biogeography of the early placental mammal radiation. J. Hered. 92, 212–219.

Eizirik, E., Murphy, W. J., Springer, M. S., and O'Brien, S. J. 2004. Molecular phylogeny and dating of early primate divergences. In: Anthropoid Origins: New Visions (eds. C. Ross and R. F. Kay), pp. 45–61. Kluwer/Plenum.

Elliot Smith, G. 1924. The Evolution of Man. Oxford University Press.

Fleagle, J. G. 1999. Primate Adaptation and Evolution, 2nd edn. Academic Press.

Gebo, D. L. 1987. Locomotor diversity in prosimian primates. Am. J. Primatol. 13, 271–281.

Gebo, D. L. 2004. A shrew-sized origin for primates. Yb. Phys. Anthropol. 47, 40–62.

Gebo, D. L., Dagosto, M., Beard, K. C., and Qi, T. 2000. The smallest primates. J. Hum. Evol. 38, 585–594.

Geoffroy Saint-Hilaire, M. 1812a. Suite au tableau des quadrumanes. Lemuriéns. Strepsirrhini. Ann. Mus. Hist. Nat. 19, 156–170.

Geoffroy Saint-Hilaire, M. 1812b. Tableau des quadrumanes, ou des animaux composant le premier ordre de la classe des mammifères. Ann. Mus. Hist. Nat. 19, 85–122.

Graziano, M. S. A. and Gandhi, S. 2000. Location of the polysensory zone in the precentral gyrus of anesthetized monkeys. Exp. Brain Res. 135, 259–266.

Graziano, M. S. A., Reiss, L. A. J., and Gross, C. G. 1999. A neuronal representation of the location of nearby sounds. Nature 397, 428–430.

Graziano, M. S. A., Taylor, C. S. R., and Moore, T. 2002a. Complex movements evoked by microstimulation of precentral cortex. Neuron 34, 841–851.

Graziano, M. S. A., Taylor, C. S. R., Moore, T., and Cooke, D. F. 2002b. The cortical control of movement revisited. Neuron 36, 349–362.

Gregory, W. K. 1920. On the structure and relations of Notharctus, an American Eocene primate. Mem. Am. Mus. Natural Hist. 3, 49–243.

Hartwig, W. C. (ed.) 2002. The Primate Fossil Record. Cambridge University Press.

He, S. Q., Dum, R. P., and Strick, P. L. 1993. Topographic organization of corticospinal projections from the frontal lobe: Motor areas on the lateral surface of the hemisphere. J. Neurosci. 13, 952–980.

Heesy, C. P. 2003. The Evolution of Orbit Orientation in Mammals and the Function of the Primate Postorbital Bar. PhD thesis, Stony Brook University.

Heesy, C. P. 2004. On the relationship between orbit orientation and binocular visual field overlap in mammals. Anat. Rec. A 281, 1104–1110.

Heesy, C. P. 2005. Function of the mammalian postorbital bar. J. Morphol. 264, 363–380.

Heesy, C. P. and Ross, C. F. 2001. Evolution of activity patterns and chromatic vision in primates: Morphometrics, genetics and cladistics. J. Hum. Evol. 40, 111–149.

Heesy, C. P., Ross, C. F., and Demes, B. D. 2006. Oculomotor stability and the functions of the postorbital bar and septum.

In: Primate Origins: Adaptation and Evolution (*eds*. M. J. Ravosa and M. Dagosto). Springer (in press).

Heffner, R. and Heffner, H. E. 1982. Hearing in the elephant (*Elephas maximus*): Absolute sensitivity, frequency discrimination, and sound localization. *J. Comp. Physiol. Psycol.* 96, 926–944.

Heffner, R. and Masterton, B. 1975. Variation in form of the pyramidal tract and its relationship to digital dexterity. *Brain Behav. Evol.* 12, 161–200.

Heffner, R. S. 2004. Hearing in primates. *Anat. Rec. A* 281, 1111–1122.

Heffner, R. S. and Heffner, H. E. 1985. Auditory localization and visual fields in mammals. *Neurosci. Abst.* 11, 547.

Heffner, R. S. and Heffner, H. E. 1992. Evolution of sound localization in mammals. In: The Evolutionary Biology of Hearing (*eds*. D. B. Webster, R. R. Fay, and A. N. Popper), pp. 691–715. Springer.

Heffner, R. S. and Masterton, R. B. 1983. The role of the corticospinal tract in the evolution of human digital dexterity. *Brain Behav. Evol.* 23, 165–183.

Howells, W. W. 1947. Mankind So Far. Doubleday and Doran.

