

The primate semicircular canal system and locomotion

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The semicircular canal system of vertebrates helps coordinate body movements, including stabilization of gaze during locomotion. Quantitative phylogenetically informed analysis of the radius of curvature of the three semicircular canals in 91 extant and recently extinct primate species and 119 other mammalian taxa provide support for the hypothesis that canal size varies in relation to the jerkiness of head motion during locomotion. Primate and other mammalian species studied here that are agile and have fast, jerky locomotion have significantly larger canals relative to body mass than those that move more cautiously.

generalized least-squares analysis | mammals | vestibular system

Paleontologists trying to reconstruct the locomotor behavior of extinct primate species rarely have the opportunity to check the repertoires inferred from postcranial evidence against independent sources of evidence such as footprints (1). Building on previous observations (2), we examine the potential to test such hypotheses with data from nonpostcranial structures: the semicircular canals, which are commonly preserved in cranial fossils. The semicircular canals of the vertebrate inner ear are the bony tubes in the otic capsule surrounding the three membranous ducts that are part of the functionally important endolymph circuit. The term “semicircular canal system” covers the entire functional unit including both bony and soft-tissue aspects. The canal system senses self-rotation when an animal moves through the environment, and its sensory input, combined with otolithic, visual, and proprioceptive information, helps coordinate posture and body movements during locomotion.

The best understood function of the canal system is its contribution to the stabilization of gaze during locomotion (3–5). The system works to integrate optic flow, i.e., the changes in the retinal images that occur when moving and that are important clues in sensing distance as well as body position (6, 7). Stabilization is accomplished via the vestibuloocular and vestibulocollic reflexes that involve, when moving, the extraocular and neck muscles, respectively. Stabilization of vision is especially important in birds and arboreal and/or gliding mammals, such as most primates, dermopterans, scandentians, and many rodents, that have to rely on eyesight when moving quickly through the air or trees. Primates as a whole show a great diversity of locomotor types. Specialized leaping is used by many prosimians and acrobatic brachiating is used by gibbons, whereas stealthy slow climbing is characteristic of lorises. Most others are quadrupedal arboreal forms with more or less leaping and/or suspension included in their repertoire.

Several workers have investigated the correlation between semicircular canal dimensions and body mass (BM) (2, 8–10), and all report that the canals increase in several dimensions, but with strong negative allometry. On the basis of theoretical functional models of the canal system, double logarithmic plots were predicted to have slopes between 0.08 and 0.33 (8). These slopes empirically determined for different vertebrate groups indeed fall within this range (5, 8, 9), with a value of 0.14 typically being obtained for the regression of \log_{10} mean radius of curvature of the canals on \log_{10} BM in a sample of 174 noncetecean mammalian species (11).

In addition to the overall scaling pattern, it is clear from past studies that valuable information about locomotion is present in the plots of \log_{10} canal size against \log_{10} BM as well. A number of early researchers suggested, on empirical evidence, that the size of the canals reflects some quality of an animal's behavior. Gray (12), for instance, noted that sloths have very small canals for their body size and suggested that this correlated with their sluggish movements. Likewise, canals were reported as large in highly maneuverable birds, and small in species with more stable flight (13–15). Subsequent studies (9, 16–20) examined such comparative observations quantitatively by measuring the length of the membranous duct or, as a proxy, the arc radius of curvature of the surrounding canal, and by interpreting the results in the context of biomechanical models that link this trait with properties of the canal system such as its mechanical sensitivity (21–23). These previous studies were hampered by the use of limited comparative data sets, often compiled from sources with dissimilar measurement definitions, and full statistical analysis of the results was therefore not possible. Nevertheless, for primates, it was found that, once body size is accounted for, species that were acrobatic or that had very rapid locomotion clearly had larger canal arc sizes than those that were cautious or slow in their movements (9, 17, 18). It was these preliminary findings that encouraged us to undertake the present study, hoping both to document the relationship between semicircular canal size and locomotor agility as a basic biological phenomenon of this sensory system, and to provide a means for future development of analytical tools to assess the locomotor behaviors of extinct primate species, independent of postcranial evidence. To this end, by using comprehensive and phylogenetically informed statistical analyses, we examined the relationship between canal arc size and locomotion in a large comparative database.

