

CHAPTER SEVEN

Were Basal Primates Nocturnal? Evidence from Eye and Orbit Shape

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INTRODUCTION

The adaptations of basal primates are of interest to paleoprimatologists because they give insight into the context in which primates diverged from other mammals. In addition, these basal adaptations may have biased the evolutionary trajectories taken by the lineages leading to extant primates. Diel activity pattern is an important component of an animal's ecology because it has pervasive influence on many aspects of primate morphology and behavior, including body size, diet, substrate preference, communication, and adaptations of the sensory systems (Charles-Dominique, 1975; Heesy and Ross, 2001, 2004; Martin, 1979).

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Early explanations for primate origins did not specify the activity pattern of basal primates (Cartmill, 1970, 1972, 1974; Elliot Smith, 1924; Le Gros Clark, 1959; Wood Jones, 1916), with one possible exception. Writing in the spirit of the "Primatological Synthesis" (*sensu* Cartmill, 1982), in which

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Primates were defined by a set of pervasive trends, Polyak (1957) argued that trends toward diurnality, high-visual acuity, and color vision, culminating in the higher primates, suggested continuity of diurnal “potential” through the mammalian stem lineage, up through primates. According to Polyak (1957: 968–969), nocturnal strepsirrhines are divergent from the diurnal mainstream of primate evolution.

By the beginning of the 1970s, however, P. Charles-Dominique and R. D. Martin’s field studies had revealed many ecological and behavioral similarities between *Microcebus murinus* and “*Galago demidovii*,” including nocturnality, leading them to suggest that many of these aspects are likely to be both ancestral strepsirrhine and ancestral primate characteristics (Charles-Dominique and Martin, 1970). Martin (1973) bolstered the argument that the ancestral strepsirrhines were nocturnal by noting that many diurnal lemurid species possess a tapetum. Tapeta are usually found in nocturnal animals (Walls, 1942; see Ross, 2004, for a review), suggesting that their presence in extant diurnal strepsirrhines is due to “primitive retention.” Extending this “primitive retention” argument to explain the *absence* of a tapetum in *Aotus* and *Tarsius*, Martin suggested that these animals were descended from diurnal ancestors, retaining a diurnal adaptation into a nocturnal environment (Martin, 1973). This argument was reinforced by the observation that *Tarsius* also possesses a retinal fovea (Le Gros Clark, 1959)—a traditionally diurnal adaptation (Ogden, 1974; Polyak, 1957; Ross, 2004; Walls, 1942). In contrast with Martin’s “primitive retention” explanation for the imperfect correlations between primate morphology and activity pattern, Charles-Dominique (1975: 86) suggested that the last common ancestor of primates “had an eye slightly differentiated for both nocturnal and diurnal vision,” capable of evolving into an anthropoid or a strepsirrhine eye.

By the late 1970s, the issue of the activity pattern of basal primates was independently addressed by a number of workers. Martin (1979) marshaled evidence, including body size, relative size of the olfactory bulb, and the presence or absence of tapeta, to suggest “that nocturnal life involving at least some predation on small animals is a primitive feature for the lemurs and lorises, and possibly for the primates as a whole” (Martin, 1979: 72). Supporting Martin’s argument were functional interpretations of two features assumed to have characterized basal primates: high degrees of orbital convergence and relatively large orbital apertures.

ORBITAL CONVERGENCE

Primates have long been noted to have more convergent orbital apertures than most other mammals. Early explanations related convergence to arboreality (Elliot Smith, 1924; Le Gros Clark, 1959; Wood Jones, 1916). However, comparisons with other animals suggested to Cartmill (1970, 1972) that convergent orbits facilitated visual predation on insects in the fine branches of the shrub layer of tropical rainforests. Cartmill argued that “Stereoptic integration of the two visual fields improves the accuracy of the final strike; increase in visual-field overlap facilitates compensation for evasive movements of the prey” (1972: 113). Cartmill’s hypothesis did not specify whether these first primates were diurnal, nocturnal, crepuscular, or cathemeral, and was left to Jack Pettigrew and John Allman to round out the visual predation hypothesis, specifying nocturnality as an essential part of the argument (Cartmill, 1992).

Pettigrew (cited by Allman, 1977: p. 29; Pettigrew, 1978) and Allman (1977) pointed out that the dioptric benefits of orbital convergence accrue to nocturnal rather than diurnal animals. The optical axis is the axis of the dioptric apparatus of the eye (i.e., lens and cornea), around which image quality is highest, whereas the visual axis is the “physiological line of fixation” (Walls, 1942: 292), approximated by a line passing through the center of the pupil and the retinal fovea or area centralis. Thus, alignment of the optic axis with the visual axis maximizes image quality in the fovea or area centralis (Figure 1). The Allman-Pettigrew model posits that orbital convergence is correlated with convergence of the optic axes on the visual axes (Figure 2), providing improved image quality in nocturnal primates. Another way to ensure high-image quality across the retina is to restrict incoming images to the paraxial region of the dioptric apparatus. This can be achieved by decreasing diameter of the pupil, but this option is not available to nocturnal animals that must maintain large pupil sizes in order to maintain image brightness. Consequently, nocturnal animals can only improve image quality in the area of visual field overlap by optic convergence (Figure 2). This suggested to Allman (1977) that if the first primates had high degrees of orbital convergence, then they were probably nocturnal.

Convergence of the optic axes on each other increases the size of the region of visual field overlap (Heesy, 2004; Ross, 2000), something that Cartmill hypothesized was advantageous in the pursuit of evasive prey.

