

Auditory Morphology and Hearing Sensitivity in Fossil New World Monkeys

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ABSTRACT

In recent years it has become possible to investigate the hearing capabilities in fossils by analogy with studies in living taxa that correlate the bony morphology of the auditory system with hearing sensitivity. In this analysis, we used a jack-knife procedure to test the accuracy of one such study that examined the functional morphology of the primate auditory system and we found that low-frequency hearing (sound pressure level at 250 Hz) can be predicted with relatively high confidence (± 3 –8 dB depending on the structure). Based on these functional relationships, we then used high-resolution computed tomography to examine the auditory region of three fossil New World monkeys (*Homunculus*, *Dolicocebus*, and *Tremacebus*) and compared their morphology and predicted low-frequency sensitivity with a phylogenetically diverse sample of extant primates. These comparisons reveal that these extinct taxa shared many auditory characteristics with living platyrrhines. However, the fossil with the best preserved auditory region (*Homunculus*) also displayed a few unique features such as the relative size of the tympanic membrane and stapedia footplate and the degree of trabeculation of the anterior accessory cavity. Still, the majority of evidence suggests that these fossil species likely had similar low-frequency sensitivity to extant South American monkeys. This research adds to the small but growing body of evidence on the evolution of hearing abilities in extinct taxa and lays the groundwork for predicting hearing sensitivity in additional fossil primate specimens. *Anat Rec*, 293:1711–1721, 2010. © 2010 Wiley-Liss, Inc.

Key words: low frequency sensitivity; middle ear; inner ear; auditory sensitivity; evolution of hearing

INTRODUCTION

The hearing capabilities of mammals are unique among vertebrates in that extant mammals are the only group of animals that can detect sounds in the ultrasonic range (>20 kHz) (Fay, 1988). And yet, many mammals can also hear extremely low-frequency sounds (e.g., elephants, whales, primates). It has been hypothesized that primitive mammals developed good high-frequency sensitivity, at the expense of low-frequency sensitivity, to improve auditory localization ability at small body size (Masterson et al., 1969). Sensitivity to high-frequency sounds (and good localization ability) is generally considered to be a key adaptation which aided the nocturnal, small-bodied early mammals in their struggle to coexist

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with thecodonts and dinosaurs (Jerison, 1973; Kermack and Mussett, 1983). Then, starting in the Paleocene and continuing through the Eocene, various taxa reacquired low-frequency hearing abilities whilst still retaining relatively good high-frequency sensitivity (Masterson et al., 1969). While this hypothesis has received some support from comparisons of living mammals (Masterson et al., 1969; Heffner and Masterson, 1970; Rosowski, 1992; Frost and Masterson, 1994), fossil evidence bearing on this question has been limited.

The first detailed study that attempted to reconstruct ancestral hearing patterns compared cochlear structure in extinct and living cetaceans and concluded that the specialized hearing of certain odontocetes related to echolocation (sonar) evolved during the Oligocene and was essentially similar to modern patterns by the Miocene (Fleischer, 1976). Later, Rosowski and Graybeal (1991) took a quantitative approach that compared the dimensions of a few middle and inner ear structures (tympanic membrane and stapedial footplate areas, basilar membrane length) with specific hearing parameters in a select group of living mammalian and avian species with known auditory abilities. They used these relationships to infer certain hearing characteristics of a Mesozoic mammaliform (*Morganucodon*) and suggested that early mammals like *Morganucodon* were likely sensitive to ultrasonic frequencies although a more narrow auditory range (5–7 kHz) of good sensitivity for this species could not be rejected.

A few different studies have investigated auditory function in mammals from the late Cretaceous. Meng and Fox (1995) concluded that marsupials and placentals from this period (~65 Ma) likely had high-frequency sensitivity similar to modern mammals based on an analysis of a dozen petrosal bones from Montana. In contrast, multituberculate petrosals from the same locality suggest that these extinct mammals were probably inefficient at perceiving high-frequency sounds (Fox and Meng, 1997). A similar conclusion was reached about slightly younger multituberculates from China (~55 Ma) based on both inner and middle ear structures (Meng and Wyss, 1995). However, the inner ears of two late Cretaceous multituberculates from Mongolia were interpreted to suggest that at least one genus (*Chulsanbaatar*) may have been able to hear relatively high frequencies (Hurum, 1998).

A couple of studies have predicted aspects of hearing in Pleistocene fossils. Blanco and Rinderknecht (2008) proposed that extinct “ground sloths” (*Lestodon armatus* and *Glossotherium robustum*) were most sensitive to very low frequencies based on the relatively large preserved middle ear elements (tympanic ring, malleus and incus). Lastly, analog electrical models of ear function based on bony outer and middle ear structures were used to predict that Middle Pleistocene fossil humans had similar hearing in the low and middle frequencies (=5 kHz) to living humans (Martínez et al., 2004).

In recent years, numerous studies on extant taxa have continued to refine our understanding of the functional morphology of the auditory system (West, 1985; Echterler et al., 1994; Coleman and Ross, 2004; Coleman, 2007; Manoussaki et al., 2008; Kirk and Gosselin-Ildari, 2009; Coleman and Colbert, 2010). The functional relationships identified by these studies permit certain aspects of hearing to be estimated with relatively high confi-

dence in fossils that preserve bony ear morphology. Consequently, it is becoming increasingly possible to use fossils to investigate the evolution of hearing patterns in various groups of animals and test proposed evolutionary patterns like that of Masterson et al. (1969). As illustrated earlier, terrestrial Cenozoic mammals are an understudied group of fossils that could provide considerable insight into the evolution of hearing. Primates represent a potentially fertile group for this type of study as they offer a relatively rich fossil record spanning the entire Cenozoic. The research presented here is the first in a series investigating auditory abilities in fossil primates and closely related taxa.

MATERIALS AND METHODS

Fossil Sample

Three fossil New World monkeys were examined in this study: *Homunculus patagonicus* (field number KAN-CL-04-1), *Dolichocebus gaimanensis* (MACN 14128), and *Tremacebus harringtoni* (type specimen). These three taxa come from early Miocene deposits of Argentina, between about 20 and 16.5 Ma (Fleagle et al., 1995, 1997; Kay et al., 1999; Tejedor et al., 2006; Kay, 2010). As such, these specimens provide a snapshot of the early stages of New World monkey evolution. High-resolution x-ray computed tomography (HRXCT) was used to construct 3D digital models of all preserved auditory structures and measurements were taken on the models.