Results

Conventional Regression. Conventional multiple regressions on both the primate and full mammalian samples indicate significant positive effects of \log_{10} BM and \log_{10} locomotor agility (AGIL) on the \log_{10} radius of curvature of all three semicircular canals and the mean canal radius (Tables 1 and 2). Based on the natural logarithm (ln) maximum likelihood (ML) estimates obtained for both samples, the correlations are strongest for the mean canal radius (Fig. 1). The relationships between \log_{10} canal radius and \log_{10} BM were strongly negatively allometric (i.e., slopes less than one-third) in all analyses (Tables 3 and 4). All

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Abbreviations: AGIL, locomotor agility; AIC, Akaike information criterion; BM, body mass; CT, computed tomography; GLS, generalized least squares; ML, maximum likelihood.

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Table 1. Results of multiple regression with \log_{10} semicircular canal radius as the dependent variable against \log_{10} BM and \log_{10} AGIL for primates

Canal	Model	ln ML	AIC	MSE	SEE
ASCR	Star	146.7	-285.4	0.00241	0.0491
	GLS Pagel's $\lambda = 0.907$	159.3	-308.7	0.00183	0.0427
PSCR	Star	169.5	-330.9	0.00146	0.0382
	GLS Pagel's $\lambda = 0.774$	175.4	-340.7	0.00128	0.0358
LSCR	Star	165.8	-323.5	0.00158	0.0398
	GLS Grafen's $\rho = 0.349$	172.9	-335.9	0.00136	0.0368
SCR	Star	172.7	-337.5	0.00136	0.0369
	GLS Pagel's $\lambda = 0.885$	182.0	-353.9	0.00111	0.0333

Results are shown under the "star" model, which uses conventional regression analysis with no phylogenetic correction and under branch length transformations used in phylogenetic GLS models. Both Pagel's λ and Grafen's ρ are methods for estimating how well the phylogeny fits the observed variation in species tip values. ASCR, anterior semicircular canal radius; LSCR, lateral semicircular canal radius; MSE, mean squared error; PSCR, posterior semicircular canal radius; SCR, average semicircular canal radius; SEE, standard error of the estimate.

95% confidence intervals for regression slopes included 0.14 to 0.15 as reported previously for primates and other mammals (9, 20) and excluded 0.33, which would indicate isometry. The positive and statistically significant regression coefficients for \log_{10} AGIL indicate that, after controlling for variation in canal radius correlated with body size, the radius increases with increasing agility of locomotion, as hypothesized.

Phylogenetic Generalized Least-Squares (GLS) Regression. GLS analyses confirmed the results of the conventional multiple regressions. In all cases, the Akaike information criterion (AIC) was lower for GLS models than for conventional analyses, thus indicating a strong phylogenetic signal in the semicircular canal data even after controlling statistically for associations with body mass and agility. Both \log_{10} BM and \log_{10} AGIL had strong positive effects on canal radius of curvature for all three canals of both the primate and full mammalian samples (Tables 1 and 2). The slopes and their 95% confidence intervals (calculated for GLS with divergence times) for each canal and the mean canal versus \log_{10} BM fell within the range of those from the conventional multiple regression and again excluded isometry (Tables 3 and 4). The regression coefficient for \log_{10} AGIL was positive in all cases, indicating that canal size increases with increasing agility of locomotion.

Table 2. Results of multiple regression with \log_{10} semicircular canal radius as dependent variable against \log_{10} BM and \log_{10} AGIL for all mammals

Canal	Model	ln ML	AIC	MSE	SEE
ASCR	Star	265.6	-523.2	0.00473	0.0688
	GLS Grafen's $\rho = 0.561$	330.5	-650.9	0.00255	0.0505
PSCR	Star	271.5	-535.0	0.00447	0.0669
	GLS Grafen's $\rho = 0.468$	328.6	-647.1	0.00260	0.0510
LSCR	Star	243.6	-479.2	0.00584	0.0764
	GLS Grafen's $\rho = 0.568$	318.3	-626.7	0.00287	0.0535
SCR	Star	277.5	-547.0	0.00423	0.0650
	GLS Grafen's $\rho = 0.595$	355.1	-700.2	0.00202	0.0449

Results are shown for the "star" model, which uses conventional regression analysis with no phylogenetic correction and under branch length transformations used in phylogenetic GLS models. ASCR, anterior semicircular canal radius; LSCR, lateral semicircular canal radius; MSE, mean squared error; PSCR, posterior semicircular canal radius; SCR, average semicircular canal radius; SEE, standard error of the estimate.