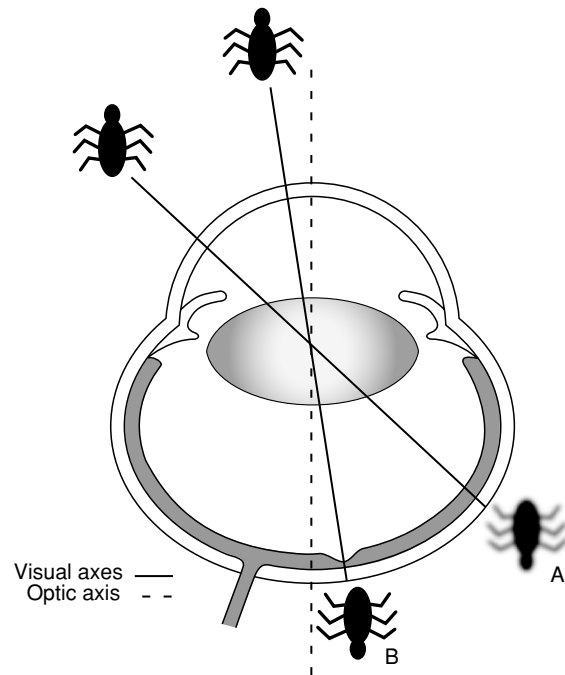


Figure 1. Diagram of eye illustrating the relationship between image quality and the orientation of the optic and visual axes. The optic axis is the axis of the dioptric apparatus (i.e., the primary refracting surfaces of the eye, the cornea, and the lens). The visual axis is the “physiological line of fixation” (Walls, 1942: 292), approximated by a line intersecting the center of the pupil and the center of the region of the retina, which the animal directs at objects of interest, and in which the animal has the highest visual acuity. In all mammals this region is the area centralis, and in haplorhine primates this region also contains a fovea. Image quality is highest for paraxial images or images close to the optic axis and deteriorates with distance from the optic axis. Image quality and visual acuity are maximized when the visual axis is close to the optic axis (A) and is minimized when the visual axis is divergent from the optic axis (B).

However, nocturnal animals also benefit from visual field overlap because it increases sensitivity to low-light levels, the eyes effectively having double the chance of registering a photon from any part of the binocular visual field. This improves the signal-to-noise ratio of the image, and improves contrast detection (Lythgoe, 1979; Pettigrew, 1986). Thus, optic (and presumably orbital) convergence provides two advantages to nocturnal animals: improved image quality, and increased image brightness in the binocular visual field.

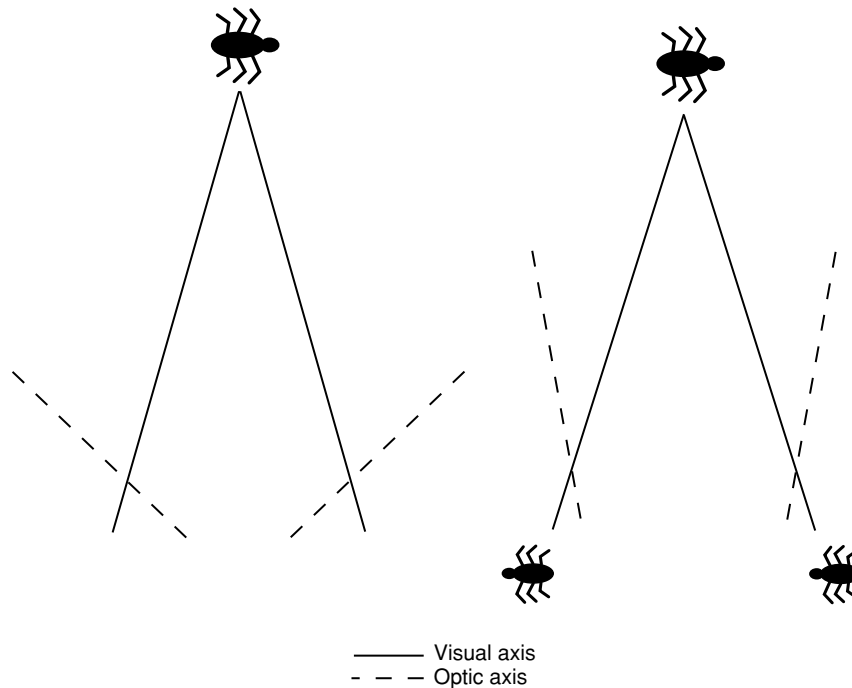


Figure 2. Diagram illustrating relationship between orientation of optic axis, visual axis, and orbits in a plesiadapiform-like animal with divergent orbits (left), and a primate with convergent orbits (right). The retinal images of objects in the binocular visual field (in front of the snout) are of lower quality in the animal with divergent orbits than in the primate. This is because the visual axis is less closely aligned with the optic axis in the animal with divergent orbits.

ORBIT SIZE AND SHAPE

Small-bodied nocturnal primates have long been noted to have larger orbital apertures than small-bodied primates of the same skull length (Cartmill, 1977; Heesy and Ross, 2001; Kay and Kirk, 2000; Walker, 1967). These differences in orbital aperture dimensions may reflect several aspects of eye size and shape (Kirk, 2004; Ross, 2000). The dioptric principles underlying the relationship between eye shape and activity pattern are illustrated in Figure 3. Nocturnal animals live in scotopic, or low-light level conditions. Low-light levels compromise image quality by providing poor sampling of the visual environment. Consequently, visually dependent nocturnal animals

