

# Evolution of eye size and shape in primates

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## Abstract

Strepsirrhine and haplorhine primates exhibit highly derived features of the visual system that distinguish them from most other mammals. Comparative data link the evolution of these visual specializations to the sequential acquisition of nocturnal visual predation in the primate stem lineage and diurnal visual predation in the anthropoid stem lineage. However, it is unclear to what extent these shifts in primate visual ecology were accompanied by changes in eye size and shape. Here we investigate the evolution of primate eye morphology using a comparative study of a large sample of mammalian eyes. Our analysis shows that primates differ from other mammals in having large eyes relative to body size and that anthropoids exhibit unusually small corneas relative to eye size and body size. The large eyes of basal primates probably evolved to improve visual acuity while maintaining high sensitivity in a nocturnal context. The reduced corneal sizes of anthropoids reflect reductions in the size of the dioptric apparatus as a means of increasing posterior nodal distance to improve visual acuity. These data support the conclusion that the origin of anthropoids was associated with a change in eye shape to improve visual acuity in the context of a diurnal predatory habitus. © 2006 Elsevier Ltd. All rights reserved.

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## Introduction

Primates are distinguished from other mammals by a suite of derived features of the visual system, including forward-facing eyes and a wide binocular visual field, relatively high visual acuity, and a proliferation of functional areas in the neocortex devoted to processing visual information (Allman, 1977, 1999; Kaas, 2002; Heesy, 2004; Ross and Kay, 2004; Martin and Ross, 2005). Although primate visual adaptations have historically been linked to an arboreal lifestyle (Elliot Smith, 1924; Le Gros Clark, 1959; Crompton, 1995), comparative data suggest that nocturnal visual predation had a major selective influence on the early evolution of the primate visual system (Cartmill, 1972; Heesy, 2003, 2004; Ravosa and

Savakova, 2004; Ross et al., 2006; Ross and Martin, 2007). In this context, convergence of the orbital and optic axes in stem primates would have improved image quality at low light levels, increased image brightness, and facilitated stereoscopic depth judgements for manual prey capture (Cartmill, 1972; Allman, 1977; Pettigrew, 1978).

Anthropoid primates (monkeys, apes, and humans) further differ from other mammals in demonstrating extreme morphological specializations for high visual acuity (Ross, 2000; Kirk and Kay, 2004). High acuity in anthropoids is the product of key derived features of the anthropoid eye and retina, including an all-cone retinal fovea, a macula lutea, and a UV-screening lens. Although retinal foveae and short-wavelength ocular filters are found in some nonanthropoid species, this complex of acuity-enhancing features is unique to anthropoid primates among all vertebrates (Kirk and Kay, 2004; Ross, 2004). Adaptive explanations for the evolution of high acuity in anthropoids emphasize the importance of a transition to diurnality in the anthropoid stem lineage (Cartmill, 1980; Ross, 1996, 2000; Kirk, 2004, 2006a,b; Kirk and Kay, 2004). Furthermore,

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comparative data and fossil evidence indicate that stem anthropoids were small-bodied and partially faunivorous, suggesting that high acuity in anthropoids originally evolved in the context of diurnal visual predation (Ross, 2000; Kirk and Simons, 2001; Heesy and Ross, 2001, 2004).

Despite the large amount of attention that has been devoted to the study of the primate visual system, relatively few studies have examined the morphology of the primate eye in a comparative context (Detwiler, 1939; Schultz, 1940; Ross, 2000; Kirk, 2004, 2006a). Evolutionary changes in the eye morphology of visually dependent vertebrates such as primates are explicable with reference to basic dioptric principles (Walls, 1942; Hughes, 1977; Motani et al., 1999; Ross, 2000; Land and Nilsson, 2002; Kirk, 2004; Kirk and Kay, 2004; Hall and Ross, 2006) (Fig. 1). Nocturnal vertebrates living in light-limited environments typically exhibit adaptations for increased retinal image brightness. Image brightness is directly related to the area of the entrance pupil of the eye and to the solid angle in space from which each receptor samples light. The angle of acceptance of a photoreceptor varies inversely with the posterior nodal distance (PND), or focal length, of the eye. In other words, eyes with shorter focal lengths generally have smaller and brighter retinal images. Hence, eyes of visually dependent nocturnal vertebrates are predicted to exhibit allometric enlargement of the pupil and cornea relative to PND. In contrast, vertebrates living in diurnal environments in which light is plentiful tend to have long focal lengths, decreasing the acceptance angle of the photoreceptors and increasing visual resolution. Moreover, because diurnal vertebrates do not need to enhance image brightness, they are predicted to have small pupils relative to focal length. This feature has the benefit of enhancing depth of focus. In both nocturnal and diurnal vertebrates, isometric enlargement of the eye improves potential visual acuity by increasing the number of photoreceptors across which the image is spread, but isometric scaling of the eye does not alter image brightness.

In the present study, we sought to determine whether primates are comparable to other mammals in terms of their eye size and shape. Because stem primates and stem anthropoids were evidently subject to selection pressures not faced by early members of most other mammalian clades, it is reasonable to expect that primate eye morphology could differ systematically from that of other mammals. To test this hypothesis, we compiled data on body size (head and body length, HBL), eye size, and corneal size for a large sample of visually dependent terrestrial mammalian species ( $n = 260$ ; see Appendix 1). We then compared eye morphology in primates with that of nonprimate mammals by examining three bivariate relationships: (1) axial eye diameter relative to body size, (2) corneal diameter relative to body size, and (3) corneal diameter relative to axial eye diameter. Regressions were used to examine the scaling relationships among these variables, and then residuals from these regression lines were used to quantify differences in relative eye size and shape. In order to assess the importance of phylogenetic effects on eye morphology in primates, scaling relationships and residuals were calculated using both ordinary data from the “tips” of the primate phylogeny, as well as independent contrasts. Several previous analyses have studied specific

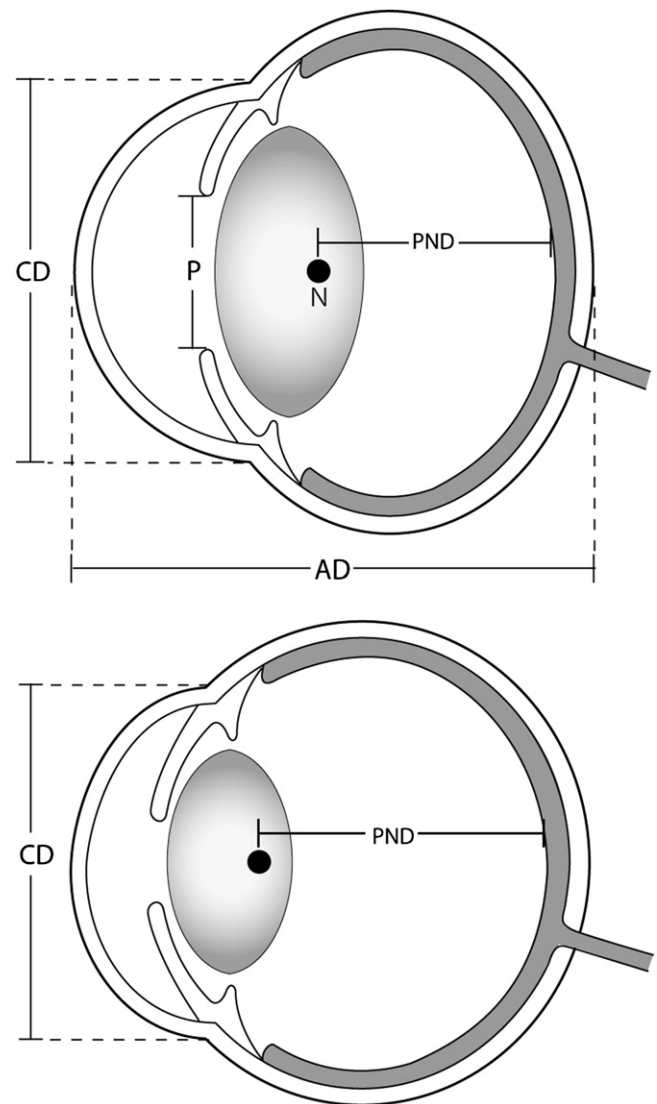


Fig. 1. Schematic diagram comparing nocturnal (above) and diurnal (below) primate eyes and illustrating the dimensions measured in this study. CD, corneal diameter, estimates maximum possible pupil diameter (P), which determines the amount of light entering the eye. CD is accordingly an important determinant of image brightness under scotopic conditions. AD, axial diameter, is an estimate of posterior nodal distance (PND), or focal length, the distance from the posterior nodal point (N) to the focal plane. PND is the principal determinant of retinal image size, which is the principal determinant of the resolving power of the eye if photoreceptor and ganglion-cell density remain constant.

features of primate eye morphology using smaller comparative samples (e.g., corneal size relative to eye size; Kirk, 2004, 2006a), but this study is the first to incorporate comparative phylogenetic methods in order to examine changes in relative eye and corneal size at primate and anthropoid origins.

## Materials and methods

### Data collection

Eye dimensions were measured in eyeballs dissected from preserved specimens in museum, university, and private

collections. The eyeballs were cleaned of connective tissue and maximally inflated with the preservative in which they were stored using a syringe and 25-gauge needle inserted on an angle into the posterior chamber of the eye. Corneal diameter (CD) was estimated as the mean of maximum and minimum diameters; axial diameter (AD) was measured as the maximum eye diameter from the front of the cornea to the back of the sclera, near the optic nerve. Head and body length (HBL), used as an estimate of overall body size, was taken from the same specimens as the eye measures or was estimated as the median of ranges published in the literature (Nowak, 1991; Rowe, 1996). Eye- and body-length data from Ritland (1982) were culled to eliminate juvenile specimens (body lengths falling outside the range of adult values in the literature) and combined with our own observations on primates and dermopterans (Ross, 2000; Kirk, 2004, 2006a). Species were assigned to one of three activity-pattern categories: diurnal, nocturnal, or cathemeral. Solely aquatic, fossorial, and echolocating species, as well as other microphthalmic species (e.g., tenrecs), were excluded from the analyses. Data are supplied in [Appendix 1](#).

#### *Eye size and corneal size relative to body size*

Comparisons of relative eye and corneal size were made using residuals from least-squares (LSR) and reduced major-axis (RMA) regression equations calculated for  $\log_{10}AD$  against  $\log_{10}HBL$  across all mammals and  $\log_{10}CD$  against  $\log_{10}HBL$  across all mammals. Residuals from this “all mammal” line were then grouped into primates and nonprimates, and these groups were further subdivided by activity pattern (i.e., diurnal, nocturnal, or cathemeral). Further subdivisions into (1) diurnal haplorhines and strepsirrhines and (2) nocturnal strepsirrhines and haplorhines were also made in order to identify the taxonomic and activity-pattern contributions to the observed effects. ANOVA or nonparametric alternatives (Mann–Whitney *U*-test for two groups; Kruskal–Wallis for more than two groups) were then used to investigate the significance of taxonomic affiliation and activity pattern on the values of these residuals. Post-hoc tests after ANOVA used the Games and Howell procedure, which does not assume homogeneity of variance, and a Bonferroni adjustment of levels of significance.

For a subset of the taxa including primates and their closest living relatives (Euarchontoglires<sup>1</sup>), a phylogenetic tree was assembled from the literature and a phylogenetically “adjusted” LSR equation was calculated using PDAP (Garland et al., 1993). This phylogenetically “adjusted” line represents the regression equation derived from independent contrasts and mapped back into the original data space (Garland and Ives, 2000). Residuals from this phylogenetically “adjusted” line were analyzed for effects of taxonomic affiliation and

activity pattern. To investigate the relative importance of taking phylogeny into account when analyzing primate eye size and shape, residuals were also derived from an ordinary LSR equation calculated using the terminal taxa only (“tips” data), and analyzed for effects of taxonomic affiliation and activity pattern. It should be noted that, in calculating and analyzing the residuals from the LSR and RMA lines, we are not attempting to “remove” or “correct for” body size (HBL). Rather, we use these residuals to investigate whether certain taxonomic groups or clades have larger or smaller measures of CD or AD at comparable head and body lengths once general trends in the data are accounted for. For comparative purposes, the LSR lines for the “tips” and contrasts for the order Primates are also presented.

#### *Corneal size relative to eye size*

To test for effects of taxonomic affiliation and activity pattern on corneal size relative to eye size, residuals from both LSR and RMA of  $\log_{10}CD$  on  $\log_{10}AD$  across all mammals were calculated and analyzed. In addition, within Euarchontoglires, residuals were calculated and analyzed from both an LSR calculated using contrasts and an LSR derived from the “tips” data. Once again, these analyses do not attempt to “remove” or “correct for” axial diameter; rather, they ask whether certain taxonomic groups or clades have larger or smaller measures of CD once general trends in AD are accounted for. For comparative purposes, the LSR lines for the “tips” and contrasts for the order Primates are also presented.

## Results

#### *Axial eye diameter (AD) relative to head and body length (HBL)*

[Table 1](#) presents LSR and RMA regression equations for the “tips” data of AD against HBL across all mammals, across Euarchontoglires, and across Primates. [Figure 2A](#) plots eye AD against HBL across all mammals, and includes the LSR and RMA lines calculated across all mammals. [Table 1](#) also includes the LSR equations for Euarchontoglires and Primates calculated from independent contrasts and mapped back into the original data space (Garland and Ives, 2000). [Figure 3A](#) plots AD against HBL within Euarchontoglires only, and includes the LSR regression line calculated using “tips” data, as well as that calculated using independent contrasts.

Axial diameter scales with negative allometry against HBL across all mammals, across Euarchontoglires, and across Primates, whether RMA or LSR of “tips” data are used, and when the LSR is calculated using independent contrasts ([Table 1](#)). The slopes of the LSR lines derived from “tips” data are steeper across euarchontoglirans (LSR = 0.609; RMA = 0.708) than across mammals as a whole (LSR = 0.551; RMA = 0.637), but shallower across Primates (LSR = 0.374; RMA = 0.434). The LSR slopes calculated across Euarchontoglires (0.419) and Primates (0.261) using independent

<sup>1</sup> Euarchontoglires is a eutherian clade that includes Euarchonta (primates + tree shrews + colugos) and Glires (rodents + lagomorphs). Within Euarchonta, tree shrews (Scandentia), and colugos (Dermoptera) together constitute the clade Sundatheria.