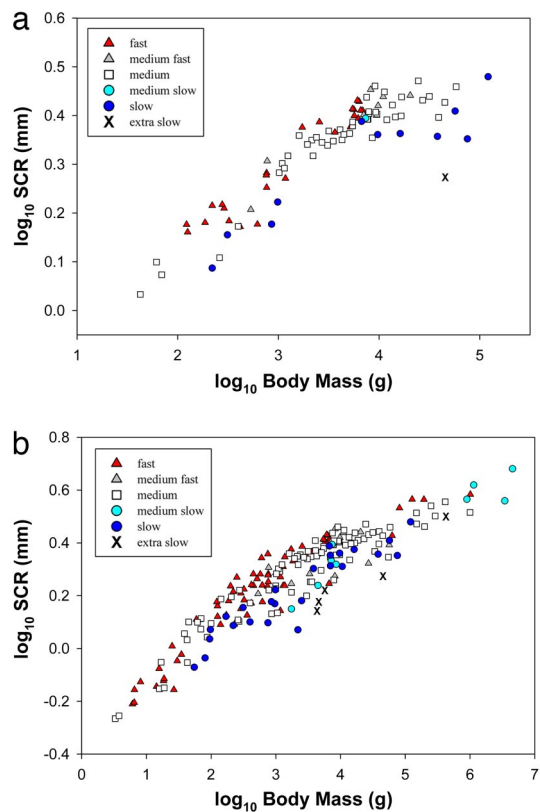


Fig. 1. Graphical relationship between canal sizes, body mass, and agility. Double logarithmic plots of mean [average semicircular canal radius (SCR)] canals against body mass for 91 primates (a) and 210 mammals (b).

Discussion

As can be seen in Fig. 1 and as demonstrated by phylogenetically informed statistical analyses, semicircular canal radius of curvature is positively correlated with agility of locomotion in primates and other mammals. Animals with faster or more agile locomotion have large canals relative to their body size, whereas animals with slower, more deliberate locomotion have small canals for their body size. This relationship between canal size and locomotor behavior is consistent across primates and other mammals representing a wide array of body sizes, life histories, and locomotor modes. As such, these findings confirm quantitatively what past studies suggested based on small samples and more incidental observations (9, 13–15, 17, 18).

The strong relationship between semicircular canal size and locomotor agility is clearly evident in a variety of primate groups. The leaping tarsiers and galagos have large canals relative to their body size, whereas the slow quadrupedal lorises, although of similar body size, lie on the lower end of the distribution with relatively small canals. At larger body masses, this relationship also holds. The acrobatic brachiating gibbons have relatively large canals for their body size, compared with the great apes. The sloth lemurs and koala lemurs have small canals for their body size, and *Palaeopropithecus* in particular has very small canals to match its reconstructed extremely slow locomotion.

In some cases, canal size does not seem to match expectations based on the locomotor behavioral classification. This could occur when a small, unrepresentative sample falls toward the margins of a species' morphological range of variation, especially when combined with a less secure estimate of body mass. It may also be that locomotor behavior was misclassified because certain aspects critical to the perception of angular rather than linear motion were not recognized. A possible example is *Ateles*

Table 3. Coefficients of the regression equations for the best-fit model for each canal: Primates

Canal	Variable	Coef	SE	F	df	P
ASCR	log ₁₀ BM	0.141	0.013	125.556	1, 88	<0.0001
	log ₁₀ AGIL	0.171	0.040	17.894	1, 88	<0.0001
	y intercept	-0.225	0.062	—	—	—
PSCR	log ₁₀ BM	0.134	0.010	193.261	1, 88	<0.0001
	log ₁₀ AGIL	0.172	0.033	27.962	1, 88	<0.0001
	y intercept	-0.249	0.047	—	—	—
LSCR	log ₁₀ BM	0.117	0.009	161.061	1, 88	<0.0001
	log ₁₀ AGIL	0.236	0.032	53.591	1, 88	<0.0001
	y intercept	-0.271	0.043	—	—	—
SCR	log ₁₀ BM	0.128	0.010	175.138	1, 88	<0.0001
	log ₁₀ AGIL	0.177	0.031	31.859	1, 88	<0.0001
	y intercept	-0.229	0.047	—	—	—

Coef, coefficient; ASCR, anterior semicircular canal radius; LSCR, lateral semicircular canal radius; PSCR, posterior semicircular canal radius; SCR, average semicircular canal radius; —, not applicable.