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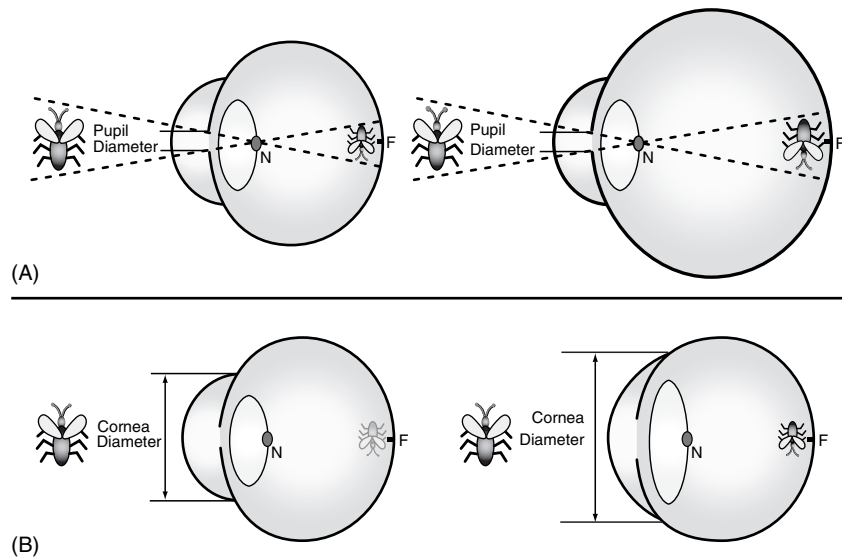


Figure 3. Diagrams illustrating relationship between eye shape and activity pattern. N = nodal point. Distance from nodal point to retina is focal length. Visually dependent diurnal animals are expected to have large focal lengths relative to pupil diameter in order to maximize image size and, hence, the resolution of the image (A). Visually dependent nocturnal animals are expected to have large pupil diameters relative to focal length in order to maximize image brightness (B). Nocturnal animals can also increase image brightness by increasing eye size while also increasing the effective size of the photoreceptor units (Land and Nilsson, 2002).

exhibit adaptations for increasing the number of photons captured from the visual field, or image brightness. Image brightness is directly related to the area of the pupil and to the solid angle in space from which each receptor samples light (Land and Nilsson, 2002). The first determines the number of photons that can enter the eye simultaneously, the second determines the number of photons that can enter each photoreceptor (Land, 1981). The angle of acceptance of a photoreceptor is inversely related to the focal length of the eye (or posterior nodal distance), roughly the distance from the lens to the retina (see Figure 4), so the longer the focal length of the eye, the dimmer the image. An intuitive sense of this can be achieved by shining a flashlight on a wall: the closer the flashlight is to the wall, the smaller and brighter the image. The same is true of the eye: the shorter the focal length of the eye, the smaller and brighter the image on the retina. Hence, visually dependent

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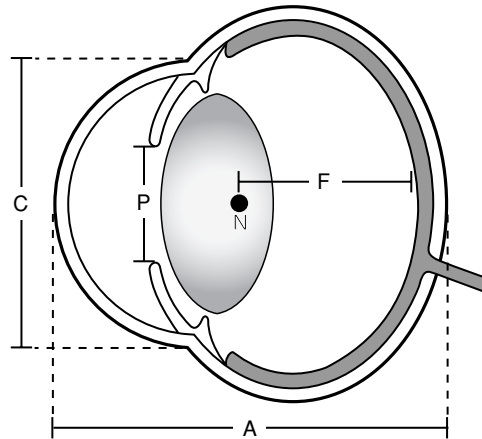


Figure 4. Diagram illustrating measures of eye shape used in this study and the variables they estimate. N=Nodal point; F=Focal length or posterior nodal distance; P=Pupil diameter; C=Cornea diameter; A=Axial diameter or length of the eye. Cornea diameter is a reasonable estimator of pupil diameter (see Ross, 2000). Axial diameter of the eye is assumed to be a sufficiently good estimator of focal length of the eye, following Hughes (1977).

nocturnal animals are predicted to have large corneas relative to their focal length regardless of body or eye size (Figure 3B).

In addition to these effects on eye shape, nocturnality is also predicted to be associated with increased eye size. The pupil obviously cannot be larger than the eye, so eye size limits the amount that the pupil can be expanded. If pupil diameter is increased by making the eye bigger, focal length will also increase, reducing image brightness by decreasing the angle of acceptance of the photoreceptors. However, this latter effect can be compensated for by increasing the effective size of the photoreceptors. In vertebrates this is done by pooling many receptors into one functional unit by connecting many of them up to a single ganglion cell—a phenomenon widespread among vertebrates, including primates (Kay and Kirk, 2000; Rohen and Castenholtz, 1967). Thus, photoreceptor pooling allows image brightness to be increased purely by increasing eye size, so it is expected that nocturnal animals will have larger eyes than similarly sized diurnal animals.

It has also been argued that photoreceptor pooling has the added benefit of widening the range of “image brightness,” or luminance, to which an

animal is sensitive (Martin, 1999). This hypothesis assumes that the size of the photoreceptor (rod) pools of nocturnal animals is flexible at the retinal level, allowing changes in the size of the pool in response to different luminance levels. This would be valuable in nocturnal environments that are characterized by a much wider range of luminance levels than diurnal environments (Lythgoe, 1979; Martin, 1990, 1999). The hypothesis argues that increases in eye size would augment the number of photoreceptor pools, creating the possibility of greater flexibility to the greater range of light levels in nocturnal environments (Martin, 1990, 1999). The validity of this hypothesis remains in doubt until mechanisms for adjusting receptive field size in scotopic conditions are demonstrated. Primates lack rod-rod coupling that might be one mechanism to accomplish this (Djamgoz et al., 1999), but there do appear to be up to three pathways for information to pass from rods to the inner retina, and these pathways may operate under different ambient light conditions (Bloomfield and Dacheux, 2001).