Jenkins, P. D. 1987. Catalogue of Primates in the British Museum (Natural History) and Elsewhere in the British Isles. Part 4: Suborder Strepsirrhini, Including the Subfossil Madagascan Lemurs and Family Tarsiidae. British Museum (Natural History).

Jerison, H. J. 1973. Evolution of the Brain and Intelligence. Academic Press.

Kaas, J. H. 2000. Why is brain size so important: Design problems and solutions as neocortex gets bigger or smaller. *Brain Mind* 1, 7–23.

Kaas, J. H. 2002. Convergences in the modular and areal organization of the forebrain of mammals: Implications for the reconstruction of forebrain evolution. *Brain Behav. Evol.* 59, 262–272.

Kaas, J. H. 2004. Evolution of somatosensory and motor cortex in primates. *Anat. Rec. A* 281, 1148–1156.

Kay, R. F. and Cartmill, M. 1977. Cranial morphology and adaptation of *Palaechthon nacimienti* and other Paromomyidae (Plesiadapoidea? Primates), with a description of a new genus and species. *J. Hum. Evol.* 6, 19–35.

Kay, R. F. and Kirk, E. C. 2000. Osteological evidence for the evolution of activity pattern and visual acuity in primates. *Am. J. Phys. Anthropol.* 113, 235–262.

Kay, R. F., Thewissen, J. G. M., and Yoder, A. D. 1992. Cranial anatomy of *Ignacius graybullianus* and the affinities of the Plesiadapiformes. *Am. J. Phys. Anthropol.* 89, 477–498.

Kay, R. F., Ross, C., and Williams, B. A. 1997. Anthropoid origins. *Science* 275, 797–804.

Kay, R. F., Williams, B. A., Ross, C. F., Takai, M., and Shigehara, N. 2004. Anthropoid origins: A phylogenetic analysis. In: Anthropoid Origins: New Visions (*eds*. C. F. Ross and R. F. Kay), pp. 91–135. Kluwer/Plenum.

Kiltie, R. A. 2000. Scaling of visual acuity with body size in mammals and birds. *Funct. Ecol.* 14, 226–234.

Larson, S. G., Schmitt, D., Lemelin, P., and Hamrick, M. 2001. Limb excursion during quadrupedal walking: How do primates compare to other mammals? *J. Zool., Lond.* 255, 353–365.

Le Gros Clark, W. E. 1934. Early Forerunners of Man: A Morphological Study of the Evolutionary Origin of the Primates. Bailliere, Tindall and Cox.

Le Gros Clark, W. E. 1959. The Antecedents of Man. Harper.

Lemelin, P. 1996. The Evolution of Manual Prehensility in Primates. PhD dissertation, State University of New York at Stony Brook.

Lemelin, P. 1999. Morphological correlates of substrate use in didelphid marsupials: Implications for primate origins. *J. Zool., Lond.* 247, 165–175.

Lemelin, P., Schmitt, D., and Cartmill, M. 2003. Footfall patterns and interlimb co-ordination in opossums (family Didelphidae): Evidence for the evolution of diagonal-sequence walking gaits in primates. *J. Zool., Lond.* 260, 423–429.

Lemme, M., Liu, Z. J., Rafferty, K. L., and Herring, S. 2005. *In vivo* postorbital ligament deformation: Temporalis incursion or masseteric pull. *IADR Conf. Abst.* CD publication.

Li, W.-H. 2000. Genetic systems of color vision in primates. *Am. J. Phys. Anthropol. Suppl.* 30, 318.

Liu, F.-G. R., Miyamoto, M. M., Freire, N. P., *et al.* 2001. Molecular and morphological supertrees for eutherian (placental) mammals. *Science* 291, 1786–1789.

Martin, L. 1986. Relationships among extant and extinct great apes and humans. In: Major Topics in Primate and Human Evolution (*eds*. B. Wood, L. Martin, and P. Andrews), pp. 161–187. Cambridge University Press.

Martin, R. D. 1972. Adaptive radiation and behaviour of the Malagasy lemurs. *Philos. Trans. R. Soc. Lond.* 264, 295–352.

Martin, R. D. 1973. Comparative anatomy and primate systematics. *Symp. Zool. Soc. Lond.* 33, 301–337.

Martin, R. D. 1979. Phylogenetic aspects of prosimian behavior. In: The Study of Prosimian Behavior (*eds*. G. A. Doyle and R. D. Martin), pp. 45–78. Academic Press.

Martin, R. D. 1990. Primate Origins and Evolution. A Phylogenetic Reconstruction. Princeton University Press.

Martin, R. D. 1993. Primate origins: Plugging the gaps. *Nature* 363, 223–234.