Table 1

Regression statistics for axial diameter (AD) and corneal diameter (CD) against head and body length (HBL) and CD vs. AD

Variables	Data set	<i>r</i>	LSR slope	Lower 95%	Upper 95%	LSR intercept	Lower 95%	Upper 95%	RMA slope	Lower 95%	Upper 95%
Tips data											
AD vs. HBL	All mammals	0.865	0.551	0.512	0.590	−0.296	−0.399	−0.195	0.637	0.598	0.676
CD vs. HBL	All mammals	0.824	0.471	0.431	0.510	−0.223	−0.327	−0.118	0.571	0.531	0.611
CD vs. AD	All mammals	0.934	0.838	0.799	0.877	0.049	0.003	0.094	0.897	0.857	0.936
CD vs. AD	Diurnal nonprimate mammals	0.977	0.844	0.771	0.918	0.054	−0.026	0.134	0.864	0.790	0.938
CD vs. AD	Nocturnal nonprimate mammals	0.988	0.935	0.897	0.973	0.009	−0.029	0.048	0.946	0.870	1.022
AD vs. HBL	Euarchontoglires	0.860	0.609	0.548	0.670	−0.403	−0.554	−0.253	0.708	0.647	0.769
CD vs. HBL	Euarchontoglires	0.710	0.387	0.322	0.451	−0.020	−0.180	0.140	0.545	0.480	0.609
CD vs. AD	Euarchontoglires	0.874	0.672	0.609	0.735	0.196	0.126	0.266	0.769	0.706	0.832
AD vs. HBL	Primates	0.809	0.351	0.298	0.405	0.304	0.165	0.443	0.434	0.380	0.487
CD vs. HBL	Primates	0.374	0.182	0.087	0.278	0.521	0.274	0.768	0.487	0.392	0.583
CD vs. HBL	Primates (diurnal)	0.808	0.457	0.376	0.539	−0.244	−0.459	0.028	0.566	0.485	0.647
CD vs. HBL	Primates (nocturnal)	0.457	0.187	−0.013	0.387	0.626	0.161	1.091	0.409	0.209	0.609
CD vs. AD	Primates	0.689	0.774	0.603	0.946	0.055	−0.154	0.263	1.123	0.9515	1.295
CD vs. AD	Primates (diurnal)	0.892	1.003	0.879	1.127	−0.261	−0.413	−0.109	1.244	1.120	1.360
CD vs. AD	Primates (nocturnal)	0.953	0.736	0.608	0.865	0.209	0.061	0.358	0.772	0.644	0.900
Independent contrasts											
AD vs. HBL	Euarchontoglires		0.419	0.351	0.487	0.067	−0.123	0.258			
CD vs. HBL	Euarchontoglires		0.358	0.283	0.433	0.114	−0.096	0.325			
CD vs. AD	Euarchontoglires		0.910	0.834	0.987	0.187	0.09	0.286			
AD vs. HBL	Primates		0.261	0.167	0.354	0.556	0.306	0.806			
CD vs. HBL	Primates		0.229	0.113	0.345	0.487	0.176	0.798			
CD vs. AD	Primates		0.876	0.716	1.037	0.002	−0.208	0.212			

Notes: LSR, least-squares regression equations calculated using SPSS, 12.0. Confidence limits provided for slope and intercept. RMA, reduced major-axis equations calculated from least-squares equations. Confidence limits about the RMA slope were estimated from LSR confidence limits. Independent-contrasts analysis performed in PDAP. Phylogenetically “adjusted” LSR equations are mapped back into the original data space (Garland and Ives, 2000). All calculations were performed using  $\log_{10}$ .

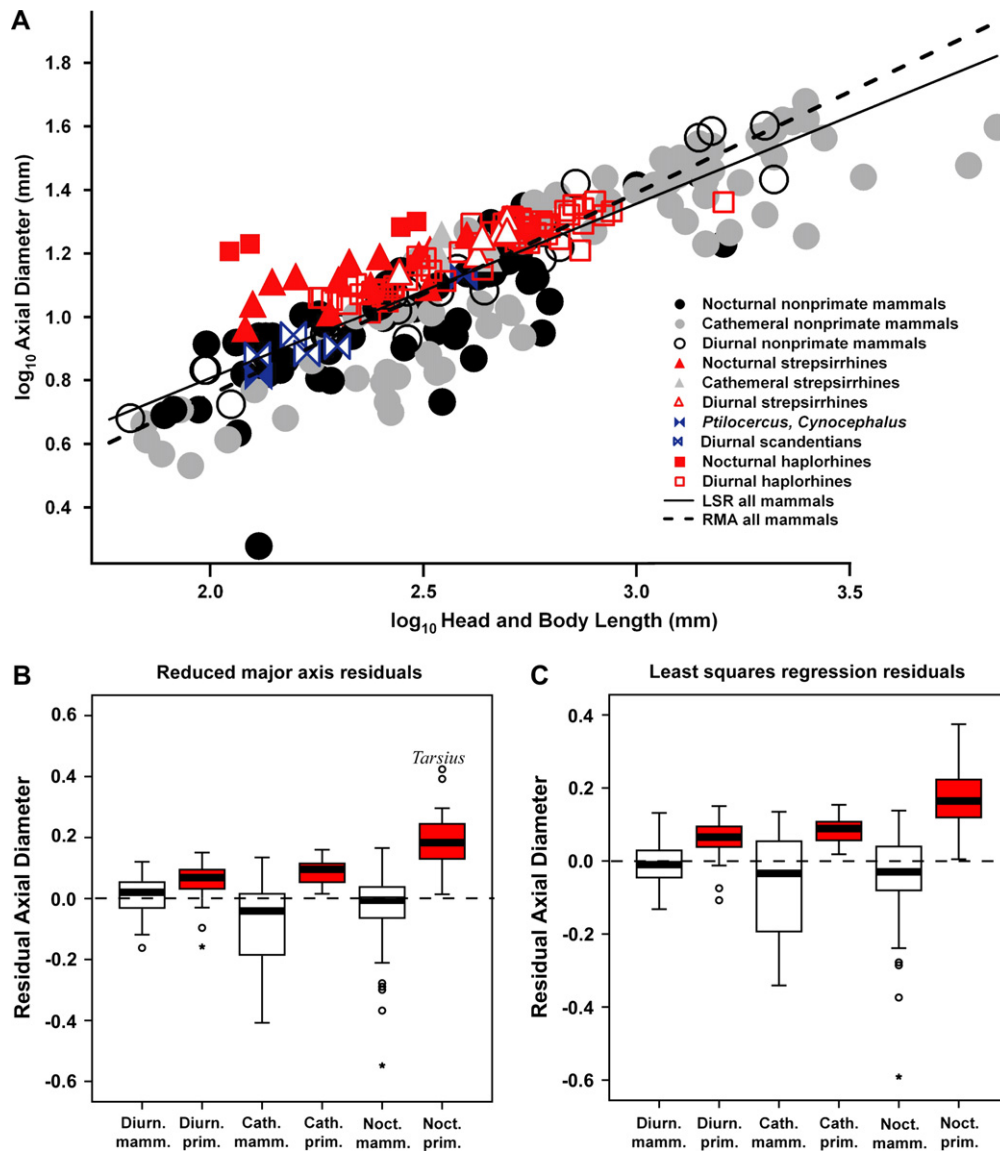


Fig. 2. (A) Bivariate plot of  $\log_{10}$ AD against  $\log_{10}$ HBL for all of the mammals measured. LSR and RMA lines calculated across all mammals are included. (B) Box plots of residuals from RMA regression line of  $\log_{10}$ AD against  $\log_{10}$ HBL calculated across all mammals. Black line, median; box, interquartile range; circles, outside values; stars, far-out values. (C) Box plots of residuals from LSR line of  $\log_{10}$ AD against  $\log_{10}$ HBL calculated across all mammals. Black line, median; box, interquartile range; circles, outside values; stars, far-out values. Abbreviations: cath., cathemeral; diurn., diurnal; haps., haplorhines; mamm., nonprimate mammals; noct., nocturnal; prim., primates; streps., strepsirrhines.

contrasts are shallower than the slopes derived from the “tips” data (Table 1; Fig. 3A).

Primate and nonprimate residuals from the RMA of  $\log_{10}$ AD against  $\log_{10}$ HBL across all primates are significantly different (Mann–Whitney  $U$ , 2557;  $Z$ ,  $-8.873$ ;  $p < 0.0001$ ), with primates having larger (more positive) residuals than nonprimates (Fig. 2B). A one-way ANOVA comparing primate with nonprimate RMA residuals within the three activity-pattern categories (diurnal, nocturnal, cathemeral) revealed significant effects ( $F = 26.299$ ;  $p < 0.001$ ). Post-hoc tests indicate that cathemeral primates have larger residual ADs than other cathemeral ( $p < 0.006$ ) or nocturnal mammals ( $p < 0.05$ ), diurnal primates have larger residual ADs than all nonprimate mammals ( $p \leq 0.01$ ), and nocturnal primates have larger residual ADs than all other groups ( $p \leq 0.001$ ), except

cathemeral primates. These results were replicated when residuals from a LSR of  $\log_{10}$ AD against  $\log_{10}$ HBL were analyzed (Fig. 2C). One-way ANOVA reveals significant differences among taxon/activity-group categories ( $F = 18.26$ ,  $p < 0.0001$ ). Post-hoc tests reveal cathemeral primates to have larger residuals than cathemeral nonprimates ( $p = 0.006$ ); diurnal primates to have larger ADs than diurnal nonprimates ( $p < 0.001$ ); and nocturnal primates to have larger ADs than nocturnal nonprimates ( $p < 0.001$ ). Thus, irrespective of the regression model used, primates tend to have larger axial diameters of the eye than other mammals of comparable body size and activity pattern (Fig. 2B, C).

Figure 3B plots the residuals from the LSR of  $\log_{10}$ AD against  $\log_{10}$ HBL across the euarchontogloran “tips” data. On average, the primate activity/taxonomic subgroups



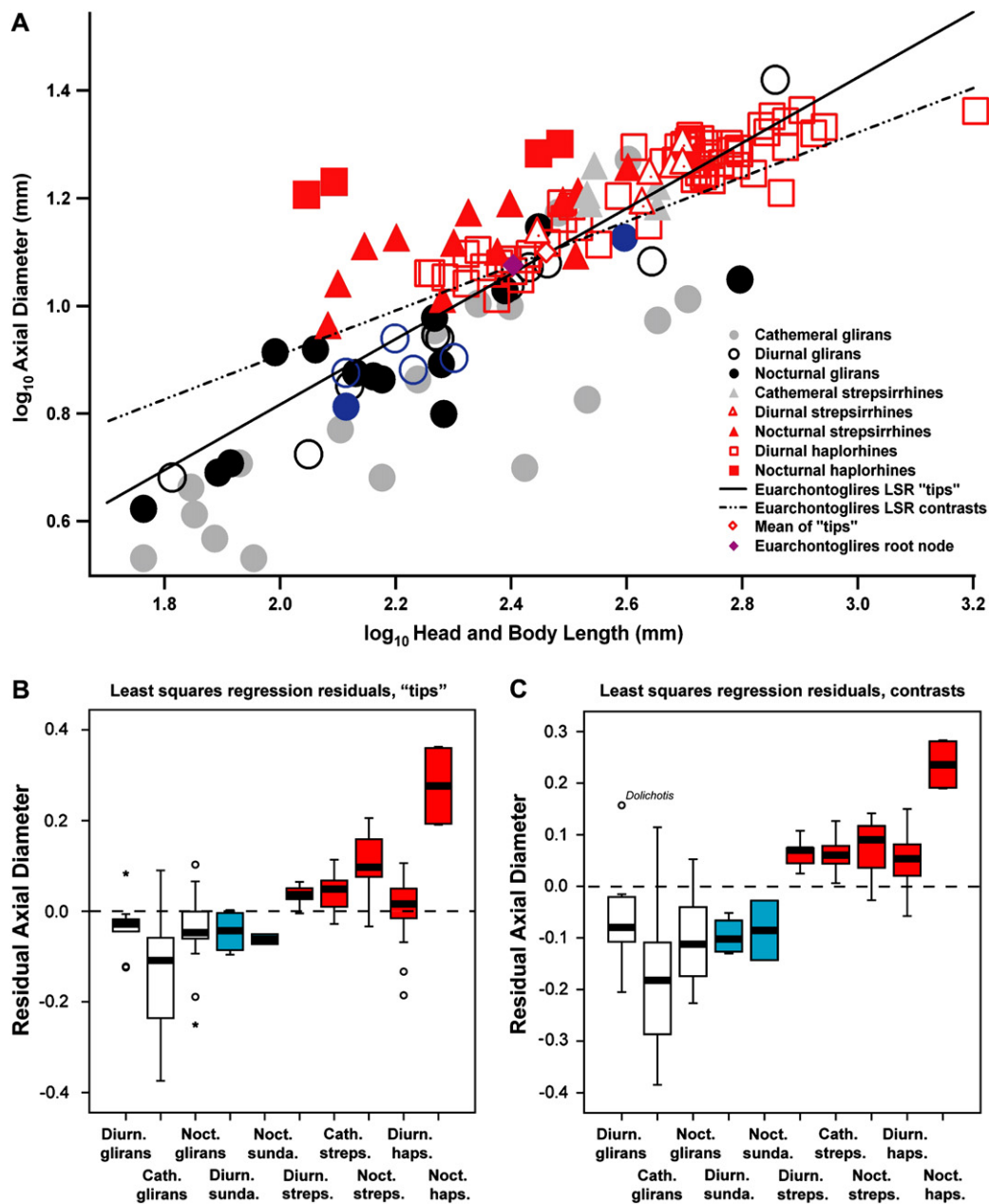


Fig. 3. (A) Bivariate plot of  $\log_{10}$ AD against  $\log_{10}$ HBL for the Euarchontoglires measured. LSR lines calculated using “tips” data and contrasts are included, as is a point representing the estimated values for the euarchontan root node. (B) Box plots of residuals from LSR regression line of  $\log_{10}$ AD against  $\log_{10}$ HBL calculated using euarchontogliran “tips” data. Black line, median; box, interquartile range; circles, outside values; stars, far-out values; nocturnal sundatherians includes *Ptilocercus* and *Cynocephalus*. (C) Box plots of residuals from LSR regression line of  $\log_{10}$ AD against  $\log_{10}$ HBL calculated using euarchontogliran independent-contrasts data. Black line, median; box, interquartile range; circles, outside values; stars, far-out values. Abbreviations: cath., cathemeral; diurn., diurnal; haps., haplorhines; noct., nocturnal; streps., strepsirrhines; sunda., sundatherians (i.e., scandentians and *Cynocephalus*).

have positive residuals and the nonprimate euarchontoglirans have negative residuals. There is a significant effect of taxonomic grouping (Primates, Glirans, Sundatheria) on mean rank of residuals (Kruskal–Wallis test, chi-square, 44.838,  $p < 0.001$ ), with primates having the highest mean rank. Post-hoc tests from a one-way ANOVA of these residuals reveal that cathemeral primates have larger residuals than cathemeral glirans ( $p = 0.008$ ), and both nocturnal strepsirrhines ( $p \leq 0.003$ ) and nocturnal haplorhines ( $p \leq 0.04$ ) have larger residual ADs than any gliran or sundatherian subgroup.

Diurnal strepsirrhines and haplorhines only have significantly larger residual ADs than cathemeral glirans ( $p = 0.001$ ,  $p = 0.002$ , respectively).