Diurnal animals, in contrast, are not constrained by the need to shorten focal length or enlarge the pupil, because image brightness is not a problem in the photopic or light rich environment. Consequently, visually dependent diurnal animals are able to have long focal lengths, thereby decreasing the acceptance angle of each photoreceptor in the retina, and increasing visual resolution (Figure 3A). Another way of saying this is that increased focal length spreads the image over a larger number of photoreceptors, increasing visual resolution. Moreover, because diurnal animals do not need to enhance image brightness, they are predicted to have small pupils relative to focal length.

RECONSTRUCTIONS OF ORBIT SIZE AND SHAPE IN BASAL PRIMATES

Functional interpretations of orbital convergence and enlargement only suggest that basal primates were nocturnal if these features were present in basal primates. The last common ancestor of primates is not known from fossil evidence, and nor are their immediate outgroups. Consequently, the assumption that basal primates had orbital apertures that were convergent and enlarged rests on interpretation of the available evidence from fossils and extant taxa.

The objectives of this study are: (a) to document the relationship between eye size and shape, and activity patterns in extant primates; (b) to document

the relationships between eye size and shape, and activity patterns in extant amniotes and use these data to interpret primate eye shape; and (c) to use orbit shape data to reconstruct activity pattern in fossil primates.

MATERIALS AND METHODS

Eye Shape Measures

On the basis of the dioptric principles outlined in the Introduction, visually dependent nocturnal animals are predicted to have large pupils relative to focal length, and visually dependent diurnal animals are predicted to have small pupil diameters for their focal lengths. These dimensions cannot be measured accurately in preserved eyes and are known for only a small number of vertebrates (e.g., Arrese, 2002; Hughes, 1977; Martin, 1999). Here, we use the axial diameter of the eye as a surrogate for focal length, and cornea diameter as a surrogate for pupil diameter (Figure 4). Hughes (1977, Figure 9B) has shown that, across a range of vertebrates of differing activity patterns, focal length is approximately 0.6 axial diameter of the eye. Assuming that this relationship is constant across vertebrates, we use axial diameter of the eye as a surrogate for focal length. Cornea diameter is a reasonable surrogate for pupil diameter as there is no obvious reason to have a cornea that is significantly larger than the pupil.

To investigate scaling relationships of cornea diameter and axial length, head and body length is used as a measure of body size for comparisons across different groups of amniotes.

Orbit Shape Measures

The relationship between relative size of the orbital aperture and activity pattern has long been of interest to paleoprimatologists because it provides a method for reconstructing activity pattern in moderately well-preserved fossils (Beard et al., 1991; Heesy and Ross, 2001; Kay and Cartmill, 1977; Kay and Kirk, 2000; Martin, 1990; Rasmussen and Simons, 1992; Walker, 1967). Given the relationship between eye shape and activity pattern predicted above, we also predict that there will be a relationship between orbit shape and activity pattern. Specifically, we predict that the size of the orbital aperture relative to the axial depth of the orbit should be correlated with activity pattern. The underlying assumptions, that pupil or cornea area is correlated

with orbital aperture area, and that the axial length of the eye is correlated with the axial depth of the orbit, have not yet been evaluated using measures of orbit and eye shape taken from the same individuals.

Orbital aperture size is estimated by the diameter of the orbital aperture, measured from orbitale inferius to the orbitale superius (Cartmill, 1970). Orbit depth is calculated as the distance from the midpoint of orbitale superius–orbitale inferius chord to the superiormost point along the rim of the optic canal. These measures were extracted using customized Macros in Microsoft Excel, from 3D coordinates of points collected using a Microscribe 3DX digitizer (Immersion Corp., San Jose, CA).

Orbit diameter data for *Cantius abditus* are from Heesy and Ross (2001). The optic canal of *Cantius abditus* (USNM 494881: Rose et al., 1999) is not preserved. A minimum estimate of the axial depth of the orbit in *C. abditus* was obtained by combining the length of the orbit floor in *C. abditus* (USNM 494881) with that of another specimen of this taxon (USNM 93938). Comparisons of *C. abditus* (USNM 494881) orbit and preserved braincase with similar-sized extant strepsirrhines (e.g., *Otolemur crassicaudatus*) suggest that the orbit depth was not substantially longer than this estimate.

The majority of the eye shape data were derived from Ritland (1982). Data from nonadult individuals were excluded. The primate eye shape data were derived in part from Ritland (1982), as well as from unpublished observations made by C. F. Ross. Additional data on bats and birds were collected by M. I. Hall. The orbit shape data were collected from different specimens than the eye shape data.

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Reduced major axis (RMA) regression equations for all Aves, Primates, and Mammalia were calculated from least squares equations generated by SPSS. The RMA slopes, intercepts, and correlation coefficients are given in Table 1.