A recently discovered *Homunculus patagonicus* cranium preserves the entire right ear region and most of the inner ear on the left side. The excellent state of preservation of this specimen permitted numerous auditory measurements to be taken including the length of the cochlea, the areas of the tympanic membrane and oval window, and the volumes of individual middle ear cavities. The *Dolichocebus gaimanensis* cranium preserves portions of both ears but due to distortion of the basicranium and complete infilling of matrix, lengths of the cochleae were the only measurements that could be estimated with confidence. The *Tremacebus harringtoni* cranium preserves only the inner ear and parts of the middle ear on the left side. Consequently, the length of the left cochlea was the only measurement that could be taken on this specimen.

CT scanning of these specimens was conducted at the HRXCT Facility at the University of Texas at Austin. The voxel dimensions of the CT scans for *Homunculus* measured $0.0449 \times 0.0449 \times 0.0484$, those for *Dolichocebus* measured $0.0422 \times 0.0422 \times 0.0466$, and those for *Tremacebus* measured $0.0420 \times 0.0420 \times 0.0466$. All measurements were taken using 3D Slicer 2.6 (Open Source, 2008). Thresholding protocols follow the HMH method outlined in Coleman and Colbert (2007). The specific measurement techniques for each structure are described by Coleman and Colbert (2010) but are briefly summarized below.

To measure the length of the cochlea and volume of the middle ear cavity, digital endocasts were created of these structures by filling their internal spaces using the “change island” function in 3D Slicer (Fig. 1). Cochlear length was measured by tracing the outer circumference of the endocasts (using the “fiducials” module) starting at the distal edge of the round window and continuing until the approximate location of the

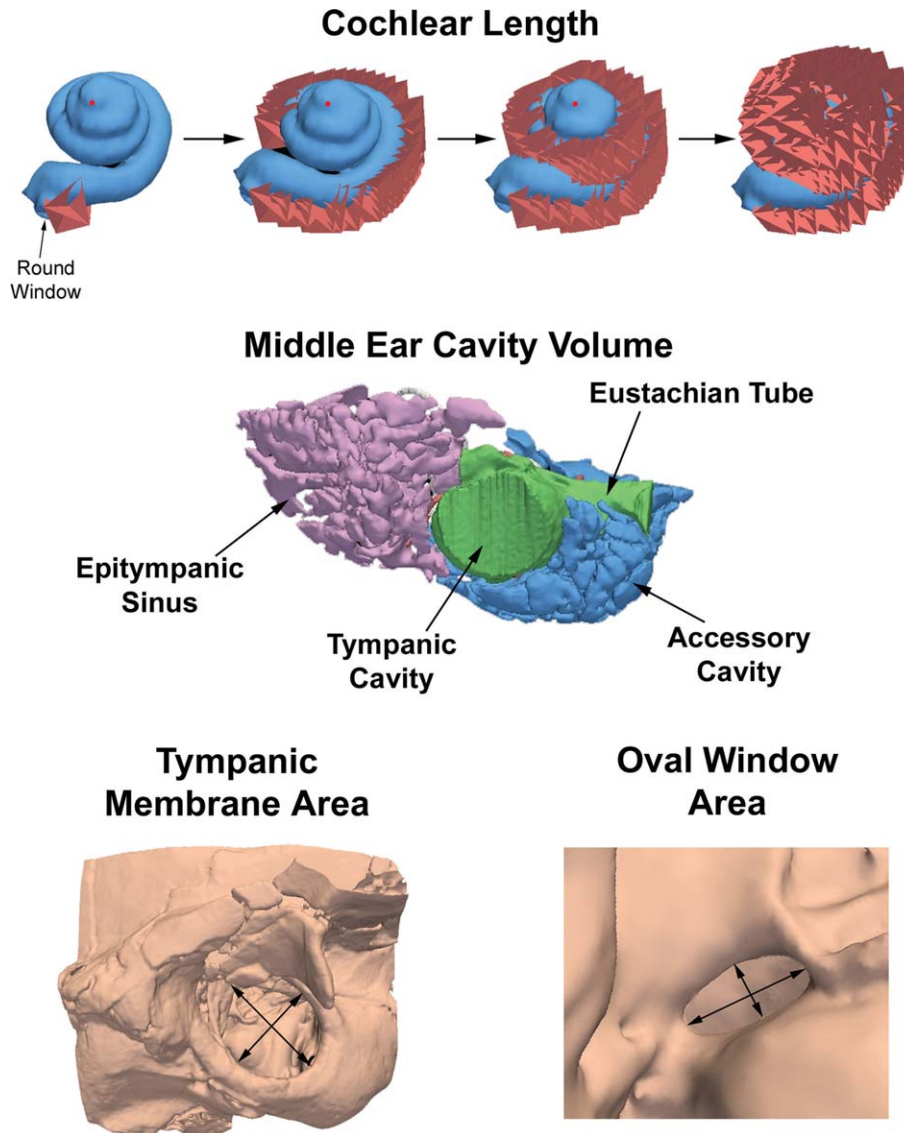


Fig. 1. Representative CT models demonstrating techniques used to measure cochlear length, middle ear cavity volume, tympanic membrane area and oval window area. Cochlear and middle ear cavity models are of *Saimiri*, tympanic ring and oval window models are of *Homunculus*. See text for more information about each measurement technique.

helicotrema. In addition, the number of spiral turns was counted (using the same starting and ending landmarks as for cochlear length) by placing a radial grid over 2D digital images of the cochlear endocasts in apical view.

Middle ear cavity volume was taken on the endocasts using the “measurevol” module in 3D Slicer. Total cavity volume was further divided into tympanic cavity volume (which included the space within the bony auditory tube), epitympanic sinus volume (which included mastoid and squamosal sinuses), and anterior cavity volume (which included the medial accessory cavity of lorisooids and the anterior accessory cavity of anthropoids—see MacPhee and Cartmill (1986) for definitions of these spaces). Tympanic membrane area and stapedial footplate area were estimated by creating 3D models of the middle ear and measuring two perpendicular axes along

the inner margins of the ectotympanic ring and oval window, respectively (Fig. 1), with the area calculated using the formula for an ellipse.