Figure 3C plots residuals from the LSR of  $\log_{10}$ AD against  $\log_{10}$ HBL across euarchontoglirans calculated using contrasts, and primates are more clearly distinguished from nonprimate euarchontoglirans than when “tips” data are used. An ANOVA of these “phylogenetically adjusted” residuals grouped by taxon reveal that primates as a whole have larger ADs than glirans or sundatherians (post hoc tests,  $p < 0.001$ ),

whereas residual ADs do not differ between glirans and sundatherians. ANOVA of “phylogenetically adjusted” residuals grouped by taxon and activity pattern were also significant ( $F = 27.764$ ,  $p < 0.001$ ). Post-hoc tests reveal most strepsirrhine activity-pattern groups to have larger residual ADs than all gliran groups ( $p \leq 0.002$ ) (Fig. 3). The only exceptions were cathemeral strepsirrhines, which do not differ significantly from cathemeral glirans. All strepsirrhine activity-pattern groups also have larger residual ADs than diurnal sundatherians ( $p \leq 0.01$ ), but they do not differ significantly from nocturnal sundatherians. However, this latter result is due to the small sample size of nocturnal sundatherians ( $n = 2$ , *Ptilocercus* and *Cynocephalus*), both of which have relatively smaller ADs than primates (Fig. 3C). The residual ADs of diurnal haplorhines (i.e., diurnal anthropoids) are larger than those of diurnal sundatherians ( $p = 0.024$ ), but they do not differ significantly from those of diurnal strepsirrhines or diurnal glirans ( $p = 0.092$ ). The lack of a difference from diurnal glirans is primarily the effect of the extraordinarily large residual AD of *Dolichotis*. When this taxon is excluded, diurnal anthropoids have larger residual ADs than all groups except strepsirrhines and nocturnal sundatherians.

#### Corneal diameter (CD) relative to head and body length (HBL)

Table 1 presents LSR and RMA regression equations for the “tips” data of CD against HBL across all mammals, across Euarchontoglires only, and across Primates. Table 1 also includes the LSR equations for Euarchontoglires and Primates calculated from independent contrasts and mapped back into the original data space (Garland and Ives, 2000). Corneal diameter scales with negative allometry against HBL across all mammals, across Euarchontoglires, and across Primates, whether RMA or LSR of “tips” data are used or whether LSR of independent-contrasts data are used (Table 1). When slopes derived from “tips” data are compared, the slopes of the lines are shallowest across Primates (LSR = 0.182; RMA = 0.487), intermediate across Euarchontoglires (LSR = 0.387; RMA = 0.545), and steepest across mammals as a whole (LSR = 0.471; RMA = 0.571). The shallow slope across Primates is partly attributable to the dramatic offset between diurnal and nocturnal primates in CD (Fig. 5). When slopes are calculated for diurnal and nocturnal primates separately, the diurnal primate slope is more similar to that for other mammals (0.457), whereas that for nocturnal primates is still very shallow (0.187). The LSR slopes calculated across Euarchontoglires (0.358) and Primates (0.229) using independent contrasts are similar to those calculated using “tips” data, and they lie within their 95% confidence limits.

Figure 4B plots the residuals from the RMA of  $\log_{10}CD$  against  $\log_{10}HBL$  calculated across all mammals. Comparisons of primate and nonprimate residuals were not significantly different at  $p < 0.05$ , but this result obscures effects of activity pattern across taxonomic groups. Post-hoc tests from a one-way ANOVA comparing primate and nonprimate CD residuals within the three activity-pattern categories

( $F = 21.798$ ,  $p < 0.001$ ) reveal that nocturnal primates have relatively larger residual CDs than any other subgroup ( $p < 0.0001$ ) except cathemeral primates ( $p = 0.055$ ), and cathemeral primates have relatively larger corneas than cathemeral nonprimate mammals ( $p = 0.002$ ) and diurnal primates ( $p = 0.004$ ). Diurnal strepsirrhines do not differ significantly from diurnal nonprimate mammals, whereas diurnal haplorhines have significantly smaller residual CDs than all other groups ( $p \leq 0.004$ ) except cathemeral mammals (Fig. 4A). Figure 4C plots the residuals from the LSR of  $\log_{10}CD$  against  $\log_{10}HBL$  calculated across all mammals. These results are essentially identical to those obtained from analysis of residuals from the RMA line. When compared with other mammals, and controlling for activity pattern, nocturnal and cathemeral primates have significantly larger residual CDs than nocturnal and cathemeral nonprimate mammals.

Figure 5A plots  $\log_{10}CD$  against  $\log_{10}HBL$  within euarchontoglires only. The LSR lines calculated with “tips” data and independent contrasts are included, and the estimated root node values for Euarchontoglires are also shown. Figure 5B plots the residuals from the LSR line calculated from the “tips” data. All primate groups except diurnal haplorhines have, on average, larger residual CDs than nonprimate euarchontoglires ( $p$ -values ranging from 0.025 to  $< 0.001$ ). Cathemeral, diurnal, and nocturnal strepsirrhines all have significantly larger residual CDs than cathemeral or diurnal glirans ( $p \leq 0.042$ ), and nocturnal strepsirrhines also have significantly larger residual CDs than nocturnal glirans ( $p = 0.002$ ) and diurnal sundatherians ( $p = 0.014$ ). In contrast, diurnal haplorhines have significantly smaller residual CDs than other primates (nocturnal haplorhines,  $p = 0.043$ ; other primate groups,  $p \leq 0.003$ ), but they do not differ significantly from the nonprimate groups.

Figure 5C plots residuals from the phylogenetically “adjusted” euarchontoglian LSR line (i.e., the line calculated using independent contrasts). The relative ranks of the residual CDs are similar to those in Fig. 5B. However, the upward shift of the line—away from the means for CD and HBL to pass through the estimated root node values—positions all of the scandentians and most of the glirans below the line. A one-way ANOVA comparing residual CD of primates as a whole with glirans and sundatherians is significant ( $F = 3.759$ ,  $p = 0.026$ ), and post-hoc tests reveal that, on average, primates have larger residual CDs than glirans ( $p = 0.021$ ) but not sundatherians. However, when a one-way ANOVA of residual CD across taxon and activity-pattern categories is performed ( $F = 18.344$ ,  $p < 0.001$ ), post-hoc tests reveal consistent differences in CD residuals for cathemeral and nocturnal primates: (1) cathemeral strepsirrhines have larger CD residuals than all glirans ( $p \leq 0.02$ ) and diurnal sundatherians ( $p = 0.031$ ); (2) nocturnal and diurnal strepsirrhines have larger CD residuals than all glirans ( $p \leq 0.04$ ); and (3) nocturnal haplorhines have larger CD residuals than glirans ( $p \leq 0.02$ ), diurnal sundatherians ( $p = 0.038$ ), and diurnal haplorhines ( $p = 0.037$ ) (Fig. 3B). However, diurnal haplorhines do not differ from nonprimate mammals in residual CDs, although they do have smaller CD residuals than all

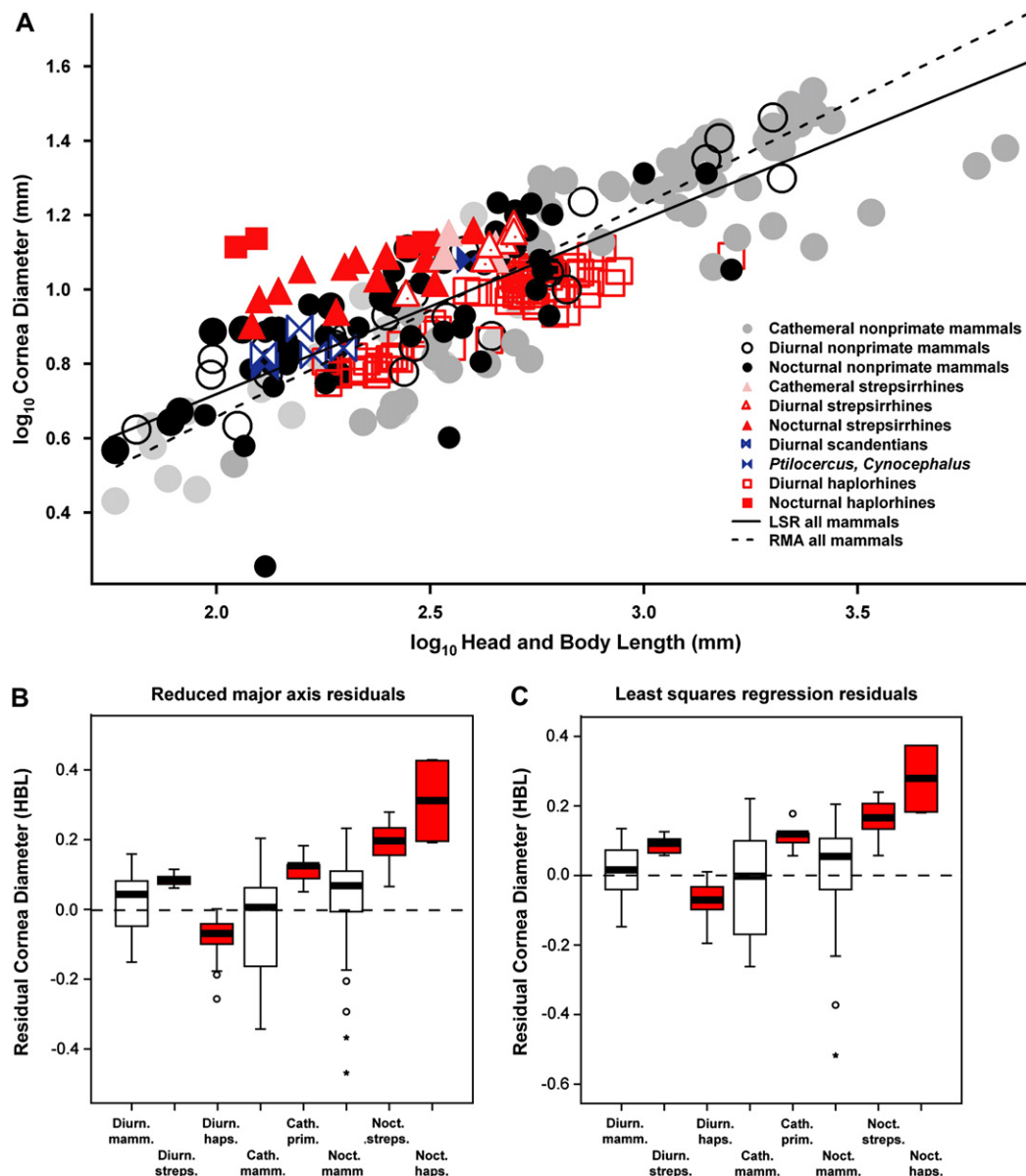


Fig. 4. (A) Bivariate plot of  $\log_{10}$ CD against  $\log_{10}$ HBL for all of the mammals measured. LSR and RMA lines calculated across all mammals are included. (B) Box plots of residuals from RMA regression line of  $\log_{10}$ CD against  $\log_{10}$ HBL calculated across all mammals. Black line, median; box, interquartile range; circles, outside values; stars, far-out values. (C) Box plots of residuals from LSR line of  $\log_{10}$ CD against  $\log_{10}$ HBL calculated across all mammals. Black line, median; box, interquartile range; circles, outside values; stars, far-out values. Abbreviations: cath., cathemeral; diurn., diurnal; haps., haplorhines; mamm., nonprimate mammals; noct., nocturnal; prim., primates; streps., strepsirrhines.

other primates (nocturnal haplorhines,  $p = 0.039$ ; all other primate groups,  $p \leq 0.002$ ). Thus, analyses controlling for phylogenetic relatedness, whether by examining only euarchontoglires using “tips” data or by using independent contrasts, yield results similar to those obtained across all mammals: nocturnal and cathemeral primates have larger corneas than their close relatives of comparable body size.

#### Corneal diameter (CD) relative to axial eye diameter (AD)

Table 1 presents LSR and RMA regression equations for the “tips” data of CD against AD across all mammals, across

Euarchontoglires, and across Primates. Table 1 also includes the LSR equation calculated from the independent contrasts and mapped back into the original data space (Garland and Ives, 2000). Corneal diameter scales with negative allometry against AD across all mammals and across euarchontoglires, whether RMA or LSR of “tips” data are used and whether LSR of independent-contrasts data is applied (Table 1). Across Primates, CD scales with negative allometry against AD when “tips” data are used, but the upper 95% confidence limit of the independent-contrasts slope includes 1.00 (LSR = 0.876, upper 95% confidence limit = 1.037). When slopes derived from “tips” data are compared across taxa, the slopes are shallower across euarchontoglires (LSR = 0.672; RMA = 0.769)