geoffroyi, which is classified as medium in agility, but its rather large canals fit well with its acrobatic behavior. Importantly, the three canals do not necessarily express locomotor behavior in equal measure, because this may depend on the planes of head motion involved. For example, during hominin evolution only the anterior and posterior canals enlarge with the emergence of modern-human-like bipedal locomotion (2). In contrast, tarsiers and galagos on the one hand, and lorises on the other are most distinct in lateral canal size. Likewise, the small lateral canal of *Alouatta seniculus* is consistent with its less agile behavior. However, its anterior canal appears unexpectedly large, possibly the consequence of spatial constraints of the subarcuate fossa (24), which opens into the endocranial cavity through the arc of the anterior canal, and houses a lobule of the cerebellum. In all, the species that most strikingly seem to contrast with the overall canal–agility correlation are the four callitrichids. These are classified as agile, but their anterior and lateral canals fall between the middle and lower end of the canal size distribution. It is unclear why this is, and more work will need to be done to understand the factors underlying this exceptional morphology.

In nearly all cases, the phylogenetic GLS models employing some type of branch length transformation outperformed both the star phylogeny (conventional regression) and the GLS method by using untransformed divergence times gathered from the literature. Of the three branch length transformations used, Grafen’s ρ and Pagel’s λ typically performed best. The addition of well dated extinct species throughout our phylogenetic tree

will result in more accurate reconstructions of the ancestral nodes, which in turn may then allow a better reconstruction of the evolution of characters. Nevertheless, as was found here, transformed trees may still perform better than those based on divergence times. This may be for a variety of reasons, including the presence of unavoidable measurement error in the estimates of species’ mean BM and canal radii (25).

The similarity of results between the conventional and the phylogenetic regression models indicates that the semicircular canal system holds a very strong functional signal related to head motion and locomotor agility. Such an apparently robust functional relationship across primates and other mammals suggests that adjusting arc size, and thus endolymph circuit length, constitutes a prime adaptive mechanism of how the canal system is tuned to the kinematic characteristics of different locomotor repertoires. This finding will contribute to a more fundamental understanding of the biomechanics of the canal system. On a more practical level, it confirms the potential utility of the semicircular canals for the reconstruction of behavior from fossil specimens.

Materials and Methods

The present sample has been collected from several sources [see [supporting information \(SI\)](#)]. Ninety-one species of primate are placed in a wider mammalian context of 210 species in total. Cetaceans were not included because they have a highly derived vestibular system compared with all other mammals, and other tetrapods (11, 20, 26). The mammalian sample included, in

Table 4. Coefficients of the regression equations for the best-fit model for each canal: All mammals

Canal	Variable	Coef	SE	F	df	P
ASCR	log ₁₀ BM	0.145	0.005	810.606	1, 207	<0.0001
	log ₁₀ AGIL	0.113	0.026	19.127	1, 207	<0.0001
	y intercept	-0.280	0.038	—	—	—
PSCR	log ₁₀ BM	0.149	0.005	927.291	1, 207	<0.0001
	log ₁₀ AGIL	0.119	0.026	21.253	1, 207	<0.0001
	y intercept	-0.344	0.035	—	—	—
LSCR	log ₁₀ BM	0.142	0.005	694.619	1, 207	<0.0001
	log ₁₀ AGIL	0.168	0.027	37.317	1, 207	<0.0001
	y intercept	-0.407	0.041	—	—	—
SCR	log ₁₀ BM	0.145	0.005	1005.332	1, 207	<0.0001
	log ₁₀ AGIL	0.128	0.023	30.653	1, 207	<0.0001
	y intercept	-0.338	0.035	—	—	—

Coef, coefficient; ASCR, anterior semicircular canal radius; LSCR, lateral semicircular canal radius; PSCR, posterior semicircular canal radius; SCR, average semicircular canal radius; —, not applicable.

particular, the canals of groups of arboreal and terrestrial eutherian and metatherian mammals with body masses in the primate range. Previously published measurements of some species that were compatible with those taken in the current study were added (12, 16–19, 27–30). Wild-shot specimens were used whenever possible, and the petrosal region of each was scanned by using medical or high-resolution computed tomography (CT) at a sufficiently high resolution for accurately measuring the canals.