RESULTS

Eye Size and Shape

Figure 5 plots axial eye diameter against head and body length in extant primates and other mammals. Nocturnal primate eyes have larger axial diameters than most similarly sized nonprimate mammals. Tarsiers have longer eyes relative to body size than any other mammals. Axial diameter of the eye scales with negative allometry across all diurnal and nocturnal mammals, and all

Table 1. Reduced major axis (RMA) regression statistics

Variables	Activity	n	RMA slope	RMA intercept	r
CD vs. AD					
Aves	Nocturnal	129	0.967	-0.100	0.951
	Diurnal	166	0.930	-0.174	0.971
Mammals	Nocturnal	174	0.912	0.0194	0.979
	Diurnal	103	1.138	-0.332	0.921
Primates	Nocturnal	30	0.765	0.179	0.971
	Diurnal	49	0.963	-0.192	0.892
CD vs. HBL					
Aves	Nocturnal	146	0.875	-0.799	0.864
	Diurnal	193	0.678	-0.590	0.826
Mammals	Nocturnal	174	0.802	-0.941	0.699
	Diurnal	103	0.576	-0.480	0.852
Primates	Nocturnal	30	0.417	0.103	0.539
	Diurnal	49	0.450	-0.182	0.895
AD vs. HBL					
Aves	Nocturnal	129	0.906	-0.726	0.85
	Diurnal	166	0.729	-0.446	0.837
Mammals	Nocturnal	197	0.882	-1.059	0.724
	Diurnal	107	0.507	-0.132	0.881
Primates	Nocturnal	30	0.546	-0.100	0.603
	Diurnal	56	0.467	0.011	0.903

AD = axial diameter; CD = cornea diameter; HBL = head and body length.

diurnal and nocturnal primates. However, as noted elsewhere (Ross, 2000), the relationship between these variables across all mammals is not linear, being positively allometric at small body sizes and negatively allometric at large body sizes. Because small primates have relatively larger eyes than other mammals, the primate slopes are significantly less steep than those for all mammals combined.

Figure 6 plots axial diameter of the eye against head and body length in extant primates and birds. Tarsiers fall within the range of nocturnal birds, i.e., strigiforms (owls) and caprimulgiforms (nightjars, frogmouths). Most of the diurnal birds lying between the nocturnal bird and diurnal primate distributions are falconiforms. The rest of the diurnal birds are parrots, pigeons, and procellariiform sea-birds, which fall among and below the primate distributions. Across nocturnal and diurnal birds, eye axial diameter is negatively allometric. However, the 95% confidence limits for nocturnal birds almost include 1.00 (= 0.99), and are significantly steeper than either mammals or primates.

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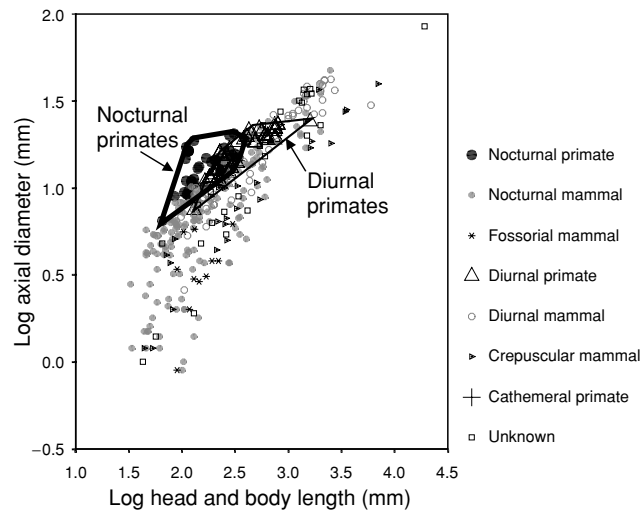


Figure 5. Bivariate plot of axial diameter (\log_{10}) against head and body length (\log_{10}) across all mammals. Minimum spanning polygons for nocturnal primates and diurnal primates are added. Nocturnal primates have longer axial lengths for their body size than similarly sized nonprimate mammals.

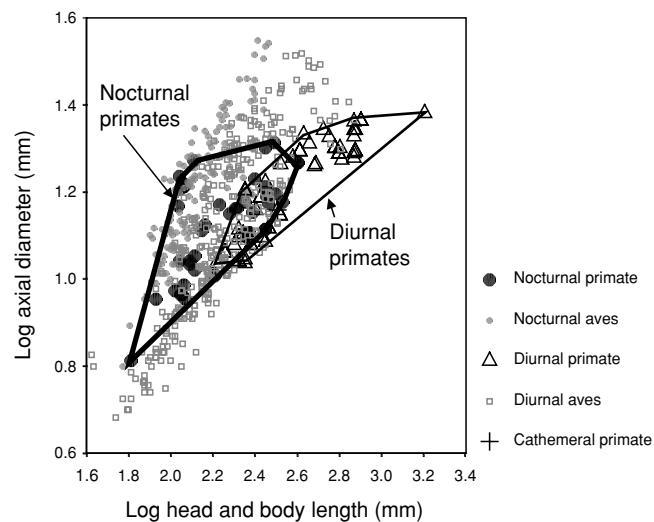


Figure 6. Bivariate plot of axial diameter (\log_{10}) against head and body length (\log_{10}) across birds and primates. Minimum spanning polygons for nocturnal primates and diurnal primates are added. The nocturnal primates with the longest axial lengths for their body size are tarsiers, which plot with the nocturnal birds represented here; i.e., strigiforms (owls) and caprimulgiforms (nightjars and frogmouths).

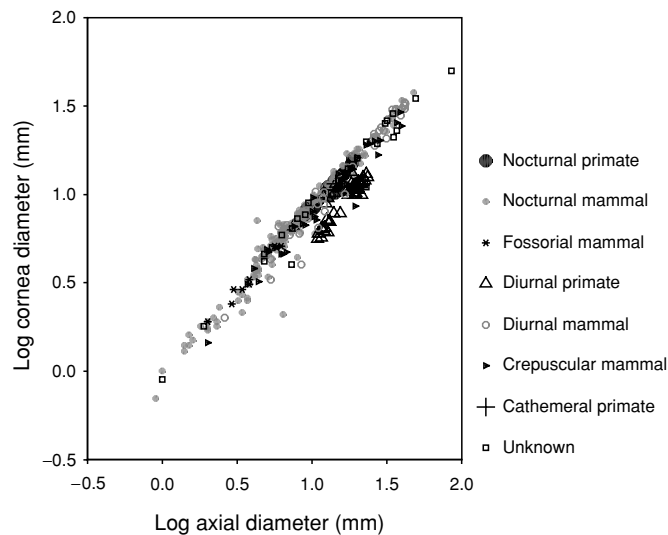


Figure 7. Bivariate plot of corneal diameter (\log_{10}) against axial diameter (\log_{10}) across mammals.