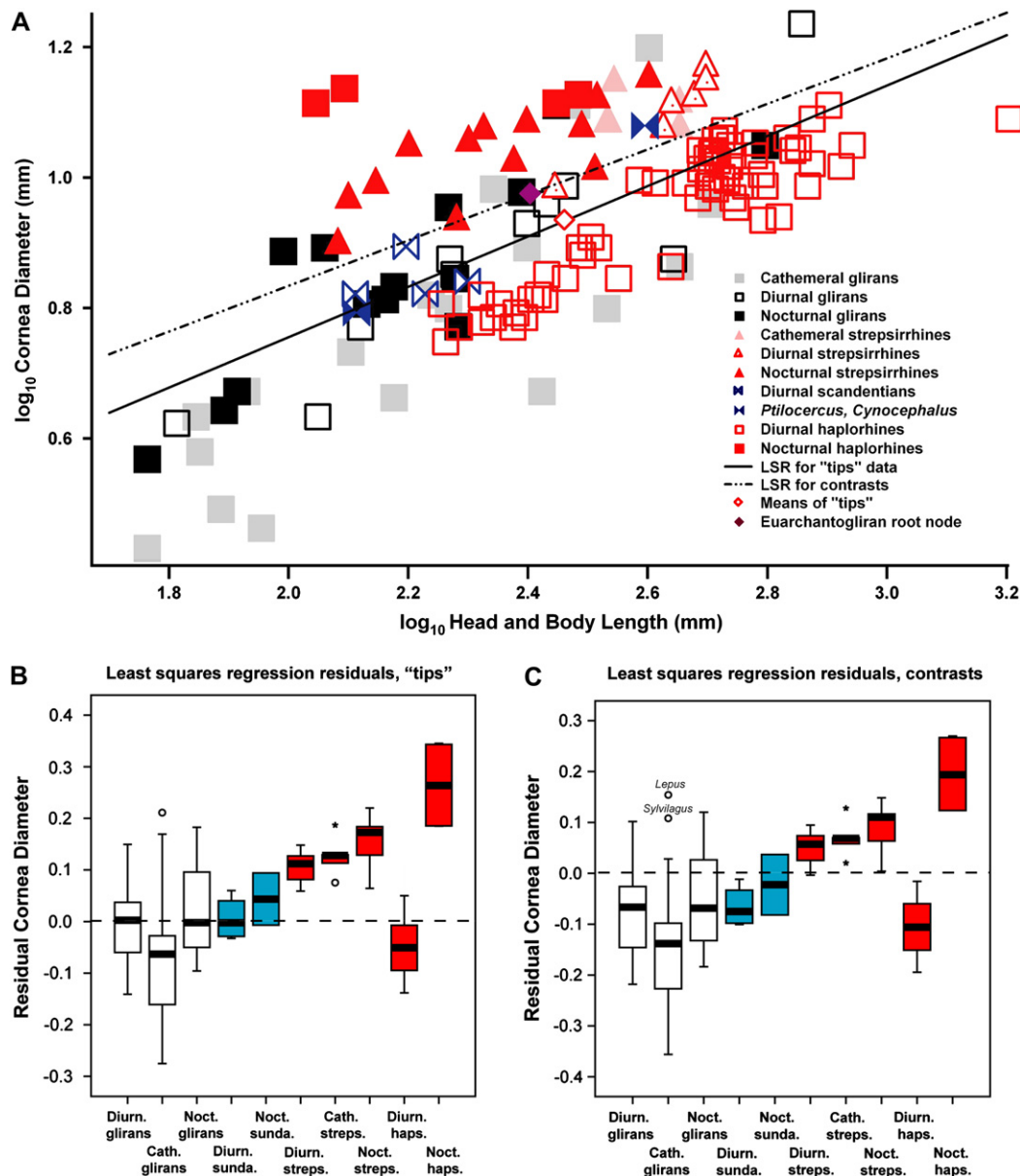


Fig. 5. (A) Bivariate plot of  $\log_{10}$ CD against  $\log_{10}$ HBL for the Euarchontoglires measured. LSR lines calculated using “tips” data and contrasts are included, as is a point representing the estimated values for the euarchontan root node. (B) Box plots of residuals from LSR regression line of  $\log_{10}$ CD against  $\log_{10}$ HBL calculated using euarchontogiliran “tips” data. Black line, median; box, interquartile range; circles, outside values; stars, far-out values; nocturnal sundatherians includes *Ptilocercus* and *Cynocephalus*. (C) Box plots of residuals from LSR regression line of  $\log_{10}$ CD against  $\log_{10}$ HBL calculated using euarchontogiliran independent-contrasts data. Black line, median; box, interquartile range; circles, outside values; stars, far-out values. Abbreviations: cath., cathemeral; diurn., diurnal; haps., haplorhines; noct., nocturnal; streps., strepsirrhines; sunda., sundatherians (i.e., scandentians and *Cynocephalus*).

than across mammals as a whole (LSR = 0.838; RMA = 0.897), but the LSR slope calculated across euarchontoglires using independent contrasts (0.910) is steeper than the slopes for the “tips” data. Across primates, the low correlation coefficient means that, although the LSR slope is intermediate between the mammal and euarchontogiliran slopes (0.774), the RMA slope is steepest (1.123) and the 95% confidence limits of the RMA line include isometry.

Figure 6A plots  $\log_{10}$ CD against  $\log_{10}$ AD across all mammals, and includes both LSR and RMA lines. Figure 6B plots the residuals from the RMA line across all mammals. A

Mann–Whitney *U*-test revealed significant differences between primate and nonprimate residuals ( $U$ , 2075;  $Z$ , -9.708;  $p < 0.0001$ ), with primates having smaller CDs relative to AD than other groups. However, this result is almost entirely attributable to the effect of diurnal haplorhines. A one-way ANOVA comparing primates with nonprimate mammals across the three activity-pattern categories (diurnal, nocturnal, cathemeral) was significant ( $F = 143.280$ ,  $p < 0.001$ ). Post-hoc tests reveal that diurnal haplorhines have significantly lower residuals (i.e., smaller corneas relative to eye size) than any other group ( $p < 0.0001$ ). Furthermore, nocturnal

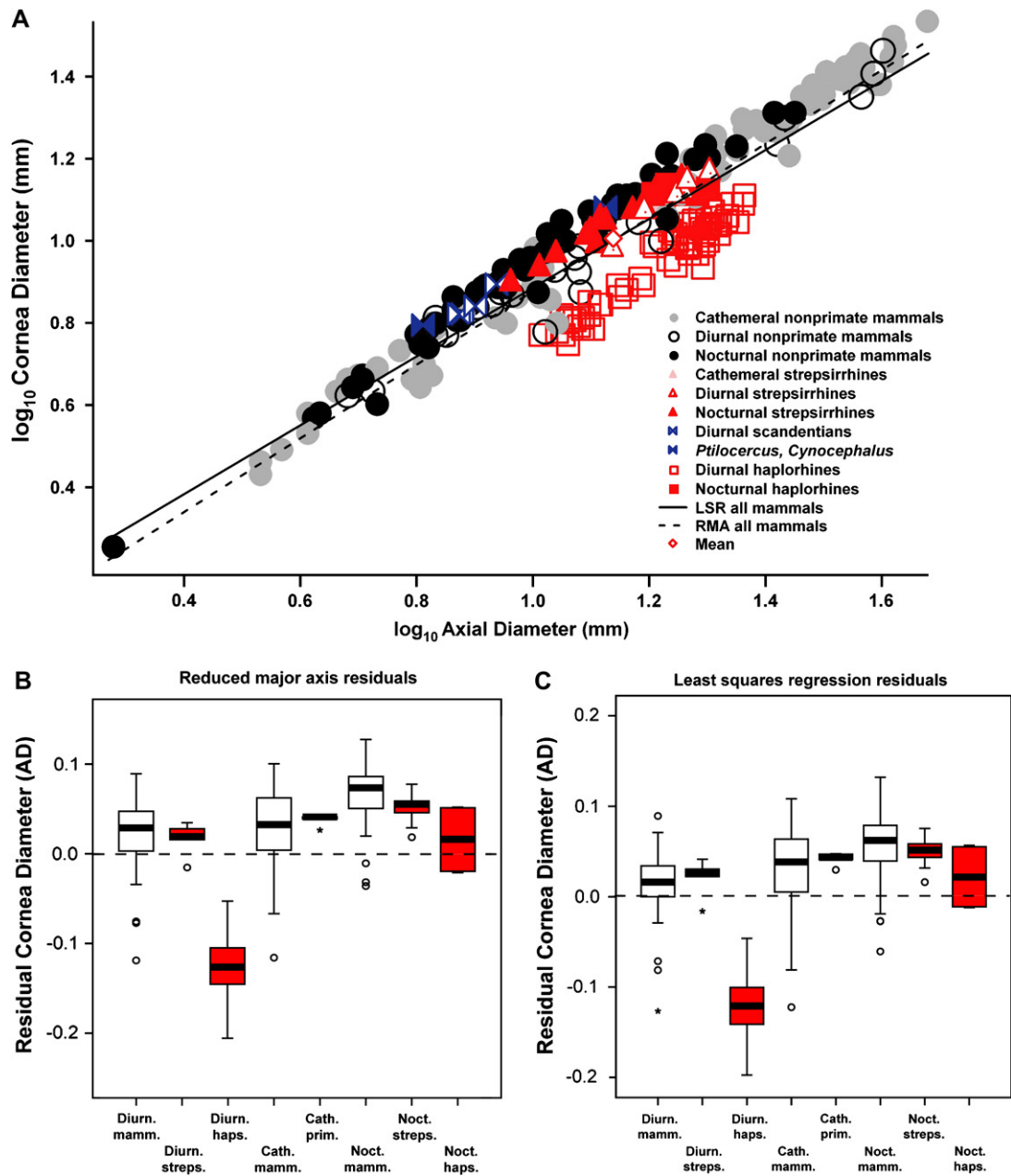


Fig. 6. (A) Bivariate plot of  $\log_{10}$ CD against  $\log_{10}$ AD for all of the mammals measured. LSR and RMA lines calculated across all mammals are included. (B) Box plot of residuals from RMA regression line of  $\log_{10}$ CD against  $\log_{10}$ AD. Black line, median; box, interquartile range; circles, outside values; stars, far-out values. (C) Box plots of residuals from LSR regression line of  $\log_{10}$ CD against  $\log_{10}$ AD. Black line, median; box, interquartile range; circles, outside values; stars, far-out values. Abbreviations: cath., cathemeral; diurn., diurnal; haps., haplorhines; mamm., nonprimate mammals; noct., nocturnal; prim., primates; streps., strepsirrhines.

mammals have significantly larger residuals than all groups ( $p \leq 0.002$ ) except nocturnal primates ( $p = 0.056$ ). Figure 6C plots residuals from the LSR line of  $\log_{10}$ CD on  $\log_{10}$ AD across all mammals. These results are almost identical to those obtained using an RMA equation. These analyses suggest that, with the exception of diurnal haplorhines, there are only subtle differences in CD dimensions relative to AD between primates and other mammals of comparable activity pattern.

Figure 7A plots  $\log_{10}$ CD against  $\log_{10}$ AD for euarchontoglirans only. The LSR lines calculated with “tips” and

contrasts data are included, along with the estimated root-node value for the Euarchontoglires clade. Figure 7B plots residuals from the LSR line calculated from “tips” data. Cathemeral ( $p \leq 0.009$ ) and nocturnal strepsirrhines ( $p \leq 0.02$ ) have larger residual CDs than diurnal and cathemeral glirans and diurnal sundatherians ( $p = 0.02$ ,  $p = 0.03$ , respectively). Diurnal haplorhines have significantly smaller residual CDs than all other groups except nocturnal sundatherians ( $p$ -values range from 0.012 to 0.000). As noted above, the latter result is attributable to small sample size of the nocturnal sundatherian group ( $n = 2$ ).

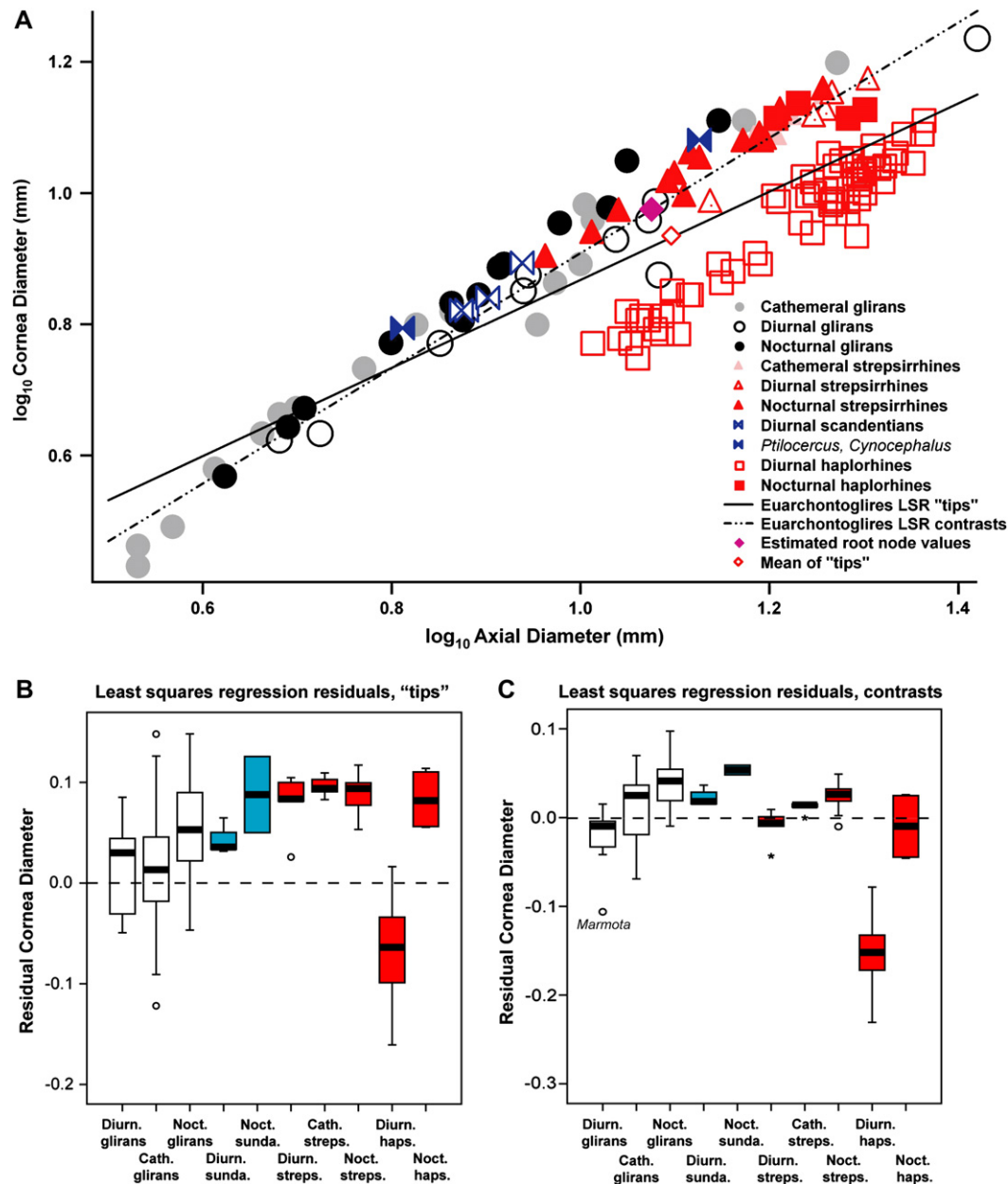


Fig. 7. (A) Bivariate plot of  $\log_{10}$ CD against  $\log_{10}$ AD for the Euarchontoglires measured. LSR lines calculated using “tips” data and contrasts are included, as is a point representing the estimated values for the euarchontan root node. (B) Box plots of residuals from LSR regression line of  $\log_{10}$ CD against  $\log_{10}$ AD calculated using euarchontoglian “tips” data. Black line, median; box, interquartile range; circles, outside values; stars, far-out values; nocturnal sundatherians includes *Ptilocercus* and *Cynocephalus*. (C) Box plots of residuals from LSR regression line of  $\log_{10}$ CD against  $\log_{10}$ AD calculated using euarchontoglian independent-contrasts data. Black line, median; box, interquartile range; circles, outside values; stars, far-out values. Abbreviations: cath., cathemeral; diurn., diurnal; haps., haplorhines; noct., nocturnal; streps., strepsirrhines; sunda., sundatherians (i.e., scandentians and *Cynocephalus*).

Figure 7C plots residuals from the “phylogenetically adjusted” LSR line of  $\log_{10}$ CD on  $\log_{10}$ AD across euarchontoglian. Analyses of these “phylogenetically adjusted” residuals yield results comparable to those obtained using unadjusted residuals. A one-way ANOVA of the effect of taxon (primates, glirans, sundatherians) is significant ( $F = 54.73$ ,  $p < 0.001$ ). Post-hoc tests reveal primates as a group to have smaller residuals than sundatherians or glirans ( $p < 0.001$ ), but nonprimate taxa do not differ from each other. ANOVA of activity-pattern and taxon categories is also significant ( $F = 134.151$ ,  $p < 0.001$ ). Post-

hoc tests reveal diurnal haplorhines to have smaller CDs relative to ADs than any other groups ( $p < 0.001$ ; nocturnal haplorhines,  $p = 0.045$ ) and diurnal strepsirrhines to have smaller CDs relative to ADs than nocturnal glirans ( $p = 0.001$ ), diurnal sundatherians ( $p = 0.017$ ), or nocturnal sundatherians ( $p = 0.002$ ). No other comparisons yield significant differences. As with the analyses of residuals from the “all mammal” lines, the most significant and pervasive pattern is one in which diurnal haplorhines have smaller corneas relative to axial eye diameter than other primates or nonprimates.