Extant Comparative Sample and Predictive Equations

The main comparative dataset that was used to analyze the fossil ears comes from data presented in Coleman and Colbert (2010). Although there are other studies on the functional morphology of primate ears (e.g., Kirk and Gosselin-Ildari, 2009) that could also be used to evaluate these fossils, Coleman and Colbert (2010) examined correlations between hearing sensitivity and auditory structures from both the middle and inner ears which permits all of the structures investigated

here to be analyzed with a single, internally consistent dataset. Their study sample was composed of all primate species (and one outgroup) for which hearing sensitivity data were available (Coleman, 2009) and included two platyrrhines (*Aotus* sp., *Saimiri* sp.), four catarrhines (*Macaca fascicularis*, *M. fuscata*, *M. mulatta*, *Papio cynocephalus*), two lemuroids (*Lemur catta*, *Phaner furcifer*), three lorisooids (*Galago senegalensis*, *Nycticebus coucang*, *Perodicticus potto*), and a tree shrew (*Tupaia glis*) (Order Scandentia). Coleman and Colbert (2010) found that low-frequency sensitivity was highly correlated with several auditory structures including cochlear length, tympanic membrane area, stapedial footplate area, and the volume of the middle ear cavity. In addition, supplementary data on tympanic membrane area and stapedial footplate area for numerous other extant primates were taken from revised estimates of the data presented in Coleman and Ross (2004). These data were measured using the same methods as described in Coleman and Colbert (2010) and provide tympanic membrane and stapedial footplate area measurements for 39 genera of primates including all 16 genera of extant New World monkeys (Appendix). The findings of these previous studies (Coleman and Ross, 2004; Coleman and Colbert, 2010) serve as the basis for our reconstruction of low-frequency sensitivity in the fossil taxa.

To evaluate the accuracy of the predictions of low-frequency sensitivity, a jack-knife procedure was employed. The exact method involved removing a species from the dataset, calculating the slope and intercept, and then comparing the predicted value using this slope and intercept with the actual value for the removed species. The auditory structures that were used for prediction included cochlear length, tympanic membrane area, stapedial footplate area, and middle-ear cavity volume and the measure of low-frequency sensitivity that was predicted was sound pressure level at 250 Hz (SPL at 250 Hz). Because Coleman and Colbert (2010) used both traditional (ahistoric) and phylogenetic comparative methods (phylogenetic independent contrasts—Felsenstein, 1985) to test for correlations, the results from both analyses were assessed. Although it is fairly straightforward to use regression analyses to predict unknown values using raw data, developing predictive statistics for phylogenetic methods is more involved.

The major difficulty in using phylogenetic independent contrasts for predicting actual species values relates to determining the y -intercept (Rohlf, 2001). Garland and Ives (2000) have shown that the y -intercept for a slope based on phylogenetic independent contrast data can be estimated by forcing the regression line through estimates of the root node values for the x and y variables, expressed by the relationship:

$$b = y^{\text{RN}} - (m * x^{\text{RN}})$$

where b is the intercept, y^{RN} is the root node value of the y variable, m is the phylogenetically adjusted slope, and x^{RN} is the root node value of the x variable. Once the intercept is determined, the phylogenetically adjusted slope can be used in the standard slope-intercept form for a linear equation ($y = mx + b$) to predict raw species values. The root node values for x and y variables were calculated using the “trace characters” func-

TABLE 1. Jack-knife procedure results showing mean differences between known and predicted values for SPL at 250 Hz using tympanic membrane area (TMA), stapedial footplate area (SFA), middle-ear cavity volume (MEV), and cochlear length (CL) as the predictive variables

Variable	Raw	PIC
TMA	6.750	7.375
SFA	4.875	5.625
MEV	7.750	8.375
CL	3.125	6.125
Mean	5.625	6.875

In all cases, the predictions made using raw data outperformed those using phylogenetic independent contrasts (PIC).

tion in Mesquite 1.12 (Maddison and Maddison, 2006). Ancestral character states were reconstructed using squared-change parsimony and the slope was based on least squares regression.

The mean differences for all jack-knife comparisons between the actual and predicted values for SPL at 250 Hz are given in Table 1. All variables were slightly better predictors using raw data than using predictions from phylogenetic independent contrasts. Regressions using raw data generally produced higher coefficients of determination and higher y -intercept values than the regression lines defined using phylogenetic independent contrasts (Fig. 2). These results suggest that the method used here to estimate the y -intercepts for phylogenetically adjusted regression lines may be underestimating the true intercept values. Therefore, the estimates of low-frequency sensitivity in fossils presented later were based solely on the predictive equations derived using raw data.

RESULTS

Mean values for the auditory structures measured in the fossils are given in Table 2, along with the values for the extant species that were measured using CT data. The results for those structures preserved only in *Homunculus* (tympanic membrane area, stapedial footplate area, middle ear cavity volume) will be presented first. Based on absolute values (Appendix), tympanic membrane area in *Homunculus* (23.7 mm²) falls within the range of values for extant platyrrhines, but is most similar to the value for *Callimico* (24.8 mm²). However, when the log of tympanic membrane area is regressed against the log of body mass (Fig. 3a), *Homunculus* appears to have a slightly smaller eardrum than expected based on body size (body mass estimates for *Homunculus* (1860g) derived using molar size data from Fleagle (1990) and predictive equations presented in Meldrum and Kay (1997)). This result could be skewed by overestimates of the body mass in this taxon or underestimates of tympanic membrane size, but the current data suggest that *Homunculus* had a tympanic membrane area that was proportionately smaller than living primates. Assuming a value of 23.7 mm², *Homunculus* has a predicted sound pressure level at 250 Hz (SPL at 250 Hz) of 31.9 dB (± 17 dB).

Oval window area was the most difficult measurement to take on the fossil specimens. This was due primarily