Martin, R. D. and Ross, C. F. 2005. The evolutionary and ecological context of primate vision. In: The Primate Visual System (*ed*. J. J. Kremers), pp. 1–36. Wiley.

Martino, A. M. and Strick, P. L. 1987. Corticospinal projections originate from the arcuate premotor area. *Brain Res.* 404, 307–312.

Ni, X., Wang, Y., Hu, Y., and Li, C. 2004. A euprimate skull from the Early Eocene of China. *Nature* 427, 65–68.

Niemitz, C. 1979. Outline of the behavior of *Tarsius bancanus*. In: The Study of Prosimian Behavior (*eds*. G. A. Doyle and R. D. Martin), pp. 631–660. Academic Press.

Noble, V. E., Kowalski, E. M., and Ravosa, M. J. 2000. Orbit orientation and the function of the mammalian postorbital bar. *J. Zool., Lond.* 250, 405–418.

Nudo, R. J. and Masterton, R. B. 1988. Descending pathways to the spinal cord: A comparative study of 22 mammals. *J. Comp. Neurol.* 277, 53–79.

Nudo, R. J. and Masterton, R. B. 1990a. Descending pathways to the spinal cord. IV: Some factors related to the amount of cortex devoted to the corticospinal tract. *J. Comp. Neurol.* 296, 584–597.

Nudo, R. J. and Masterton, R. B. 1990b. Descending pathways to the spinal cord. III: Sites of origin of the corticospinal tract. *J. Comp. Neurol.* 296, 559–583.

O'Brien, S. J., Menotti-Raymond, M., Murphy, W. J., *et al.* 1999. The promise of comparative genomics in mammals. *Science* 286, 458–481.

Petras, J. M. 1969. Some efferent connections of the motor and somatosensory cortex of simian primates and felid, candid and procyonid carnivores. *Ann. NY Acad. Sci.* 167, 469–505.

Pettigrew, J. D. 1978. Comparison of the retinotopic organization of the visual Wulst in nocturnal and diurnal raptors, with a note on the evolution of frontal vision. In: Frontiers of Visual Science (*eds*. S. J. Cool and E. L. Smith), pp. 328–335. Springer.

Phillips, C. G. and Porter, R. 1977. Corticospinal Neurones: Their Role in Movement. Academic Press.

Preuss, T. M. 1993. The role of the neurosciences in primate evolutionary biology, historical commentary and prospectus. In: Primates and Their Relatives in Phylogenetic Perspective (ed. R. D. E. MacPhee), pp. 333–362. Plenum.

Rasmussen, D. T. 1990. Primate origins: Lessons from a neotropical marsupial. Am. J. Primatol. 22, 263–277.

Ravosa, M. J. and Savakova, D. G. 2004. Euprimate origins: The eyes have it. J. Hum. Evol. 46, 355–362.

Ravosa, M. J., Noble, V. E., Johnson, K. R., Kowalski, E. M., and Hylander, W. L. 2000. Masticatory stress, orbital orientation, and the evolution of the primate postorbital bar. J. Hum. Evol. 38, 667–693.

Ritland, S. 1982. The Allometry of the Vertebrate Eye. Unpublished PhD dissertation, Department of Biology, University of Chicago.

Ross, C., Williams, B. A., and Kay, R. F. 1998. Phylogenetic analysis of anthropoid relationships. J. Hum. Evol. 35, 221–306.

Ross, C. F. 1995. Allometric and functional influences on primate orbit orientation and the origins of the Anthropoidea. J. Hum. Evol. 29, 201–227.

Ross, C. F. 2000. Into the light: The origin of Anthropoidea. Ann. Rev. Anthropol. 29, 147–194.

Ross, C. F., Lockwood, C. A., Fleagle, J. G., and Jungers, W. L. 2002. Adaptation and behavior in the primate fossil record. In: Reconstructing Behavior in the Primate Fossil Record (eds. J. M. Plavcan, R. F. Kay, W. L. Jungers, and C. P. van Schaik), pp. 1–41. Kluwer/Plenum.

Ross, C. F., Hall, M. I., and Heesy, C. P. 2006. Were basal primates nocturnal? Evidence of eye and orbit shape. In: Primate Origins: Adaption and Evolution (eds. M. J. Ravosa and M. Dagosto). Springer (in press).

Schiller, P. and Stryker, M. 1972. Single-unit recording and stimulation in superior colliculus of the alert rhesus monkey. J. Neurophysiol. 35, 915–924.

Schmitt, D. 2003. Insights into the evolution of human bipedalism from experimental studies of humans and other primates. J. Exp. Biol. 206, 1437–1448.

