

Evolution of locomotion in Anthroidea: the semicircular canal evidence

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Our understanding of locomotor evolution in anthropoid primates has been limited to those taxa for which good postcranial fossil material and appropriate modern analogues are available. We report the results of an analysis of semicircular canal size variation in 16 fossil anthropoid species dating from the Late Eocene to the Late Miocene, and use these data to reconstruct evolutionary changes in locomotor adaptations in anthropoid primates over the last 35 Ma. Phylogenetically informed regression analyses of semicircular canal size reveal three important aspects of anthropoid locomotor evolution: (i) the earliest anthropoid primates engaged in relatively slow locomotor behaviours, suggesting that this was the basal anthropoid pattern; (ii) platyrrhines from the Miocene of South America were relatively agile compared with earlier anthropoids; and (iii) while the last common ancestor of cercopithecoids and hominoids likely was relatively slow like earlier stem catarrhines, the results suggest that the basal crown catarrhine may have been a relatively agile animal. The latter scenario would indicate that hominoids of the later Miocene secondarily derived their relatively slow locomotor repertoires.

Keywords: vestibular system; generalized least-squares analysis; primates

1. INTRODUCTION

The fossil record documenting anthropoid evolution over the last 40 million years (Ma) is comparatively rich, but the locomotor behaviours of many taxa remain poorly understood owing to a paucity of well-preserved, relevant postcranial remains. In the fossil record, the presence of cranial remains preserving inner ear structures, in particular the semicircular canals, presents an opportunity to generate an alternative set of locomotor reconstructions throughout the Cenozoic in the absence of

postcranial material, and to provide an independent test of competing hypotheses about locomotor mode in taxa known from the postcranium [1–3]. The semicircular canals are three bony tubes in the otic capsule surrounding membranous ducts that are part of the organ of balance [4]. The semicircular canal system detects angular rotations of the head as an animal moves through the environment, and coordinates posture and body movements during locomotor activities in conjunction with otolithic, visual and proprioceptive information [5–7]. Recent experimental work has demonstrated a strong relationship between canal size and the afferent sensitivity of the vestibular nerve [8,9]. It has also been demonstrated that mammalian semicircular canal arc size scales with body mass (BM) with strong negative

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2012.0939> or via <http://rspb.royalsocietypublishing.org>.

allometry and that the residuals of this regression are positively correlated with locomotor agility [1–3,10].

Here, we reconstruct locomotor agility in 16 fossil anthropoid species dating from the Late Eocene to the Late Miocene based on semicircular canal size and provide new insights into the evolution of anthropoid locomotion over the last 35 Ma. Our analysis provides an insight into three important questions regarding phases in the evolution of anthropoid primates. First, we reconstruct locomotor agility in the earliest undisputed anthropoids of the Late Eocene and Early Oligocene from the Fayum Depression of northern Egypt (*Catopithecus browni*, *Proteopithecus sylviae*, *Apidium phiomense*, *Parapithecus grangeri*) and, in doing so, identify one aspect of the likely primitive locomotor mode for anthropoids. Second, we reconstruct the locomotor behavioural adaptations in five fossil platyrrhine species, most of which have no attributed postcranial material: *Dolichocebus gaimanensis*, *Homunculus patagonicus*, *Lagonimico conclucatus*, *Tremacebus harringtoni* and *Chilecebus carrascoensis*. Using these data, we reconstruct the basal locomotor adaptation in platyrrhines and the dynamics of their subsequent radiation in the New World since the Oligocene. Finally, we reconstruct locomotor agility in fossil catarrhines both predating (*Aegyptopithecus zeuxis*, *Saadanius hijazensis*) and post-dating (*Victoriapithecus macinnesi*, *Proconsul heseloni*, *Rudapithecus hungaricus*, *Hispanopithecus laietanus* and *Oreopithecus bambolii*) the cercopithecoid–hominoid split to determine the locomotor behavioural changes associated with this divergence and the likely basal locomotor adaptations of both Old World monkeys and apes.

