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# Evolution of activity patterns and chromatic vision in primates: morphometrics, genetics and cladistics

Hypotheses for the adaptive origin of primates have reconstructed nocturnality as the primitive activity pattern for the entire order based on functional/adaptive interpretations of the relative size and orientation of the orbits, body size and dietary reconstruction. Based on comparative data from extant taxa this reconstruction implies that basal primates were also solitary, faunivorous, and arboreal. Recently, primates have been hypothesized to be primitively diurnal, based in part on the distribution of color-sensitive photoreceptor opsin genes and active trichromatic color vision in several extant strepsirrhines, as well as anthropoid primates (Tan & Li, 1999 *Nature* **402,** 36; Li, 2000 *Am. J. phys. Anthrop. Supple.* **30,** 318). If diurnality is primitive for all primates then the functional and adaptive significance of aspects of strepsirrhine retinal morphology and other adaptations of the primate visual system such as high acuity stereopsis, have been misinterpreted for decades. This hypothesis also implies that nocturnality evolved numerous times in primates. However, the hypothesis that primates are primitively diurnal has not been analyzed in a phylogenetic context, nor have the activity patterns of several fossil primates been considered.

This study investigated the evolution of activity patterns and trichromacy in primates using a new method for reconstructing activity patterns in fragmentary fossils and by reconstructing visual system character evolution at key ancestral nodes of primate higher taxa. Results support previous studies that reconstruct omomyiform primates as nocturnal. The larger body sizes of adapiform primates confound inferences regarding activity pattern evolution in this group. The hypothesis of diurnality and trichromacy as primitive for primates is not supported by the phylogenetic data. On the contrary, nocturnality and dichromatic vision are not only primitive for all primates, but also for extant strepsirrhines. Diurnality, and possibly X-linked polymorphic trichromacy, evolved at least in the stem lineage of Anthropoidea, or the stem lineage of all haplorhines.



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## Introduction

The time of day during which a primate species is active is an important component of its ecology. Activity pattern is interrelated with resource availability, predation pressure, social structure, mating system and diet, among other factors. Nocturnal primates tend to be solitary or live in small monogamous groups, are often insectivorous or frugivorous, and are never habitually terrestrial (Crook & Gartlan, 1966; Clutton-Brock & Harvey, 1977; Terborgh & Janson, 1986; Janson, 1992). Diurnal species, on the other hand, often live in larger groups with more diverse and complex social systems, are arboreal and terrestrial, and are more frugivorous or folivorous (Crook &

Gartlan, 1966; Clutton-Brock & Harvey, 1977; Terborgh & Janson, 1986; Janson, 1992). Data on a primate species' activity pattern open a window into its ecology.

Current theory posits that the original adaptive niche into which primates evolved was that of a nocturnal visual predator locomoting on small diameter supports in the shrub layer (Cartmill, 1972, 1974, 1992; Allman, 1977; Pettigrew, 1978; Lemelin, 1996, 1999; Ravosa *et al.*, 2000). Even those who dispute the importance of visual predation accept that ancestral primates were nocturnal (e.g., Rasmussen, 1990; Crompton, 1995), suggesting that they were also probably solitary or monogamous, largely insectivorous, and arboreal (Charles-Dominique, 1975; Bearder, 1987). However, in a recent analysis of the genetic basis of color vision in Malagasy strepsirrhines, Tan & Li (1999; Li, 2000) suggest that: (1) the last common ancestor of strepsirrhines was polymorphic at the X-linked opsin locus and therefore trichromatic and, by association, diurnal, and (2) the last common ancestor of tarsiers and strepsirrhines was trichromatic and diurnal. If the ancestral primates were indeed diurnal, as Tan & Li suggest, much of what is currently thought about the polarity and adaptive significance of distinctive primate features associated with nocturnal visual predation—such as the enlarged, convergent orbits and postorbital bar (Cartmill, 1972, 1974)—needs to be reassessed.

Although fossil evidence of the earliest primates is not available to determine directly whether they were nocturnal or diurnal, data from the visual systems of living and fossil archontans provide relevant evidence. Biomechanical and trait-function association analyses among living primates can determine the functional significance of distinctive features of the primate visual system and the distribution of morphological features, activity patterns, and genetic data on a primate phylogeny can determine whether nocturnal visual predation is parsimoniously interpreted as arising as a unit in the primate stem lineage (Ross *et al.*, n.d.). Here we argue that the hypothesis that the last common ancestors of strepsirrhines and primates were trichromatic and diurnal (Tan & Li, 1999; Li, 2000) is in conflict with morphological, phylogenetic and behavioral data.

In addition, we present a new technique for reconstructing activity pattern in fragmentary fossil primates, apply this technique to the basal adapiform, *Cantius*, and to the omomyiform, *Omomys*, and integrate these new data into our analysis. Reconstructing activity patterns in fossil primates, particularly when combined with data on diet (Kay, 1975, 1984; Kay & Covert, 1984; Strait, 1991, 1997), locomotor adaptations (Bown *et al.*, 1982; Dagosto, 1993; Covert, 1995; Fleagle & Simons, 1995) and sexual dimorphism (a correlate of mating competition intensity) (Fleagle *et al.*, 1980; Plavcan & van Schaik, 1993/1994, 1997; Simons *et al.*, 1999), provides a powerful tool for inferring the behavior and ecology of fossil primate species. These data can be used to test hypotheses regarding important adaptive transitions in the evolution of primate higher taxa, such as whether the last common ancestor of all primates or the last common ancestor of all strepsirrhines was primitively nocturnal or diurnal (Cartmill, 1972; Tan & Li, 1999; Li, 2000), and whether diurnality arose in haplorhines prior to or following the tarsiid–anthropoid divergence (Cartmill, 1980; Ross, 1996, 2000, n.d.; Kay *et al.*, 1997).

*Osteological data*

Kay & Cartmill (1977) pioneered a method for reconstructing activity pattern in fossil primates by analyzing the effect that activity pattern has on orbit dimensions. When orbit diameter is plotted against skull length nocturnal taxa are differentiated from diurnal taxa below a skull length of 75 mm

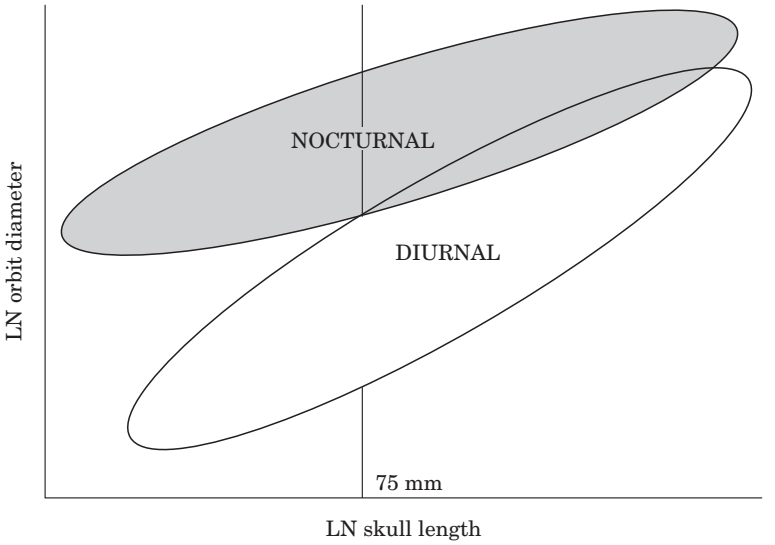



Figure 1. Diagram illustrating the relationship between orbit diameter and skull length. Kay & Cartmill (1977) compared the orbit diameters of several orders of small-bodied mammals and noted that nocturnal primates have larger orbits than diurnal primates of similar body size. Above a skull length of 75 mm the distributions of nocturnal and diurnal animals overlap at least partially.

[Figure 1, derived from Kay & Cartmill (1977)]. Above this skull length activity pattern cannot be definitively reconstructed from relative orbit diameter. The reason for this is not clear. At smaller body sizes the orbit closely approximates the size of the eye, whereas at larger body sizes the eye accounts for much less of the volume of the orbit (Schultz, 1940; Kay & Cartmill, 1977). Because orbit size becomes an increasingly inaccurate measure of eye size with increasing body size, activity pattern may not be reflected in relative orbit size because orbit size is not indicative of eye size. Another possibility is that orbit size is a sufficiently good estimator of eye size at large body size, but that eye size is not reflective of activity pattern at large body size (Cartmill, 1972; Ross, 1995). Regardless of the reasons for the breakdown of this relationship at larger skull sizes, relative orbit size can discriminate between nocturnal and diurnal primates at small skull sizes.

Kay & Cartmill's (1977) method for inferring activity pattern in fossil taxa has been applied to *Shoshonius*, *Tetonius*, *Rooneyia*, *Necrolemur*, *Adapis* and *Catopithecus* (Gingerich & Martin, 1981; Martin, 1990; Beard *et al.*, 1991; Rasmussen & Simons, 1992; Kay & Kirk, 2000). Broader application of this method is limited by the fact that fossil specimens that preserve reasonably complete undistorted orbits, as well as both prosthion and inion, are few in number. This precludes the analysis of activity pattern in important fossils, such as *Cantius abditus*, an early notharctid adapiform (Rose *et al.*, 1999). A method is required for reconstructing activity patterns in fragmentary fossils.

How fragmentary a fossil specimen can yield an accurate reconstruction of activity pattern? Estimates of orbit diameter and some surrogate of body size are necessary for this type of analysis. Kay & Cartmill (1977) used prosthion–inion length as a size estimate, but often one or both of these landmarks is not preserved in fossils. Here we utilize measures of $M^1$ as an estimate of overall size and the radius of the curvature

of the inferior orbital margin adjacent to the $M^1$ as an estimate of orbit size. Using a portion of the inferior orbital margin to estimate the radius of curvature of the orbit and measures of $M^1$ to estimate body size has several advantages. Dental remains predominate in the fossil record, $M^1$ crown area is highly correlated with body mass in primates ($r^2$=0·946, Gingerich *et al.*, 1982; Gingerich & Smith, 1985), and the proximity of the inferior orbital margin to the tooth row increases the likelihood that both the orbital margin and the $M^1$ will be preserved together in a specimen. It is worth noting that the use of $M^1$ crown area as a size surrogate, as other surrogates used in the past, like skull length, must be done with some caution. The residual variance in body mass unexplained by crown area can introduce significant error in mass estimates (Smith, 1996). Nonetheless, the frequency of preservation of fragmentary orbit diameters and $M^1$s makes possible the inference of activity patterns for more fossil primate taxa.

*Genetic data*

Tan & Li's (1999) hypothesis that the ancestral primates were diurnal is based on the claim that the ancestral primate population included some individuals that possessed genes for trichromacy—i.e., possessed genes that coded for three different cone photopigments, each maximally sensitive to a different wavelength. Cone photoreceptors are not sensitive at the low light levels typical of the nocturnal (scotopic) environment, but they have short integration times (meaning they can fire at a high frequency) and different cones can be tuned to be maximally sensitive to different wavelengths. Diurnal animals have more cones than nocturnal animals, especially in the area centralis, the part of the retina with maximal acuity (see review by Ross, 2000). Rods, in contrast, are highly sensitive to small numbers of photons and have long integration times, so nocturnal mammals, including nocturnal primates, utilize rods for scotopic vision and have rod-dominated retinae. Rods contain only one type of visual pigment: they never contain photopigments with different maximal sensitivities. The reasons for this are debated, but the most likely explanation is that there are not enough photons in a nocturnal environment for neighboring photoreceptor arrays to reliably distinguish light of different wavelengths (Gouras, 1991; Mollon, 1991). The genes that code for the photopigment molecules of different wavelengths have been well studied, and it is possible to determine whether an animal has the genes for one, two, or three cone photopigments. Tan & Li (1999) provide these important data, indicating those species that have the genetic capability for trichromacy. To determine whether a species has expressed the genes for different photopigments, photomicrospectrometry or histological techniques are needed (Jacobs, 1993). Archontans for which these data are available are listed in Table 1. To know for sure whether an animal is trichromatic it is advisable to test animals behaviorally while carefully controlling luminance differences (Jacobs, 1993). Archontans on which these tests have been performed are also listed in Table 1. Note that the nocturnal strepsirrhine *Cheirogaleus major* has the genetic potential for trichromacy, but it has not been studied histologically or using microphotospectrometry. Here we analyze these genetic, histologic, and behavioral data in a phylogenetic context to evaluate Tan & Li's (1999) hypothesis that the ancestral primates were trichromatic and hence diurnal.

The purpose of this study is twofold. First, we address two questions: (1) Can the diameter of the orbit be reconstructed using just a segment of the inferior orbital margin and, if so, how large a segment is required? (2) How accurate is such an orbital diameter estimate for reconstructing activity patterns

in small-bodied primates (when orbit scaling trends are considered)? The results are then applied to the analysis of two specimens of *Omomys carteri*, one *C. abditus*, and one *C. ralstoni*, taxa that were previously unavailable for activity pattern reconstruction. Second, the evolution of activity patterns and trichromatic color vision are then investigated by mapping the evolution of these traits on a phylogenetic tree of primates.

## Material and methods

*Materials*

In order to establish a method for reconstructing the orbital diameters and activity patterns for fragmentary fossil specimens, measurements were taken on 210 specimens representing 47 species of primates (Table 2). The samples are housed in the Department of Mammalogy at the American Museum of Natural History and the Museum of Comparative Anatomy at the Department of Anatomical Sciences at the State University of New York at Stony Brook. Small-bodied strepsirrhines and haplorhines were selected so as to (a) encompass the range for which Kay & Cartmill (1977) were able to distinguish nocturnal and diurnal species, i.e., animals with skull lengths less than 75 mm prosthion–inion length, and (b) encompass the tooth size range for the fossil taxa examined in this study. The activity patterns of extant taxa (Table 2) were obtained from the literature (Martin, 1990; Fleagle, 1999). Fossil omomyiform, adapiform and anthropoid specimens with various amounts of orbital margin preserved were also analyzed (Table 3). In addition, comparative data on *C. abditus* (UM 93938; data kindly provided by G. F. Gunnell), *Shoshonius cooperi* (Beard *et al.*, 1991), *Catopithecus browni* (Rasmussen & Simons, 1992), *Proteopithecus sylviae* (Simons, 1997), *Tremacebus harringtoni* (Rusconi, 1935*a*, *b*; Hershkovitz, 1974), and *Homunculus patagonicus* (e.g., MACN 5768) are included (Table 2) in order to reconstruct the evolution of activity patterns in basal primate taxa.

*Measurements*

*Body size.* Measurements of $M^1$ crowns were taken utilizing a stereoscopic microscope equipped with a reticle calibrated to 0·1 mm. Crown areas were computed from measures of mesiodistal crown lengths (greatest lengths) and buccolingual crown widths (greatest widths). The left $M^1$s were measured for all specimens barring those missing teeth, in which cases the right $M^1$s were measured. Skull lengths (prosthion–inion) were measured with digital calipers to the nearest 0·1 mm.