We analyzed the extant primate sample together with the subfossil lemurs of Madagascar. These latter species have only become extinct very recently and can be regarded as part of the same ecological community as living lemurs (31, 32). Most of the subfossil lemurs were much larger than their living relatives and so extend the size range of strepsirrhines to that of large anthropoids. Locomotor reconstructions for the subfossil Malagasy lemurs were based on postcranial skeletal anatomy. The giant koala lemurs of the genus *Megaladapis* are very large footed, slow climbing animals with at least three species (33). The three genera of sloth lemurs are increasingly more adapted for suspensory locomotion in the order, *Mesopropithecus* (34), *Babakotia* (35), and *Palaeopropithecus*. The last of these, also the largest at the size of a chimpanzee, is a remarkably close mimic of the living South American sloths, with longer forelimbs than hindlimbs, very elongated curved hands and feet, and the loss of the necessary wrist and ankle stability for moving effectively on the ground (36, 37). The monkey-like lemurs of the Archaeolemuridae were large brained, stocky quadrupeds with dental adaptations that closely parallel those of Old World monkeys, and locomotor adaptations for ground living, although they were undoubtedly capable of moving arboreally (38).

Most of the smaller extant primate skulls were scanned on the OMNI-X high-resolution x-ray CT scanner at the Center for Quantitative Imaging at Pennsylvania State University with voxel dimensions ranging from ≈ 0.02 to 0.1 mm. Other specimens were scanned with CT scanners at various locations with voxel dimensions ranging from ≈ 0.07 to 0.5 mm. The CT images were cropped to the maximum extents of the bony labyrinth. By using VoxBlast 3.1 software (VayTek, Fairfield, IA), image stacks were resliced along the plane of each of the three canals. The height and width of each canal (16) were measured, and the radius of curvature was calculated as $R = 0.5 \times (\text{height} + \text{width})/2$. The species mean radius of curvature was used for all analyses. Body masses for primates were taken from Smith and Jungers (39) and for other mammals mainly from Silva and Downing (40). To test the hypothesis that canal radius is positively correlated with agility of locomotion, each taxon was assigned one of six agility categories, from extra slow (scored as 1) to fast (scored as 6), based on the field observations of three workers [J. Fleagle (Stony Brook University, Stony Brook, NY), S. McGraw (Ohio State University, Columbus, OH), and A.W.] and supplemented from the literature (41, 42) and video footage (see SI).

Regression analyses were performed independently on the primate sample and on the complete mammalian sample. Con-

ventional least-squares multiple regression analyses were run for \log_{10} transformed canal radius against \log_{10} BM and \log_{10} AGIL. AGIL was treated as a quantitative variable with increasing AGIL expected to correspond to increasing canal size.

For phylogenetic GLS analyses, phylogenies were constructed by using the results of molecular analyses, where possible, and branch lengths were taken from the paleontological literature or from molecular clock analyses (see SI). The phylogenetic trees for primates and all mammals were converted to variance–covariance matrices by using the PDDIST module of Phenotypic Diversity Analysis Programs (PDAP) in which the diagonals represented the branch length from the root to each tip species and the off-diagonals represented the branch length shared by pairs of tips (43–45). For each canal, multiple regressions were performed by using the phylogenetic GLS model for \log_{10} canal radius against \log_{10} BM and \log_{10} AGIL. GLS regression analyses were run by using the original branch lengths as well as after transforming the branch lengths by using the maximum likelihood estimates for the Ornstein–Uhlenbeck transform (45, 46), Grafen's ρ (47, 48), and Pagel's λ (49, 50), to determine the optimal regression model. Models were compared by using the natural logarithm (ln) ML likelihood and the AIC. The presence of phylogenetic signal in these data were tested by comparing the likelihoods for phylogenetic and nonphylogenetic regression analyses by using the AIC (51). A significantly lower AIC indicated a phylogenetic signal in the data. The three branch length transformations generally performed equally well and all gave significantly higher ML estimates than either the star phylogeny or the true divergence time branches. Pagel's λ branch length transformation generally yielded the highest ln ML estimates, although all three branch length transformations produced results that were equally robust with very similar values.

All statistical analyses were run by using the REGRESSIONv2.M program [available from A. R. Ives (University of Wisconsin, Madison, WI) and T.G.] in Matlab vR2006a (43, 52).

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Spoor *et al.* 10.1073/pnas.0704250104.

Supporting Information

Files in this Data Supplement:

[SI Data Set](#) = an Excel file that can be downloaded (04250Dataset.xls)

[SI Text](#)

SI Text

Phylogeny for All Mammals in Newick Format.