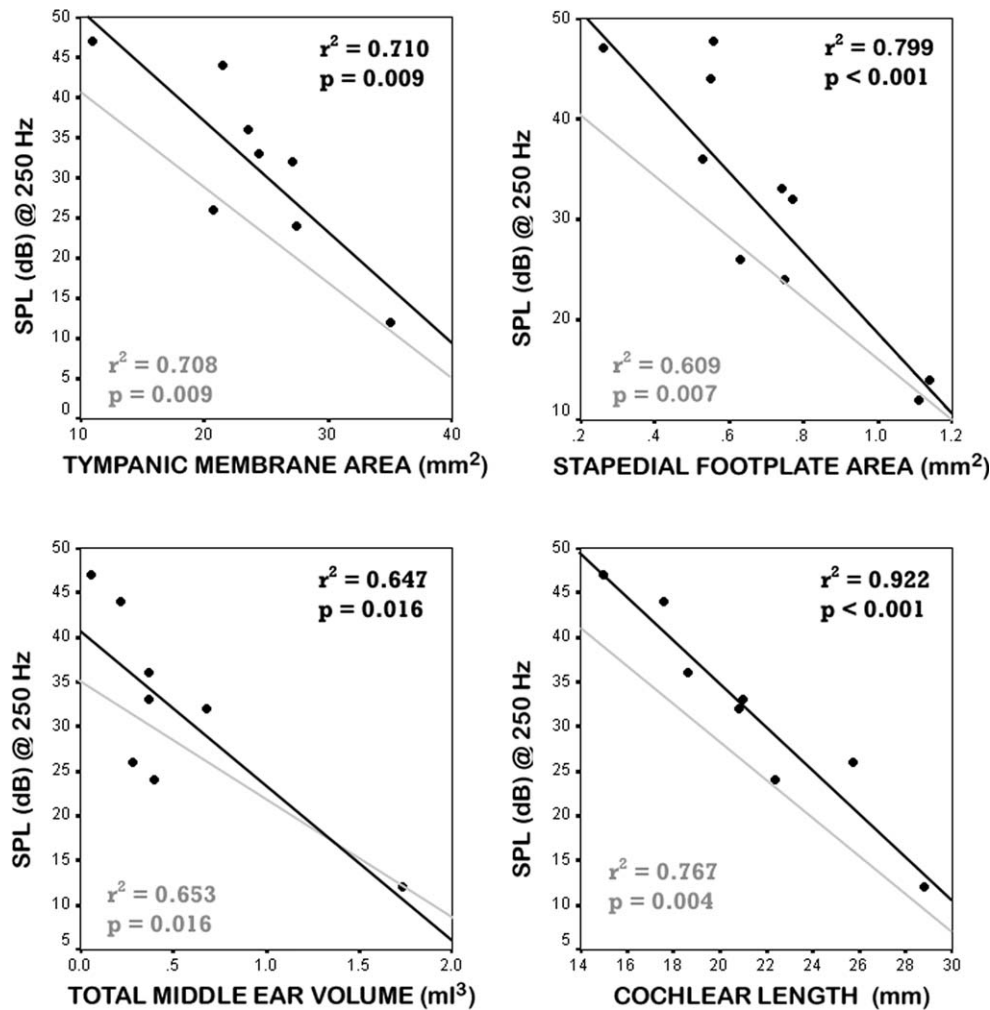


Fig. 2. Regression lines for four auditory variables versus SPL at 250 Hz computed using both raw (black lines) and phylogenetic independent contrasts (grey lines) data. In all cases except for middle ear volume, the regression lines computed using raw data show higher coefficients of determination.

to the small size of the measurements being taken (relative to the voxel dimensions) and the fragile nature of the edge of the oval window where the footplate of the stapes actually attaches. Still, estimates were obtained for *Homunculus* producing a mean value of 0.61 mm². The calculated area of the right (0.57 mm²) and left (0.65 mm²) oval windows show relatively good agreement, suggesting this is a reasonable estimate. As with tympanic membrane area, the raw values for stapedial footplate area fall within the range for extant platyrrhines but when compared with body mass (Fig. 3b), *Homunculus* apparently had an oval window (and stapedial footplate) that was relatively smaller than most of the extant taxa examined. Using stapedial footplate area, *Homunculus* has a predicted value for SPL at 250 Hz of 35.6 dB (± 14.8 dB).

Coleman and Colbert (2010) also detected a significant relationship between stapedial footplate area and one measure of high-frequency sensitivity (SPL at 32 kHz, $r^2 = 0.579$), although the correlation coefficient was lower than with SPL at 250 Hz and the relationship was

nonsignificant using phylogenetic comparative methods. Still, stapedial footplate area provides a first estimate of high-frequency sensitivity and the value for *Homunculus* produces a predicted value for SPL at 32 kHz of 13.4 dB (± 12.6 dB). This estimate is very similar to the values for *Saimiri* (14.3 dB) and *Aotus* (14.0 dB) which is not too surprising considering the similarity in size of the stapedial footplate among these New World taxa. In comparison, the range of values of SPL at 32 kHz for Old World monkeys is higher (22–39 dB), suggesting less high-frequency sensitivity, while those for lemurs (8–14 dB), lorises (7–23 dB) and tree shrews (6.6 dB) are generally lower, suggesting better sensitivity in this range.

One variable that has long been considered to be functionally relevant for hearing sensitivity is the areal convergence ratio (Helmholtz, 1885; Wever and Lawrence, 1954; Dallos, 1973; Hemilä et al., 1995). This ratio is calculated as the tympanic membrane area divided by the oval window area (stapedial footplate area). It models the increase in pressure produced by the smaller surface

TABLE 2. Auditory measurements taken on fossils along with the values from the extant comparative CT dataset from Coleman and Colbert (2010)

Taxon	TMA	SFA	MEV	TCV	ESV	ACV	CL	CS
<i>Homunculus patagonicus</i>	23.7	0.61	0.48	0.1	0.18	0.2	24.6	3
<i>Dolichocebus gaimanensis</i>							24.4	3 1/8
<i>Tremacebus harringtoni</i>							22	2 3/4
<i>Aotus</i> spp.	27.4	0.75	0.4	0.07	0.12	0.22	22.4	2 3/4 - 3
<i>Callitrix jacchus</i> ^a	20.5	0.56	0.15	0.05	0.05	0.05	20.3	2 1/2 - 2 7/8
<i>Saimiri</i> spp.	20.7	0.63	0.28	0.04	0.09	0.16	25.7	2 7/8 - 3
<i>Cercopithecus mitis</i> ^a	47.3	1.25	1.85	0.16	1.17	0.52	30.9	3 - 3 1/8
<i>Macaca fascicularis</i>	35	1.11	1.73	0.11	1.17	0.45	28.8	2 7/8 - 3 1/8
<i>Eulemur fulvus</i> ^a	27.1	0.67	0.39				21.2	2 1/2
<i>Lemur catta</i>	27.1	0.77	0.68				20.8	2 3/8 - 2 1/2
<i>Galago senegalensis</i>	21.5	0.55	0.22	0.08	0.1	0.03	17.6	2 1/2 - 2 3/4
<i>Nyctcebus coucang</i>	23.5	0.53	0.37	0.06	0.23	0.07	18.6	2 1/8 - 2 1/2
<i>Perodicticus potto</i>	24.4	0.74	0.37	0.06	0.21	0.09	21	2 1/4 - 2 1/2
<i>Tupaia glis</i>	11	0.26	0.06				15	2 3/4 - 3

^aPreviously unpublished data [all measurements made using the same methods as described in Coleman and Colbert (2010)]. TCV, tympanic cavity volume; ESV, epitympanic sinus volume; ACV, anterior cavity volume; CS, number of cochlear spirals. All other abbreviations are as in Table 1.