*Orbit diameter.* Measurements of orbital diameters and the radii of curvature used to estimate orbit diameters were taken from video images of all sampled skulls. Each skull was oriented such that the planes of the orbital margin and video camera lens were parallel. These images were videoed at distances exceeding 15 times the maximum diameter of the bony orbit in order to minimize distortion due to parallax (Spencer & Spencer, 1995). The video images were downloaded into *Adobe Photoshop 3* (Adobe Systems, Inc.) and reoriented so that the line representing the shortest distance between orbitale inferius (point on the inferior orbital margin that lies closest to the lateral margin of the maxillary tooth row) and the tooth row was vertically aligned with an overlying grid. Mediolateral orbit diameters were measured from orbitale medialis (most medial point on the medial orbital margin) to orbitale lateralis (most lateral point on the lateral orbital margin). Radii of curvature were calculated from three points along the orbital margin (Figure 2). Using the formula derived from Susman *et al.*, 1984:

**Table 1 Distribution of cone photoreceptors and their peak spectral sensitivities, when known, and type of color vision in primates and other archontans**

| Taxon | Activity pattern | Short (blue) | Medium (green) | Polymorphic medium* (green–red) | Long* (red) | Type of color vision | Reference |
|---|---|---|---|---|---|---|---|
| Megachiroptera | Nocturnal | 430 nm | 520 nm | — | — | Dichromatic? | Jacobs, 1993 |
| Microchiroptera | Nocturnal | ? | ? | ? | ? | ? | |
| Dermoptera | Nocturnal | ? | ? | ? | ? | ? | |
| Tupaiinae | Diurnal | 440 nm | 556 nm | — | — | Dichromatic | Jacobs, 1993 |
| Ptilocercinae | Nocturnal | ? | ? | ? | ? | ? | |
| Loridae | Nocturnal | 430–440 nm | 543 nm | — | — | Dichromatic | Tan & Li, 1999 |
| Galagonidae | Nocturnal | X† | 545 nm | — | — | Monochromatic | Jacobs *et al.*, 1995, 1996*a* |
| *Daubentonia* | Nocturnal | 430–440 nm | 543 nm | — | — | Dichromatic | Tan & Li, 1999 |
| *Microcebus* | Nocturnal | 430–440 nm | — | — | 558 nm | Dichromatic | Tan & Li, 1999 |
| *Mirza* | Nocturnal | 430–440 nm | — | — | 558 nm | Dichromatic | Tan & Li, 1999 |
| *Allocebus* | Nocturnal | ? | ? | ? | ? | Dichromatic? | |
| *Cheirogaleus major* | Nocturnal | 430–440 nm | | 543/558 nm | | Polymorphic trichromatic | Tan & Li, 1999 |
| *Cheirogaleus medius* | Nocturnal | 430–440 nm | 543 nm | — | — | Dichromatic | Tan & Li, 1999 |
| *Phaner* | Nocturnal | ? | ? | ? | ? | Dichromatic? | |
| *Lepilemur* | Nocturnal | ? | ? | ? | ? | Dichromatic? | |
| *Propithecus* | Diurnal | 430–440 nm | 543 nm | — | — | Dichromatic | Tan & Li, 1999 |
| *Propithecus v. coquereli* | Diurnal | 430–440 nm | — | 543/558 nm | — | Polymorphic trichromatic | Tan & Li, 1999 |
| *Avahi* | Nocturnal | ? | ? | ? | ? | Dichromatic? | |
| *Varecia variegata* | Diurnal | 430–440 nm | 543 nm | — | — | Dichromatic | Tan & Li, 1999 |
| *Varecia v. rubra* | Diurnal | 430–440 nm | — | 543/558 nm | — | Polymorphic trichromatic | Tan & Li, 1999 |
| *Hapalemur* | Cathemeral | 430–440 nm | — | — | 558 nm | Dichromatic | Tan & Li, 1999 |
| *Lemur catta* | Diurnal | 437 nm | 545 nm | — | — | Dichromatic | Jacobs & Deegan, 1993 |
| *Eulemur fulvus* | Cathemeral | 437 nm | 545 nm | — | — | Dichromatic | Jacobs & Deegan, 1993 |
| *Eulemur mongoz* | Cathemeral | 430–440 nm | 543 nm | — | — | Dichromatic | Tan & Li, 1999 |
| *Tarsius syrichta* | Nocturnal | 430–440 nm | — | — | 558 nm | Dichromatic | Tan & Li, 1999 |
| *Tarsius bancanus* | Nocturnal | 430–440 nm | 543 nm | — | — | Dichromatic | Tan & Li, 1999 |
| *Callimico* | Diurnal | 430–440 nm | — | 543/556/563 nm | — | Polymorphic trichromatic | Bowmaker, 1998; Jacobs, 1998 |

**Table 1** ***Continued.***

| Taxon | Activity pattern | Short (blue) | Medium (green) | Polymorphic medium* (green–red) | Long* (red) | Type of color vision | Reference |
|---|---|---|---|---|---|---|---|
| *Saguinus* | Diurnal | 430–440 nm | — | 543/556/563 nm | — | Polymorphic trichromatic | Bowmaker, 1998; Jacobs, 1998 |
| *Leontopithecus* | Diurnal | 430–440 nm | — | 543/556/563 nm | — | Polymorphic trichromatic | Bowmaker, 1998; Jacobs, 1998 |
| *Cebuella* | Diurnal | 430–440 nm | — | 543/556/563 nm | — | Polymorphic trichromatic | Bowmaker, 1998; Jacobs, 1998 |
| *Callithrix* | Diurnal | 430–440 nm | — | 543/556/563 nm | — | Polymorphic trichromatic | Bowmaker, 1998; Jacobs, 1998 |
| *Cebus* | Diurnal | 430–440 nm | — | 535/550/563 nm | — | Polymorphic trichromatic | Bowmaker, 1998; Jacobs, 1998 |
| *Saimiri* | Diurnal | 430–440 nm | — | 535/550/563 nm | — | Polymorphic trichromatic | Jacobs, 1998; Mollon *et al.*, 1984 |
| *Aotus* | Nocturnal | X† | 545 nm | — | — | Monochromatic | Jacobs *et al.*, 1996*a* |
| *Cacajao* | Diurnal | 430–440 nm | — | X | — | Polymorphic trichromatic | Jacobs, 1996, 1998 |
| *Chiropotes* | Diurnal | 430–440 nm | — | X | — | Polymorphic trichromatic | Jacobs, 1996, 1998 |
| *Pithecia* | Diurnal | 430–440 nm | — | X | — | Polymorphic trichromatic | Jacobs, 1996, 1998 |
| *Callicebus* | Diurnal | 430–440 nm | — | X/549/562 nm | — | Polymorphic trichromatic | Jacobs, 1996, 1998; Jacobs & Neitz, 1987 |
| *Alouatta* | Diurnal | 430–440 nm | X | — | X | True trichromatic | Jacobs *et al.*, 1996*b* |
| *Lagothrix* | Diurnal | 430–440 nm | — | X | — | Polymorphic trichromatic | Jacobs, 1996, 1998 |
| *Brachyteles* | Diurnal | 430–440 nm | — | X | — | Polymorphic trichromatic | Jacobs, 1996, 1998 |
| *Ateles* | Diurnal | 430–440 nm | — | X/550/563 nm | — | Polymorphic trichromatic | Jacobs, 1993, 1996, 1998 |
| Catarrhini | Diurnal | 430 nm | 530 nm | | 560 nm | True trichromatic | Hunt *et al.*, 1995 |

X denotes that this cone type is present, but the peak spectral sensitivity has not been measured. A — denotes that this cone type is not present.

*Tan & Li (1999) assign peak spectral sensitivities to medium and polymorphic medium wavelengths opsins in strepsirrhines and *Tarsius* based on amino acid composition at critical exon sites (3, 4 and 5) known to code for spectral shifts using comparative data from platyrrhines.

†Jacobs *et al.* (1995, 1996*a*) contend that the short cone type is non-functioning in *Otolemur crassicaudatus* and *Aotus* due to deleterious mutations in the *S* opsin gene.

Note that possession of *L* opsin alleles does not imply homology between haplorhines and strepsirrhines or within strepsirrhines.

**Table 2 Extant and fossil taxa of known orbit diameters used in this study**

| Taxon | *n* | Activity pattern | Prosthion–inion length | | $M^1$ crown area | | $M^1$ crown length | | Mediolateral orbital diameter | | Diameter estimate from 2 mm | | Diameter estimate from 5 mm | | Diameter estimate from 10 mm | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| *Aotus trivirgatus* | 7 | Nocturnal | 61·4 | 1·42 | 14·5 | 1·21 | 3·5 | 0·12 | 19·6 | 1·63 | 11·7 | 5·37 | 17·6 | 2·72 | 18·0 | 0·67 |
| *Avahi laniger* | 5 | Nocturnal | 53·6 | 2·12 | 16·8 | 0·63 | 4·3 | 0·20 | 17·5 | 0·60 | 17·4 | 1·08 | 17·3 | 0·58 | 17·5 | 0·59 |
| *Callicebus caligatus* | 6 | Diurnal | 63·7 | 3·20 | 19·6 | 0·93 | 4·0 | 0·15 | 15·5 | 0·77 | 11·7 | 2·48 | 15·7 | 1·53 | 15·6 | 1·30 |
| *Callimico goeldi* | 5 | Diurnal | 50·2 | 1·96 | 12·3 | 0·84 | 3·0 | 0·14 | 12·7 | 0·68 | 8·0 | 3·10 | 12·3 | 2·49 | 12·3 | 0·61 |
| *Callithrix argentata* | 6 | Diurnal | 46·2 | 0·93 | 7·9 | 0·44 | 2·5 | 0·07 | 10·6 | 0·15 | 9·6 | 2·20 | 11·3 | 1·64 | 10·7 | 0·47 |
| *Callithrix jacchus* | 3 | Diurnal | 45·1 | 1·35 | 7·3 | 0·50 | 2·5 | 0·13 | 10·6 | 0·22 | 10·0 | 0·54 | 10·6 | 0·17 | 10·7 | 0·07 |
| *Cebuella pygmaea* | 6 | Diurnal | 34·6 | 1·03 | 4·7 | 0·27 | 2·0 | 0·10 | 9·1 | 0·40 | 7·6 | 1·82 | 9·8 | 0·92 | | |
| *Cebus albifrons* | 1 | Diurnal | 91·3 | | 27·7 | | 4·7 | | 19·6 | | 18·0 | | 20·0 | | 19·6 | |
| *Cebus apella* | 4 | Diurnal | 86·4 | 4·78 | 27·4 | 3·58 | 4·7 | 0·33 | 18·6 | 1·7 | 16·9 | 1·22 | 16·3 | 3·94 | 18·8 | 1·16 |
| *Cebus capucinus* | 1 | Diurnal | 89·6 | | 27·0 | | 4·6 | | 20·0 | | 18·3 | | 19·6 | | 20·2 | |
| *Cheirogaleus major* | 1 | Nocturnal | 56·5 | | 12·3 | | 3·4 | | 15·6 | | 14·7 | | 14·8 | | 15·4 | |
| *Daubentonia madagascariensis* | 3 | Nocturnal | 85·3 | 4·17 | 16·3 | 1·30 | 4·3 | 0·50 | 20·7 | 1·23 | 18·9 | 0·88 | 20·0 | 1·00 | 20·8 | 1·24 |
| *Eulemur fulvus* | 6 | Cathemeral | 91·0 | 1·22 | 38·2 | 3·78 | 5·8 | 0·33 | 18·5 | 0·84 | 18·3 | 1·31 | 18·2 | 0·88 | 18·3 | 0·78 |
| *Eulemur rubriventer* | 3 | Cathemeral | 87·6 | 4·19 | 38·6 | 4·82 | 5·8 | 0·38 | 19·6 | 0·84 | 19·4 | 1·92 | 19·4 | 1·04 | 19·5 | 0·72 |
| *Galago alleni* | 5 | Nocturnal | 50·7 | 2·74 | 13·3 | 1·01 | 3·3 | 0·19 | 16·2 | 1·21 | 15·7 | 3·43 | 15·9 | 0·81 | 16·5 | 1·33 |
| *Galago senegalensis* | 6 | Nocturnal | 43·2 | 2·16 | 8·9 | 0·67 | 2·7 | 0·08 | 15·8 | 0·97 | 8·9 | 1·73 | 14·7 | 2·02 | 15·1 | 1·25 |
| *Galagoides demidoff* | 6 | Nocturnal | 35·1 | 2·60 | 5·9 | 0·42 | 2·1 | 0·09 | 10·7 | 0·57 | 9·5 | 1·68 | 10·5 | 0·60 | 10·7 | 0·46 |
| *Hapalemur griseus* | 6 | Cathemeral | 64·3 | 1·62 | 24·7 | 2·84 | 4·8 | 0·19 | 18·0 | 1·12 | 16·1 | 1·49 | 17·1 | 2·32 | 17·0 | 1·91 |
| *Hylobates agilis*⋆ | 4 | Diurnal | 99·3 | 2·05 | 34·5 | 2·58 | 6·0 | 0·42 | 23·2 | 0·74 | | | | | | |
| *Hylobates hoolock*⋆ | 6 | Diurnal | 111·7 | 8·54 | 41·8 | 3·48 | 6·7 | 0·31 | 22·6 | 1·46 | | | | | | |
| *Hylobates lar*⋆ | 3 | Diurnal | 102·1 | 8·14 | 31·8 | 2·77 | 5·3 | 0·27 | 22·4 | 0·50 | | | | | | |
| *Hylobates moloch*⋆ | 3 | Diurnal | 93·1 | 2·83 | 37·3 | 3·35 | 6·1 | 0·27 | 22·1 | 1·14 | | | | | | |
| *Indri indri* | 5 | Diurnal | 102·5 | 3·23 | 54·6 | 1·91 | 8·0 | 0·10 | 22·4 | 0·36 | 22·2 | 1·19 | 22·3 | 0·37 | 22·4 | 0·27 |
| *Lemur catta* | 4 | Diurnal | 82·2 | 1·97 | 28·4 | 1·33 | 5·0 | 0·30 | 16·9 | 0·33 | 16·1 | 0·6 | 16·8 | 0·32 | 17·2 | 0·67 |
| *Leontopithecus rosalia* | 5 | Diurnal | 55·6 | 1·88 | 15·3 | 0·84 | 3·5 | 0·10 | 12·1 | 0·50 | 10·4 | 1·80 | 12·4 | 1·27 | 12·1 | 0·84 |
| *Lepilemur mustelinus* | 6 | Nocturnal | 50·6 | 1·17 | 14·2 | 0·90 | 3·7 | 0·20 | 14·8 | 0·33 | 12·2 | 1·82 | 13·9 | 1·78 | 14·8 | 0·83 |
| *Loris tardigradus* | 5 | Nocturnal | 50·0 | 3·60 | 12·7 | 1·51 | 3·2 | 0·14 | 15·8 | 0·55 | 10·8 | 3·04 | 14·5 | 1·41 | 14·9 | 0·63 |

**Table 2** *Continued*

| Taxon | *n* | Activity pattern | Prosthion–inion length | | $M^1$ crown area | | $M^1$ crown length | | Mediolateral orbital diameter | | Diameter estimate from 2 mm | | Diameter estimate from 5 mm | | Diameter estimate from 10 mm | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| *Microcebus murinus* | 6 | Nocturnal | 31·5 | 0·72 | 4·3 | 0·47 | 1·7 | 0·11 | 10·1 | 0·32 | 9·5 | 1·51 | 10·4 | 1·38 | 10·5 | 0·46 |
| *Microcebus rufus* | 1 | Nocturnal | 30·2 | | 4·1 | | 1·9 | | 9·3 | | 9·3 | | 9·4 | | | |
| *Miopithecus talapoin* | 3 | Diurnal | 72·3 | 2·78 | 21·4 | 4·80 | 4·5 | 0·38 | 18·1 | 0·84 | 9·3 | 1·78 | 16·4 | 1·56 | 16·6 | 3·45 |
| *Nycticebus coucang* | 6 | Nocturnal | 57·1 | 1·73 | 21·0 | 1·13 | 4·1 | 0·19 | 16·7 | 0·51 | 11·8 | 3·47 | 16·7 | 1·94 | 16·5 | 0·56 |
| *Otolemur crassicaudatus* | 6 | Nocturnal | 69·8 | 1·72 | 28·8 | 1·63 | 4·7 | 0·18 | 18·8 | 0·38 | 15·2 | 3·04 | 18·4 | 2·46 | 20·1 | 1·40 |
| *Otolemur garnettii* | 6 | Nocturnal | 66·5 | 4·59 | 20·8 | 2·02 | 4·0 | 0·33 | 17·7 | 0·92 | 17·0 | 0·89 | 17·7 | 0·98 | 17·7 | 0·80 |
| *Pan troglodytes** | 5 | Diurnal | 189·1 | 3·65 | 115·1 | 10·84 | 10·8 | 0·54 | 34·4 | 1·43 | | | | | | |
| *Papio anubis** | 6 | Diurnal | 193·5 | 17·19 | 102·8 | 9·08 | 10·5 | 0·79 | 29·2 | 1·23 | | | | | | |
| *Perodicticus potto* | 4 | Nocturnal | 62·2 | 3·29 | 20·2 | 3·87 | 4·1 | 0·38 | 15·4 | 0·89 | 11·1 | 1·87 | 14·8 | 1·45 | 16·1 | 1·66 |
| *Phaner furcifer* | 2 | Nocturnal | 55·0 | 2·23 | 7·7 | 0·32 | 2·7 | 0·30 | 14·9 | 0·53 | 14·4 | 0·72 | 15·5 | 0·75 | 15·0 | 0·47 |
| *Pithecia pithecia* | 5 | Diurnal | 75·6 | 3·59 | 18·9 | 2·07 | 4·0 | 0·21 | 16·9 | 1·16 | 10·1 | 1·26 | 19·7 | 3·13 | 17·3 | 1·35 |
| *Propithecus diadema* | 5 | Diurnal | 89·9 | 4·50 | 45·0 | 4·18 | 7·1 | 0·32 | 21·0 | 0·8 | 21·0 | 1·20 | 21·2 | 1·12 | 21·1 | 0·87 |
| *Propithecus verreauxi* | 2 | Diurnal | 85·9 | 1·8 | 44·3 | 2·55 | 7·0 | 0·10 | 18·6 | 0·08 | 16·8 | 2·30 | 18·1 | 0·47 | 18·6 | 0·20 |
| *Saguinus oedipus* | 6 | Diurnal | 48·8 | 1·78 | 10·7 | 1·56 | 2·9 | 0·22 | 11·8 | 0·36 | 9·4 | 1·97 | 11·7 | 1·29 | 12·2 | 0·33 |
| *Saimiri sciureus* | 6 | Diurnal | 64·3 | 4·38 | 14·2 | 1·96 | 3·2 | 0·25 | 14·4 | 1·12 | 6·7 | 2·68 | 10·7 | 3·17 | 13·2 | 1·21 |
| *Tarsius bancanus* | 3 | Nocturnal | 36·7 | 2·17 | 12·9 | 1·72 | 2·9 | 0·28 | 17·3 | 1·66 | 13·0 | 4·86 | 12·2 | 2·63 | 16·9 | 1·35 |
| *Tarsius syrichta* | 4 | Nocturnal | 39·1 | 1·36 | 12·0 | 1·80 | 2·8 | 0·20 | 16·7 | 0·67 | 13·8 | 0·88 | 16·6 | 1·62 | 17·6 | 2·00 |
| *Theropithecus gelada** | 3 | Diurnal | 164·6 | 5·33 | 94·2 | 7·27 | 11·5 | 1·08 | 25·6 | 2·04 | | | | | | |
| *Varecia variegata* | 7 | Diurnal | 103·4 | 3·93 | 56·2 | 2·81 | 7·2 | 0·19 | 20·1 | 1·36 | 19·9 | 0·82 | 20·2 | 1·32 | 20·3 | 1·32 |
| *Varecia variegata rubra* | 3 | Diurnal | 104·5 | 0·91 | 54·8 | 1·02 | 6·9 | 0·22 | 20·8 | 0·72 | 18·8 | 1·55 | 19·9 | 1·22 | 20·6 | 0·69 |
| *Cantius abditus*† | 1 | ? | | | 34·5 | | 5·0 | | 22·4 | | | | | | | |
| *Catopithecus browni*‡ | 1 | Diurnal | | | 12·7 | | 3·1 | | 11·5 | | | | | | | |
| *Proteopithecus sylviae*§ | 2 | Diurnal | 44·2 | | 12·3 | | 3·0 | | 8·4 | | | | | | | |
| *Tremacebus harringtoni*‖ | 1 | ? | | | 15·9 | | 3·4 | | 14·3 | | | | | | | |
| *Shoshonius cooperi*¶ | 1 | Nocturnal | | | 6·6 | | 2·2 | | 12·8 | | | | | | | |

*Data on large-bodied catarrhines are included for comparative purposes.