(Ornithorhynchus_anatinus:135.0,((Didelphis_virginiana:64.0,(Isoodon_obesulus:51.0,(((Phascolarctos_cinereus:21.0,Cercartetus_nanus:21.0):21.0,(((Trichosurus_vulpecula:25.0,(Ailurops_ursinus:19.5,(Spilococus_maculatus:14.0,Phalanger_orientalis:14.0):5.5):5.5):4.0,(Acrobates_pygmaeus:21.5,(Pseudocheirus_peregrinus:5.0,(Hemibelideus_lemuroides:4.0,Petauroides_volans:4.0):1.0):9.0,(Dactylopsila_trivirgata:9.5,(Petaurus_breviceps:5.0,Petaurus_norfolcensis:5.0):4.5):4.5):7.5):7.5):4.0,(Petrogale_penicillata:5.0,Macropus_fuliginosus:5.0):28.0):9.0):4.5,(Notoryctes_typhlops:36.0,(Phascogale_tapoatafa:24.3,(Sminthopsis_laniger:13.8,Sminthopsis_macroura:13.8):10.5):11.7):10.5):4.5):13.0):61.0,(((Elephas_maximus:15.0,Loxodonta_africana:15.0):47.0,Dugong_dugon:62.0):45.0,((((Bradypus_variegatus:9.0,Bradypus_tridactylus:9.0):9.0,Choloepus_hoffmanni:18.0):36.0,Tamandua_tetradactyla:54.0):9.0,Zaedyus_pichiy:63.0):39.0,((((Camelus_dromedarius:64.0,(Sus_scrofa:61.0,(Hippopotamus_amphibius:56.0,(Giraffa_camelopardalis:29.0,(Bos_taurus:23.0,(Gazella_bennetti:20.0,(Oryx_beisa:15.0,Ovis_aries:15.0):5.0):3.0):6.0):27.0):5.0):3.0):18.0,(Equus_caballus:56.0,Diceros_bicornis:56.0):25.0,(((Procyon_cancrivorus:28.0,(((Lutra_lutra:9.9,Enhydra_lutris:9.9):10.1,Mustela_nivalis:20.0):1.0,Taxidea_taxus:21.0):7.0):8.0,(Odobenus_rossicus:24.0,(Phoca_groenlandica:12.0,(Halichoerus_grypus:7.0,Phoca_vitulina:7.0):5.0):12.0):12.0):6.0,(Vulpes_vulpes:13.0,(Canis_familiaris:9.0,Nyctereutes_procyonoideus_viverrinus:9.0):4.0):29.0):13.0,(Herpestes_ichneumon:38.0,(Proteles_cristatus:35.0,(((Felis_catus:6.7,Puma/Felis_concolor:6.7):0.5,Lynx_rufus:7.2):3.6,(Panthera_tigris:3.72,Panthera_leo:3.72):7.08):24.2):3.0):17.0):26.0):1.0):1.0,(Pteropus_giganteus:59.0,Rhinolophus_cornutus_cornutus:59.0):6.0,(Eptesicus_fuscus:33.0,(Pipistrellus_pipistrellus:13.0,Nyctalus_lasipterus:13.0):20.0):20.0,(Myotis_lucifugus:43.0,Myotis_macroductylus:43.0):10.0):12.0):18.0):2.0,(Scalopus_aquaticus:41.0,Talpa_europaea:41.0):31.0,(Erinaceus_europaeus:55.0,(Blarina_brevicauda:27.5,(Sorex_hoyi:5.0,Sorex_cinereus:5.0):22.5):27.5):17.0):13.0):9.0,((((Castor_canadensis:53.5,(Pedetes_capensis:49.0,(Anomalurus_derbianus:24.6,(Idiurus_macrotis:12.3,Idiurus_zenkeri:12.3):12.3):19.9,(Dipus_sagitta:40.0,(Spalax_ehrenbergi:35.5,(((Ondatra_zibethicus:13.5,Microtus_pennsylvanicus:13.5):13.5,Peromyscus_man