Figure 7 plots cornea diameter against axial diameter in extant primates and other mammals. Nocturnal primates, as well as diurnal and cathemeral strepsirrhines, fall with other mammals on a plot of cornea diameter versus axial diameter of the eye (see also Ross, 2000). Diurnal anthropoids differ from all other mammals in having small corneas relative to axial length, or longer eyes relative to cornea diameter. The separation between nocturnal and diurnal primates extends to all body sizes sampled. The RMA slopes for nocturnal and diurnal primates are not significantly different, and the intercept for diurnal primates is significantly lower than that for nocturnal primates. Eye shape does not sort nocturnal and diurnal nonprimate mammals. Cornea diameter scales isometrically with axial diameter in diurnal primates, with positive allometry across all diurnal mammals, with negative allometry across nocturnal primates, and with slight negative allometry across all nocturnal mammals.

Figure 8 plots cornea diameter against axial diameter in extant primates and birds. Nocturnal primates and diurnal strepsirrhines plot with nocturnal birds in relative cornea and axial diameter, whereas diurnal anthropoids plot amongst diurnal birds. Eye shape sorts nocturnal and diurnal birds from each other, and diurnal anthropoids from other primates. Cornea diameter scales

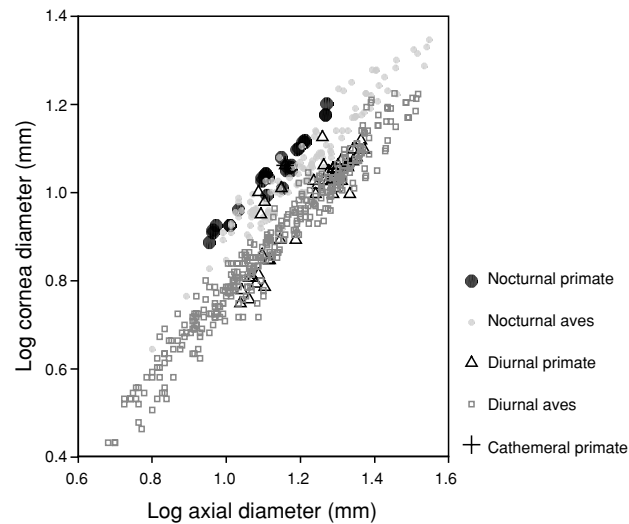


Figure 8. Bivariate plot of corneal diameter (\log_{10}) against axial diameter (\log_{10}) across birds and primates.

isometrically with axial diameter in nocturnal birds, and with slight negative allometry in diurnal birds.

The RMA slopes of corneal diameter against axial diameter are not significantly different from each other in diurnal primates, diurnal birds, nocturnal birds, and nocturnal mammals. Nocturnal primates have a significantly shallower slope than diurnal primates, and diurnal mammals have a significantly steeper slope than all other groups.

Figure 9 diagrams the distributions of cornea and axial diameters in mammals and birds with minimum spanning polygons. There is surprisingly little variability in eye shape across these clades. Diurnal anthropoids and diurnal birds have longer axial lengths for their cornea diameters than other birds and mammals, whereas nocturnal birds, nocturnal primates, and diurnal strepsirrhines (asterisks) plot among nonprimate mammals, without regard for their activity pattern.

Orbit Size and Shape

Figure 10 plots orbit aperture diameter against orbital depth in extant primates and some fossils. Orbital aperture diameter is positively correlated with orbit depth in both nocturnal and diurnal taxa, and within each activity group there is little variation in orbit diameter at any given orbit depth. In this

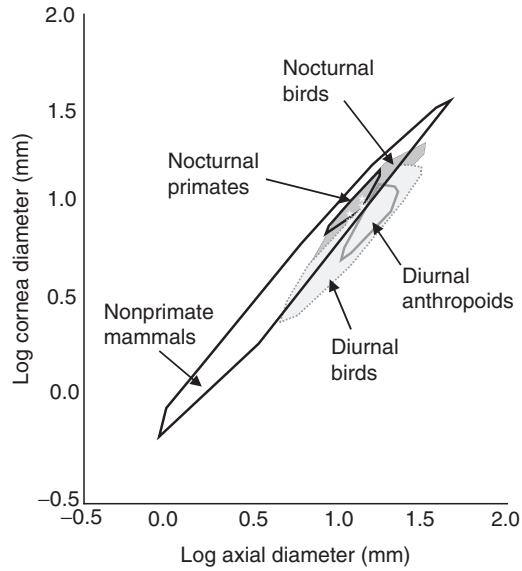
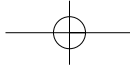


Figure 9. Bivariate plot of corneal diameter (\log_{10}) against axial diameter (\log_{10}) across birds, nonprimate mammals, and primates. Minimum spanning polygons are illustrated, excluding two outliers for nonprimate mammals. White asterisks on nocturnal primate polygon are diurnal strepsirrhine primates.