†Data on orbit diameter and $M^1$ dimensions provided by Gunnell, personal communication (1997).

‡Data on *Catopithecus browni* are from Rasmussen & Simons (1992).

§Data on *Proteopithecus sylviae* orbit and skull dimensions are from Simons (1997).

‖The mediolateral diameter of *Tremacebus* was established from the more complete right orbit because the left orbit is partially compressed dorsoventrally. Upper $M^1$ crown area is from Hershkovitz (1974).

¶Data on orbit diameter and skull length from Beard *et al.* (1991), and $M^1$ dimensions from K. C. Beard, personal communication (2000).

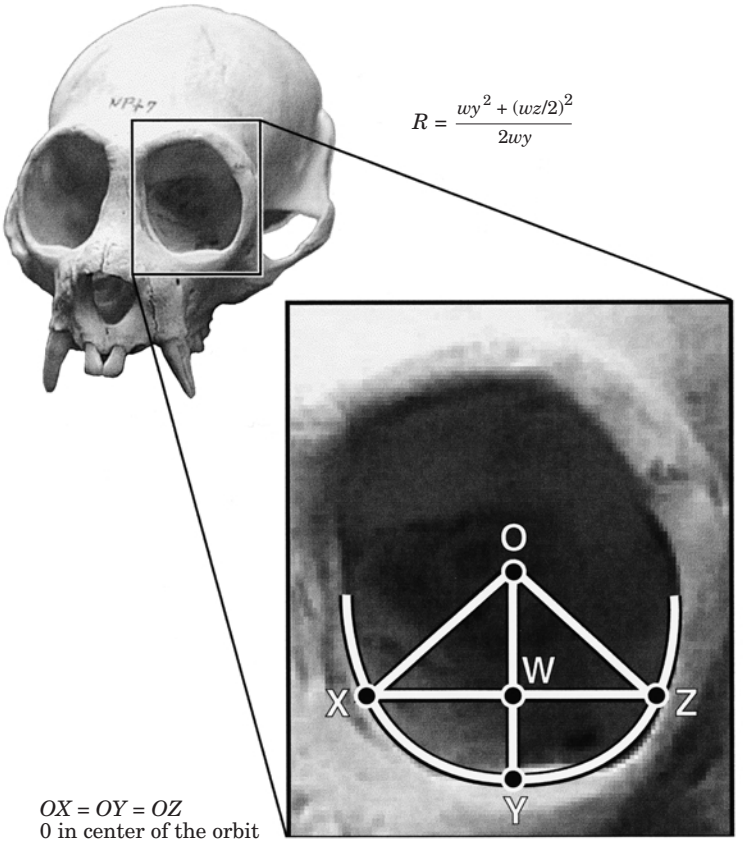



Figure 2. Diagram illustrating the method for estimating orbit diameter from the radius of curvature of an arc fitted to the inferior orbital margin. Radii of curvature can be calculated from three points along the orbital margin where the radius $R=OX=OY=OZ$, $Y$ is orbitale inferius, and $X$ and $Z$ are the endpoints of the included arc. From these data radii of curvature can be calculated by the formula: $R=(WY^2+(WZ/2)^2)/2WY$. Orbit diameter$=2R$.

$$R=(WY^2+(WZ/2)^2)/2WY$$

where the radius $R=OX=OY=OZ$, $O$ is the origin or center of the circle, $W$ is point of perpendicular intersection between $XZ$ and $OY$, $Y$ is orbitale inferius, and $X$ and $Z$ are the endpoints of the included arc (see Figure 2).

Orbit diameters and the diameters estimated from the radii of curvature for the sample studied were measured using *MacMorph 2.1* morphometric video analysis software designed by Spencer & Spencer (1995), which computes radii of curvature using the above formula. A calibrated grid was superimposed over the image of the orbit and arcs were laid over the orbital margin. Orbitale inferius was used for the midpoint of the arcs (point *Y*) and radii were computed from endpoints (points $X$ and $Z$ in the formula above) placed 1 mm, 2·5 mm and 5 mm on each side of the midpoint, which equated to arcs taken at three increments on the orbital margin: 2 mm, 5 mm and 10 mm total arc length segments. These three arc lengths were chosen to quantify the errors associated with progressively smaller segments of the inferior orbital margin in order to determine the minimum required length of inferior orbital margin necessary

**Table 3 Fossil taxa analyzed in this study**

| Taxon | Specimen no. | $M^1$ crown area | $M^1$ crown length | Length of orbital margin preserved | Diameter reconstruction | | Activity pattern reconstruction |
|---|---|---|---|---|---|---|---|
| | | | | | Mean | S.D. | |
| *Cantius abditus* | USNM 494881 | 39·9 | 5·9 | 8·2 | 24·1 | 1·40 | Nocturnal? |
| *Cantius ralstoni* | DMNH 40488 | 21·6* | 4·0 | 5·3 | 19·5 | 0·73 | Nocturnal? |
| *Homunculus patagonicus* | MACN 6768 | 21·4† | 4·0 | 20·6 | 16·6 | 0·01 | ? |
| *Omomys carteri* | UCM 67762 | 7·5 | 2·2 | 8·7 | 20·3 | 1·0 | Nocturnal |
| *Omomys carteri* | UCM 67854 | 7·9 | 2·4 | 5·4 | 19·2 | 0·9 | Nocturnal |

*The buccal 1/3 of the crown was broken off so the buccolingual measurement was estimated based on the dimensions of the tooth root [this specimen is currently being described by Robert V. Hill and Maureen O'Leary of SUNY Stony Brook (Hill *et al.*, 2000)].

†The upper $M^1$ of *Homunculus patagonicus* (MACN 6768) is missing so data on upper $M^1$ crown area are from an isolated molar, MACN-SC 334 (Tejedor, n.d.).

from which a reasonably accurate orbit diameter could be estimated and activity pattern could be inferred.

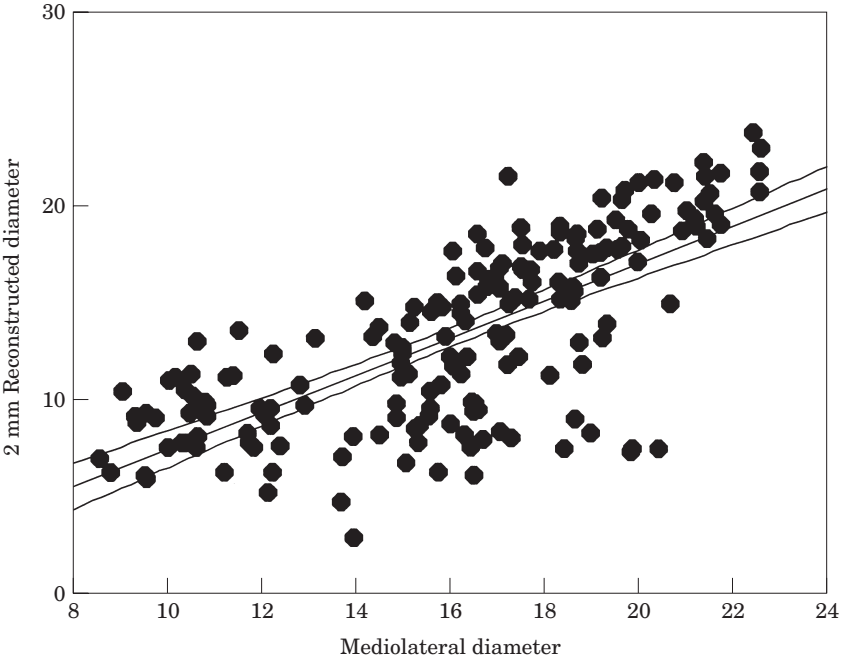
*Analysis of orbit diameter estimates*

To determine the accuracy of the estimates of orbit diameter derived from each arc length increment, Pearson's correlation coefficients were computed between the estimated and actual orbit diameters. In addition, percentage errors were computed for the three orbital margin increments for a more intuitive understanding of the amount of error generated from the three orbital margin estimates. Subsequently, bivariate plots of estimated diameters and $M^1$ crown areas as well as estimated diameters and prosthion–inion lengths were examined to determine the degree to which nocturnal and diurnal taxa are differentiated.

*Character mapping of activity pattern and color vision evolution*

The phylogeny of primates advocated by Ross *et al.* (1998) was expanded with strepsirrhine and platyrrhine phylogenies (extant taxa only) from Yoder (1997) and Fleagle (1999). The monophyly of Scandentia, Chiroptera and Dermoptera was assumed, but the relationships of these taxa to Primates were arbitrarily resolved because they did not materially affect the results of this analysis. Extant primate and archontan taxa were coded for activity pattern, number of middle polymorphic and long wavelength sensitive opsin genes, as well as type of chromatic vision these taxa possess (Appendix 1).

The evolution of these visual system characters was reconstructed in *MacClade 3.05* by optimizing the characters on to the tree using maximum parsimony (Maddison & Maddison, 1992). The maximum parsimony option in *MacClade* yields the set of equally most parsimonious solutions to the optimization of a trait for a given phylogeny. Nodes and internodes for which multiple solutions are possible are reconstructed as equivocal. This set of equally most parsimonious solutions includes optimizations that favor parallelisms (ACCTRAN) and reversals (DELTRAN) as well as all of the solutions in between. ACCTRAN and DELTRAN are the extremes of character optimization and do not necessarily demonstrate the most appropriate solution to the evolution of the trait of interest. Maddison & Maddison (1992) argued that in those cases where multiple equally most parsimonious solutions are found, all the alternative solutions must be examined in detail unless independent data are available



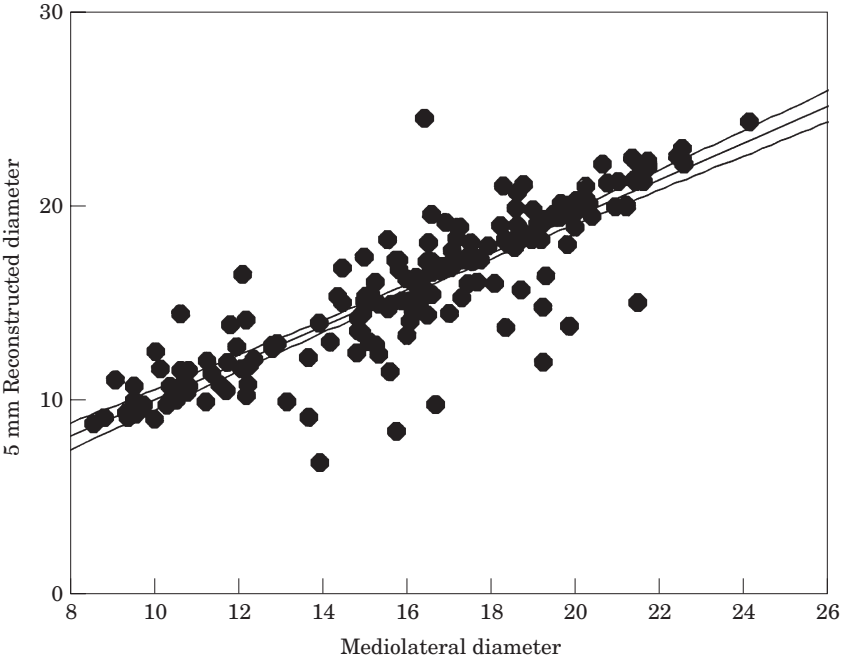




Figure 3. (a) and (b).

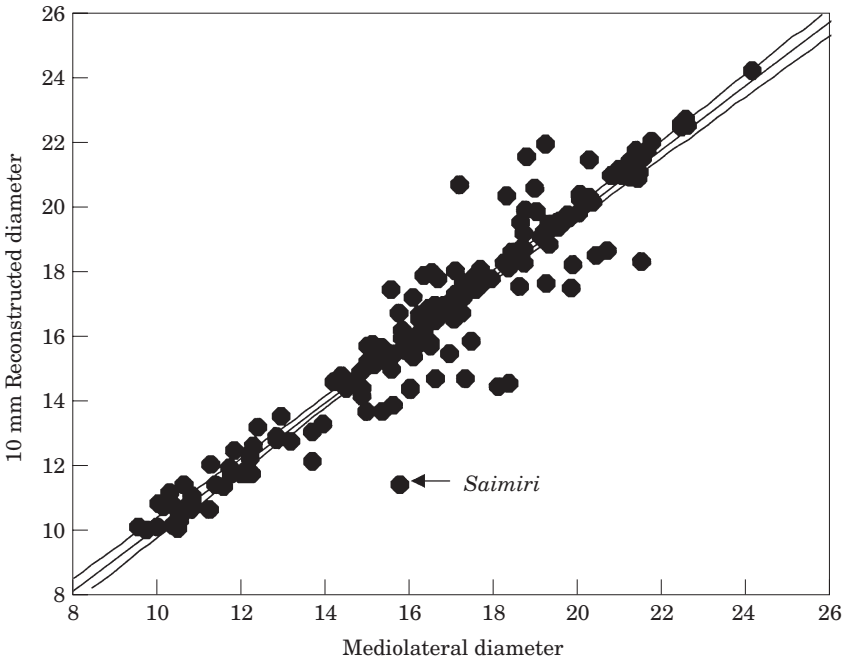



Figure 3. (c).

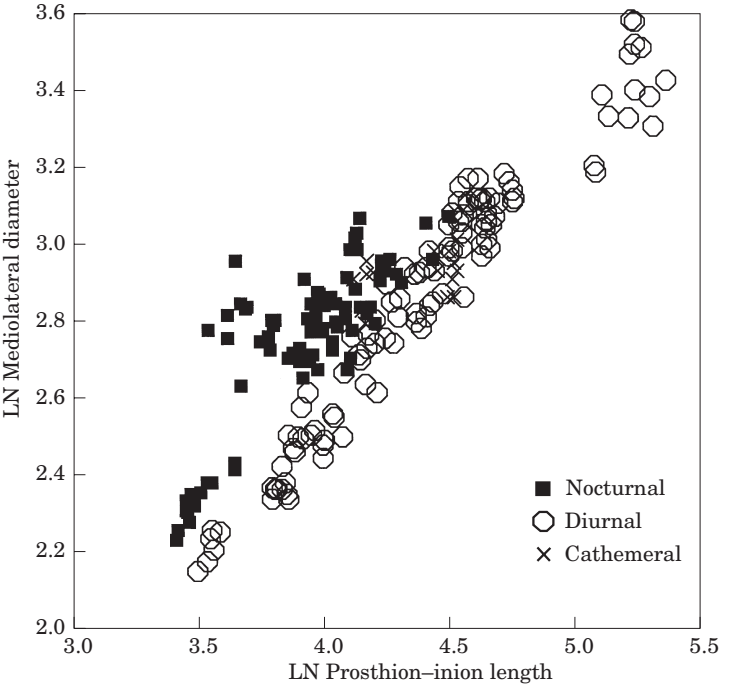
Figure 3. Bivariate plots of actual mediolateral orbit diameter against estimates of orbit diameter made from (a) 2 mm arc length fitted to the inferior orbital margin ($\rho=0{\cdot}654$, $P<0{\cdot}01$), (b) 5 mm arc length fitted to the inferior orbital margin ($\rho=0{\cdot}869$, $P<0{\cdot}01$), (c) 10 mm arc length fitted to the inferior orbital margin ($\rho=0{\cdot}964$, $P<0{\cdot}01$). The dip in the inferior orbital margin of *Saimiri* (indicated by arrow) leads to an underestimate of orbit diameter in this species (see Discussion).

to suggest that either ACCTRAN and DELTRAN best model the evolution of the trait (see also Swofford & Maddison, 1992). Each most parsimonious solution can be evaluated by using *MacClade*'s equivocal cycling option and displaying the number of state changes of the trait. The number of solutions that reconstruct alternative activity patterns and chromacy for important primate nodes are presented. Additionally, optimizing and analyzing the evolution of characters that were used to generate phylogenies potentially introduces circularity into the analysis of trait evolution because the topology of the tree may be intimately liked to the trait's distribution (Felsenstein, 1985; Coddington, 1988; Brooks & McLennan, 1991; Garland *et al.*, 1993). In those cases where the inclusion or exclusion of a character alters tree topology, the phylogeny is not robust enough to support the analysis of historical ecology and the adaptive significance of character evolution (Brooks & McLennan, 1994). Trait mapping onto independently derived phylogenies, the method used in this study, is advantageous and preferred because it avoids this bias.