## Discussion

### Eye scaling

The data presented here demonstrate that eye size scales with negative allometry against body size across all mammals (Figs. 2–3). This result corroborates the findings of previous analyses of eye-size scaling in mammals and birds (Ritland, 1982; Brooke et al., 1999; Kiltie, 2000; Hall, 2005; Ross et al., 2006; Hall and Ross, 2006). The present analysis also demonstrates that cornea size scales with even greater negative allometry relative to head–body length (Figs. 4–5) than does eye size. Regardless of which taxonomic group is examined, the slopes of regressions of CD on HBL are almost always lower than the slopes of comparable regressions of AD on HBL (Table 1).

Regressions of CD on AD demonstrate that cornea size also scales with negative allometry against eye size across all mammals. Regression slopes of CD on AD are generally steeper than those for either CD or AD on HBL. Within Euarchontoglires, negative allometry of CD relative to AD is observed when “tips” data are used (LSR slope = 0.672; RMA slope = 0.769), an effect that is diminished by use of independent contrasts (LSR slope = 0.910). Across Primates as a whole, the LSR slope and 95% confidence limits calculated using “tips” data suggest negative allometry of CD relative to AD, but the RMA confidence limits include isometry. Similarly, the LSR calculated using contrasts for primates also suggest isometry. When analyses are performed within activity-pattern categories, CD scales with negative allometry relative to AD across nocturnal primates (LSR slope = 0.736; RMA slope = 0.772) but with isometry or slight positive allometry across diurnal primates (LSR slope =  $1.003 \pm 0.124$  95% CI; RMA slope =  $1.244 \pm \text{ca. } 0.124$  95% CI). These results are consistent with those of Ross et al. (2006), who reported negative allometry of CD relative to AD across nocturnal primates (using “tips” data; RMA slope = 0.765) but near isometry for diurnal primates (RMA slope = 0.963).

The tendency for mammals as a whole to show negative allometry of CD relative to AD may partly reflect the fact that diurnal and cathemeral mammals tend to be larger than nocturnal mammals (Eisenberg, 1981). The largest absolute eye sizes among mammals are found in diurnal and cathemeral mammals, whereas nocturnal mammals tend to have smaller eyes, consistent with their smaller body sizes (Kirk, 2006a). In terms of  $\log_{10}\text{AD}$ , nocturnal animals range from 0.28 to 1.45 (mean, 1.031), diurnal mammals range from 0.68 to 1.60 (mean 1.178), and cathemeral mammals range from 0.53 to 1.68 (mean 1.20). Diurnal and cathemeral mammals also have smaller corneas relative to eye length than nocturnal mammals. As a result, a regression of CD on AD is expected to be negatively allometric since the ratio of cornea size to eye size will be lower in species with the largest absolute eye sizes (i.e., diurnal and cathemeral taxa) and greater in species with the smallest absolute eye sizes (i.e., nocturnal taxa).

These considerations suggest that the scaling relationship between cornea size and eye size should be considered within activity-pattern subgroups. The LSR and RMA equations for diurnal and nocturnal nonprimate mammals are provided in Table 1 for comparison with the primate equations. Among diurnal nonprimate mammals, CD scales with negative allometry relative to AD whether LSR or RMA equations are considered. In this context, the isometry of eye shape across different body sizes of diurnal primates is of interest. This isometric relationship indicates that diurnal primates maintain a geometrically constant eye shape across a range of eye and body sizes. (This isometry of eye shape is seen in both diurnal strepsirrhines and diurnal haplorhines.) Nocturnal nonprimates resemble diurnal nonprimates in having cornea sizes that scale with negative allometry relative to eye size (LSR slope = 0.935; RMA slope = 0.946; 95% confidence interval estimated for the RMA line includes isometry). However, unlike diurnal primates, CD scales with strong negative allometry relative to AD in nocturnal primates. This strong negative allometry of CD relative to AD in nocturnal primates is only partly explained by the unusual eye shapes of *Aotus*, the largest-eyed nocturnal primate genus in the sample. When *Aotus* is excluded from the sample, nocturnal primates still show negative allometry of CD relative to AD (LSR slope = 0.864).

### Functional equivalence

The analyses of residuals presented here reveal some clear differences between primate and nonprimate mammals in relative eye size and shape. Before functional interpretations of these differences are presented, it is necessary to make explicit our underlying assumptions regarding the functional equivalence represented by the regression lines from which the residuals were calculated. The LSR, RMA, or “phylogenetically adjusted” regression lines from which the residuals were calculated are empirically derived lines summarizing the overall trends in the data. Although it is clear that eye size scales with negative allometry against body size across mammals, as across other vertebrate groups (see above), there is no body of theory that precisely explains how this negatively allometric relationship maintains or does not maintain “functional equivalence” across body sizes. For example, increases in absolute eye size allow increases in photoreceptor number and increases in PND, both of which can augment acuity, but there are no data to suggest that visual acuity increases with body size in mammals. Many other variables contribute to the determination of visual acuity, so lines of functional equivalence for eye size and shape have not yet been derived. In the absence of such theory, we opt to proceed using empirically derived lines, to assume that these scaling patterns represent some degree of “functional equivalence” across mammalian body sizes, and to further assume that common positive or negative deviations (residuals) from these lines at different body sizes represent common functional differences.



### Evolution of eye size and shape

Primates tend to have larger eye axial diameters than nonprimate mammals of equivalent body size, whether compared en masse or within activity-pattern subgroups (i.e., diurnal, nocturnal, cathemeral) (Fig. 2). This difference persists when phylogenetic relationships within Euarchontoglires are considered in the calculation of the regression line (Fig. 3). In addition to having larger axial diameters, cathemeral and nocturnal primates also exhibit larger corneas than nonprimate mammals of similar body size (Fig. 4). Diurnal primates, in contrast, have cornea sizes that either do not differ from those of nonprimate mammals of the same body size (e.g., as with diurnal strepsirrhines) or are smaller. Notably, diurnal haplorhine primates have smaller corneal diameters than other similarly sized primates (Figs. 4 and 5).

The uniqueness of diurnal haplorhine eye shape is confirmed by comparison of residuals derived from an RMA regression of CD against AD (Figs. 6 and 7). Across a broad range of eye sizes ( $\sim 9$ – $20$  mm AD), strepsirrhines and nocturnal haplorhines have corneal sizes that are comparable to those of nonprimate mammals. Diurnal haplorhines, in contrast, have uniformly very low CD residuals (Figs. 6 and 7), indicating that corneal size is very small relative to eye size. In this respect, diurnal haplorhines are nearly unique among mammals. Indeed, the only nonprimate taxa with comparably low CD residuals are marmots (*Marmota*) and two mongooses (*Suricata* and *Cynictis*).

These results have several important implications for adaptive hypotheses of primate evolution. The first primates are generally accepted to have been nocturnal (Charles-Dominique and Martin, 1970; Martin, 1979; Martin and Ross, 2005; Ross et al., 2006; Ross and Martin, 2007), although some authors have recently argued that ancestral primates were instead diurnal or cathemeral (Tan and Li, 1999; Ni et al., 2004; Tan et al., 2005). The data presented here suggest that basal primates had larger eyes than nonprimate mammals of similar body size, but comparable corneal sizes relative to eye size. These data favor the conclusion that the origin of crown primates involved an increase in eye size without a major shift in eye morphology. Comparisons of relative eye size within primates have recently demonstrated that nocturnal herbivores and diurnal species are generally comparable in relative eye size. By contrast, nocturnal and faunivorous primates have larger eyes than most other primate species, suggesting that nocturnal visual predation favors increased eye size (Kirk, 2006b). If this conclusion is correct, then the occupation of a nocturnal and predatory niche by the crown-primate common ancestor could explain the initial evolution of increased relative eye size in primates. In contrast, if the last common ancestor of crown primates was diurnal (Tan and Li, 1999; Ni et al., 2004; Tan et al., 2005) or a nocturnal frugivore (Sussman, 1991), then there is no expectation that ancestral primates would have undergone selection for increased eye size relative to that seen in nonprimate euarchontans.

Some evidence for the generality of an association between nocturnal visual predation and increased relative eye size is provided by an examination of the data presented here for carnivorans (Appendix 1). Although members of the Carnivora exhibit a diverse array of lifestyles, the visual ecology and anatomy of felids has been suggested to provide comparative evidence in favor of the nocturnal visual predation hypothesis of primate origins (Cartmill, 1972, 1992). Specifically, most felids are highly faunivorous, hunt by sight under nocturnal conditions, and use their forelimbs to capture or entrap prey (Nowak, 1991). Felids also have forward-facing eyes and wide binocular fields similar to those of primates (Heesy, 2003, 2004). Comparison of the residuals for carnivorans from the all-mammal LSR regressions of  $\log_{10}AD$  on  $\log_{10}HBL$ , or  $\log_{10}CD$  on  $\log_{10}HBL$ , further demonstrates that felids have significantly larger residuals than nonfelid carnivorans (Wilcoxon rank-sum;  $Z$  ranges from 2.922 to 4.339;  $p$ -values range from  $< 0.001$  to 0.003). These results indicate that felids resemble primates not only in their degree of optic convergence, but also in having relatively large eyes. Indeed, in terms of eye size relative to body size, felids are more comparable to primates than they are to most other carnivorans. These observations strengthen the case for an association between relatively large eyes and nocturnal visual predation. However, it is important to note that nocturnal visual predation is unlikely to be the only factor favoring increased eye size in mammals, as indicated by the existence of relatively large eyes in some herbivorous species (e.g., various bovids, camelids, and leporids) that rely partly on keen sight to spot predators at a distance.

If we are correct in our conclusion that early primates were nocturnal, the functional implications of the changes in relative eye size documented here are fairly straightforward. An increase in eye size within the nocturnal primate stem lineage without a substantial change in cornea size relative to axial length would have improved visual acuity by increasing the total number of photoreceptors per degree of visual angle (Land and Nilsson, 2002). By the same token, these changes alone would not have diminished the high visual sensitivity required in a nocturnal setting. Image quality in early primates would also have been improved by the increased convergence of orbital and optical axes characteristic of the order (Cartmill, 1972; Allman, 1977; Pettigrew, 1978; Heesy, 2003, 2004; Heesy and Ross, 2004; Ravosa and Savakova, 2004). These changes in the peripheral visual system were associated with a reorganization of the visual areas of the brain. Changes to the cerebral cortex included an expansion and multiplication of (1) extrastriate visual areas, which process information on fine-grained stereopsis, acuity, color, and movement (Allman and McGuinness, 1988; Allman, 1999; Kaas, 2002; Ross and Martin, 2007), and (2) cortical premotor areas associated with the refinement of visually guided hand movements (Preuss, 1993; Allman, 1999; Dum and Strick, 2002). Changes to the visual system were accompanied by improved ability to localize sounds or movements in space, increased manual dexterity, and changes to the somatosensory and somatic motor systems that provided for

improved control of visually guided reaching and grasping movements (for a review, see Ross and Martin, 2007). Together, these features support the hypothesis that the origin of euprimates was associated with improved ability to feed in terminal branches (Cartmill, 1972; Ross and Martin, 2007).

In contrast with the primate stem lineage, the lineage leading to extant anthropoids saw a significant decrease in cornea diameter relative to eye axial length without a major change in relative eye size. This analysis provides support for the conclusion that diurnal anthropoids are highly derived among mammals in having very small corneas relative to eye length. We have suggested elsewhere that this change in anthropoid eye shape was part of a suite of changes related to increased visual acuity in the haplorhine or anthropoid stem lineage (Ross, 2000; Kirk, 2004, 2006a,b). One possibility is that the unusual eye shape of anthropoids reflects increased axial diameter of the eye, enhancing image size and, possibly, visual acuity (Ross and Kay, 2004; Ross et al., 2006). However, this hypothesis is not tenable in the context of the results presented here, in which the relative AD of diurnal haplorhines is not significantly different from that in other primates (Fig. 3). Given this result, it is relevant to ask what advantage might accrue to a lineage in which CD is decreased. One possibility, which we favor, is that the decrease in relative corneal size documented here reflects a decrease in the overall size of the lens and anterior chamber, effectively moving the dioptric apparatus of the eye further from the retina (Kirk, 2004, 2006a). Anterior displacement of the dioptric apparatus would increase PND and focal length, resulting in a larger retinal image and improved visual acuity without increasing the (already large) AD of the eye (Fig. 1). The fact that diurnal mammals have a greater PND than nocturnal mammals has been demonstrated by Hughes (1977) and Pettigrew et al. (1988), and reduction in the size of the anterior chamber is one way to achieve this result. A reduction in corneal size in stem anthropoids must have occurred in a diurnal setting because increases in focal length and decreases in corneal diameter reduce the brightness of the retinal image and decrease visual sensitivity. Such changes would have been disadvantageous under nocturnal conditions.

The unusual eye morphology of living anthropoids documented here is consistent with hypotheses that the origin of anthropoids was associated with a shift from nocturnal to diurnal visual predation (Ross, 1996, 2000; Kirk and Kay, 2004; Kirk, 2004, 2006a,b). Some nonanthropoid mammals do resemble anthropoids in having small cornea diameters relative to eye diameter (Fig. 6). These taxa include three species of small, diurnal mammals (*Marmota*, *Cynictis*, *Suricata*). The latter two genera resemble hypothesized basal anthropoids in being visual predators that consume insects and small vertebrates (Ross, 1996, 2000). They also live in complex social systems, another context in which visual acuity has been hypothesized to be important (Allman, 1977; Barton, 1998). However, all three nonanthropoid species also live in open country, and their enhanced visual

acuity might function to increase the distance over which they can detect predators.

### *Eye and orbit size*

The results presented here also help to explain the differences in relative orbital-aperture size that characterize nocturnal and diurnal primates (Walker, 1967; Kay and Cartmill, 1977). Kirk (2006b) showed that the relatively large orbital apertures of nocturnal primates do not always reflect the presence of relatively large eyes. Although most nocturnal primates have relatively larger orbital apertures than diurnal primates, as noted above, many nocturnal and diurnal primates differ little in terms of relative eye size. This discrepancy probably reflects the fact it is the cornea (rather than the sclera) that protrudes through the orbital aperture, making it likely that orbital aperture size is constrained by cornea size. As a result, the relatively small orbital apertures of diurnal anthropoid primates partly reflect differences in eye shape rather than eye size (Kirk, 2006b).