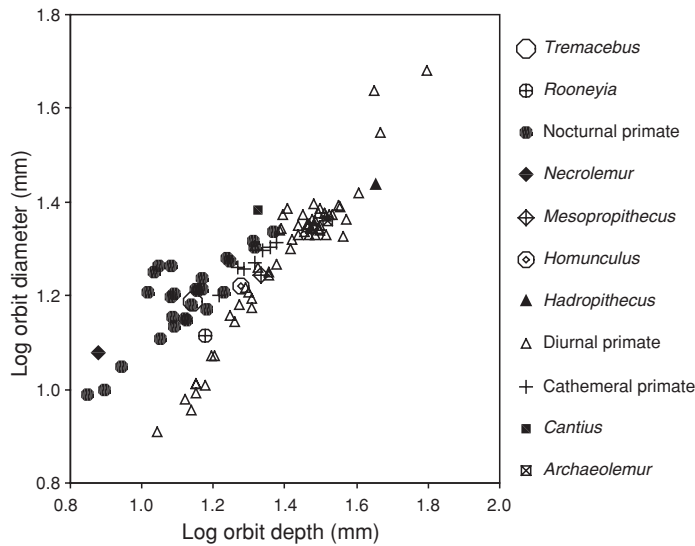
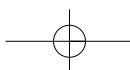


Figure 10. Bivariate plot of orbital aperture diameter (\log_{10}) against axial depth of the orbit (\log_{10}) across primates.



respect this plot resembles the plot of cornea diameter against axial length of the eye in birds and primates (Figure 7). However, the slopes of the two distributions differ, so that at small body sizes nocturnal primates have larger orbital apertures than diurnal primates with the same axial depths, but above an axial depth = 1.3 (\log_{10}) the nocturnal and diurnal distributions begin to overlap.

The activity patterns of several fossil taxa can be reconstructed by plotting them on this distribution. As noted by others, *Necrolemur* was almost certainly nocturnal. *Tremacebus* and *Homunculus* also plot as nocturnal, and *Mesopropithecus* plots as diurnal. *Rooneyia* plots closest to the diurnal primates, and was probably diurnal, although it has a slightly larger orbit diameter than extant diurnal primates. At orbit depths greater than that of *Mesopropithecus* there are no nocturnal extant primates, so it is not possible to estimate the activity patterns of larger fossil forms, such as *Hadropithecus*. *Cantius* falls above the distribution of extant nocturnal primates, suggesting that it was nocturnal, confirming the results of Heesy and Ross (2001). However, because of the uncertainty of orbit depth in this taxon, this conclusion must be regarded as preliminary.

DISCUSSION

The Eyes of Basal Primates

There is debate as to the precise ecological significance of the relatively high levels of orbital convergence seen in primates. Cartmill attributes it to selection for nocturnal visual predation (Cartmill, 1992), whereas others associate it with manual manipulation, or visual detection of small objects, including fruits, insects, and small branches in a nocturnal rainforest environment (Crompton, 1995; Rasmussen, 1990; Sussman, 1991, 1995). Common to all these models is the relationship between orbital convergence and nocturnality. Although relatively high degrees of orbital convergence have not been extrapolated down to basal primates using rigorous character optimization methods, all primates, living and fossil, with only one exception (*Megaladapis*) have more highly convergent orbits (Heesy, 2003; Ni et al., 2004; Ravosa and Savokova, 2004) than seen in nonprimate mammals, including plesiadapiforms. It, therefore, seems probable that basal primates also had relatively high degrees of orbital convergence, and hence were nocturnal.

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This conclusion is congruent with character optimization studies of the evolution of activity pattern and chromacy in primates, and their relatives (Heesy and Ross, 2001, 2004), but runs counter to recent claims that basal primates were diurnal (Li, 2000; Ni et al., 2004; Tan and Li, 1999). We have discussed our objections to Tan and Li's arguments elsewhere (Heesy and Ross, 2001, 2004).

The eye shape data presented here suggest that the eyes of these basal primates were probably not distinguished from those of their ancestors on the basis of shape, as anthropoids are the only mammals with a distinctive eye shape (Figure 7). The reason for the lack of correlation between eye shape and diel activity pattern in nonprimate mammals is not obvious. One possibility is that the nocturnality generally assumed for the mammalian stem lineage resulted in a nocturnal-shaped eye (i.e., with a large cornea relative to axial length), and that nocturnality and its characteristic eye shape persisted in the lineage leading from basal mammals to basal primates. Of course, this does not explain why all nonanthropoid diurnal mammals possess a "nocturnal eye shape," including many visually dependent diurnal mammals. Another possibility is that the measures of eye shape used here are poor indicators of image brightness; in particular, axial diameter of the eye may not accurately reflect focal length in mammals. Future work should evaluate this possibility.

In contrast with these conclusions regarding eye shape, it can be hypothesized that basal primates, if they were nocturnal, were distinguished from their ancestors by larger eye size (Figure 5): extant nocturnal primate eyes have larger axial diameters than similarly sized nonprimate mammals. As noted earlier, when accompanied by photoreceptor pooling, increase in eye size increases image brightness (Land and Nilsson, 2002). Increase in axial length of the eye in basal primates will also increase visual acuity in a nocturnal environment, the same way as it increases acuity for diurnal animals (i.e., by enlarging the image and spreading it over a greater number of photoreceptors). Of course, this would make the image dimmer if the cornea and pupil did not also increase in size to maintain image brightness, but image brightness is maintained in primates (Figure 7) regardless of differences in eye size (Figure 5).

Increased visual acuity is also expected in the context of the increased orbital convergence that also characterized basal primates. One effect of increased orbital convergence is to improve image quality along the visual axis (by aligning optic and visual axes), so it seems reasonable to expect that the

eye would be altered to take advantage of the improved image quality. Increasing axial length and spreading the image over a greater number of photoreceptors is one way to do this.