Schmitt, D. and Lemelin, P. 2002. The origins of primate locomotion: Gait mechanics of the woolly possum. Am. J. Phys. Anthropol. 118, 231–238.

Schulze, H. and Meier, B. 1995. Behavior of captive Loris tardigradus nordicus: A qualitative description, including some information about morphological bases of behavior. In: Creatures of the Dark: The Nocturnal Prosimians (eds. L. Alterman, G. A. Doyle, and M. K. Izard), pp. 221–249. Plenum.

Silcox, M. T. 2001. A Phylogenetic Analysis of Plesiadapiformes and Their Relationship to Euprimates and to Other Archontans. PhD thesis, Johns Hopkins University School of Medicine.

Springer, M. S., Cleven, G. C., Madsen, O., et al. 1997. Endemic African mammals shake the phylogenetic tree. Nature 388, 61–64.

Stepniewska, I., Fang, P.-C., and Kaas, J. H. 2005. Microstimulation reveals specialized subregions for different complex movements in posterior parietal cortex of prosimian galagos. Proc. Natl. Acad. Sci. USA 102, 4878–4883.

Sussman, R. W. 1991. Primate origins and the evolution of angiosperms. Am. J. Primatol. 23, 209–223.

Szalay, F. S. and Dagosto, M. 1988. Evolution of hallucial grasping in primates. J. Hum. Evol. 17, 1–33.

Tan, Y. and Li, W.-H. 1999. Trichromatic vision in prosimians. Nature 402, 36.

Tavaré, S., Marshall, C. R., Will, O., Soligo, C., and Martin, R. D. 2002. Using the fossil record to estimate the age of the last common ancestor of extant primates. Nature 416, 726–729.

Thier, P. and Andersen, R. A. 1998. Electrical microstimulation distinguishes distinct saccade-related areas in the posterior parietal cortex. J. Neurophysiol. 80, 1713–1735.

Walker, A. 1967. Patterns of extinction among the subfossil Madagascan lemuroids. In: Pleistocene Extinctions: The Search for a Cause (eds. P. S. Martin and H. E. Wright), pp. 425–432. Yale University Press.

Wood Jones, F. 1916. Arboreal Man. Arnold.

Wu, C. W.-H., Bichot, N. P., and Kaas, J. H. 2000. Converging evidence from microstimulation, architecture, and connections for multiple motor areas in the frontal and cingulate cortex of prosimian primates. J. Comp. Neurol. 423, 140–177.

Further Reading

Charles-Dominique, P. 1975. Nocturnality and diurnality: An ecological interpretation of these two modes of life by an analysis of the higher vertebrate fauna in tropical forest ecosystems. In: Phylogeny of the Primates: A Multidisciplinary Approach (eds. W. P. Luckett and F. S. Szalay), pp. 69–88. Plenum.

Cooke, D. F. and Graziano, M. S. A. 2004. Sensorimotor integration in the precentral gyrus: Polysensory neurons and defensive movements. J. Neurophysiol. 91, 1648–1660.

Dum, R. P. and Strick, P. L. 2005. Frontal lobe inputs to the digit representations of the motor areas on the lateral surface of the hemisphere. J. Neurosci. 25, 1375–1386.

Kay, R. F. and Kirk, E. C. 2000. Osteological evidence for the evolution of activity pattern and visual acuity in primates. Am. J. Phys. Anthropol. 113, 235–262.

Kirk, E. C. and Kay, R. F. 2004. The evolution of high visual acuity in the Anthropoidea. In: Anthropoid Origins: New Visions (eds. C. F. Ross and R. F. Kay), pp. 539–602. Kluwer/Plenum.

Milton, K. 1988. Foraging behaviour and the evolution of primate intelligence. In: Machiavellian Inheritance (eds. R. Byrne and A. Whiten), pp. 285–305. Oxford University Press.

Murphy, W. J., Eizirik, E., Johnson, W. E., Zhang, Y. P., Ryder, O. A., and O'Brien, S. J. 2001. Molecular phylogenetics and the origins of placental mammals. Nature 409, 614–618.

Nudo, R. J. and Masterton, R. B. 1989. Descending pathways to the spinal cord. II: Quantitative study of the tectospinal tract in 23 mammals. J. Comp. Neurol. 286, 96–119.

Soligo, C. and Martin, R. D. 2006. Adaptive origins of primates revisited. J. Hum. Evol. 50, 414–430.

Tan, Y. and Li, W.-H. 1999. Trichromatic vision in prosimians. Nature 402, 36.

Tan, Y., Yoder, A. D., Yamashita, N., and Li, W.-H. 2005. Evidence from opsin genes rejects nocturnality in ancestral primates. Proc. Natl. Acad. Sci. USA 102, 14712–14716.