## Conclusions

Primates are distinguished from other mammals in having large eyes relative to body size, and diurnal anthropoids exhibit unusually small corneas for their eye size. This distribution of traits suggests that two major changes in eye morphology occurred during the course of primate evolution. First, eye size increased relative to body size in the primate stem lineage. This shift in eye size is consistent with the hypothesis that basal primates were nocturnal visual predators. Accordingly, the large eyes of basal primates are hypothesized to have evolved to improve visual acuity without compromising visual sensitivity in a nocturnal setting. Second, corneal size decreased in the anthropoid stem lineage while eye size remained relatively large. The reduced relative corneal sizes of anthropoids are hypothesized to reflect reductions in the size of the dioptric apparatus as a means of increasing posterior nodal distance to improve visual acuity. These data support the conclusion that the origin of anthropoids was associated with a change in eye shape to improve visual acuity in the context of a diurnal predatory habitus.

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# Appendix 1. Data, activity patterns, and taxon and activity codes used for analyses

Genus	Species	Order	ACT	n	HBL	AD	CD
<i>Alces</i>	<i>alces</i>	Artiodactyla	c	1	2750	36.6	28.5
<i>Ammotragus</i>	<i>lervia</i>	Artiodactyla	c	2	1500	34.5	26.5
<i>Antelope</i>	<i>cervicapra</i>	Artiodactyla	c	1	1250	28.0	20.0
<i>Camelus</i>	<i>bactrianus</i>	Artiodactyla	d	2	2000	40.0	29.0
<i>Capra</i>	<i>ibex</i>	Artiodactyla	c	1	1400	35.0	25.5
<i>Capricornis</i>	<i>sumatraensis</i>	Artiodactyla	c	1	1500	29.0	22.5
<i>Cervus</i>	<i>nippon</i>	Artiodactyla	c	1	1300	20.0	16.0
<i>Connochaetes</i>	<i>gnou</i>	Artiodactyla	c	1	1750	26.5	18.8
<i>Dama</i>	<i>dama</i>	Artiodactyla	c	1	1450	34.0	25.3
<i>Elaphurus</i>	<i> davidianus</i>	Artiodactyla	c	4	1500	33.8	24.7
<i>Gazella</i>	<i>dorcas</i>	Artiodactyla	c	1	1100	26.0	18.5
<i>Kobus</i>	<i>ellipsprymnus</i>	Artiodactyla	c	1	2000	36.0	27.5
<i>Lama</i>	<i>glama</i>	Artiodactyla	d	1	1500	38.5	25.5
<i>Muntiacus</i>	<i>muntjak</i>	Artiodactyla	c	1	1000	25.0	18.5
<i>Odocoileus</i>	<i>hemionus</i>	Artiodactyla	c	4	1193	26.8	19.8
<i>Odocoileus</i>	<i>virginianus</i>	Artiodactyla	c	2	1450	27.0	19.3
<i>Okapia</i>	<i>johnstoni</i>	Artiodactyla	d	1	2100	27.1	19.9
<i>Oryx</i>	<i>gazella</i>	Artiodactyla	c	2	1975	37.1	26.4
<i>Ovis</i>	<i>dalli</i>	Artiodactyla	c	2	1263	31.7	22.7
<i>Strepsiceros</i>	<i>spekei</i>	Artiodactyla	c	2	1338	30.3	23.9
<i>Strepsiceros</i>	<i>strepsiceros</i>	Artiodactyla	c	1	2200	41.7	31.4
<i>Sylvicapra</i>	<i>grimmia</i>	Artiodactyla	n	1	1000	26.0	20.5
<i>Taurotragus</i>	<i>eurycerus</i>	Artiodactyla	c	1	2100	32.0	25.8
<i>Taurotragus</i>	<i>oryx</i>	Artiodactyla	c	2	2488	47.7	34.2
<i>Tayassu</i>	<i>tajacu</i>	Artiodactyla	c	2	794	18.6	13.4
<i>Tragulus</i>	<i>meminna</i>	Artiodactyla	n	1	500	17.0	16.3
<i>Tragulus</i>	<i>javanicus</i>	Artiodactyla	n	1	500	19.0	15.8
<i>Acinonyx</i>	<i> jubatus</i>	Carnivora	d	2	1400	36.7	22.4
<i>Ailurus</i>	<i>fulgens</i>	Carnivora	n	1	560	13.0	10.0
<i>Alopex</i>	<i>lagopus</i>	Carnivora	c	2	567	18.6	13.3
<i>Bassariscus</i>	<i>astutus</i>	Carnivora	n	1	340	12.5	11.8
<i>Canis</i>	<i>lupus</i>	Carnivora	c	1	1200	22.5	16.6
<i>Cerdocyon</i>	<i>thous</i>	Carnivora	n	1	535	17.3	14.4
<i>Galidia</i>	<i>elegans</i>	Carnivora	d	1	290	8.5	7.0
<i>Genetta</i>	<i>genetta</i>	Carnivora	n	2	500	15.0	13.0
<i>Hemigalus</i>	<i>derbyanus</i>	Carnivora	n	1	460	13.8	12.3
<i>Ichneumia</i>	<i>albicauda</i>	Carnivora	n	1	570	14.0	12.0
<i>Ictailurus</i>	<i>planiceps</i>	Carnivora	n	1	455	19.8	17.1
<i>Leopardus</i>	<i>tigrinus</i>	Carnivora	c	1	575	20.6	18.0
<i>Leopardus</i>	<i>wiedii</i>	Carnivora	c	2	575	22.9	19.8
<i>Lutra</i>	<i>annectans</i>	Carnivora	c	1	330	10.3	7.3
<i>Lutra</i>	<i>marculicollis</i>	Carnivora	c	1	285	10.4	8.6
<i>Lynx</i>	<i>canadensis</i>	Carnivora	c	2	842	27.4	19.1
<i>Martes</i>	<i>flavigula</i>	Carnivora	d	1	345	12.0	8.4
<i>Meles</i>	<i>meles</i>	Carnivora	n	1	600	8.9	8.5
<i>Melursus</i>	<i>ursinus</i>	Carnivora	n	1	1600	17.0	11.3
<i>Mustela</i>	<i>nivalis</i>	Carnivora	c	1	260	5.4	4.9
<i>Mydaus</i>	<i>sp.</i>	Carnivora	c	1	350	6.8	6.1
<i>Otocolobus</i>	<i>manul</i>	Carnivora	c	1	575	19.0	12.8
<i>Panthera</i>	<i>onca</i>	Carnivora	n	1	1400	28.2	20.5
<i>Panthera</i>	<i>uncia</i>	Carnivora	c	2	1150	31.4	22.1
<i>Panthera</i>	<i>tigris</i>	Carnivora	c	2	2000	35.0	24.2
<i>Panthera</i>	<i>leo</i>	Carnivora	c	3	1933	36.9	25.3
<i>Paracynctis</i>	<i>selousi</i>	Carnivora	c	1	430	11.0	6.3
<i>Pardofelis</i>	<i>marmorata</i>	Carnivora	n	1	545	22.4	17.0
<i>Prionailurus</i>	<i>bengalensis</i>	Carnivora	c	2	600	20.6	16.3
<i>Prionailurus</i>	<i>viverrinus</i>	Carnivora	c	1	650	24.2	19.6
<i>Procyon</i>	<i>lotor</i>	Carnivora	n	3	423	13.4	11.7
<i>Salanoia</i>	<i>concolor</i>	Carnivora	d	1	380	14.2	12.7
<i>Selenarctos</i>	<i>thibetanus</i>	Carnivora	c	1	1450	17.0	11.5
<i>Speothos</i>	<i>venaticus</i>	Carnivora	d	1	660	16.6	10.0
<i>Suricata</i>	<i>suricata</i>	Carnivora	d	1	275	10.5	6.0

## Appendix 1 (continued)

Genus	Species	Order	ACT	n	HBL	AD	CD
<i>Urocyon</i>	<i>cinereoargenteus</i>	Carnivora	c	3	540	17.4	13.9
<i>Ursus</i>	<i>arctos</i>	Carnivora	c	1	2500	18.0	13.0
<i>Ursus</i>	<i>americanus</i>	Carnivora	c	1	1650	18.5	13.8
<i>Vormela</i>	<i>peregrusna</i>	Carnivora	c	1	325	7.6	6.6
<i>Vulpes</i>	<i>vulpes</i>	Carnivora	n	3	610	20.1	15.9
<i>Dasyurus</i>	<i>viverrinus</i>	Dasyuromorphia	n	1	301	10.6	10.4
<i>Sarcophilus</i>	<i>lanarius</i>	Dasyuromorphia	n	1	471	14.5	12.9
<i>Cynocephalus</i>	<i>volans</i>	Dermoptera	n	2	394	13.4	12.0
<i>Caluromys</i>	<i>philander</i>	Didelphimorphia	n	1	140	8.7	7.9
<i>Caluromys</i>	<i>derbianus</i>	Didelphimorphia	n	2	258	10.5	9.4
<i>Caluromys</i>	<i>lanatus</i>	Didelphimorphia	n	1	260	12.7	11.2
<i>Caluromys</i>	<i>irrupta</i>	Didelphimorphia	n	1	215	8.7	7.9
<i>Chironectes</i>	<i> minimus</i>	Didelphimorphia	n	2	255	9.9	9.1
<i>Didelphis</i>	<i> marsupialis</i>	Didelphimorphia	n	1	375	8.7	7.9
<i>Didelphis</i>	<i> virginianus</i>	Didelphimorphia	n	2	381	9.7	8.5
<i>Lutreolina</i>	<i> crassicaudata</i>	Didelphimorphia	n	1	285	8.0	7.5
<i>Marmosa</i>	<i> robinsoni</i>	Didelphimorphia	n	3	120	6.6	6.1
<i>Marmosa</i>	<i> sp.</i>	Didelphimorphia	n	2	146	7.3	7.3
<i>Metachirus</i>	<i> nudicaudatus</i>	Didelphimorphia	n	1	146	6.8	6.3
<i>Bettongia</i>	<i> penicillata</i>	Diprotodontia	n	2	400	13.7	11.9
<i>Macropus</i>	<i> fuliginosus</i>	Diprotodontia	c	2	860	23.1	18.7
<i>Macropus</i>	<i> giganteus</i>	Diprotodontia	c	1	1450	24.1	19.2
<i>Petauroides</i>	<i> volans</i>	Diprotodontia	n	1	135	8.7	7.9
<i>Petaurus</i>	<i> sp.</i>	Diprotodontia	n	1	165	10.1	9.1
<i>Phalanger</i>	<i> orientalis</i>	Diprotodontia	n	1	250	11.4	10.0
<i>Phalanger</i>	<i> sp.</i>	Diprotodontia	n	1	530	16.0	14.5
<i>Pseudocheirus</i>	<i> herbertensis</i>	Diprotodontia	n	2	130	8.7	7.7
<i>Strigocuscus</i>	<i> gymnotis</i>	Diprotodontia	n	1	450	16.1	14.3
<i>Trichosurus</i>	<i> vulpecula</i>	Diprotodontia	n	1	450	13.7	12.3
<i>Hemiechinus</i>	<i> megalotis</i>	Eulipotyphla	n	1	180	6.4	5.6
<i>Hylomys</i>	<i> sp.</i>	Eulipotyphla	c	1	110	4.1	3.4
<i>Neotetracus</i>	<i> fulvescens</i>	Eulipotyphla	n	1	116	4.3	3.8
<i>Heterohyrax</i>	<i> sp.</i>	Hyracoidea	d	1	200	9.2	7.4
<i>Procavia</i>	<i> capensis</i>	Hyracoidea	d	1	600	15.2	11.1
<i>Lepus</i>	<i> californicus</i>	Lagomorpha	c	1	400	18.7	15.8
<i>Ochotona</i>	<i> rufescens</i>	Lagomorpha	c	1	185	9.0	6.3
<i>Sylvilagus</i>	<i> audubonii</i>	Lagomorpha	c	3	303	14.9	12.9
<i>Elephantulus</i>	<i> rozeti</i>	Macroscelidea	d	2	97	6.8	5.9
<i>Elephantulus</i>	<i> brachyrhynchus</i>	Macroscelidea	d	1	98	6.8	6.5
<i>Petrodromus</i>	<i> tetradactylus</i>	Macroscelidea	d	1	130	8.0	6.9
<i>Dromiciops</i>	<i> gliroides</i>	Microbiotheria	n	1	94	5.1	4.6
<i>Perameles</i>	<i> nasuta</i>	Paramelemorphia	n	2	136	6.6	5.5
<i>Diceros</i>	<i> bicornis</i>	Perissodactyla	c	1	3400	27.6	16.1
<i>Equus</i>	<i> asinus</i>	Perissodactyla	c	1	2100	39.0	24.0
<i>Equus</i>	<i> burchelli</i>	Perissodactyla	c	1	2315	41.3	28.0
<i>Equus</i>	<i> zebra</i>	Perissodactyla	c	1	2200	41.5	27.3
<i>Equus</i>	<i> caballus</i>	Perissodactyla	c	2	2500	42.0	29.9
<i>Tapirus</i>	<i> terrestris</i>	Perissodactyla	c	1	2000	21.0	14.8
<i>Manis</i>	<i> javanica</i>	Pholidota	n	1	415	7.4	6.4
<i>Manis</i>	<i> tricuspis</i>	Pholidota	n	1	340	9.0	7.7
<i>Alouatta</i>	<i> sp.</i>	Primates	d	3	737	16.2	9.7
<i>Alouatta</i>	<i> seniculus</i>	Primates	d	1	560	17.1	9.0
<i>Aotus</i>	<i> trivirgatus</i>	Primates	n	3	280	19.2	13.0
<i>Aotus</i>	<i> sp.</i>	Primates	n	2	305	20.0	13.4
<i>Ateles</i>	<i> paniscus</i>	Primates	d	4	503	18.7	9.7
<i>Ateles</i>	<i> belzebuth</i>	Primates	d	1	410	19.7	9.8
<i>Ateles</i>	<i> sp.</i>	Primates	d	2	509	20.2	10.9
<i>Cacajao</i>	<i> rubicundus</i>	Primates	d	1	553	19.2	9.3
<i>Callicebus</i>	<i> sp.</i>	Primates	d	1	356	13.0	7.0
<i>Callicebus</i>	<i> moloch</i>	Primates	d	1	290	13.1	7.0
<i>Callimico</i>	<i> goeldii</i>	Primates	d	1	270	12.5	7.1
<i>Callithrix</i>	<i> argentata</i>	Primates	d	1	210	11.0	6.0
<i>Callithrix</i>	<i> jacchus</i>	Primates	d	6	193	11.3	5.9
<i>Callithrix</i>	<i> aurita</i>	Primates	d	1	180	11.5	6.4

(continued on next page)

Appendix 1 (continued)