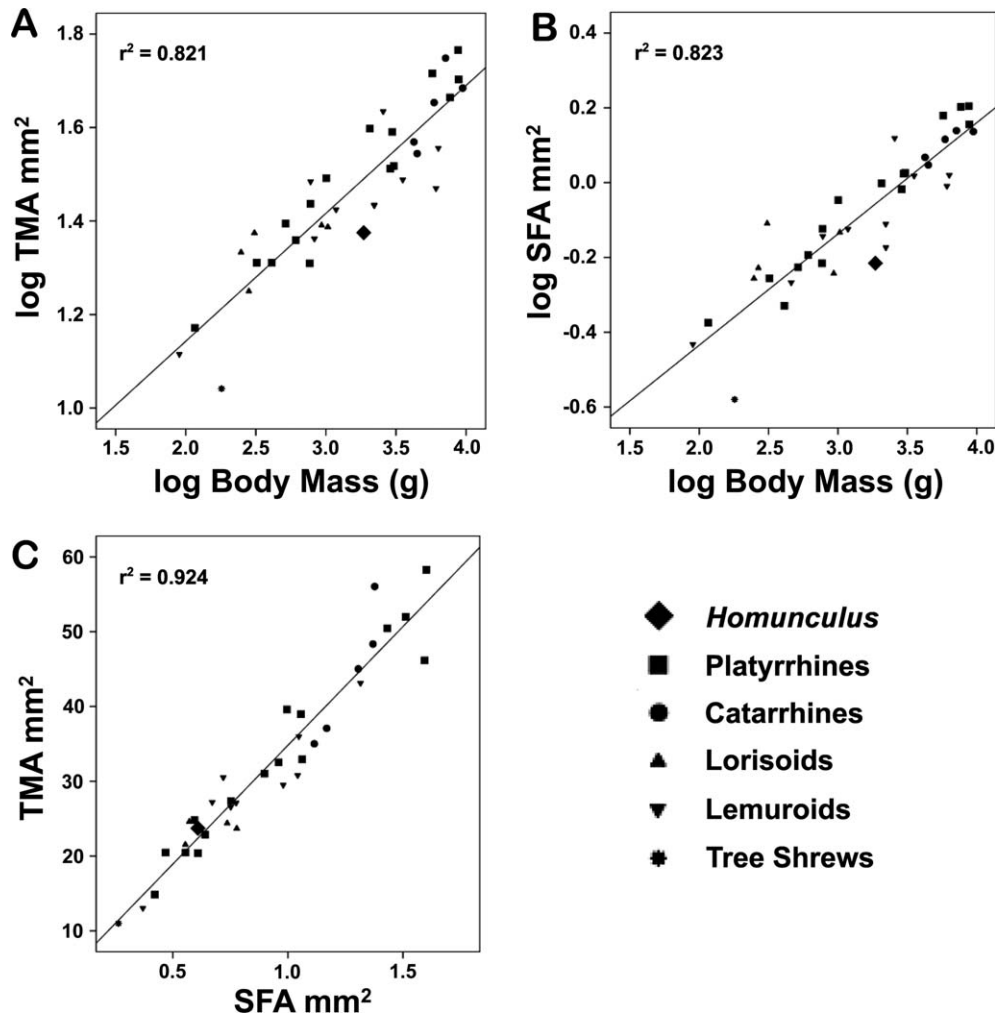


Fig. 3. Scatterplots showing tympanic membrane and oval window areas of *Homunculus* compared with extant primates. All extant body mass data from Smith and Jungers (1997).

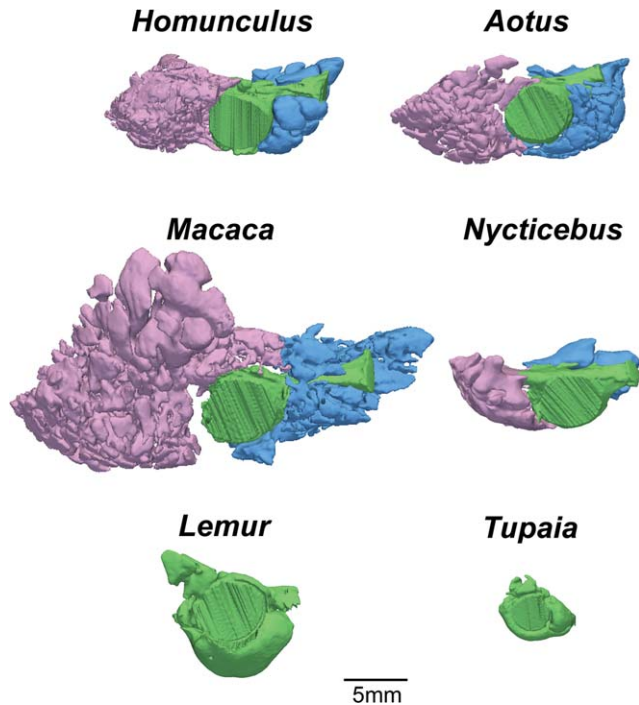


Fig. 4. CT endocast models of middle ear cavities in *Homunculus* and representatives of extant superfamilies examined here. Tympanic cavities are green, epitympanic sinuses are purple, and anterior cavities are blue.

area of the stapedial footplate compared with that of the eardrum. Figure 3c shows tympanic membrane area regressed against stapedial footplate area. In this comparison *Homunculus* falls close to but just above the overall primate regression line, suggesting that *Homunculus* is like most other primates in its areal convergence ratio.

The middle ear cavities of *Homunculus* are remarkably well preserved. Figure 4 shows a CT model of the *Homunculus* middle ear along with representative models for each of the major groups (superfamilies) examined here. As this figure demonstrates, the majority of the internal architecture (i.e., trabeculae) remains intact in *Homunculus* allowing for reasonable estimates of cavity volume. The only region that appears to be slightly damaged is the upper lateral aspect of the mastoid cavity, though the cortical bone in this region is perfectly preserved. Since some of the trabeculae seem to be broken or missing in this area, measurements of epitympanic sinus volume may be slightly overestimated. Compared with *Aotus*, *Saimiri*, and *Callithrix* (Table 2), *Homunculus* has a larger total middle ear cavity volume (0.48 mL) and epitympanic sinus volume (0.18 mL). This may be related to the slightly larger estimated body mass of *Homunculus* (compared with the extant comparisons) although the difference may also be partially influenced by slight overestimates of epitympanic sinus volume in this fossil, as mentioned earlier.