## Results

*Orbit diameter estimates*

Figure 3(a) is a bivariate plot of logged orbit diameters estimated from a 2 mm arc against the logged values of actual mediolateral diameters. The correlation is statistically significant ($P<0{\cdot}01$) but the correlation coefficient (Pearson's $r$) is only



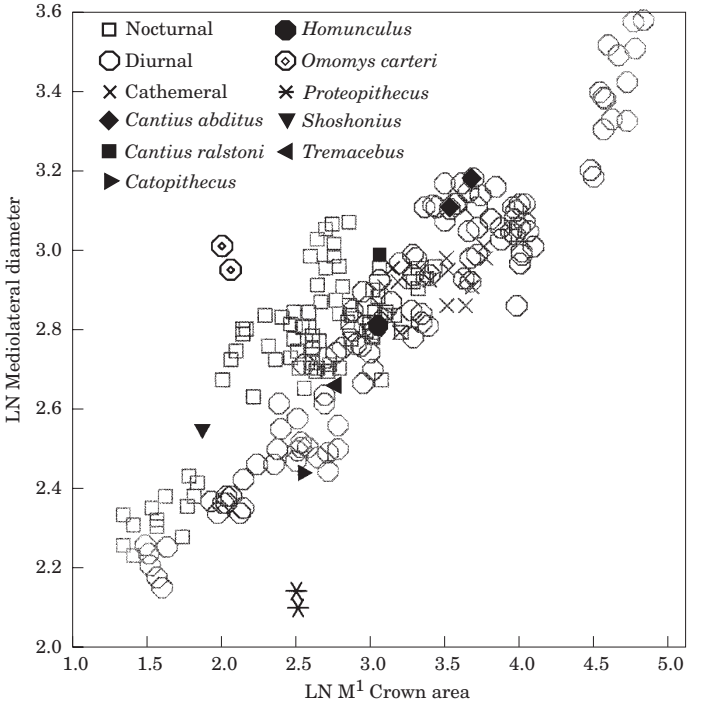




Figure 4. (a) and (b).

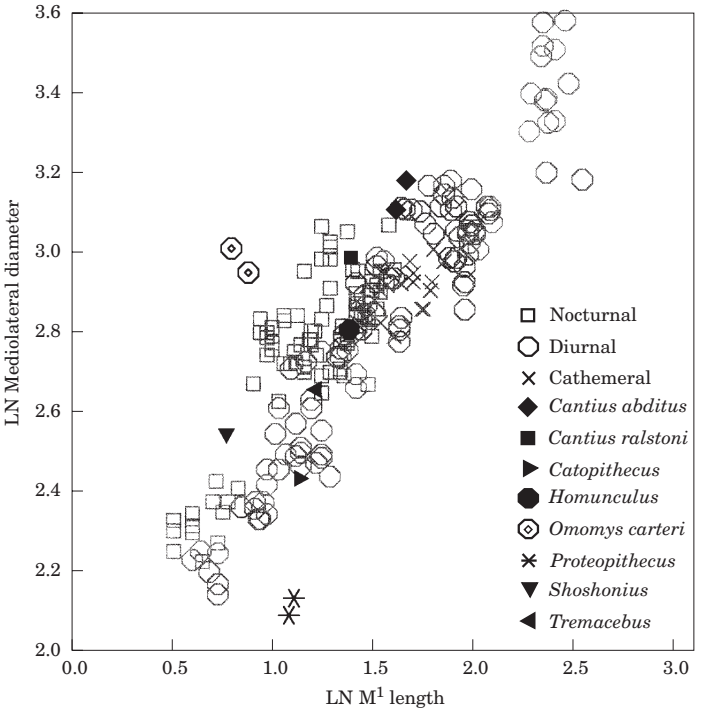



Figure 4. (c).

Figure 4. Bivariate plots of LN mediolateral orbit diameter against two body size correlates for individual specimens. (a) LN orbit diameter plotted against LN prosthion–inion length. This plot replicates the analysis coducted by Kay & Cartmill (1977). (b) LN orbit diameter plotted against LN $M^1$ crown area. *Shoshonius cooperi* and one specimen of *Cantius abditus* have been included for comparison. The estimated orbit diameter values for *Omomys carteri*, *C. abditus* and *C. ralstoni* were used. Based on this plot, *O. carteri* and *C. ralstoni* were nocturnal. (c) LN orbit diameter plotted against LN $M^1$ length. Based on this plot, *O. carteri* and *C. ralstoni* were nocturnal.

0·654. The low correlation coefficient and the broad scatter indicate that the estimates taken from this arc length are of variable accuracy. The mean percentage error of the estimates of orbit diameter made from 2 mm arc lengths for the entire sample is 19·6%. Standardized residual regression values decrease significantly with increasing orbit diameter and nearly half of the error variance is explained ($r^2$=0·48), indicating that, contrary to expectation, errors in diameter estimates decrease with increasing orbit diameter, not with increases in the proportion of the orbit sampled by a 2 mm arc. More importantly, estimates from a 2 mm arc can both underestimate and overestimate the radius (and therefore the orbit diameter).

Figure 3(b) is a bivariate plot of logged orbital diameters estimated from a 5 mm arc against the logged values of actual mediolateral orbit diameter. The correlation is statistically significant ($P$<0·01) and the correlation coefficient is 0·869. The mean percentage error of the estimates of orbit diameter made from 5 mm arc lengths for the entire sample is 7·86%. Standardized residual regression values for estimates from 5 mm arcs do not differ significantly along the range of actual mediolateral diameters and a small proportion of the error variance is explained by increases in orbit diameter

($r^2$=0·25). The higher correlation coefficient and the lower mean percentage error for the 5 mm arc lengths indicate that 5 mm arc lengths provide improved orbit diameter estimates when compared to those from 2 mm segments.

Figure 3(c) is a bivariate plot of logged orbit diameter estimates from a 10 mm arc against the logged values of actual mediolateral orbit diameters. *Cebuella pygmaea* and *Microcebus rufus* were excluded because the mediolateral orbit diameters of these taxa were smaller than 10 mm. The estimated and actual diameter values are strongly correlated. The correlation is statistically significant ($P$<0·01) and the correlation coefficient is 0·964. Standardized residual regression values do not differ significantly along the range of actual mediolateral diameters and little variance is explained by the proportion of size sampled by ($r^2$=0·08). The mean error percentage of the 10 mm arc length estimates for the entire sample is 3·7%.

*Activity pattern reconstructions*

For the purposes of applying orbit diameter estimates to activity pattern reconstructions it is necessary to plot the diameter values against correlates of body size. Figure 4(a) is a bivariate plot of logged mediolateral diameter against the logged values of prosthion–inion length, an analysis similar to that performed by Kay & Cartmill (1977). When logged mediolateral orbit diameter is plotted against logged $M^1$ crown area [Figure 4(b)], nocturnal and diurnal taxa discriminate less clearly at the low end of the range than in the plot against prosthion–inion length [cf. Figure 4(a)]. The distributions of nocturnal, diurnal and cathemeral animals begin to overlap at approximately 2·75 LN $M^1$ crown area (=16 $mm^2$), which corresponds in size with 60 mm (=LN 4·1) prosthion–inion length for this sample. This is lower than the lower range of overlap of activity patterns when using LN prosthion–inion length (75 mm, Kay & Cartmill, 1977; Kay & Kirk, 2000; this study).

The orbit diameter estimates from the 5 mm and 10 mm arc segments were compared to three size surrogates: prosthion–inion length, crown area of the $M^1$, and $M^1$ crown length in Figure 5(a)–(f). The diameter estimates taken from 5 mm arc length segments do not completely differentiate between nocturnal and diurnal taxa [Figure 5(a)–(c)]. There is less overlap between nocturnal and diurnal taxa when skull length is used as a body size substitute than there is when $M^1$ crown area or length is used. However, neither is sufficient to consistently differentiate between activity patterns.

Activity patterns are differentiated when diameter estimates from 10 mm arc length segments are plotted against skull length [Figure 5(d)]. Nocturnal, diurnal and cathemeral taxa overlap at 4·1 LN prosthion–inion length (60·3 mm). Activity patterns are also differentiated when the 10 mm diameter estimates are plotted against $M^1$ crown area [Figure 5(e)]. The two groups begin to converge at 2·75 LN $M^1$ crown area (correlated with a skull length of approximately 61 mm). However, diurnal and nocturnal taxa at the low end of crown area also tend to converge, although the two groups do not overlap. Although $M^1$ crown area or length may be adequate body size correlates for reconstructing activity pattern, nocturnal and diurnal samples are closer to overlapping than when skull length is used, and this trend can be seen in both the plots of actual mediolateral diameters or diameter estimates from 10 mm segments [Figure 4(b), 5(d)].

*Activity pattern reconstructions for fossil taxa*

The orbit diameters of two *O. carteri*, one *C. abditus* and one *C. ralstoni* were analyzed, each of which preserved portions of the inferior orbital margin that fell between the suboptimal 5 mm length and the preferred 10 mm length (Table 3). In addition, one

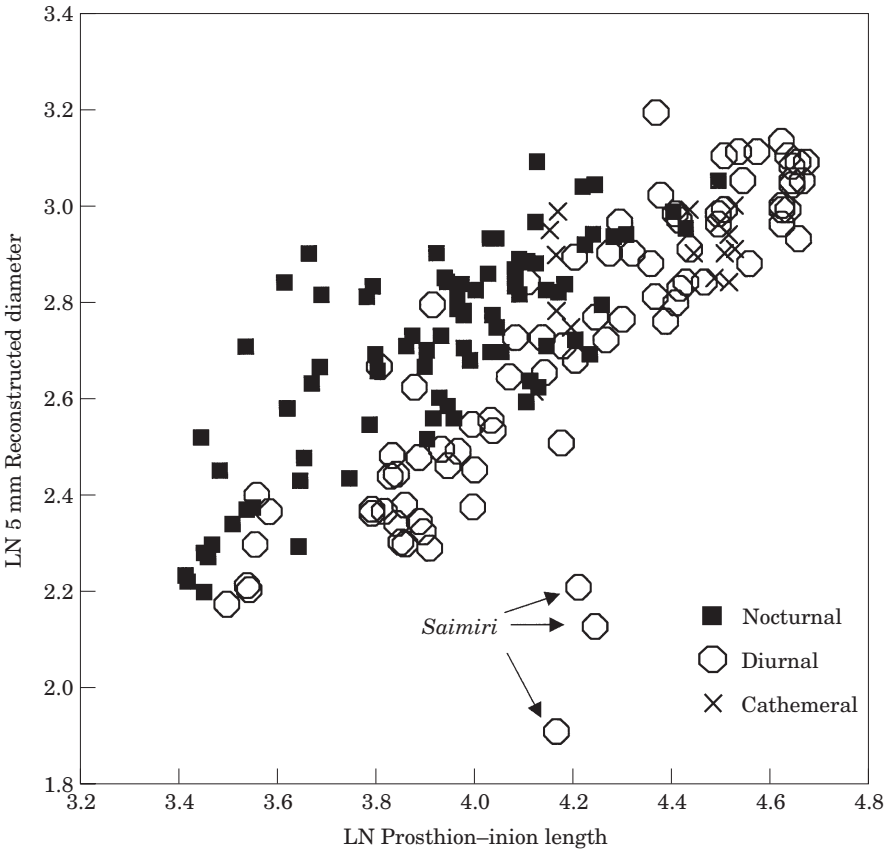



Figure 5. (a).

*H. patagonicus* was included with 20·6 mm of the inferior orbital margin preserved (Table 3). The mean diameter values of six measurements per fossil were computed (Table 3). Each fossil was plotted with the extant sample using their actual mediolateral diameters [Figure 4(b), (c)]. *C. abditus*, *S. cooperi*, *C. browni*, *P. sylviae* and *T. harringtoni* (Table 2) were plotted as well for comparison with the activity pattern inferences of *Omomys* and *Cantius* and to reassess the evolution of activity for important basal primate nodes.

Omomys carteri. Although the two *O. carteri* specimens differed in the amount of preservation of the inferior orbital margin (5·4 mm and 8·7 mm), the reconstructed diameter values for each are similar, 19·2 mm and 20·3 mm. Both specimens are also similar in inferred body size based on $M^1$ crown area (7·5 $mm^2$ and 7·9 $mm^2$). These specimens plot well above the range of extant diurnal and nocturnal animals [Figure 4(b), (c)], suggesting that not only was *O. carteri* nocturnal, but that the orbits were hypertrophied to a degree similar to the secondarily nocturnal haplorhines, *Tarsius* and *Aotus*.

Cantius abditus and C. ralstoni. *C. ralstoni* (DMNH 40488) has a reconstructed orbit diameter of 19·5 mm, and the specimen plots in the nocturnal range [Figure 4(b), (c)]. However, *C. ralstoni* (DMNH 40488)

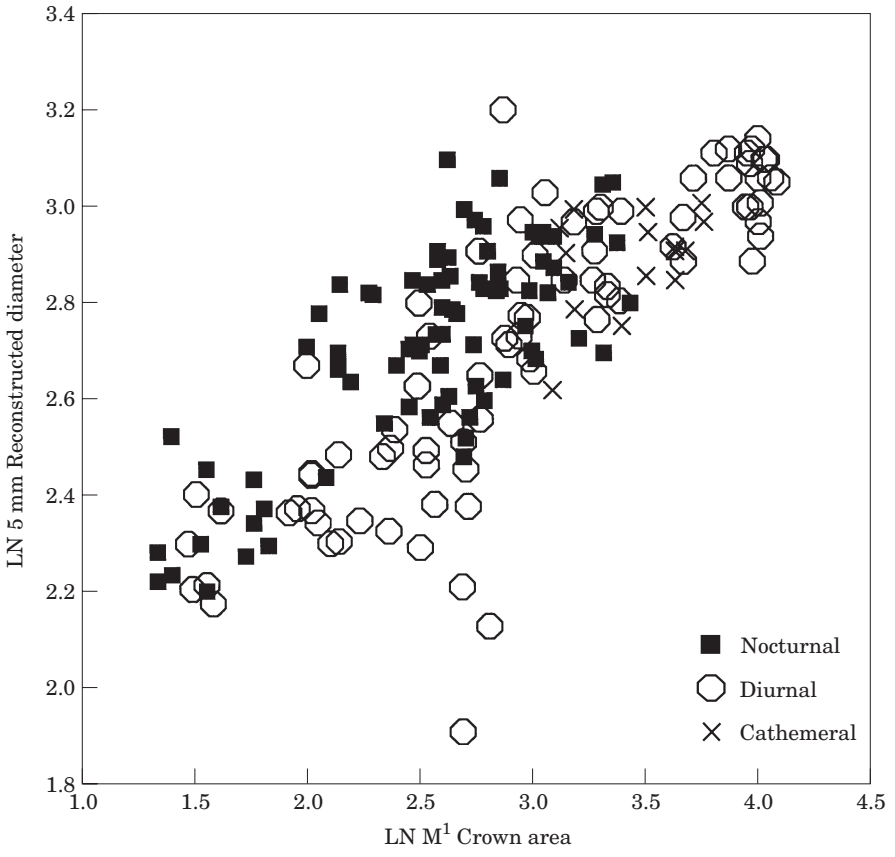



Figure 5. (b).

exceeds the size at which activity pattern can be confidently assigned to fossil taxa, suggesting that the nocturnal pattern inferred for *C. ralstoni* should be considered as preliminary. The reconstructed orbit diameter for *C. abditus* (USNM 494881) is supported by the comparison with *C. abditus* (UM 93938), a specimen of known orbit diameter but without skull length preserved. *C. abditus* also exceeds the size at which the distributions of nocturnal and diurnal animals begin to overlap but it also has relatively larger orbits than any diurnal primate of the same $M^1$ length. This suggests that *C. abditus* may also have been nocturnal, although larger than any extant nocturnal primates.

Shoshonius cooperi. *S. cooperi* is inferred to be nocturnal [Figure 4(b), (c)], as has been previously demonstrated by analyses using skull length as a surrogate for body size (Beard *et al.*, 1991; Kay & Kirk, 2000). Interestingly, the extreme orbit hypertrophy exhibited by *Shoshonius*, hypothesized by Beard *et al.* (1991) to be a synapomorphy of a *Shoshonius*+*Tarsius* clade, is exceeded by the orbit size–body size relationship in *O. carteri* [Figure 4(b), (c)].