Genus	Species	Order	ACT	n	HBL	AD	CD
<i>Callithrix</i>	sp.	Primates	d	2	183	11.5	5.6
<i>Cebus</i>	sp.	Primates	d	1	435	14.1	7.3
<i>Cebus</i>	<i>capucinus</i>	Primates	d	1	385	16.0	9.9
<i>Cercocebus</i>	<i>torquatus</i>	Primates	d	1	602	19.4	11.3
<i>Cercopithecus</i>	<i>cephus</i>	Primates	d	1	521	17.2	10.6
<i>Cercopithecus</i>	<i>nitidus</i>	Primates	d	1	546	17.6	10.4
<i>Cercopithecus</i>	<i>ascanius</i>	Primates	d	2	460	18.5	9.8
<i>Cercopithecus</i>	<i>albogularis</i>	Primates	d	2	625	19.2	9.7
<i>Cercopithecus</i>	<i>mitis</i>	Primates	d	2	517	19.4	11.0
<i>Cercopithecus</i>	<i>diana</i>	Primates	d	1	508	19.5	10.7
<i>Cercopithecus</i>	<i>neglectus</i>	Primates	d	1	512	20.7	10.9
<i>Cheirogaleus</i>	<i>medius</i>	Primates	n	4	191	10.3	8.7
<i>Cheirogaleus</i>	<i>major</i>	Primates	n	4	238	12.6	10.7
<i>Colobus</i>	<i>polykomos</i>	Primates	d	3	617	18.2	10.1
<i>Colobus</i>	<i>guereza</i>	Primates	d	1	750	19.7	10.5
<i>Daubentonia</i>	<i>madagascariensis</i>	Primates	n	2	400	18.1	14.4
<i>Erythrocebus</i>	<i>patas</i>	Primates	d	6	711	22.5	11.1
<i>Eulemur</i>	<i>macaco</i>	Primates	c	4	450	15.3	12.1
<i>Eulemur</i>	<i>mongoz</i>	Primates	c	4	343	15.5	12.3
<i>Eulemur</i>	<i>coronatus</i>	Primates	c	2	340	16.1	12.3
<i>Eulemur</i>	<i>fulvus</i>	Primates	c	6	450	16.7	13.2
<i>Eulemur</i>	<i>rubriventer</i>	Primates	c	1	350	18.2	14.2
<i>Galago</i>	<i>sengalensis</i>	Primates	n	2	140	12.9	9.9
<i>Galago</i>	<i>moholi</i>	Primates	n	8	159	13.4	11.3
<i>Galagoides</i>	<i>demidoff</i>	Primates	n	6	126	11.0	9.4
<i>Gorilla</i>	<i>gorilla</i>	Primates	d	2	1600	23.0	12.3
<i>Haplemur</i>	<i>griseus</i>	Primates	d	2	280	13.8	9.7
<i>Hylobates</i>	<i>lar</i>	Primates	d	1	530	17.7	10.0
<i>Hylobates</i>	<i>leucogenys</i>	Primates	d	1	546	18.9	11.2
<i>Hylobates</i>	sp.	Primates	d	3	500	19.9	10.7
<i>Lagothrix</i>	<i>lagotricha</i>	Primates	d	2	508	20.0	10.0
<i>Lemur</i>	<i>catta</i>	Primates	d	3	425	15.6	12.0
<i>Leontopithecus</i>	<i>rosalia</i>	Primates	d	1	261	11.2	6.6
<i>Leontopithecus</i>	sp.	Primates	d	1	268	12.2	6.5
<i>Lophocebus</i>	<i>aterrimus</i>	Primates	d	1	530	18.3	11.5
<i>Lophocebus</i>	<i>albingena</i>	Primates	d	1	600	20.0	10.8
<i>Loris</i>	<i>tardigradus</i>	Primates	n	5	212	14.9	12.0
<i>Macaca</i>	<i>fuscata</i>	Primates	d	1	540	17.4	9.9
<i>Macaca</i>	<i>fascicularis</i>	Primates	d	3	517	18.4	9.6
<i>Macaca</i>	<i>radiata</i>	Primates	d	3	483	18.6	9.3
<i>Macaca</i>	sp.	Primates	d	3	488	19.7	10.3
<i>Macaca</i>	<i>mulatta</i>	Primates	d	3	553	20.0	10.8
<i>Macaca</i>	<i>nemestrina</i>	Primates	d	3	516	20.4	11.4
<i>Macaca</i>	<i>silenus</i>	Primates	d	1	535	20.4	11.8
<i>Mandrillus</i>	<i>leucophaeus</i>	Primates	d	1	680	21.6	11.5
<i>Mandrillus</i>	<i>sphinx</i>	Primates	d	1	800	23.1	12.9
<i>Microcebus</i>	<i>murinus</i>	Primates	n	10	121	9.2	8.0
<i>Mirza</i>	<i>coquereli</i>	Primates	n	6	200	13.1	11.5
<i>Nycticebus</i>	<i>pygmaeus</i>	Primates	n	1	250	15.5	12.3
<i>Nycticebus</i>	<i>coucang</i>	Primates	n	7	309	15.7	12.1
<i>Otolemur</i>	<i>crassicaudatus</i>	Primates	n	2	328	16.3	13.4
<i>Pan</i>	<i>troglydites</i>	Primates	d	2	839	20.9	10.4
<i>Papio</i>	<i>cynocephalus</i>	Primates	d	1	660	17.6	8.7
<i>Papio</i>	sp.	Primates	d	3	696	21.0	11.0
<i>Perodicticus</i>	<i>potto</i>	Primates	n	3	325	12.4	10.4
<i>Pithecia</i>	<i>monachus</i>	Primates	d	1	330	14.0	7.8
<i>Pongo</i>	<i>pygmaeus</i>	Primates	d	2	875	21.5	11.2
<i>Procolobus</i>	<i>badius</i>	Primates	d	1	580	18.4	9.7
<i>Propithecus</i>	<i>verreauxi</i>	Primates	d	6	438	17.7	13.1
<i>Propithecus</i>	<i>tattersalli</i>	Primates	d	3	478	18.2	13.4
<i>Propithecus</i>	<i>diadema</i>	Primates	d	1	500	20.2	14.9
<i>Saguinus</i>	<i>fuscicollis</i>	Primates	d	3	237	10.3	5.9
<i>Saguinus</i>	sp.	Primates	d	1	254	11.6	6.5
<i>Saguinus</i>	<i>oedipus</i>	Primates	d	1	225	11.8	6.4
<i>Saguinus</i>	<i>labiatus</i>	Primates	d	1	240	12.0	6.2

Appendix 1 (continued)

Genus	Species	Order	ACT	n	HBL	AD	CD
<i>Saguinus</i>	<i>midas</i>	Primates	d	1	248	12.2	6.1
<i>Saguinus</i>	<i>imperator</i>	Primates	d	1	210	12.5	6.6
<i>Saguinus</i>	<i>mystax</i>	Primates	d	1	220	12.7	6.1
<i>Saimiri</i>	<i>boliviensis</i>	Primates	d	5	310	14.5	7.6
<i>Saimiri</i>	sp.	Primates	d	3	320	15.3	8.1
<i>Saimiri</i>	<i>sciureus</i>	Primates	d	4	306	15.5	7.8
<i>Semnopithecus</i>	<i>entellus</i>	Primates	d	1	750	22.0	12.3
<i>Tarsius</i>	sp.	Primates	n	3	111	16.1	13.0
<i>Tarsius</i>	<i>syrichta</i>	Primates	n	3	124	17.0	13.7
<i>Theropithecus</i>	<i>gelada</i>	Primates	d	1	620	19.6	8.6
<i>Trachypithecus</i>	<i>cristatus</i>	Primates	d	1	487	18.6	11.0
<i>Varecia</i>	<i>variegata</i>	Primates	d	5	500	18.5	14.2
<i>Elephas</i>	<i>maximus</i>	Proboscidea	c	1	6000	30.0	21.5
<i>Loxodonta</i>	<i>africana</i>	Proboscidea	c	1	7000	39.6	24.0
<i>Acomys</i>	<i>wilsoni</i>	Rodentia	c	1	70	4.6	4.3
<i>Allactaga</i>	<i>elater</i>	Rodentia	n	1	150	7.3	6.8
<i>Anomalurus</i>	sp.	Rodentia	n	1	280	14.0	12.9
<i>Aplodontia</i>	<i>rufa</i>	Rodentia	c	1	265	5.0	4.7
<i>Callosciurus</i>	<i>notatus</i>	Rodentia	d	1	186	8.8	7.5
<i>Calomyscus</i>	<i>baliwardi</i>	Rodentia	c	1	71	4.1	3.8
<i>Castor</i>	<i>canadensis</i>	Rodentia	c	1	450	9.4	7.3
<i>Cavia</i>	<i>porcellus</i>	Rodentia	c	1	250	10.0	7.8
<i>Chinchilla</i>	<i>chinchilla</i>	Rodentia	c	1	220	10.1	9.6
<i>Chroeomys</i>	<i>jelskii</i>	Rodentia	c	1	77	3.7	3.1
<i>Cricetomys</i>	<i>gambianus</i>	Rodentia	c	1	340	6.7	6.3
<i>Dactylomys</i>	sp.	Rodentia	n	1	245	10.7	9.5
<i>Dasyprocta</i>	<i>agouti</i>	Rodentia	d	1	250	10.9	8.5
<i>Dipodomys</i>	<i>spectabilis</i>	Rodentia	n	1	145	7.4	6.5
<i>Dolichotis</i>	<i>patagonum</i>	Rodentia	d	1	720	26.3	17.2
<i>Dryomys</i>	<i>nitedula</i>	Rodentia	n	1	58	4.2	3.7
<i>Erethizon</i>	<i>dorsatum</i>	Rodentia	c	1	508	10.3	9.1
<i>Glaucomys</i>	<i>volans</i>	Rodentia	n	1	115	8.3	7.8
<i>Glis</i>	<i>glis</i>	Rodentia	c	1	173	7.3	6.6
<i>Graphiurus</i>	<i>heuti</i>	Rodentia	c	1	127	5.9	5.4
<i>Hystrix</i>	<i>cristata</i>	Rodentia	n	1	625	11.2	11.2
<i>Isotrix</i>	<i>bistriata</i>	Rodentia	n	1	185	9.5	9.0
<i>Jaculus</i>	<i>jaculus</i>	Rodentia	n	2	98	8.2	7.7
<i>Marmota</i>	<i>monax</i>	Rodentia	d	1	440	12.1	7.5
<i>Microtus</i>	sp.	Rodentia	c	1	90	3.4	2.9
<i>Myosciurus</i>	<i>pumilio</i>	Rodentia	d	1	65	4.8	4.2
<i>Myoxus</i>	<i>glis</i>	Rodentia	c	1	173	7.3	6.6
<i>Oenomys</i>	<i>hypoxanthus</i>	Rodentia	c	1	150	4.8	4.6
<i>Peromyscus</i>	<i>maniculatus</i>	Rodentia	n	1	78	4.9	4.4
<i>Peromyscus</i>	sp.	Rodentia	n	5	82	5.1	4.7
<i>Phodopus</i>	<i>songorus</i>	Rodentia	c	1	85	5.1	4.7
<i>Proechimys</i>	<i>cayennensis</i>	Rodentia	n	1	190	7.8	7.0
<i>Rattus</i>	<i>rattus</i>	Rodentia	n	10	192	6.3	5.9
<i>Rhabdomys</i>	<i>pumilio</i>	Rodentia	d	1	112	5.3	4.3
<i>Sciurus</i>	<i>carolinensis</i>	Rodentia	d	1	270	11.8	9.1
<i>Sciurus</i>	<i>niger</i>	Rodentia	d	1	290	12.0	9.7
<i>Tamias</i>	<i>striatus</i>	Rodentia	d	6	132	7.1	5.9
<i>Tamiasciurus</i>	sp.	Rodentia	d	3	189	8.7	7.1
<i>Tatera</i>	<i>indica</i>	Rodentia	n	1	135	7.5	6.4
<i>Zapus</i>	<i>hudsonius</i>	Rodentia	c	1	58	3.4	2.7
<i>Plilocercus</i>	<i>lowii</i>	Scandentia	n	1	130	6.5	6.2
<i>Tupaia</i>	<i>minor</i>	Scandentia	d	1	130	7.5	6.6
<i>Tupaia</i>	<i>belangeri</i>	Scandentia	d	1	170	7.6	6.6
<i>Tupaia</i>	<i>glis</i>	Scandentia	d	2	158	8.7	7.8
<i>Urogale</i>	<i>everetti</i>	Scandentia	d	1	200	8.0	6.9
<i>Cabassous</i>	<i>centralis</i>	Xenarthra	n	1	350	5.4	4.0
<i>Chaetophractus</i>	<i>vellerosus</i>	Xenarthra	c	1	260	6.7	4.7
<i>Chlamyphorus</i>	<i>truncatus</i>	Xenarthra	n	1	130	1.9	1.8
<i>Choloepus</i>	<i>hoffmanni</i>	Xenarthra	n	1	580	13.3	11.2
<i>Cyclopes</i>	<i>didactylus</i>	Xenarthra	n	1	180	10.2	7.5

(continued on next page)



## Appendix 1 (continued)

Genus	Species	Order	ACT	n	HL	AD	CD
<i>Euphractus</i>	<i>sexcinctus</i>	Xenarthra	c	1	540	8.6	6.5
<i>Myrmecophaga</i>	<i>tridactyla</i>	Xenarthra	c	1	500	10.7	7.2
<i>Tolypeutes</i>	<i>tricinctus</i>	Xenarthra	c	2	220	6.4	4.4
<i>Tolypeutes</i>	<i>matacus</i>	Xenarthra	c	1	275	6.5	5.0
<i>Zaedyus</i>	<i>pichiy</i>	Xenarthra	c	1	255	6.2	4.6

Notes: ACT, activity code: c = cathemeral, d = diurnal, n = nocturnal; n, sample size; HBL, head and body length (mm); AD, axial diameter of eye (in mm); CD, cornea diameter of eye (mm).