Homunculus apparently demonstrates a distinctive platyrrhine pattern (among primates) in having the largest portion of middle ear volume within the anterior (accessory) cavity. In the comparative sample examined here, both catarrhines and lorisooids show the largest

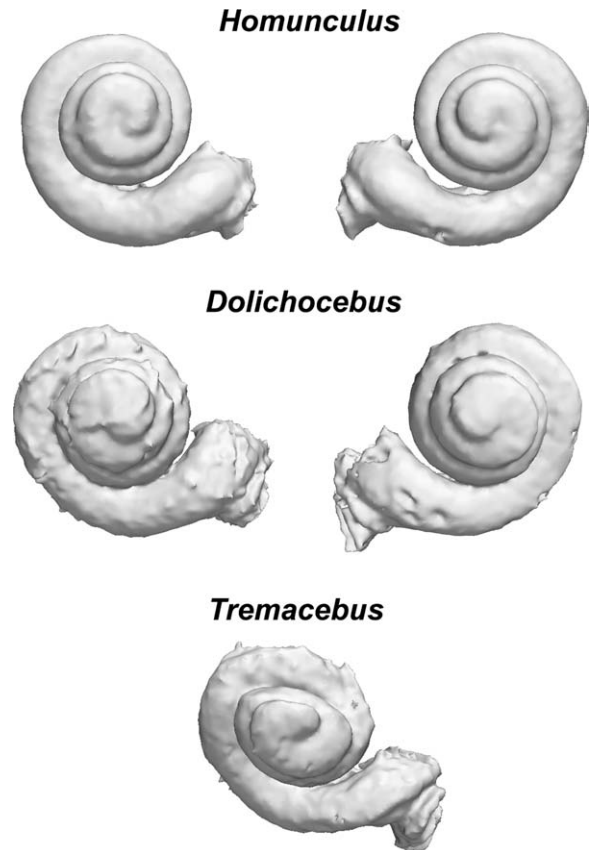


Fig. 5. CT endocast models of cochleae for the three fossil platyrrhines examined here. The models for *Homunculus* and *Dolichocebus* are very similar and show the excellent preservation of the auditory region in these specimens but the model for *s* appears to illustrate some compression along the superior edges of the spirals.

portion of middle ear volume within the epi tympanic sinus while lemuroids and *Tupaia* are essentially devoid of any sinuses other than the tympanic cavity itself. The main difference between sampled catarrhines and platyrrhines is that the epitympanic sinus of Old World monkeys invaginates into both the mastoid and squamosal portions of the tympanic bone while in New World monkeys pneumatization is limited almost exclusively to the mastoid. Sherwood (1999) found that chimpanzees and gorillas also show substantial invagination of the squamosal region, suggesting that this may be a typical platyrrhine-catarrhine distinction although more taxa need to be sampled before generalizing about the groups as a whole. Based on the value for total middle ear cavity volume (0.48 mL), *Homunculus* has a predicted SPL at 250 Hz of 32.3 dB (± 18.8 dB) and using the value for anterior cavity volume (0.20 mL) gives a predicted value of 27.1 dB (± 10.9).

Cochlear length was the only measurement that could be taken on all three fossil specimens (Table 2). The cochlea is frequently the best preserved region of the auditory system in fossils and these specimens attest to this preservation bias. Figure 5 shows the endocasts that were used to estimate cochlear length and it can be seen that, in general, these cochleae are intact. This is

TABLE 3. Predicted values of SPL at 250 Hz for the fossil specimens using cochlear length (CL), total middle ear cavity volume (MEV), anterior cavity volume (ACV), tympanic membrane area (TMA), and stapedial footplate area (SFA)

	CL	MEV	ACV	TMA	SFA
<i>Homunculus</i>	23.6 ± 9.1	32.3 ± 18.8	27.1 ± 10.9	31.9 ± 17.0	35.6 ± 14.8
<i>Dolichocebus</i>	24.1 ± 9.1				
<i>Tremacebus</i>	29.9 ± 8.9				

particularly true of the *Homunculus* cochleae which show 3 full spiral turns and produced a mean value of 24.6 mm for cochlear length. The individual values for the right and left cochleae were very similar with the right cochlea measuring 24.4 mm and the left cochlea measuring 24.8 mm. Using the mean value (24.6), *Homunculus* yields a predicted value of 23.6 dB (± 9.1 dB) for SPL at 250 Hz.

The cochleae of *Dolichocebus* show many resemblances to those of *Homunculus*, and had an average length of 24.4 mm and just over 3 spiral turns. The CT scans revealed several cracks in the left cochlea of *Dolichocebus*, which produced some artifacts in the digital endocast (Fig. 5). However, the length of the left cochlea (24.6 mm) was only marginally longer than that of the right cochlea (24.2 mm), indicating this slight damage did not greatly impact the length measurement. Using a length of 24.4 mm for *Dolichocebus*, the predicted value for SPL at 250 Hz is 24.1 dB (± 9.1 dB).

The left cochlear endocast for *Tremacebus* produced a measurement of 22 mm. The CT scans for *Tremacebus* do not seem to demonstrate any substantial damage to the auditory region in this specimen, but the cochlear endocast (Fig. 5) appears to show some distortion (compression) along the superior borders of the first, second and third spirals (turns). This potential artifact could be caused by the partial infilling of matrix in this specimen, although attempts to take this into account did not remedy the (apparent) problem. Therefore, it is possible that this measurement underestimates the true length of the cochlea. However, the *Tremacebus* cochlea does appear to demonstrate only $\sim 2 \frac{3}{4}$ spiral turns, which is about $\frac{1}{4}$ turn less than in the other two species suggesting it may be somewhat shorter. In any case, using a value of 22 mm, the predicted sound pressure level at 250 Hz is 29.9 dB (± 8.9 dB).

DISCUSSION

The auditory structures in *Homunculus*, *Dolichocebus* and *Tremacebus* are similar in many ways to those found in living primates, particularly the platyrrhines in our sample. The length of the cochlea in all three fossil specimens falls within the range of the extant platyrrhines examined here. In addition, the proportions and configuration of the middle ear cavities in *Homunculus* strongly resemble the patterns found in living South American monkeys. One interesting distinction in middle ear cavity structure between *Homunculus* and its extant counterparts is in the degree of trabeculation of the anterior (accessory) cavity. Instead of displaying the honeycomb-like pattern typical of modern anthropoids, *Homunculus* shows fewer struts and exhibits more of a septated pattern similar to the way lorisooids divide their mastoid cavities (Fig. 4). This finding suggests that the

relatively dense trabecular bone found in the anterior accessory cavity of both catarrhines and platyrrhines (Ross, 1994) may have developed independently. It also raises the possibility that the ancestral condition of anthropoids for this structure was nontrabeculated, which could impact discussions related to the homology of the anterior accessory cavity in tarsiers and anthropoids (e.g., Packer and Sarmento, 1984; MacPhee and Cartmill, 1986; Simons and Rasmussen, 1989; Ross, 1994). However, before this possibility can be evaluated, more studies are needed on the variability of trabecular development in living anthropoids and its expression in geologically older fossils.