iculatus:27.0):4.0,((Meriones_unguiculatus:13.5,Lophiomys_imhausi:13.5):13.5,(Rattus_norvegicus:16.0,Mus_musculus:16.0):11.0):4.0):4.5):4.5):4.5):4.5):16.5,(((Hydrochaeris_hydrochaeris:17.0,Cavia_porcellus:17.0):14.0,(Erethizon_dorsatum:29.0,(Chinchilla_laniger:25.0,Myocastor_coyppus:25.0):4.0):2.0):23.0,(Cryptomys_hottentotus_natalensis:5.0,Cryptomys_mechowi:5.0):49.0):16.0):4.0,((Ratufa_bicolor:7.0,Ratufa_macroura:7.0):29.0,((((Spermophilus_beecheyi:14.5,(Spermophilus_tridecemlineatus:10.7,(Spermophilus_richardsoni:1.3,Spermophilus_parryi:1.3):9.4):3.8):1.5,Marmota_monax:16.0):12.0,(Xerus_rutilus:7.0,Xerus_erythropus:7.0):21.0):6.0,((Petaurista_petaurista:18.0,Glaucomys_volans:18.0):5.0,(Sciurus_vulgaris:8.6,(Sciurus_richmondi:7.5,(Sciurus_niger:6.4,(Sciurus_aberti:5.3,(Sciurus_granatensis:2.8,Sciurus_carolinensis:2.8):2.5):1.1):1.1):1.1):14.4):11.0):2.0):38.0):9.0,(Lepus_europaeus:3.65,Oryctolagus_cuniculus:3.65):79.35):4.0,(((Cynocephalus_variegatus:22.1,Cynocephalus_volans:22.1):59.9,(Ptilocercus_lowii:45.0,(Dendrogale_murina:27.5,(Tupaia_minor:10.0,(Urogale_everetti:7.0,(Tupaia_glis:3.5,Tupaia_tana:3.5):3.5):3.0):17.5):17.5):37.0):4.5,((((Nycticebus_cougang:36.0,Loris_tardigradus:36.0):6.0,(Arctocebus_labarensis:36.0,Perodicticus_potto:36.0):6.0):13.0,((Galagoides_alleni:5.0,Galagoides_demidoff:5.0):25.0,(Galago_elegantulus:15.0,((Galago_moholi:5.0,Galago_senegalensis:5.0):3.0,(Otolemur_crassicaudatus:5.0,Otolemur_garnetti:5.0):3.0):7.0):15.0):25.0):14.0,(Daubentonia_madagascariensis:62.7,((((Megaladapis_madagascariensis:4.9994,Megaladapis_edwardsi:4.9994):31.0,(Varecia_variegata:32.0,((Lemur_catta:13.0,(Hapalemur_griseus:5.0,Hapalemur_simus:5.0):8.0):14.0,(Eulemur_macaco:10.0,(Eulemur_mongoz:8.0,Eulemur_fulvus_ssp.:8.0):2.0):17.0):5.0):4.0):2.0,(((Arc_haeolemur_edwardsi:19.9992,Hadropithecus_stenognathus:19.9986):10.5,((Avahi_laniger:24.0,(Indri_indri:13.0,(Propithecus_verreauxi:5.0,Propithecus_diadema:5.0):8.0):11.0):5.5,(Mesopropithecus_pithecoides:24.999,(Babakotia_radofilai:19.999,Palaeopropithecus_ingens:19.9995):5.0):4.5):1.0):4.5,Lepilemur_sp.:35.0):3.0):4.7,((Cheirogaleus_medius:9.0,Cheirogaleus_major:9.0):20.0,(Microcebus_murinus:9.0,Microcebus_rufus:9.0):20.0):13.7):20.0):6.3):8.0,((((Pongo_pygmaeus:11.3,(Gorilla_gorilla:6.4,(Homo_sapiens:5.4,(Pan_troglodytes:2.4,Pan_paniscus:2.4):3.0):1.0):4.9):3.7,((((Hylobates_klossii:3,Hylobates_moloch:3):3,Hylobates_lar:6):3,Hylobates_pileatus:9):3,Hylobates_hoolock:12):2,Hylobates_syndactylus:14):1.0):19.7,(((Macaca_sylvanus:5.6,((Macaca_nemestrina:3.0,(Macaca_nigra:1.5,Macaca_tonkeana:1.5):1.5):2.0,(Macaca_fascicularis:2.5,(Macaca_fuscata:1.5,(Macaca_cyclopis:1.0,Macaca_mulatta:1.0):0.5):1.0):2.5):0.6):4.2,((Mandrillus_sphinx:4.1,Cercocebus_torquatus:4.1):2.8,(Lophocebus_albigena:4.0,(Theropithecus_gelada:3.0,Papio_hamadryas_ssp.:3.0):1.0):2.9):2.9):1.8,((Chlorocebus_aethiops:5.0,Erythrocebus_patas:5.0):3.0,(((Cercopithecus_mitis:0.5,Cercopithecus_nictitans:0.5):0.5,Cercopithecus_cephus:1.0):0.5,(Cercopithecus_diana:0.5,Cercopithecus_mona:0.5):1.0):6.5):3.6):4.4,((Procolobus_badius:2.0,(Colobus_polykomos:1.0,Colobus_guereza:1.0):1.0):9.0,(((Trachypithecus_vetellus:1.0,Trachypithecus_obscurus:1.0):7.0,Semnopithecus_entellus:8.0):2.0,Nasalis_larvatus:10.0):0.5,Pygathrix_nemaues:10.5):0.5):5.0):18.7):8.9,(((Callimico_goeldi:14.0,(Callithrix_jacchus:13.0,(Leontopithecus_rosalia:10.4,Saguinus_oedipus:10.4):2.6):1.0):9.5,(Saimiri_sciureus:22.0,Cebus_apella:22.0):1.5):1.5,((Aotus_trivirgatus:22.0,(Callicebus_moloch:5.0,Callicebus_torquatus:5.0):17.0):1.0,((Cacajao_calvus:2.5,Cacajao_melanocephalus:2.5):5.5,Pithecia_pithecia:8.0):15.0):1.0,(Alouatta_seniculus:23.0,(Lagothrix_lagotricha:10.0,Ateles_geoffroyi:10.0):13.0):1.0):1.0):18.6):11.4,(Tarsius_syricta:6.5,Tarsius_bancanus:6.5):48.5):22.0):9.5):0.5):7.0):8.0):5.0):18.0):10.0);