Catopithecus browni. Previous analyses that reconstructed *C. browni* as diurnal using skull length as a body size surrogate (Rasmussen & Simons, 1992; Kay & Kirk, 2000) are supported here using $M^1$

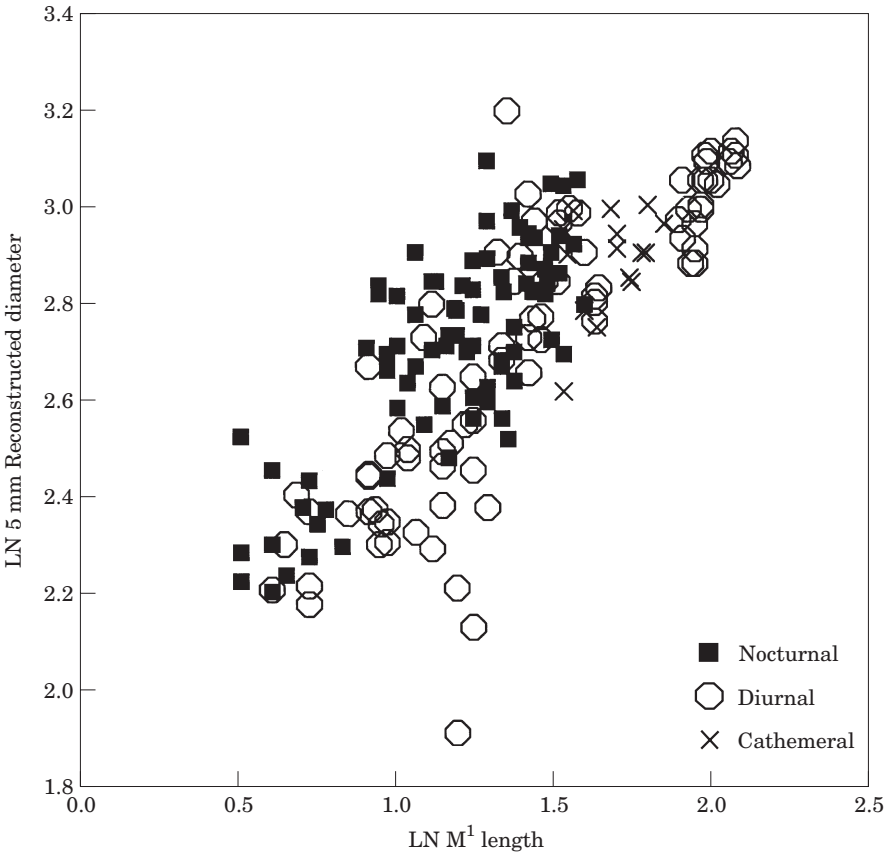



Figure 5. (c).

dimensions as a surrogate of body size [Figure 4(b), (c)].

Proteopithecus sylviae. *P. sylviae* has very small orbits that are similar in size to small callitrichids, such as *Saguinus*. However, the $M^1$ dimensions are similar to much larger animals. As a result, *Proteopithecus* plots beneath the extant diurnal cluster [Figure 4(b), (c)] and is inferred to have been diurnal (see also Kay & Kirk, 2000).

Homunculus patagonicus. *H. patagonicus* MACN 5768 preserves a large portion of the inferior orbital margin, allowing confidence in the diameter reconstruction of 16·6 mm. However, the activity pattern of *Homunculus* cannot be inferred based on orbit diameter because it plots in the area where activity patterns overlap [Figure 4(b), (c)].

Tremacebus harringtoni. *T. harringtoni* plots primarily among diurnal taxa when using $M^1$ crown area as a body size surrogate [Figure 4(b)], but it must be noted that this specimen plots adjacent to nocturnal taxa when $M^1$ is used [Figure 4(c)]. The activity pattern of *Tremacebus* cannot be inferred based on this analysis.

*Trait mapping of activity pattern and color vision evolution*

Mapping activity patterns and opsin gene evolution on a tree of primates demonstrates

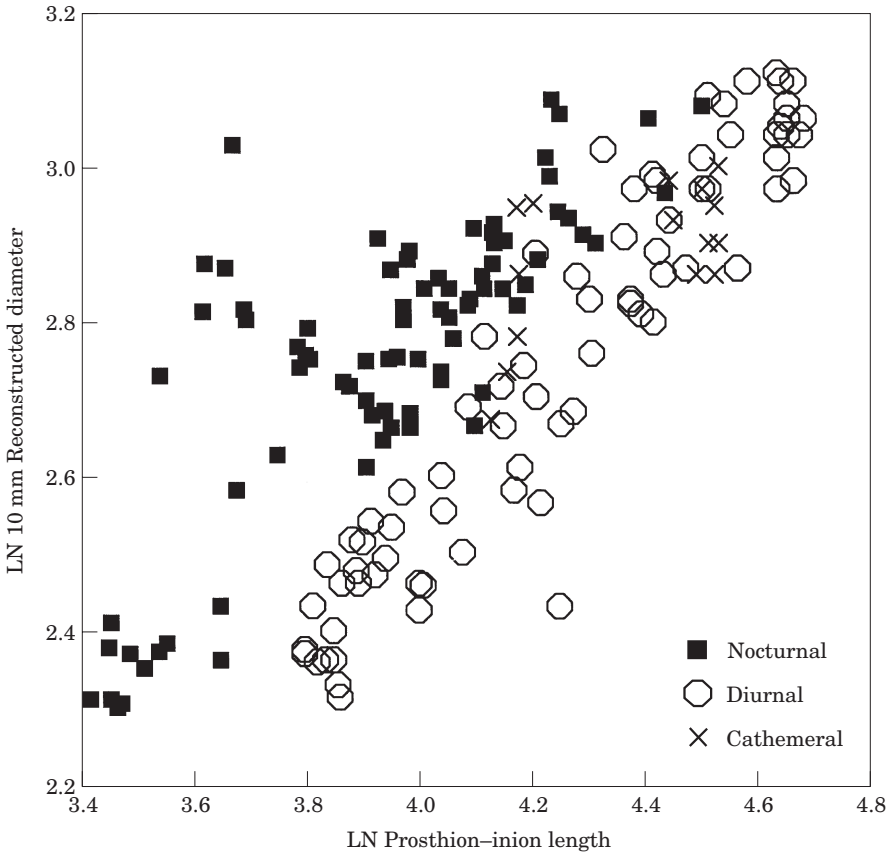



Figure 5. (d).

the most parsimonious reconstruction of opsin and activity pattern evolution at the nodes of primate higher level taxa [Figure 6(a–d)].

*Presence of* L. Tan & Li's (1999) hypothesis that the ancestral primate and strepsirrhine were trichromatic can be evaluated by determining whether these ancestors possessed "long"/"red" wavelength opsins. The majority of primates possess both *S* ("blue") and *M* ("green") opsins and it is parsimonious to reconstruct an *M* opsin as present in the primate and strepsirrhine ancestors. Therefore, Tan & Li's hypothesis predicts that these ancestors possessed an *L* opsin gene in addition to an *M*. It seems to us unlikely that all *L* opsin genes found in extant primates are homologous because they code for at least eight different wavelengths of longer wavelength sensitivity (see Table 1 for the distribution of peak wavelength sensitivities among primates). However, if Tan & Li's (1999) hypothesis is valid, the differences in wavelength sensitivity that these genes code for might be secondarily derived from some ancestral *L* opsin. Therefore, to evaluate this hypothesis we coded all *L* opsin genes as the same, and therefore potentially homologous, and reconstructed the evolution of these genes in Figure 6(a). Based upon this analysis, it is not parsimonious to hypothesize that the last common ancestors of strepsirrhines and of

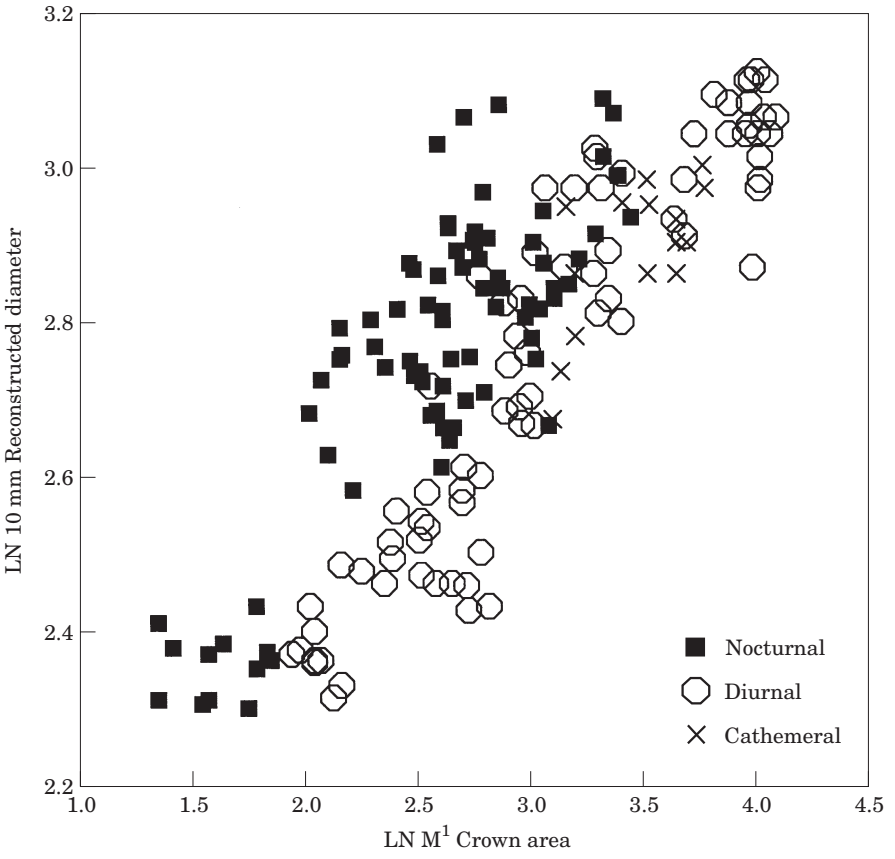



Figure 5. (e).

primates had a gene coding for *L* wavelength sensitivity. Using the equivocal cycling option in *MacClade 3.05* demonstrates that 0% of the equally most parsimonious solutions reconstruct an *L* opsin at these nodes (Table 4). It is more parsimonious to suggest that *L* wavelength opsins evolved independently in several Malagasy strepsirrhine taxa. Such a reconstruction is also possible for the ancestral haplorhine or anthropoid, although nearly half of the equally most parsimonious solutions support an *M* opsin at these nodes (Table 4).

*Number of genes.* Tan & Li's (1999) hypothesis predicts that in addition to the *S* opsin gene, universally present in extant primates, the last common ancestors of strepsirrhines and primates also possessed two genes for longer wavelength sensitive opsins: *M* and *L*. This could include the possession of a single polymorphic *M* opsin that codes for slightly different peak wavelength spectra, as in most platyrrhines, or two individual *M* and *L* opsin genes as in catarrhines and *Alouatta*. In Figure 6(b) we plot the number of opsin coding genes in extant primates and reconstruct the evolution of the number of opsin genes. It is most parsimonious to presume that polymorphic middle wavelength opsins arose independently in *C. major*, *Propithecus v. coquereli*, *Varecia variegata rubra*, and stem anthropoids, or possibly stem haplorhines. If the

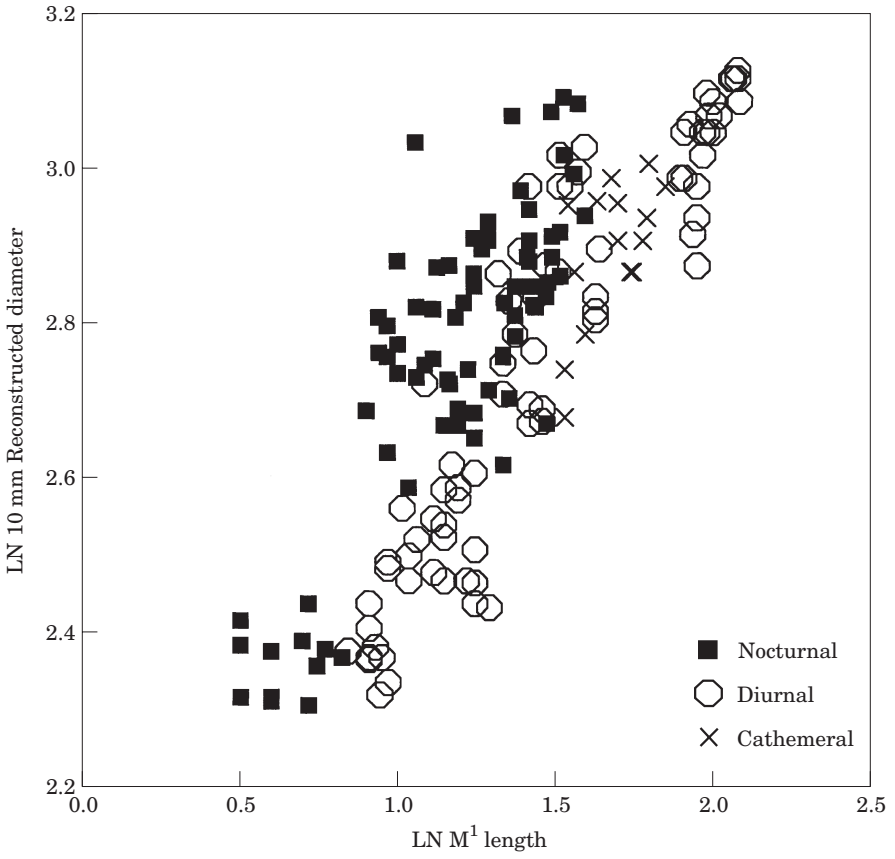



Figure 5. (f).

Figure 5. Bivariate plots of LN diameter estimates from 5 mm and 10 mm arcs fitted to the inferior orbital margin plotted against LN skull length, $M^1$ crown area, and length. The 7·86% mean percentage error of the estimates of orbital diameter associated with 5 mm arc lengths lead to noctural and diurnal taxa overlapping along much of the range of body sizes. The 3·7% mean error percentage error of the estimates of orbital diameter associated with 10 mm arc lengths lead to better differentiation between nocturnal and diurnal taxa. The dip in the inferior orbital margin of *Saimiri* (indicated by arrow) leads to an underestimate of orbit diameter in this species (see Discussion).

polymorphic *M* opsin was present in basal primates, as Tan & Li (1999) have suggested, then it has been lost numerous times during primate evolution. This result is also supported by the optimization of wavelength evolution (Appendix: character 5 and/or 6) at the nodes of primate higher taxa. 0% of the equally most parsimonious solutions for wavelength evolution (either wavelength coding method for character 5 and 6) reconstructs similar wavelength sensitivity for the last common ancestor of strepsirrhines and haplorhines (i.e., the basal primate node), as would be expected if polymorphic trichromacy were primitive for primates.

*The origins of trichromacy.* Tan & Li's (1999) hypothesis can also be evaluated simply by optimizing the presence of trichromacy and dichromacy onto the phylogeny of Archonta [Figure 6(c)]. This model makes no assumptions about gene evolution or opsin homology. It merely reconstructs the evolution of degree of chromacy. It is not

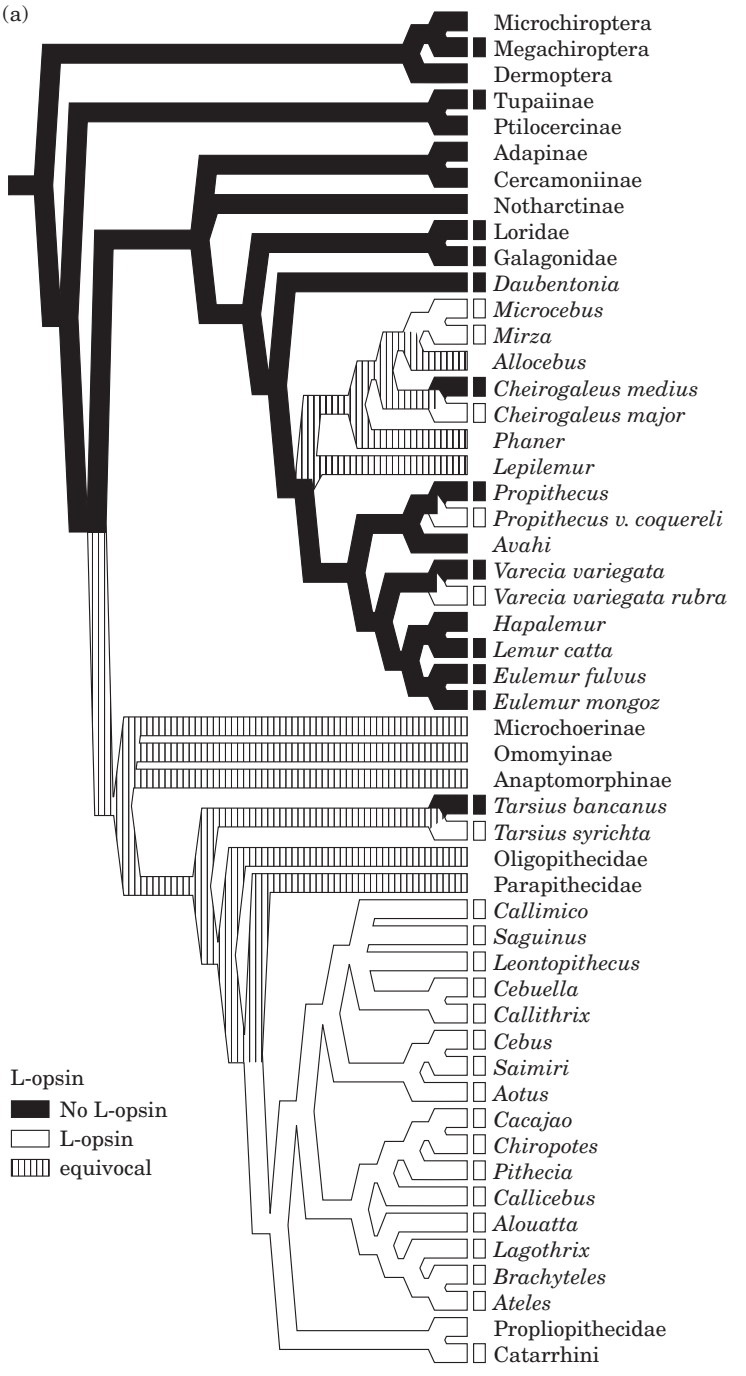

(a)
Microchiroptera
Megachiroptera
Dermoptera
Tupaiinae
Ptilocercinae
Adapinae
Cercamoniinae
Notharctinae
Loridae
Galagonidae
Daubentonia
Microcebus
Mirza
Allocebus
Cheirogaleus medius
Cheirogaleus major
Phaner
Lepilemur
Propithecus
Propithecus v. coquereli
Avahi
Varecia variegata
Varecia variegata rubra
Hapalemur
Lemur catta
Eulemur fulvus
Eulemur mongoz
Microchoerinae
Omomyinae
Anaptomorphinae
Tarsius bancanus
Tarsius syrichta
Oligopithecidae
Parapithecidae
Callimico
Saguinus
Leontopithecus
Cebuella
Callithrix
Cebus
Saimiri
Aotus
Cacajao
Chiropotes
Pithecia
Callicebus
Alouatta
Lagothrix
Brachyteles
Ateles
Propliopithecidae
Catarrhini
L-opsin
No L-opsin
L-opsin
equivocal

Figure 6. (a).