The other minor differences between *Homunculus* and extant platyrrhines were in the areas of the tympanic membrane and oval window. Based on the estimated body mass for this species, *Homunculus* appears to have had a relatively small tympanic membrane and stapedial footplate. In contrast, *Homunculus* does demonstrate a typical primate value for the areal convergence ratio (tympanic membrane area / oval window area), although the utility of this parameter to predict auditory sensitivity is open to question (Coleman and Colbert, 2010). Considered collectively, the general characteristics of the group of auditory structures measured here imply that fossil platyrrhines had low-frequency hearing sensitivity that was similar to that of living platyrrhines. Still, there are also hints that the auditory system may have undergone subtle modifications in crown platyrrhines, including a slight increase in relative tympanic membrane and oval window areas and increased trabeculation in the anterior cavity, possibly "fine-tuning" the fundamentally modern patterns illustrated by the fossils.

The predicted values for SPL at 250 Hz in the fossil specimens provide significant support for the idea that extinct platyrrhines had modern levels of sensitivity to low-frequency sounds. Table 3 provides a summary of the predicted values for all of the auditory structures that were investigated. Predictions using cochlear length had the lowest overall estimates and also had the smallest confidence intervals, although this last finding is not unexpected since cochlear length produced the highest coefficient of determination of any structure examined ($r^2 = 0.922$). Anterior cavity volume also predicted a relatively low value for SPL at 250 Hz (27.1 dB) and showed reduced confidence intervals compared with the other structures (except cochlear length). The other three variables (total middle ear volume, tympanic membrane area, oval window area) predicted sound pressure levels that were a bit higher (31.9–35.6 dB) and were associated with considerably larger confidence intervals. It should be noted that the predicted value for *Homunculus* using cochlear length falls within the range of predictions for all other structures. However, the predicted

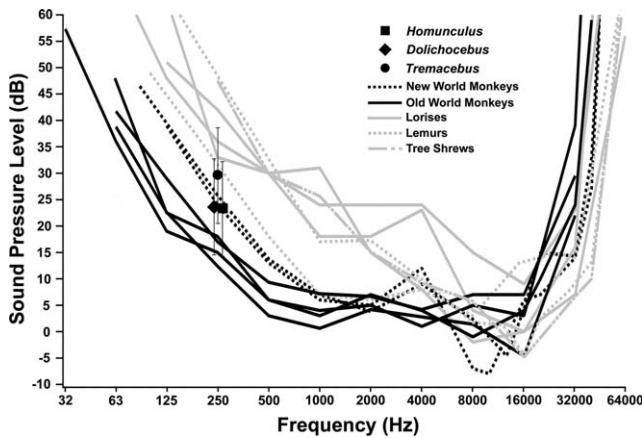


Fig. 6. Predicted low frequency sensitivity (SPL at 250 Hz) for all three Miocene platyrrhines based on cochlear length along with the audiograms for extant primates from Coleman (2009).

value using oval window area is outside of the range of the values derived using cochlear length and furthermore, the predicted values for middle ear volume and tympanic membrane area are just at the upper limits of the cochlear length prediction.

These several facts suggest that cochlear length may provide the best overall estimate of low-frequency hearing: (1) cochlear length shows the strongest correlation with SPL at 250 Hz in extant taxa (Coleman and Colbert, 2010); (2) cochlear length demonstrates the highest predictive accuracy in the jack-knife procedure presented above; (3) the confidence intervals associated with cochlear length predictions are narrower than for any other variable; (4) the predicted value using cochlear length was comfortably encompassed by the ranges for the other variables although the opposite was not always the case.

The predicted values of SPL at 250 Hz (using cochlear length) for all three fossil specimens are shown in Figure 6, along with the hearing curves (audiograms) for primates from Coleman (2009). The predicted values for *Homunculus* and *Dolichocebus* are nearly identical to the two platyrrhines (*Aotus* and *Saimiri*) for which hearing sensitivity is known. The upper range for the confidence intervals does not overlap with the lorisooids that have been tested but there is slight overlap with one of the lemuroids (*Lemur catta*). The lower bounds of the confidence intervals also show some overlap with catarhines. The relatively wide confidence intervals are partially the product of using single specimens for species predictions (predictions based on mean values would have reduced the confidence intervals to just over ± 3 dB). Still, the predictions for both specimens fall essentially on the audiograms for extant platyrrhines and there is limited overlap with other groups, strongly suggesting that *Homunculus* and *Dolichocebus* had low-frequency sensitivity very much like living representatives of this group.

The predicted value for *Tremacebus* falls above the extant platyrrhine audiograms (indicating less sensitivity) and the confidence intervals overlap with two lorisooids and *Lemur catta* but also with the platyrrhines. Although this finding suggests that *Tremacebus* had

low-frequency hearing that was intermediate between platyrrhines and lorisooids, it should be kept in mind that the cochlear length measurement for this specimen is in question since it appears that some postdepositional distortion has compressed part of the cochlea. Therefore, it remains uncertain whether *Tremacebus* is unlike the other fossil platyrrhines sampled, displaying less sensitivity than extant New World monkeys, or whether the length of its cochlea has been underestimated.

With this reservation in mind, the preponderance of evidence presented above suggests that the early Miocene New World monkeys investigated here had low-frequency hearing sensitivity comparable to extant platyrrhines. The size of the oval window in *Homunculus* also suggests that fossil New World monkeys may have had similar high-frequency sensitivity to modern forms. These findings parallel other lines of cranial and postcranial evidence that show that living platyrrhines retain numerous characteristics possessed by their fossil ancestors (Fleagle, 1999). However, recent analyses have found that the fossil taxa examined here are likely not directly related to any of the modern genera of New World monkeys living today (Kay et al., 2008). Therefore, good low-frequency sensitivity (and possibly good high-frequency sensitivity) would seem to be a primitive platyrrhine trait that dates back at least 20 Ma.