If the basal primate eye was characterized by features functioning to increase visual acuity in a nocturnal environment, this acuity could have been put to a number of uses, including visual predation on insects (Cartmill, 1992), detection of small fruits, and locomotion in the terminal branches (Crompton, 1995; Sussman, 1995). Several workers have criticized the “nocturnal visual predation” model of primate origins by pointing out that many nocturnal primates use their auditory sense to detect prey, suggesting that this weakens the link between orbital convergence and visual predation (Crompton, 1995; Rasmussen, 1991; Sussman, 1991, 1995;). Clearly, however, basal primates could well have been using both senses to find their prey. R.S. Heffner and H.E. Heffner provide evidence that in extant mammals, increased acuity in sound localization is positively correlated with both increased width of the binocular visual field (1985) and a narrowing of the field of highest visual acuity, estimated by the width of the area centralis (in degrees) (1992). The sound localization threshold is a measure of acuity, such that the lower the threshold, the smaller the difference in the angular position of a sound source that can be detected. Hence, animals with large binocular visual fields and narrow fields of high-acuity vision tend to have the highest auditory acuity. Heffner and Heffner argue that auditory and visual acuity are correlated because hearing is used to guide the eyes toward the target more precisely. Indeed, they go so far as to suggest that “it is the function of sound localizing, i.e., directing the attention of other senses toward the sound-producing object . . . which underlies the variation in mammalian sound-localizing acuity” (R. S. Heffner and H. E. Heffner, 1992: 711). This suggests that if basal primates exhibited adaptations for prey localization, these adaptations probably were found in both the hearing and visual systems.

Heffner and Heffner’s data do not include many primates, but support for a link between visual and auditory acuity, and degree of insectivory among primates is found in Tetreault et al.’s (2004) study of retinal ganglion cell densities in *Cheirogaleus* and *Microcebus*. *Microcebus* has a higher retinal ganglion cell density than *Cheirogaleus*, is more insectivorous, and has larger more mobile pinnae, an important determinant of sound localizing ability (Brown, 1994; Coleman and Ross, 2004; Heffner and Heffner, 1992). Their

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data also suggest that *Microcebus* had a narrower field of high-acuity vision than *Cheirogaleus*. Clearly more research is needed into the sound localizing and visual acuity of strepsirrhines, as well as the interactions between the two systems.

The Eyes of Haplorhines

The increase in orbital convergence in anthropoid primates over and above that of most prosimians (Ross, 1995), combined with the decreased pupil diameter associated with diurnality, probably further improved image quality along the visual axis of anthropoids. In this context it would have been worthwhile to both further increase image size by increasing axial length of the eye (producing the unusually long eyes of extant anthropoids), and add a retinal fovea to the visual axis. It is noteworthy in this regard that diurnal anthropoids fall with diurnal birds on the plot of cornea diameter and axial diameter (Figure 9), and most diurnal birds have retinal foveae as well (Ross, 2004).

The tarsier eye exhibits adaptations for increased acuity in a nocturnal environment over and above those predicted for basal primates. The orbits of tarsiers are highly convergent for their size, suggesting that tarsiers are maximizing convergence as much as possible to improve image quality on the retina. The eyes of tarsiers are longer in axial length than any other mammals, plotting with strigiform and caprimulgiform birds. This may reflect increases in overall eye size, to increase either image brightness or the range of light levels over which their eyes are sensitive. It may also be an attempt to increase visual acuity. Tarsiers possess a retinal fovea characterized by a high density of photoreceptors and ganglion cells (Hendrickson et al., 2000), and the exclusion of blood vessels from the center of the fovea, or foveola (Hendrickson et al., 2000; Polyak, 1957; Ross, 2004). Tarsiers lack a tapetum (Hendrickson et al., 2000; Martin, 1973), also probably an adaptation for increased acuity (Cartmill, 1980; Ross, 2004) and possess a postorbital septum to insulate their fine-grained retina against movements in the temporal fossa during mastication (Cartmill, 1980, Heesy et al., this volume; Ross, 1996). In most of these features, tarsiers resemble owls, animals with similar relative axial diameters of the eye (Figure 6), supporting Niemitz' (1985) suggestion of ecological convergence between the two.

Tarsiers and anthropoids share several features of the visual system that are divergent from the basal primate condition. They both possess retinal

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foveae and lack tapeta, even when nocturnal, and their eyes exhibit large axial diameters. Their orbits are highly convergent for their size and are characterized by a postorbital septum. One explanation is that these shared features are adaptations to diurnality that have been retained by the tarsier lineage when it adopted nocturnal habits (Cartmill, 1980; Ross, 2000). These features of the tarsier eye may also be adaptations for high acuity in a nocturnal environment. Parsimony suggests that the last common ancestor of extant haplorhines was nocturnal (Heesy and Ross, 2001, 2004; Ross, 2004), but definitive resolution of this question must await discovery of fossils closer to the ancestral haplorhine node.

CONCLUSIONS

The origin of primates was accompanied by increases in eye size and orbital convergence. These changes almost certainly occurred in a nocturnal lineage and likely functioned to improve image brightness and visual acuity in a nocturnal environment. The exact use to which this increased acuity was put cannot be determined from eye shape and size alone. Comparative studies of nonprimate mammals suggest that increased visual acuity was associated with increased auditory acuity as well (Heffner and Heffner, 1992).

The changes in the visual system at the origin of primates were similar in kind to but less in degree than those that took place along the anthropoid stem lineage; i.e., anthropoids exhibit a further increase in orbital convergence, axial diameter of the eye, and visual acuity. Selections for these changes in the anthropoid visual system are most likely to have occurred in the context of the changes in visual system anatomy put in place at the origin in primates.

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