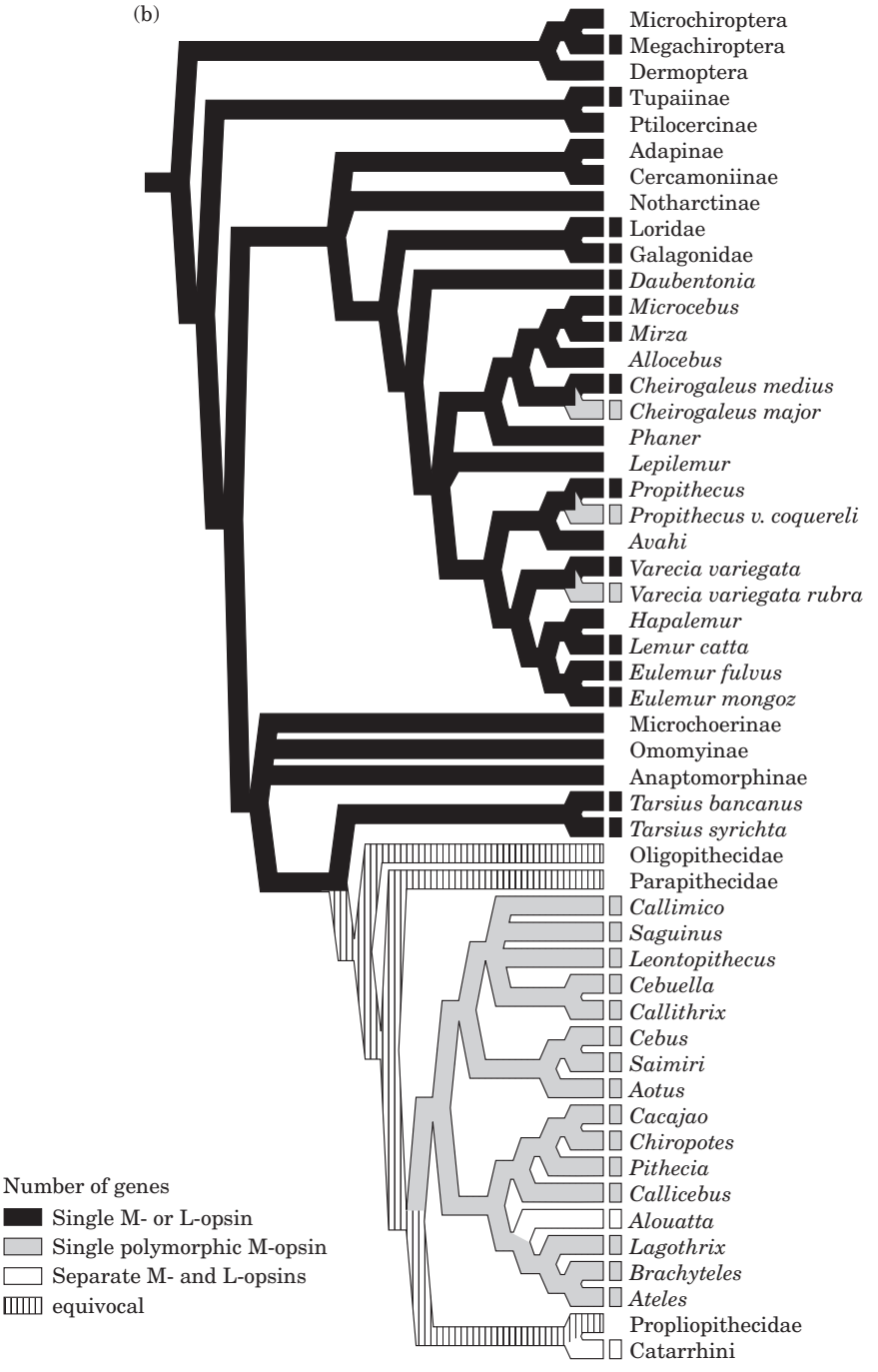

(b)
Microchiroptera
Megachiroptera
Dermoptera
Tupaiinae
Ptilocercinae
Adapinae
Cercamoniinae
Notharctinae
Loridae
Galagonidae
Daubentonia
Microcebus
Mirza
Allocebus
Cheirogaleus medius
Cheirogaleus major
Phaner
Lepilemur
Propithecus
Propithecus v. coquereli
Avahi
Varecia variegata
Varecia variegata rubra
Hapalemur
Lemur catta
Eulemur fulvus
Eulemur mongoz
Microchoerinae
Omomyinae
Anaptomorphinae
Tarsius bancanus
Tarsius syrichta
Oligopithecidae
Parapithecidae
Callimico
Saguinus
Leontopithecus
Cebuella
Callithrix
Cebus
Saimiri
Aotus
Cacajao
Chiropotes
Pithecia
Callicebus
Alouatta
Lagothrix
Brachyteles
Ateles
Propliopithecidae
Catarrhini
Number of genes
Single M- or L-opsin
Single polymorphic M-opsin
Separate M- and L-opsins
equivocal

Figure 6. (b).

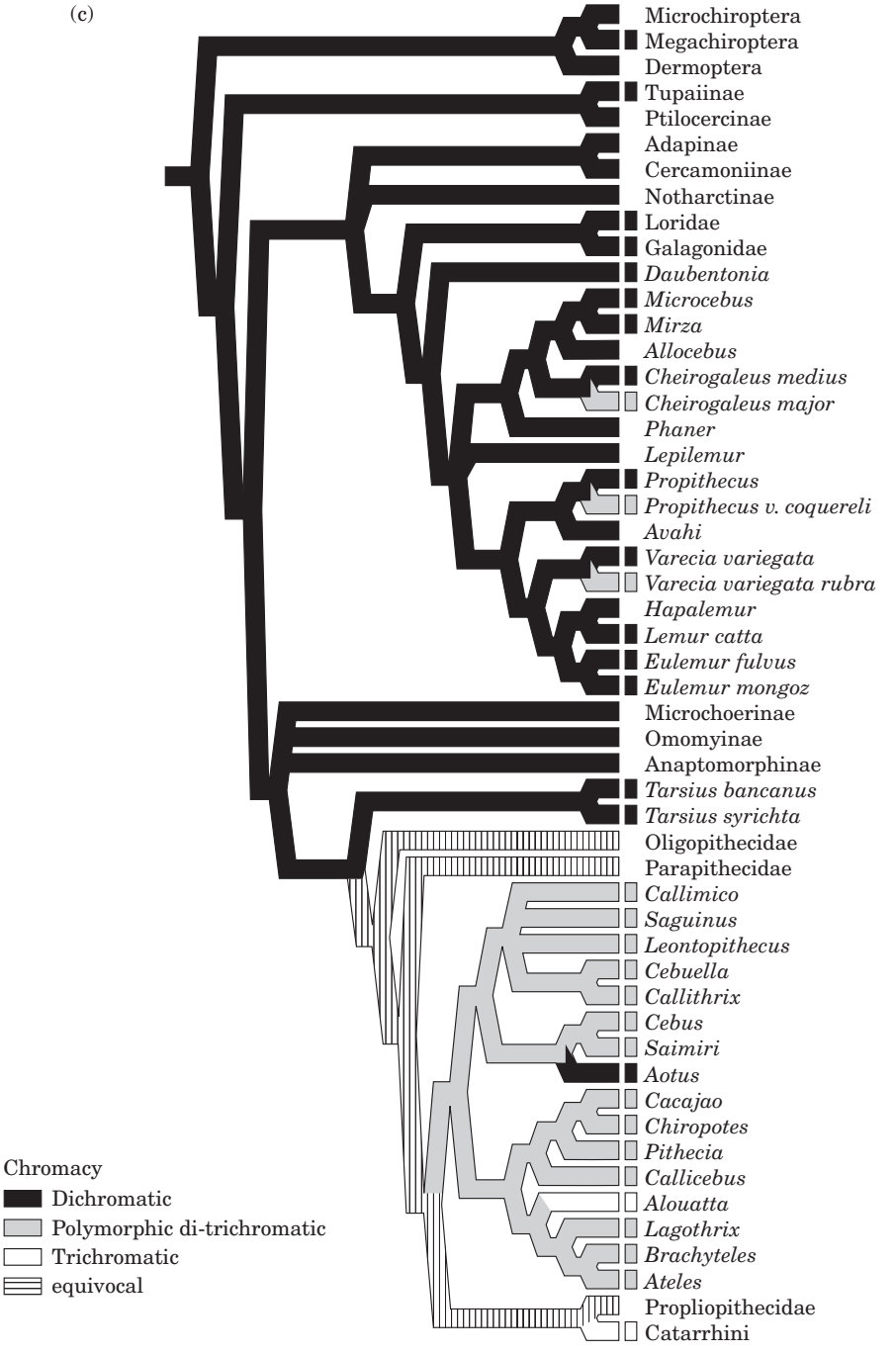

(c)
Microchiroptera
Megachiroptera
Dermoptera
Tupaiinae
Ptilocercinae
Adapinae
Cercamoniinae
Notharctinae
Loridae
Galagonidae
Daubentonia
Microcebus
Mirza
Allocebus
Cheirogaleus medius
Cheirogaleus major
Phaner
Lepilemur
Propithecus
Propithecus v. coquereli
Avahi
Varecia variegata
Varecia variegata rubra
Hapalemur
Lemur catta
Eulemur fulvus
Eulemur mongoz
Microchoerinae
Omomyinae
Anaptomorphinae
Tarsius bancanus
Tarsius syrichta
Oligopithecidae
Parapithecidae
Callimico
Saguinus
Leontopithecus
Cebuella
Callithrix
Cebus
Saimiri
Aotus
Cacajao
Chiropotes
Pithecia
Callicebus
Alouatta
Lagothrix
Brachyteles
Ateles
Propliopithecidae
Catarrhini
Chromacy
Dichromatic
Polymorphic di-trichromatic
Trichromatic
equivocal

Figure 6. (c).

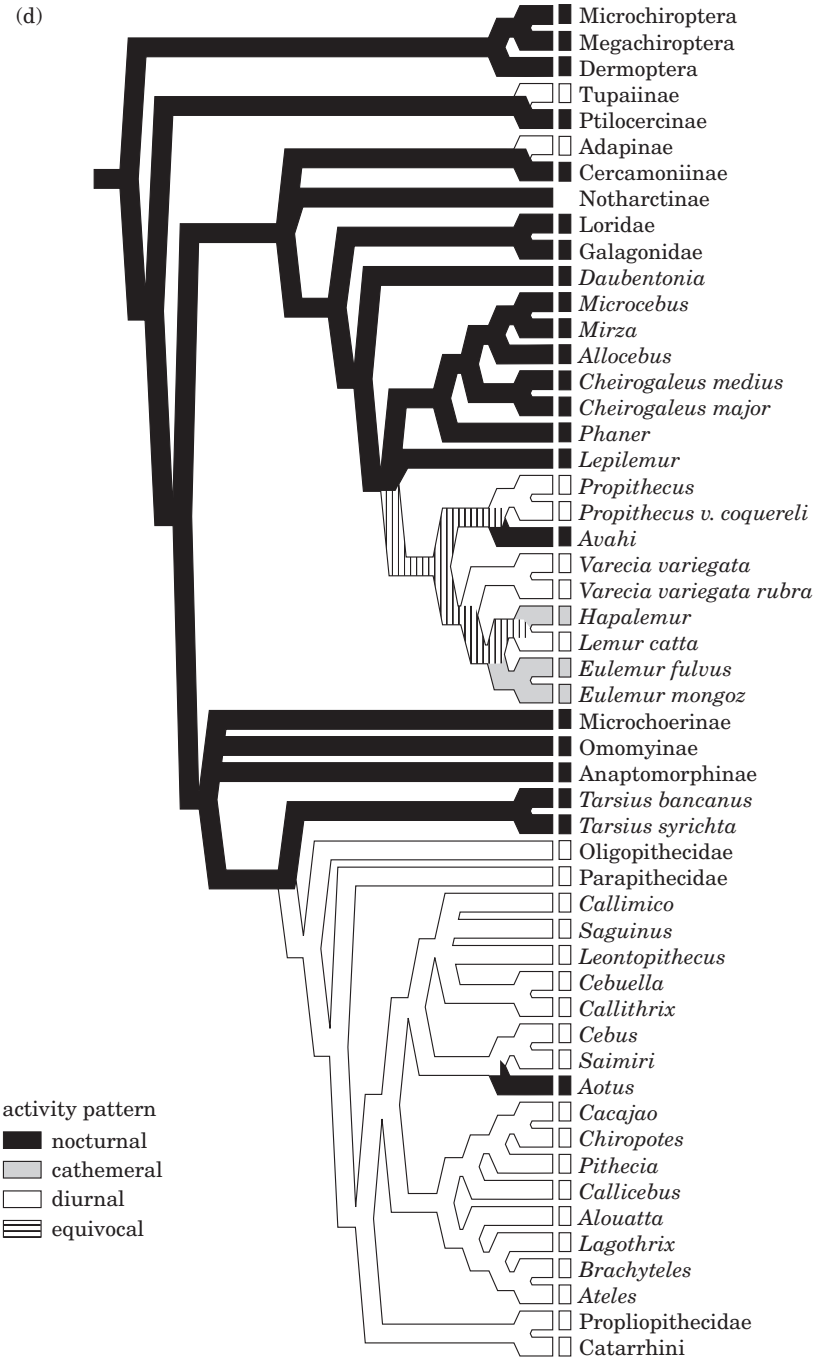

(d)
Microchiroptera
Megachiroptera
Dermoptera
Tupaiinae
Ptilocercinae
Adapinae
Cercamoniinae
Notharctinae
Loridae
Galagonidae
Daubentonia
Microcebus
Mirza
Allocebus
Cheirogaleus medius
Cheirogaleus major
Phaner
Lepilemur
Propithecus
Propithecus v. coquereli
Avahi
Varecia variegata
Varecia variegata rubra
Hapalemur
Lemur catta
Eulemur fulvus
Eulemur mongoz
Microchoerinae
Omomyinae
Anaptomorphinae
Tarsius bancanus
Tarsius syrichta
Oligopithecidae
Parapithecidae
Callimico
Saguinus
Leontopithecus
Cebuella
Callithrix
Cebus
Saimiri
Aotus
Cacajao
Chiropotes
Pithecia
Callicebus
Alouatta
Lagothrix
Brachyteles
Ateles
Propliopithecidae
Catarrhini
activity pattern
nocturnal
cathemeral
diurnal
equivocal

Figure 6. (d).

parsimonious to suggest that the last common ancestors of strepsirrhines and Primates were trichromatic. X-linked polymorphic trichromacy in *P. v. coquereli*, *V. v. rubra*, and *C. major* is most parsimoniously explained as three independent occurrences. Polymorphic trichromacy can only be reconstructed with confidence for stem platyrrhines, although 9% of the solutions support trichromacy at the basal anthropoid node (Table 4).

*Nocturnality and diurnality.* Tan & Li (1999) imply, and Li (2000) explicitly states, that the last common ancestors of primates and strepsirrhines were diurnal as well as trichromatic. In Figure 6(d) we evaluate this hypothesis by optimizing onto our primate tree the presence of nocturnal and diurnal activity patterns. In living taxa these data are available; for fossils they are estimated from the relative size of the orbital aperture as discussed above. Nocturnality is most parsimoniously reconstructed as the primitive condition for all primates, all strepsirrhines, Malagasy strepsirrhines, and basal haplorhines [Figure 6(d); Table 4]. These results are unchanged even when two diurnal "dummy" outgroup taxa are added as the sister taxa to primates (Table 4), suggesting a highly robust reconstruction of nocturnality for these nodes. On the other hand, all analyses support a diurnal reconstruction for the basal anthropoid node [Figure 6(d); Table 4].