While these results do not directly test the idea that mammals went through a low-frequency bottleneck phase during the early Cenozoic as part of achieving good high-frequency hearing (Masterson et al., 1969), they do support the notion that mammals had achieved modern-levels of low-frequency hearing by the end of the Eocene (or at least by the Miocene). Good low-frequency sensitivity is an essential part of the communication system in animals that use low-frequency, long-distance vocalizations. For example, blue monkeys (*Cercopithecus mitis*) have been shown to use low-frequency vocalizations that are adapted to the rainforest environments in which they live (Brown et al., 1995), and the audible range of these calls is greatly increased by the heightened low-frequency hearing sensitivity in this species (Brown and Waser, 1984; Brown, 1986).

However, if mammals did go through a low-frequency bottleneck phase during the evolution of modern hearing patterns, this could have had considerable implications on the evolution of vocal communication, predator-prey interactions and the development of hearing specializations. A transition to good high- and poor low-frequency hearing would likely have been paralleled by a shift to higher vocalization frequencies: a lack of good low-frequency sensitivity make it improbable that early mammals were able to use low-frequency, long-range communication signals like those that are utilized by many species of mammals today. Therefore, forested environments during the early part of the Cenozoic may have sounded quite different from those of recent times. Our results indicate that at least the auditory component of the communication system in fossil New World monkeys was developed to the degree that would have permitted the use of long calls like those that resonate through the South American forests today (e.g., howler monkey roars, titi monkey duet calls).

However, before we can begin fully exploring the implications of the evolutionary sequence articulated by Masterson et al., (1969), additional research is needed

on fossils from the Paleocene-Oligocene to better understand the hearing patterns which characterized early members of the modern orders of mammals.

CONCLUSIONS

This study examined correlations between auditory morphology and hearing sensitivity in living primates to predict certain aspects of hearing sensitivity in early Miocene New World monkeys. Among the structures investigated, the length of the cochlea provides the most accurate predictions of low-frequency sensitivity, which is fortunate considering the relative abundance of inner ears (petrosals) in the fossil record. Based on these findings, we show that the low-frequency sensitivity of fossil New World monkeys was likely very similar to living platyrrhines, although some fine-tuning of the auditory system may have occurred in crown groups. This suggests that primates had developed low-frequency hearing similar to modern forms by at least the early Miocene, which generally agrees with ideas about the evolution of hearing in mammals. However, to fully understand the timing and development of hearing patterns in primates (and mammals), additional studies are needed that sample fossils from key transitional periods during primate evolution. Research is currently underway investigating a broad sample of Paleogene primate fossil taxa to help fill this void.

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APPENDIX

Revised estimates of tympanic membrane area (TMA) and stapedial footplates area (SFA) data from Coleman and Ross (2004)

Taxon	TMA	N	S.D.	SFA	N	S.D.	BM
<i>Alouatta</i> spp.	51.99	29	4.82	1.51	22	0.14	5738
<i>Aotus</i> spp.	27.36	105	2.84	0.75	30	0.07	775
<i>Arctocebus calabarensis</i>	23.69	2	2.33	0.78	2	0.11	309
<i>Ateles</i> spp.	58.28	27	6.98	1.60	14	0.24	875
<i>Avahi laniger</i>	26.57	4	0.92	0.75	1		1180
<i>Brachyteles arachnoides</i>	50.45	3	2.24	1.43	1		8840
<i>Cacajao</i> spp.	32.93	25	4.03	1.06	3	0.03	3050
<i>Callicebus</i> spp.	31.03	20	3.34	0.90	9	0.11	1005
<i>Callimico goeldii</i>	24.81	5	2.27	0.59	3	0.09	516
<i>Callithrix jacchus</i>	20.46	48	1.60	0.56	6	0.04	321
<i>Cebuella pygmaea</i>	14.84	5	1.42	0.42	2	0.05	116
<i>Cebus</i> spp.	38.96	76	3.86	1.06	29	0.14	2977
<i>Cercopithecus</i> spp.*	45.02	5	3.77	1.31	6	0.14	5915
<i>Chiropotes satanus</i>	32.52	19	3.00	0.96	5	0.12	2885
<i>Chlorocebus aethiops</i>	37.08	2	1.18	1.17	2	0.01	4240
<i>Daubentonia madagascariensis</i>	43.11	5	2.65	1.31	2	0.17	2560
<i>Erythrocebus patas</i> *	48.35	4	7.23	1.37	3	0.12	9450
<i>Eulemur</i> spp.*	27.20	42	2.14	0.67	2	0.00	2215
<i>Euoticus elrgantulus</i>	17.78	2	0.21				282
<i>Galago senegalensis</i>	21.53	42	1.79	0.55	9	0.05	248
<i>Hapalemur griseus</i>	23.02	13	2.18				827
<i>Indri indri</i>	35.98	5	2.89	1.05	2	0.18	6335
<i>Lagothrix lagotricha</i>	46.16	13	3.66	1.59	3	0.21	7683
<i>Lemur catta</i>	27.12	26	2.16	0.77	13	0.10	2210
<i>Leontopithecus rosalia</i>	22.86	12	2.76	0.64	6	0.07	609
<i>Lepilemur mustelinus</i>	30.51	8	3.30	0.72	5	0.15	777
<i>Lophocebus albigena</i> *	56.04	1		1.38	1		7135
<i>Loris tardigradus</i> *				0.59	2	0.05	267
<i>Macaca fascicularis</i> *	35.01	8	2.94	1.11	8	0.12	4475
<i>Microcebus murinus</i>	13.04	8	4.27	0.37	2	0.11	90
<i>Nycticebus</i> spp.*	24.59	8	4.49	0.57	5	0.06	932
<i>Perodicticus potto</i>	24.40	29	2.25	0.74	12	0.05	1032
<i>Phaner furcifer</i>				0.54	1		460
<i>Pithecia</i> spp.	39.60	24	4.55	1.00	8	0.11	2060
<i>Propithecus</i> spp.	29.51	17	2.83	0.98	2	0.12	6100
<i>Saguinus</i> spp.	20.47	17	1.07	0.47	4	0.07	411
<i>Saimiri</i> spp.	20.40	85	2.09	0.61	19	0.06	766
<i>Tupaia glis</i> *	11.00	6	1.38	0.26	6	0.07	180
<i>Varecia variegata</i>	30.79	18	1.80	1.04	1		3533

Species marked with asterisks indicate previously unpublished data for that species. The methods used to produce these revised estimates are the same as those employed by Coleman and Ross (2004). All body mass (BM) data from Smith and Jungers (1997).