Explanation of Mammal Phylogeny. The mammal phylogeny used in this study was constructed based primarily on molecular studies of relationships and divergence times. Priority in generating the phylogeny was placed on molecular studies. Morphological studies and the fossil record (1) were used to supplement the molecular phylogeny where necessary. The general relationships among major mammal groups were taken from Springer *et al.* (2, 3).

General relationships among primates and initial trees were taken from a variety of sources (4-9). A divergence date of 86 mya for Primates and (Scandentia-Dermoptera) was taken from Springer *et al.* (2). An estimate of 77 mya for the Strepsirrhine-Haplorhine split was used based on Springer *et al.* (2). The base of Strepsirrhines was placed at 69 mya from Yoder and Yang (10), the base of Lorisiformes at 55 from Yoder (8), and the base of Lemuriformes at 62.7 mya from Yoder and Yang (10). Internal branching patterns and divergence dates for Strepsirrhines based on several molecular studies (8, 10-12). The split between African and Asian lorises was set at 42 mya and the splits between the respective loris genera were set at 36 mya (12). The divergence between *Galagoides* and the *Galago-Otolemur* clade was set to 30 mya with the splits between *G. elegantulus* and the other bushbabies arbitrarily set to 15 mya. *Daubentonia* is set as the initial branch from the other Lemuriformes at 62.7 mya. The split between cheirogaleids and the rest of the Malagasy taxa is set at \approx 43 mya (10, 12). Internal branching dates within cheirogaleids after Yoder and Yang (10). Phylogenetic positions of the subfossil lemurs taken from Karanth *et al.* (11). Branch lengths for the subfossils are slightly shorter than contemporary to reflect their status as recently extinct. Estimates of last occurrence are from Burney *et al.* (13).

The base of the Haplorhines was set at 55 mya following Ross *et al.* (6) based on the presence of *Tarsius eoacaenus* at 45 mya (14). The platyrrhine-catarrhine split is placed at 43.6 mya based on the molecular data from Eizirik *et al.* (15). The platyrrhine relationships and branching dates largely follows the phylogeny and explanation used by Ross *et al.* (6) and based on molecular data (5, 16) and fossil evidence. The base of the platyrrhine radiation is set at 25 mya based on the initial appearance of platyrrhines in the fossil record during the early Miocene. The presence in the Miocene of fossils purported to belong to modern clades suggests a rapid radiation of known clades after 25 mya.

The divergence dates and branching patterns within catarrhines were based on both molecular and fossil evidence (5, 10, 17-21). The cercopithecoid-hominoid split was placed at 34.7 based on Yoder and Yang (10), which is similar to other estimates (15). The phylogeny of hylobatids was based Roos and Geissmann (22), and the divergence dates were arbitrary following the 15 mya split with hominids. The divergence dates within hominids were based on Stauffer *et al.* (19). Relationships and dates within cercopithecoids were based on both molecular and morphological sources (17, 18, 20, 21).

Detailed phylogenies and divergence dates were estimated for all other mammal groups in the study including Marsupialia (23-28), Xenarthra (29, 30), Cetartiodactyla (31), Carnivora (32, 33), Rodentia (34-42), Eulipotyphla (35, 43, 44), Chiroptera (45-48), and Scandentia (49, 50).

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