## Appendix 2. Nexus tree file, including branch lengths in years, followed by abbreviations used (see Fig. A1)

### #NEXUS

Begin trees;

Translate

1 Oh,2 Sy,3 Le,4 Gh,5 My,6 Gi,7 Ds,8 Ar,9 Cl,10 M2,11 M1,12 T1,13 G1,14 Ta,15 Sn,16 Sc,17 Hx,18 Dt,19 Ix,20 Pr,21 C5,22 En,23 Da,24 CV,25 Dl,26 Dy,27 An,28 C9,29 Zp,30 Aa,31 Jc,32 C2,33 C1,34 Ry,35 Rt,36 Oe,37 Tt,38 Ay,39 M3,40 Ph,41 Ak,42 P1,43 P2,44 Cv,45 P1,46 Ue,47 Tm,48 T1,49 Tu,50 Pq,51 Lt,52 Nc,53 Np,54 Gd,55 Oc,56 Gs,57 Gm,58 Dm,59 Mm,60 Mc,61 Co,62 Ch,63 Pd,64 Pt,65 Px,66 Vv,67 Lc,68 Hg,69 Eo,70 Ec,71 Ef,72 Ez,73 Er,74 Ts,75 Ty,76 Pi,77 Cr,78 Cy,79 Cm,80 Ao,81 At,82 Al,83 Ap,84 L1,85 As,86 Au,87 Af,88 Cb,89 Ck,90 Sp,91 Sb,92 Ss,93 Cg,94 Cw,95 Cf,96 Cj,97 Cu,98 Lp,99 Lr,100 Sf,101 Su,102 So,103 Sd,104 Sm,105 Sl,106 Sx,107 Hy,108 Ho,109 Hl,110 Po,111 Gg,112 Py,113 Tc,114 Se,115 Pb,116 Cp,117 Cz,118 Ep,119 Cq,120 Cd,121 Cn,122 Ce,123 Ci,124 Cs,125 Cc,126 Ct,127 Ml,128 Mx,129 La,130 Lu,131 Tg,132 Pa,133 Pu,134 Mq,135 Ms,136 Ma,137 Mn,138 Mr,139 Mf,140 Mu;

tree (((((Oh: 37000000,(Sy: 18500000,Le: 18500000): 18500000): 28000000,(((Gh: 28500000,(My: 14250000,(Gi: 72500000,Ds: 72500000): 70000000): 14250000): 22850000,(Ar: 44350000,(Cl: 37000000,(M2: 15500000,(M1: 75000000,T1: 75000000): 80000000): 80000000,(G1: 15500000,(Ta: 75000000,(Sn: 37500000,Sc: 37500000): 37500000): 80000000): 80000000): 13500000): 73500000): 70000000): 46500000,(Hx: 46000000,(Dt: 21000000,(Ix: 11000000,Pr: 11000000): 10000000): 10000000,((C5: 11000000,En: 11000000): 12000000,(Da: 15000000,(CV: 70000000,Dl: 70000000): 80000000): 80000000): 80000000): 15000000): 39000000,An: 39000000): 13000000,((C9: 41500000,(Zp: 33000000,(Aa: 16000000,Jc: 16000000): 17000000): 85000000): 85000000,((C2: 20000000,C1: 20000000): 59000000,(((Ry: 10300000,Rt: 10300000): 12200000,(Oe: 21500000,(Tt: 11500000,Ay: 11500000): 10000000): 10000000): 22000000,(M3: 92000000,Ph: 92000000): 100000000,(Ak: 176000000,(P1: 96000000,P2: 96000000): 80000000): 16000000): 55000000): 12000000): 24100000): 20000000): 20000000): 20000000): 90000000):

25000000,((Cv: 85000000,(Pl: 80000000,(Ue: 70000000,(Tm: 60000000,(Tl: 50000000,Tu: 50000000): 10000000): 10000000): 10000000): 77000000): 40000000,(((Pq: 30000000,(Lt: 20000000,(Nc: 10000000,Np: 10000000): 10000000): 10000000): 10000000,(Gd: 30000000,(Oc: 20000000,(Gs: 10000000,Gm: 10000000): 10000000): 10000000): 10000000): 28500000,(Dm: 62000000,((Mm: 20000000,Mc: 20000000): 90000000,(Co: 14500000,Ch: 14500000): 14500000): 13000000,((Pd: 10000000,(Pt: 90000000,Px: 90000000): 10000000): 30000000,(Vv: 32000000,(Lc: 17000000,Hg: 17000000): 11000000,(Eo: 10000000,(Ec: 90000000,(Ef: 80000000,(Ez: 70000000,Er: 70000000): 10000000): 10000000): 18000000): 40000000): 80000000): 20000000): 20000000): 65000000): 16500000,((Ts: 80000000,Ty: 80000000): 59500000,(((Pi: 80000000,Cr: 80000000): 15000000,((Cy: 11000000,Cm: 11000000): 11000000,(Ao: 11000000,At: 11000000): 11000000): 10000000): 10000000,((Al: 11500000,Ap: 11500000): 11500000,(Ll: 90000000,(As: 60000000,(Au: 30000000,Af: 30000000): 30000000): 30000000): 14000000): 10000000): 10000000,(((Cb: 17000000,Ck: 17000000): 50000000,(Sp: 15000000,(Sb: 75000000,Ss: 75000000): 75000000): 70000000): 15000000,(Cg: 14000000,((Cw: 90000000,(Cf: 50000000,(Cj: 40000000,Cu: 40000000): 10000000): 40000000): 40000000,(Lp: 52000000,Lr: 52000000): 52000000,(Sf: 94000000,(Su: 84000000,(So: 64000000,Sd: 64000000): 10000000,(Sm: 64000000,(Sl: 54000000,Sx: 54000000): 10000000): 10000000): 10000000): 10000000): 26000000): 10000000): 95000000): 15000000): 25000000,(((Hy: 60000000,(Ho: 30000000,Hl: 30000000): 30000000): 12000000,(Po: 12000000,(Gg: 90000000,Py: 90000000): 30000000): 60000000): 17000000,(((Tc: 80000000,Se: 80000000): 20000000,(Pb: 90000000,(Cp: 80000000,Cz: 80000000): 10000000): 10000000): 20000000,((Ep: 80000000,(Cq: 65000000,(Cd: 50000000,(Cn: 40000000,((Ce: 20000000,Ci: 20000000): 10000000,(Cs: 20000000,Cc: 20000000): 10000000): 10000000): 10000000): 15000000): 15000000): 20000000,(((Ct: 50000000,(Ml: 30000000,Mx: 30000000): 20000000): 20000000,(La: 30000000,Lu: 30000000): 10000000,(Tg: 30000000,(Pa: 15000000,Pu: 15000000): 15000000): 10000000): 30000000): 10000000,(Mq: 70000000,(Ms: 60000000,(Ma: 50000000,(Mn: 40000000,(Mr: 20000000,(Mf: 10000000,Mu: 10000000): 10000000): 20000000): 10000000): 10000000): 10000000): 20000000): 20000000): 23000000): 15000000): 17500000): 17500000): 40000000): 10000000) 00000000); End;

Ap, *Alouatta seniculus*; Al, *Alouatta* sp.; At, *Aotus* sp.; Ao, *Aotus trivirgatus*; Af, *Ateles belzebuth*; Au, *Ateles paniscus*; As, *Ateles* sp.; Cr, *Cacajao rubicundus*; Cm, *Callicebus moloch*; Cy, *Calli-  
cebus* sp.; Cg, *Callimico goeldii*; Cf, *Callithrix argentata*; Cu, *Callithrix aurita*; Cj, *Callithrix jacchus*; Cw, *Callithrix* sp.; Ck, *Cebus capucinus*; Cb, *Cebus* sp.; Ct, *Cercopithecus torquatus*; Cq, *Cercopithecus albogularis*; Cs, *Cercopithecus ascanius*; Cc,

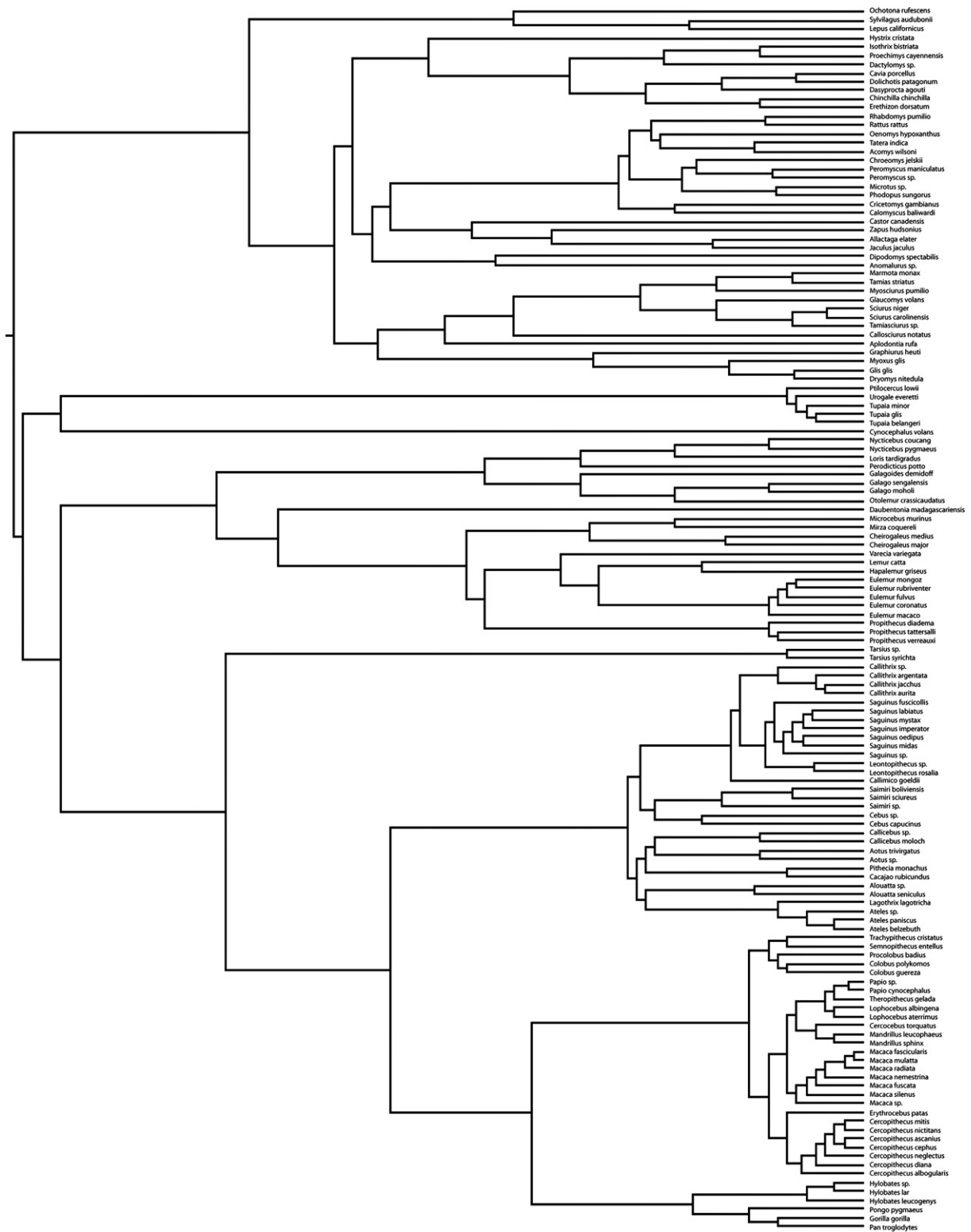


Fig. A1. Phylogenetic tree of Euarchontoglires used for analyses in PDAP. Branch lengths are given in accompanying Nexus file.

*Cercopithecus cephus*;Cd, *Cercopithecus diana*;Ce, *Cercopithecus mitis*;Cn, *Cercopithecus neglectus*;Ci, *Cercopithecus nictitans*;Ch, *Cheirogaleus major*;Co, *Cheirogaleus medius*;Cz, *Colobus guereza*;Cp, *Colobus polykomos*;Cv, *Cynocephalus volans*;Dm, *Daubentonia madagascariensis*;Ep, *Erythrocebus patas*;Ec, *Eulemur coronatus*;Ef, *Eulemur fulvus*;Eo, *Eulemur macaco*;Ez, *Eulemur mongoz*;Er, *Eulemur rubriventer*;Gm, *Galago moholi*;Gs, *Galago sengalensis*;Gd, *Galagoides demidoff*;Gg, *Gorilla gorilla*;Hg, *Hapalemur griseus*;Ho, *Hylobates lar*;Hl, *Hylobates leucogenys*;Hy, *Hylobates sp.*;Ll, *Lagothrix lagotricha*;Lc, *Lemur catta*;Lr, *Leontopithecus rosalia*;Lp, *Leontopithecus sp.*;La, *Lophocebus albingena*;Lu, *Lophocebus aterrimus*;Lt, *Loris tardigradus*;Mf, *Macaca fascicularis*;Ma, *Macaca fuscata*;Mu, *Macaca mulatta*;Mn, *Macaca nemestrina*;Mr, *Macaca radiata*;Ms, *Macaca silemus*;Mq, *Macaca sp.*;Ml, *Mandrillus leucophaeus*;Mx, *Mandrillus sphinx*;Mm, *Microcebus murinus*;Mc, *Mirza coquereli*;Nc, *Nycticebus coucang*;Np, *Nycticebus pygmaeus*;Oc, *Otolemur crassicaudatus*;Py, *Pan troglodytes*;Pu, *Papio cynocephalus*;Pa, *Papio sp.*;Pq, *Perodicticus potto*;Pi, *Pithecia monachus*;Po, *Pongo pygmaeus*;Pb, *Procolobus badius*;Pd, *Propithecus diadema*;Pt, *Propithecus tattersalli*;Px, *Propithecus verreauxi*;Pl, *Ptilocercus lowii*;Sf, *Saguinus fuscicollis*;Sm, *Saguinus imperator*;Sl, *Saguinus labiatus*;Sd, *Saguinus midas*;Sx, *Saguinus mystax*;So, *Saguinus oedipus*;Su, *Saguinus sp.*;Sb, *Saimiri boliviensis*;Ss, *Saimiri sciureus*;Sp, *Saimiri sp.*;Se, *Semnopithecus entellus*;Ty, *Tarsius sp.*;Ts, *Tarsius syrichta*;Tg, *Theropithecus gelada*;Tc, *Trachypithecus cristatus*;Tu, *Tupaia belangeri*;Tl, *Tupaia glis*;Tm, *Tupaia minor*;Ue, *Urogale everetti*;Vv, *Varecia variegata*;Ay, *Acomys wilsoni*;Aa, *Allactaga elater*;An, *Anomalurus sp.*;Ar, *Aplodontia rufa*;Cl, *Callosciurus notatus*;C1, *Calomyscus baliwardi*;C9, *Castor canadensis*;CV, *Cavia porcellus*;C5, *Chinchilla chinchilla*;Ak, *Chroeomys jelskii*;C2, *Cricetomys gambianus*;Dt, *Dactylomys sp.*;Da, *Dasyprocta agouti*;Dy, *Dipodomys spectabilis*;Dl, *Dolichotis patagonum*;Ds, *Dryomys nitedula*;En, *Erethizon dorsatum*;G1, *Glaucomys volans*;Gi, *Glis glis*;Gh, *Graphiurus heuti*;Hx, *Hystrix cristata*;Ix, *Isotrix bistriata*;Jc, *Jaculus jaculus*;Le, *Lepus californicus*;M1, *Marmota monax*;M3, *Microtus sp.*;M2, *Myosciurus pumilio*;My, *Myoxus glis*;Oh, *Ochotona rufescens*;Oe, *Oenomys hypoxanthus*;P1, *Peromyscus maniculatus*;P2, *Peromyscus sp.*;Ph, *Phodopus sungorus*;Pr, *Proechimys cayennensis*;Rt, *Rattus rattus*;Ry, *Rhabdomys pumilio*;Sc, *Sciurus carolinensis*;Sn, *Sciurus niger*;Sy, *Sylvilagus audubonii*;T1, *Tamias striatus*;Ta, *Tamiasciurus sp.*;Tt, *Tatera indica*;Zp, *Zapus hudsonius*;

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