## Discussion

*Orbital diameter estimates*

The nocturnal and diurnal clusters begin to converge at approximately 61 mm prosthion–inion length in this analysis, whereas in Kay & Cartmill's (1977) analysis these groups converge at 75 mm prosthion–inion length. This discrepancy is probably explained by the fact that Kay & Cartmill used species mean values for their analysis, whereas individual values were used in this study. When mean values are used, nocturnal and diurnal taxa converge above 70 mm prosthion–inion length (Figure 7). Plotting mean values tends to underestimate the variation in diameter size. For the purposes of inferring activity patterns of individual fossils, as was performed here, individual values should be used for comparison.

Figure 6. Cladograms illustrating the optimization (using parsimony) of visual system traits on a phylogeny of primates. (a) The most parsimonious distribution of *L* ("red") opsin alleles indicates that the last common ancestor of all extant strepsirrhines had not evolved the *L* opsin allele and was not trichromatic, implying that *L* opsins have evolved convergently at least four times in strepsirrhines. *Microcebus* and *Mirza* possess *L* opsin alleles but have lost *M* opsin alleles, suggesting that *M* opsins may have mutated into *L* opsins, so only *Varecia variegata rubra*, *Propithecus v. coquereli*, and *Cheirogaleus major* have the genes for trichromacy [see Figure 6(c)]. It is not parsimonious to hypothesize that the last common ancestors of strepsirrhines and primates had a gene coding for *L* wavelength sensitivity. (b) According to Tan & Li (1999) the last common ancestors of strepsirrhines and primates also possessed two genes for longer wavelength sensitive opsins: *M* and *L*. Scoring extant primates for the number of opsin coding genes and optimizing the number of opsin genes onto the primate phylogeny does not support this hypothesis. X-linked polymorphic trichromacy requires that the *M* opsin evolve multiple paralogous alleles sensitive to dissimilar peak wavelengths. This polymorphism is not parsimoniously reconstructed at any of the key strepsirrhine nodes. (c) Optimizing the presence of trichromacy and dichromacy onto the phylogeny of Archonta demonstrates that the X-linked *M* polymorphism probably arose multiple times, and it is not parsimonious to suggest that the last common ancestors of strepsirrhines and primates were trichromatic. This model makes no assumptions about gene evolution or opsin homology. (d) Nocturnality is also reconstructed at many nodes, an activity pattern that is hypothesized here and by Tan & Li (1999) to be functionally incompatible with trichromacy. This analysis demonstrates that all primates, all strepsirrhines, Malagasy strepsirrhines, and haplorhines were primitively nocturnal.

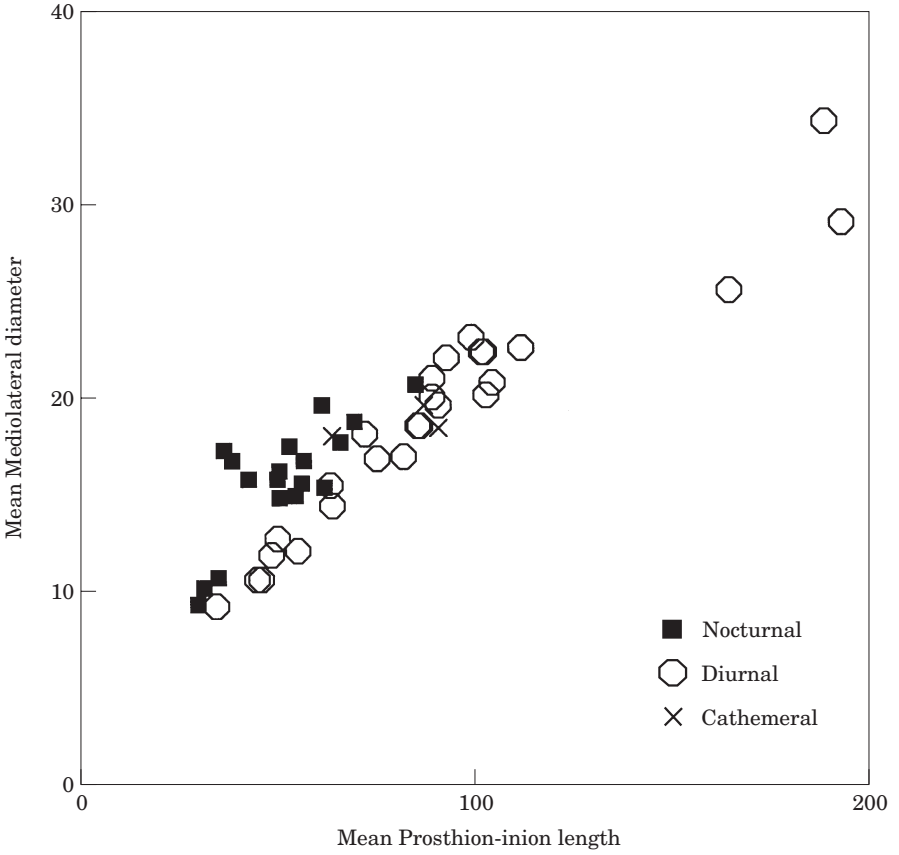



Figure 7. Bivariate plot of mean mediolateral orbit diameter against mean prosthion–inion length for each extant species sampled. When mean values are used, nocturnal and diurnal taxa converge above 70 mm prosthion–inion length, a result similar to that found by Kay & Cartmill (1977).

The orbit diameters estimated from a 10 mm arc length of the inferior orbital margin are more highly correlated with the actual mediolateral diameters in comparison to the smaller 2 mm and 5 mm segment sizes. This is to be expected given that many of the taxa studied have orbit diameters not much larger than 10 mm. The radii (and subsequently diameters) are computed from arcs that are formed from three points. The placement of these points strongly influences the computed values due to the irregularities in the shape of the orbital margin. For example, note in Figure 3(c) and Figure 5(a) the indicated position of *Saimiri*. The morphology of the inferior orbital margin in *Saimiri* is irregular with large dips. These dips affect the placement of orbitale inferius, the center point used to form the arc from which the radii (and diameters) are estimated. This irregularity reduces the calculated radii of curvature for the orbit, causing this method to significantly underestimate orbit diameter.

The 2 mm and 5 mm arc lengths produce estimated values that are sensitive to small irregularities in the orbital margin. The placement of points over a larger arc length, like 10 mm, is less sensitive to the variations in the shape of the inferior orbital margin. So, regardless of the size of the margin that is encompassed in the arc (i.e., a 5 mm arc

**Table 4 Analysis of the number of solutions possible for equivocally resolved nodes**

| Trait Analysis | Total solutions | Number of solutions at nodes | | | | |
|---|---|---|---|---|---|---|
| | | Basal primates | Basal strepsirrhini | Malagasy strepsirrhini | Basal haplorhini | Basal anthropoidea |
| *L*-opsin | 20 solutions | 0% *L*-opsin | 0% *L*-opsin | 0% *L*-opsin | 40% *L*-opsin | 60% *L*-opsin |
| Number of genes | 11 solutions | 100% 1-gene | 100% 1-gene | 100% 1-gene | 100% 1-gene | 9% 2-gene solution |
| Chromacy | 11 solutions | 100% dichromatic | 100% dichromatic | 100% dichromatic | 100% dichromatic | 91% dichromatic† |
| Activity pattern | 6 solutions | 100% nocturnal | 100% nocturnal | 100% nocturnal | 100% nocturnal | 100% diurnal |
| Activity pattern w/2 diurnal outgroups | 6 solutions | 100% nocturnal | 100% nocturnal | 100% nocturnal | 100% nocturnal | 100% diurnal |

The equivocal cycling option in *MacClade 3.05* (Maddison & Maddison, 1992) permits the examination of all the possible solutions at equivocal nodes. The total number of solutions and the percentage of these solutions that support alternative reconstructions for the evolution visual traits are reported for the nodes discussed in the text. †Note that the ancestral node for crown anthropoids is parsimoniously reconstructed as trichromatic for 82% of the solutions. Ambiguity in resolving chromatic vision in basal anthropoids is a product of the placement of fossil taxa.

used to estimate the diameter from a segment that is 10 mm in length), irregularities in the shape will have a greater effect on the estimated value for the smaller arc lengths. This contributes to the higher variance in diameter estimates from 2 mm and 5 mm arc lengths. In addition, the smaller lengths also represent a smaller percentage of the total orbital margin. Ten millimeter segments are preferred for estimating the actual orbital diameter. However, this large segment size limits the number of incomplete fossils that can be analyzed using this method.

Although the diameter estimates from 5 mm segments are correlated with mediolateral diameter, these estimates incorporate 7·86% mean error. This amount of error is sufficient to group some nocturnal and diurnal specimens together when plotted. However, along any part of the range, nocturnal and diurnal taxa differ on average approximately 15% in orbit diameter, so 5 mm diameter predictions have utility for activity pattern reconstructions, as was demonstrated by the analysis of *O. carteri*. Additionally, although $M^1$ crown area is correlated with body mass, nocturnal and diurnal taxa fall more closely when crown area is used as a body size correlate. Variance in crown size is likely affected by dietary factors, suggesting that $M^1$ crown area may be a problematic variable for estimating body size. Although skull length is correlated with $M^1$ crown area (Spearman's $\rho=0{\cdot}928$, $P<0{\cdot}01$; Figure 8), the scatter inherent in using $M^1$ crown area as a body size correlate detracts from activity pattern reconstructions.

### *Reconstruction of activity patterns of fossil primates*

*Fossil strepsirrhines.* Adapine and notharctine adapiformes (e.g., *Adapis*, *Leptadapis* and *Notharctus*) are often reconstructed as diurnal, whereas the cercamoniines *Pronycticebus gaudryi* and *Mahgarita stevensi* are nocturnal (Kay & Cartmill, 1977; Kay & Kirk, 2000). The question of importance to the evolution of activity pattern in primates is what is the primitive activity pattern of all adapiformes? Adapiformes are the sister taxon to modern strepsirrhines (Beard *et al.*, 1988; Kay *et al.*, 1997; Ross *et al.*, 1998), therefore the primitive condition for adapiformes bears on the reconstruction of activity pattern at the basal strepsirrhine and primate nodes [Figure 6(d)]. However, inferring the activity patterns for the basal adapiforms *C. abditus* and *C. ralstoni* is confounded in part by the large size of these taxa. Although *C. ralstoni* exceeds the upper size range for strict inference of activity pattern, the very large orbit diameter indicates that this species was almost certainly nocturnal [Figure 4(b), (c)]. On the other hand, the analysis of *C. abditus* supports two interpretations. If *C. abditus* was a diurnal primate, then the orbits (and possibly eyes) of this species were significantly larger than any diurnal primate within this body size range. On the other hand, if *C. abditus* was nocturnal, then this species was nocturnal at a body size larger than the largest extant nocturnal primate, *Daubentonia*. *C. abditus* does not, however, exceed the theoretical asymptotic upper limit for nocturnal primates that was suggested by Kay & Kirk (2000), further supporting the preliminary nocturnal inference for *Cantius* and, by extension, all basal adapiforms.

*Fossil haplorhines.* *O. carteri* was nocturnal, indicating that the 7·86% mean percentage error of the estimates of orbital diameter associated with 5 mm arc lengths (which was approximately the preservation of UCM 67854) does not negate the utility of fossils that preserve less than 10 mm of the inferior orbital margin. In these cases, however, inferring activity pattern for such specimens should be considered preliminary until additional specimens of the same taxon can also be analyzed, as was the case here for

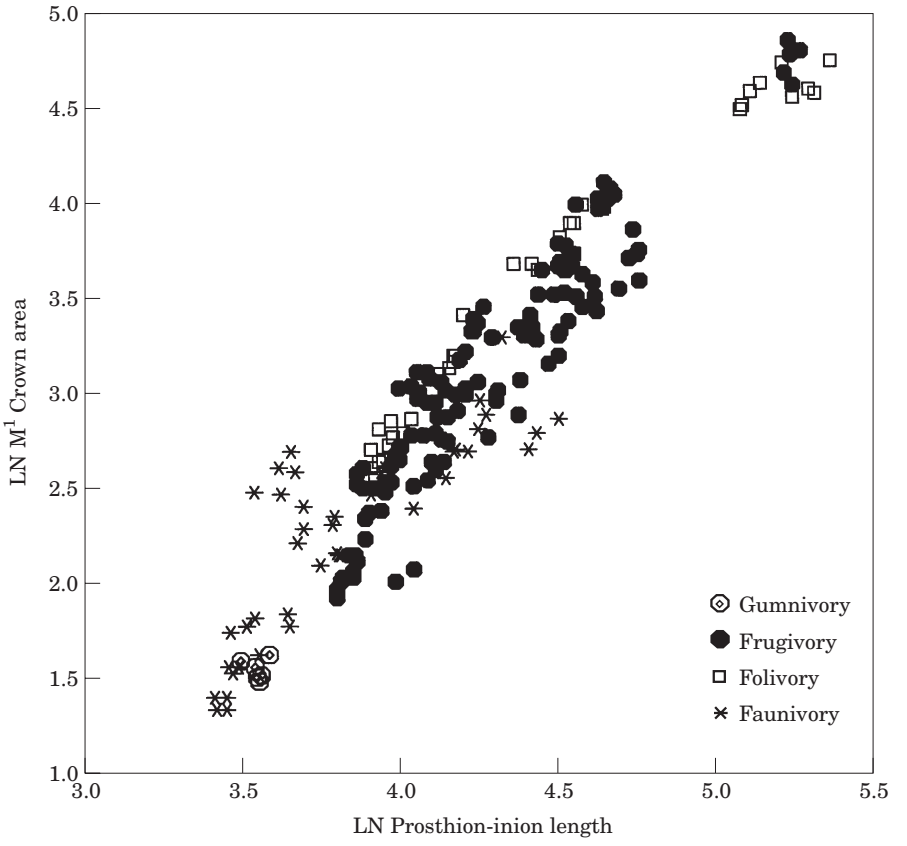



Figure 8. Bivariate plot of LN $M^1$ crown area against LN prosthion–inion length, two of the body size surrogates used in this analysis. Skull length is correlated with $M^1$ crown area (Spearman's $\rho=0{\cdot}947$, $P<0{\cdot}01$); however, the variance inherent in using $M^1$ crown area (possibly due to diet) as a size surrogate, especially at larger body sizes, introduces additional error and causes greater overlap between nocturnal and diurnal taxa.

*Omomys*. Since the two specimens were so similar in body size and reconstructed orbit diameter, this supports the robustness of each reconstruction and the inference of nocturnality for the taxon. These data provide further support for the inferred nocturnal activity pattern of omomyiform primates (Kay & Cartmill, 1977; Beard *et al.*, 1991; Kay & Kirk, 2000).

*O. carteri* has very large orbits for its size [Figure 4(b), (c)], exceeding the extreme orbit hypertrophy exhibited by *Shoshonius*, hypothesized by Beard *et al.* (1991) to be a synapomorphy of a *Shoshonius*+*Tarsius* clade. The only extant primates that have similarly-sized eyes relative to orbit size are the secondarily nocturnal haplorhines *Tarsius* and *Aotus*. This extreme hypertrophy has been suggested to increase visual sensitivity or, possibly, visual acuity in a nocturnal primate that lacks a reflective tapetum lucidum (Cartmill, 1980; Kay & Kirk, 2000). However, all omomyiformes were nocturnal (Kay & Cartmill, 1977; Beard *et al.*, 1991; Kay & Kirk, 2000; this study), and tapetum loss is probably a synapomorphy of nonomomyiform haplorhines (Ross, 1996, 2000). If the extreme orbit dimensions of *O. carteri* are the result of tapetum loss, then this loss would necessarily have occurred in a

nocturnal animal. At present, it is more reasonable to hypothesize that the factors leading to extreme orbit and eye size increases in putatively nocturnal taxa are unknown.

*C. browni* was a diurnal anthropoid, based both on previous analysis that used skull length as a body size surrogate (Rasmussen & Simons, 1992; Kay & Kirk, 2000) and the use of $M^1$ dimensions used here. On the other hand, if estimates of orbit diameter suggested for the similarly sized anthropoid *P. sylviae* are correct, this species has smaller orbits relative to $M^1$ crown dimensions of any primate, extant or fossil. If this is indeed the case, then *Proteopithecus* had a visual system and ecology dissimilar to any extant primate. Although the crushed skulls of *Proteopithecus* may have led to underestimates of orbit diameter, it seems unlikely that the orbits of *Proteopithecus* are large enough to support a reconstruction of nocturnality, suggesting that it was diurnal [Figure 6(d); Simons, 1997).

Rusconi (1935*a*,*b*) and Hershkovitz (1974) suggested that *T. harringtoni* was nocturnal or, possibly, crepuscular, based on the size of the orbits. This suggestion cannot be evaluated by the analysis of orbit diameters presented here because the results using $M^1$ dimensions as size surrogates are not consistent [Figure 4(b), (c)]. *H. patagonicus*, the additional fossil platyrrhine in this analysis, exceeds the size at which activity pattern can be inferred with confidence. Although the activity patterns of both these taxa cannot be inferred, mapping this trait on the most parsimonious tree of primates indicates that diurnality is primitive for platyrrhines [Figure 6(d)]. If either *Tremacebus* or *Homunculus* were nocturnal, then these taxa evolved nocturnality secondarily.

### *The evolution of activity patterns and chromatic vision in primates*

Tan & Li (1999) reconstruct the last common ancestor of strepsirrhines as trichromatic, based upon the distribution of *M* and *L* opsin alleles. These alleles code for middle and long wavelength sensitive cone photopigments, and their presence in addition to *S* (which apparently is primitive for mammals) grants trichromatic vision. However, the most parsimonious distribution of these alleles published by Tan & Li (1999) actually leads to the opposite conclusion [Figure 6(a), (b)]. All of the lorid species (galagos and lorises) that were sampled by Tan & Li (1999) lacked the *L* opsin allele, meaning that none of these species has functional trichromatic color vision. Also, the *L* opsin allele is highly variable in Malagasy strepsirrhines and was not found in many lemurids. It is more parsimonious, therefore, to suggest that the last common ancestor of these two superfamilies lacked the *L* allele, and therefore lacked functional trichromacy. In addition, since several taxa that possess *L* opsin alleles have lost *M* opsin alleles, only *V. variegata rubra*, *P. v. coquereli*, and *C. major* are trichromatic. Indeed, if trichromacy is primitive not for just strepsirrhines but for all primates, then this requires that trichromacy be lost a minimum of eight times during primate evolution [Figure 6(c)]. This distribution also begs the question that if the ancestral strepsirrhine was trichromatic, why have some extant diurnal strepsirrhines lost one allele?

The suggestion that trichromacy and diurnality are primitive for strepsirrhines is also at odds with known retinal morphology. Nocturnal mammals are predominantly monochromatic, or occasionally dichromatic, because their retinae sacrifice cones to pack in rods so as to increase visual sensitivity in a light-deficient environment (Jacobs, 1993). The few diurnal or cathemeral Malagasy strepsirrhines are more similar to nocturnal strepsirrhines in their ratios of cones to rods than they are to habitually diurnal anthropoid species (Pariente, 1979), implying that these diurnal strepsirrhines have only recently evolved relatively diurnal

activity patterns from a nocturnal ancestor (van Schaik & Kappeler, 1996). This latter point is also supported by the known distribution of tapeta lucida in strepsirrhines. The tapetum is a reflecting layer between the choroid and retina that functions to increase visual sensitivity in nocturnal animals (Walls, 1942). Tapeta lucida are found in all strepsirrhines (Pariente, 1979), including the diurnal or cathemeral (i.e., exhibiting both nocturnal and diurnal habits) lemurids studied by Tan & Li (1999), suggesting that the last common ancestor of strepsirrhines had a tapetum to enhance scotopic vision and was, therefore, nocturnal.

What is less clear is how recently diurnality evolved in indriids and lemurids. Van Schaik & Kappleler (1996) argued that (based primarily on other data) the low levels (compared to diurnal anthropoids) of glutathione, an enzyme known to counter ultraviolet damage to the lens of diurnal primates, found in the lens of strepsirrhines, *Aotus* and *Tarsius* (Holleschau & Rathbun, 1994; Rathbun *et al.*, 1994) support the hypothesis that diurnality and trichromacy evolved only recently in indriids and lemurids. However, a comparison of the glutathione reductase levels [the enzyme product specifically cited by van Schaik & Kappeler (1996)] between primates and nonprimate mammals demonstrates that strepsirrhines, *Aotus* and *Tarsius* are more similar to other mammals (both diurnal and nocturnal) than any of these species are to diurnal anthropoids (Rathbun *et al.*, 1986). Anthropoids appear to be unique in the high levels of glutathione present in their lens, and a comparison between diurnal strepsirrhines and anthropoids does not clarify how recently diurnal and cathemeral Malagasy strepsirrhines evolved these activity patterns. What is clear, however, is that the last common ancestor of Malagasy strepsirrhines was nocturnal [Figure 6(d); Table 4], indicating that the presence of tapeta lucida and the high proportion of rods in their retinae support a nocturnal ancestry of indriids and lemurids.

Tan & Li (1999) suggest that the last common ancestor of tarsiers and strepsirrhines must have been trichromatic and diurnal. Tarsiers are generally agreed to be more closely related to anthropoids than to strepsirrhines (Purvis, 1995; Kay *et al.*, 1997; Ross *et al.*, 1998; Fleagle, 2000), so the last common ancestor of tarsiers and stepsirrhines was arguably the last common ancestor of all primates. The last common ancestor of all primates was nocturnal, as inferred from high degrees of orbital convergence characteristic of all primates (Allman, 1977; Pettigrew, 1978; Cartmill, 1992), as was the Eocene fossil group most closely related to tarsiers and anthropoids, the Omomyiformes (Kay & Cartmill, 1977; Beard *et al.*, 1991; this study). The Eocene Adapiformes, the putative sister taxon of strepsirrhines, were also probably primitively nocturnal based on the activity pattern reconstruction of the cercamoniine adapiforms *P. gaudryi* and *M. stevensi* (Kay & Cartmill, 1977; Kay & Kirk, 2000), and the reconstructed activity pattern for *C. ralstoni* (this study). Nocturnality is reconstructed as the primitive activity pattern for all primates [Figure 6(d)]. In addition, that all extant archontans, except tupaiines, are nocturnal also strongly suggests that archontans, including stem primates, were primitively nocturnal [Figure 6(d)].

Diurnality is probably primitive for anthropoids, based on the activity patterns of all extant anthropoids and the best inferences for the early oligopithecid *C. browni* (Rasmussen & Simons, 1992) and *P. sylviae* (Kay & Kirk, 2000; this study) [Figure 6(d)]. The only evidence for the origin of polymorphic trichromacy claimed by Tan & Li (1999) to be primitive for all primates is, in fact, present in platyrrhines. Female platyrrhines that are X-chromosome heterozygous for the *M* opsin allele (also known as the *M*/*L* opsin allele), meaning that each

*M* opsin photopigment is photosensitive at dissimilar peak spectra, have functional trichromacy (Jacobs, 1994/95; Shyue *et al.*, 1995). Homozygous female and all male platyrrhines are dichromatic. The only exception among platyrrhines is *Alouatta*, which has multiple, duplicate X-chromosome heterozygous alleles and both males and females are routinely trichromatic (Jacobs *et al.*, 1996*b*). On the other hand, all catarrhines have *S*, *M* and *L* opsins and are all trichromatic (Jacobs, 1993, 1994/95). The link between diurnality and trichromacy is easier to make for anthropoids because all but one species, *Aotus*, is diurnal and all species have polymorphic or true trichromacy. Polymorphic trichromacy probably evolved first in either stem anthropoids or in the ancestor to platyrrhines, not in the ancestor to all primates or strepsirrhines, as has been hypothesized by Tan & Li (1999). Therefore, the hypothesis that diurnality is primitive for all primates or strepsirrhines cannot be supported based on the available evidence.

## Summary and conclusions

The hypothesis that diurnality and trichromacy are primitive for all primates or strepsirrhines fails when the weight of the comparative evidence is considered. The highly variable distribution of long wavelength sensitive opsin alleles (whatever their origin) among diurnal strepsirrhines, the absence of X-linked polymorphic trichromacy in all but three extant strepsirrhines, the nocturnal morphology of strepsirrhine eyes, and the reconstruction of activity patterns at nodes of the most parsimonious tree of primates, strongly indicate that not only the last common ancestors of strepsirrhines, but also of all primates, were dichromatic and nocturnal, not trichromatic and diurnal as was suggested by Tan & Li (1999; Li, 2000).

This study also investigates the extent to which activity patterns can be reconstructed for fossils, using orbit diameters estimated from segments of the inferior orbital margin in order to examine fossil primate taxa that were previously considered to be too fragmentary to infer activity patterns. Fossil specimens in which a minimum of 10 mm arc length of the inferior orbital margin, and an $M^1$ crown area no greater than LN 2·75 (approximately 16 $mm^2$), or 61 mm prosthion–inion length, are preferred for activity pattern reconstruction; however, specimens that are more fragmentary are not beyond the scope of this method. The orbital diameters of specimens that preserve a minimum of 5 mm of the inferior orbital margin can also be estimated, but the errors associated with these estimates suggest that caution be used.

*O. carteri* can be inferred to have been nocturnal. The analysis of the two *O. carteri* specimens used here also demonstrates that highly fragmentary fossils are not necessarily excluded from activity pattern inferences. This analysis provides additional evidence that omomyiform taxa were nocturnal, and that nocturnality was probably primitive for all of the Omomyiformes (Kay & Cartmill, 1977; Beard *et al.*, 1991). *C. ralstoni* (e.g., Hill *et al.*, 2000) was nocturnal. *C. abditus* possibly was also nocturnal, but exhibited this activity pattern at a body size larger than any extant nocturnal primate.

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## Appendix

*Character list and coded matrix*

1. Activity Pattern. Nocturnality is scored as 0, diurnality is scored as 1, and cathemerality is scored as 2. Data on extant taxa are

| Taxon | Characters | | | | | |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| Microchiroptera | 0 | ? | ? | ? | ? | ? |
| Megachiroptera | 0 | 0 | 0 | 0 | 0 | 0 |
| Dermoptera | 0 | ? | ? | ? | ? | ? |
| Tupaiinae | 1 | 0 | 0 | 0 | 3 | 5 |
| Ptilocercinae | 0 | ? | ? | ? | ? | ? |
| Adapinae | 1 | ? | ? | ? | ? | ? |
| Cercamoniinae | 0 | ? | ? | ? | ? | ? |
| Notharctinae | ? | ? | ? | ? | ? | ? |
| Anaptomorphinae | 0 | ? | ? | ? | ? | ? |
| Microchoerinae | 0 | ? | ? | ? | ? | ? |
| Omomyinae | 0 | ? | ? | ? | ? | ? |
| Oligopithecidae | 1 | ? | ? | ? | ? | ? |
| Parapithecidae | 1 | ? | ? | ? | ? | ? |
| Propliopithecidae | 1 | ? | ? | ? | ? | ? |
| Catarrhini | 1 | 1 | 2 | 2 | 0/4 | 1/6 |
| *Saguinus* | 1 | 1 | 1 | 1 | 1/3/4 | 3/5/7 |
| *Leontopithecus* | 1 | 1 | 1 | 1 | 1/3/4 | 3/5/7 |
| *Callithrix* | 1 | 1 | 1 | 1 | 1/3/4 | 3/5/7 |
| *Cebuella* | 1 | 1 | 1 | 1 | 1/3/4 | 3/5/7 |
| *Cebus* | 1 | 1 | 1 | 1 | 0/2/4 | 2/4/7 |
| *Saimiri* | 1 | 1 | 1 | 1 | 0/2/4 | 2/4/7 |
| *Aotus* | 0 | 1 | 1 | 0 | 1 | 3 |
| *Cacajao* | 1 | 1 | 1 | 1 | ? | ? |
| *Chiropotes* | 1 | 1 | 1 | 1 | ? | ? |
| *Pithecia* | 1 | 1 | 1 | 1 | ? | ? |
| *Callicebus* | 1 | 1 | 1 | 1 | 2/4 | 4/7 |
| *Callimico* | 1 | 1 | 1 | 1 | 1/3/4 | 3/5/7 |
| *Alouatta* | 1 | 1 | 2 | 2 | ? | ? |
| *Lagothrix* | 1 | 1 | 1 | 1 | ? | ? |
| *Brachyteles* | 1 | 1 | 1 | 1 | ? | ? |
| *Ateles* | 1 | 1 | 1 | 1 | 2/4 | 4/7 |
| Loridae | 0 | 0 | 0 | 0 | 1 | 3 |
| Galagonidae | 0 | 0 | 0 | 0 | 1 | 3 |
| *Microcebus* | 0 | 1 | 0 | 0 | 3 | 5 |
| *Mirza* | 0 | 1 | 0 | 0 | 3 | 5 |
| *Allocebus* | 0 | ? | ? | ? | ? | ? |
| *Daubentonia* | 0 | 0 | 0 | 0 | 1 | 5 |
| *Cheirogaleus major* | 0 | 1 | 1 | 1 | 1/3 | 3/5 |
| *Cheirogaleus medius* | 0 | 0 | 0 | 0 | 3 | 3 |
| *Phaner* | 0 | ? | ? | ? | ? | ? |
| *Lepilemur* | 0 | ? | ? | ? | ? | ? |
| *Propithecus* | 1 | 0 | 0 | 0 | 1 | 3 |
| *P. v. coquereli* | 1 | 1 | 1 | 1 | 1/3 | 3/5 |
| *Avahi* | 0 | ? | ? | ? | ? | ? |
| *Varecia v. rubra* | 1 | 1 | 1 | 1 | 1/3 | 3/5 |
| *Varecia variegata* | 1 | 0 | 0 | 0 | 1 | 3 |
| *Hapalemur* | 2 | ? | ? | ? | 3 | 5 |
| *Lemur catta* | 1 | 0 | 0 | 0 | 1 | 3 |
| *Eulemur mongoz* | 2 | 0 | 0 | 0 | 1 | 3 |
| *Eulemur fulvus* | 2 | 0 | 0 | 0 | 1 | 3 |
| *Tarsius bancanus* | 0 | 0 | 0 | 0 | 1 | 3 |
| *Tarsius syrichta* | 0 | 1 | 0 | 0 | 3 | 5 |

from Martin (1990), Nowak (1991) and Fleagle (1999). Data on fossil primate taxa are from Kay & Cartmill (1977), Beard *et al.* (1991), Gingerich & Martin (1981), Martin (1990), Rasmussen & Simons (1992), Kay & Kirk (2000), and this study.

2. *L* Opsin. Several primate taxa possess opsins coding for peak wavelength spectral sensitivities that are longer in wavelength than is typically considered to be analogous to the middle wavelength or *M* opsin. For example, the peak spectral wavelength sensitivity of the *M* in *Tarsius bancanus* is 543 nm whereas that of *T. syrichta* is 558 nm, which is in the "red" range of the spectrum. However, primates, including the example of *Tarsius*, do not possess functional trichromacy without both middle and long wavelength opsins. It is possible that the strepsirrhine and tarsiid species with longer wavelength opsins have middle wavelength opsins that have simply mutated longer wavelength sensitivity, implying that an *L* opsin allele is not primitive for all primates. 0 is the possession of a monomorphic *M* opsin allele. 1 indicates that this taxon has long wavelength spectral sensitivity, regardless of whether or not it still retains middle wavelength spectral sensitivity.

3. Number of middle and long wavelength sensitive genes. Dichromatic mammals, including archontans, have a short wavelength gene (sensitive to blue spectra) and typically a middle wavelength gene (sensitive to green spectra). X-linked polymorphic trichromats, such as female platyrrhines and possibly *Varecia variegata rubra*, *Cheirogaleus major*, and *Propithecus v. coquereli*, have polymorphic middle wavelength alleles that are sensitive to slightly different peak spectral sensitivities. Heterozygous females may then have functional trichromacy because one of their middle wavelength alleles is more sensitive to longer wavelength spectra. However, these females do not have separate middle and long wavelength genes but

instead a single polymorphic middle wavelength gene. It may be possible that in taxa like *Microcebus* or *Mirza*, that possess long wavelength sensitive (i.e., red sensitive) genes but not middle wavelength sensitive genes, that the middle wavelength has mutated into a longer wavelength sensitive gene that is analogous to those in other primates. The catarrhine and *Alouatta* trichromacy system involves the possession of separate middle and long wavelength genes and is hypothesized to be a successor to X-linked polymorphic trichromacy. 0 is a single medium or long, 1 is a single polymorphic medium, 2 equals separate medium and long wavelength genes.

4. Chromacy. Dichromacy is scored as 0, X-linked polymorphic trichromacy (female platyrrhine condition) is scored as 1, and trichromacy (catarrhine and *Alouatta* condition) is scored as 2.

5. Allele wavelength sensitivity. 0=520–530 nm, 1=542–545 nm, 2=549–550 nm, 3=556–558 nm, 4=560–563 nm. The peak spectral sensitivities of primate cone photoreceptors vary among and between groups (compare the callitrichids to *Cebus* and *Saimiri*, Table 2). This variation has been argued to indicate that polymorphic trichromacy has evolved at least twice within platyrrhines (Shyue *et al.*, 1995). The genes for medium or green (*M*), polymorphic medium or green-red (*M′*), and long wavelength or red (*L*) were coded based on the distribution of measured peak spectral sensitivity. This coding makes no assumptions about gene evolution or opsin homology. It merely codes for similarities in the wavelengths that primate taxa are able to detect.

6. Allele wavelength sensitivity (alternative coding). 0=520 nm, 1=530 nm, 2=535 nm, 3=542–545 nm, 4=549–550 nm, 5=556–558 nm, 6=560 nm, 7=562–563 nm. The distribution of peak wavelength sensitivities among primates supports an alternative coding scheme. Similar to Character 5, this coding makes no assumptions about gene evolution or opsin homology. It merely codes for the wavelengths that primate taxa are able to detect.

## NOTE ADDED IN PROOF

It has recently been discovered that the allelic data in *Cheirogaleus major* are erroneous (Y. Tan, pers. comm.). *Cheirogaleus* does not possess a polymorphic gene for longer wavelength opsins, and therefore is not trichromatic. This limits the number of trichromatic strepsirrhines to two, *Varecia variegata rubra* and *Propithecus v. coquereli*. These results further support the conclusion that polymorphic trichromacy evolved independently in these diurnal strepsirrhines.