2. MATERIAL AND METHODS

Semicircular canal radii of curvature for the fossil specimens used in this study were measured from computed tomography (CT) scan data following established protocols [1–3]. The CT scan data were collected from a variety of sources using high-resolution CT (see electronic supplementary material, table S1). The radius of curvature was measured for each canal following methods used in previous studies [1–3,11]. A species mean radius of curvature was calculated for taxa with multiple fossil specimens and was used for all subsequent statistical analyses. The fossil specimens and their BMs, taken from the literature or estimated based on available regression equations, are given in the electronic supplementary material, table S2. One caveat with respect to the interpretation of our *Apidium* sample is that all three specimens assessed here are isolated petrosals, not associated with dental or postcranial material. They are attributed to *Apidium* based on primate anatomy, size and the high relative abundance of that taxon in the relevant deposits. However, until more complete cranial material is known for the genus, these attributions must remain provisional. One specimen (YPM 25972) that has been referred to both *Apidium* [12] and *Aegyptopithecus* [13,14] is identified here as pertaining to the latter genus based on semicircular canal size and shape, both of which fall within that genus' range based on specimens that include dentitions.

The fossil taxa were compared with a sample of 91 extant and recently extinct primate species (subfossil lemurs were included as part of the modern strepsirrhine radiation) used in a previous analysis of semicircular canal size in

which both conventional and phylogenetically informed multiple regression analyses were used to demonstrate a significant relationship between canal size and agility of locomotion [2]. Spoor *et al.* [2] assigned agility scores to the modern taxa based on the field observations of several primatologists, supplemented from the literature [15,16] and from video footage. These scores were based on the estimated typical angular accelerations of the head in locomotion because this is the variable of significance to the semicircular canal system. The terms 'agile' or 'acrobatic' as used in this manuscript are descriptive terms referring to this agility scoring system. A relatively more acrobatic or agile animal would have a comparatively higher agility score. Results and descriptions for fossil taxa should be interpreted within the framework of the scores assigned to the large sample of extant primate species [2].

A phylogenetic generalized least-squares (pGLS) regression approach [17–19] was used to predict locomotor agility in fossil specimens using the semicircular canal size data. For the extant primate taxa, phylogenies were constructed using the results of molecular analyses, where possible, and branch lengths were taken from the palaeontological literature or from molecular clock analyses [1–3]. Each fossil taxon was placed on this extant primate cladogram based on current hypotheses regarding the phylogenetic relationships of each species (see electronic supplementary material for phylogenetic tree). Branch lengths for the fossil taxa on this tree were estimated based on the ages of the localities from which the fossils were recovered. The pGLS method used here should provide a more robust prediction of locomotor agility in fossil taxa than an equation derived from a multiple linear regression because it accounts for the hypothesized phylogenetic relationships of each fossil specimen.

A pGLS analysis [17,18] was performed to predict the unknown agility values for each fossil by regressing \log_{10} agility (AGIL) against both \log_{10} BM and \log_{10} semicircular canal radius. The error terms in the pGLS were modelled by multivariate normal distributions whose variance–covariance matrices were determined by the phylogenetic topology and its corresponding branch lengths. The dependent variable, \log_{10} AGIL, was defined as Y , with X representing the data matrix of the two independent variables, BM and semicircular canal radius. The pGLS model can therefore be written as:

$$Y = X\beta + \varepsilon, \quad (2.1)$$

where β 's are regression coefficients and ε 's are the error terms, whose variance–covariance matrix is proportional to the distance matrix of the transformed phylogenetic tree (D). For the purpose of predicting unknown agility values for fossil specimens, the mean and the confidence intervals of the predicted value from the joint distribution of estimated Y , \hat{Y} were obtained.

The pGLS regression analyses were run for each canal and the mean canal using the original branch lengths and after transforming the branch lengths using the maximum-likelihood estimates for Grafen's arbitrary method [17] and Pagel's arbitrary method [20] to determine the optimal regression model. Models were compared using the ln maximum likelihood (ML) and the Akaike Information Criterion (AIC) [21]. The three analyses using different branch lengths generally performed equally well, but Pagel's arbitrary branch length transformation yielded the highest maximum-likelihood estimates. All statistical analyses were performed

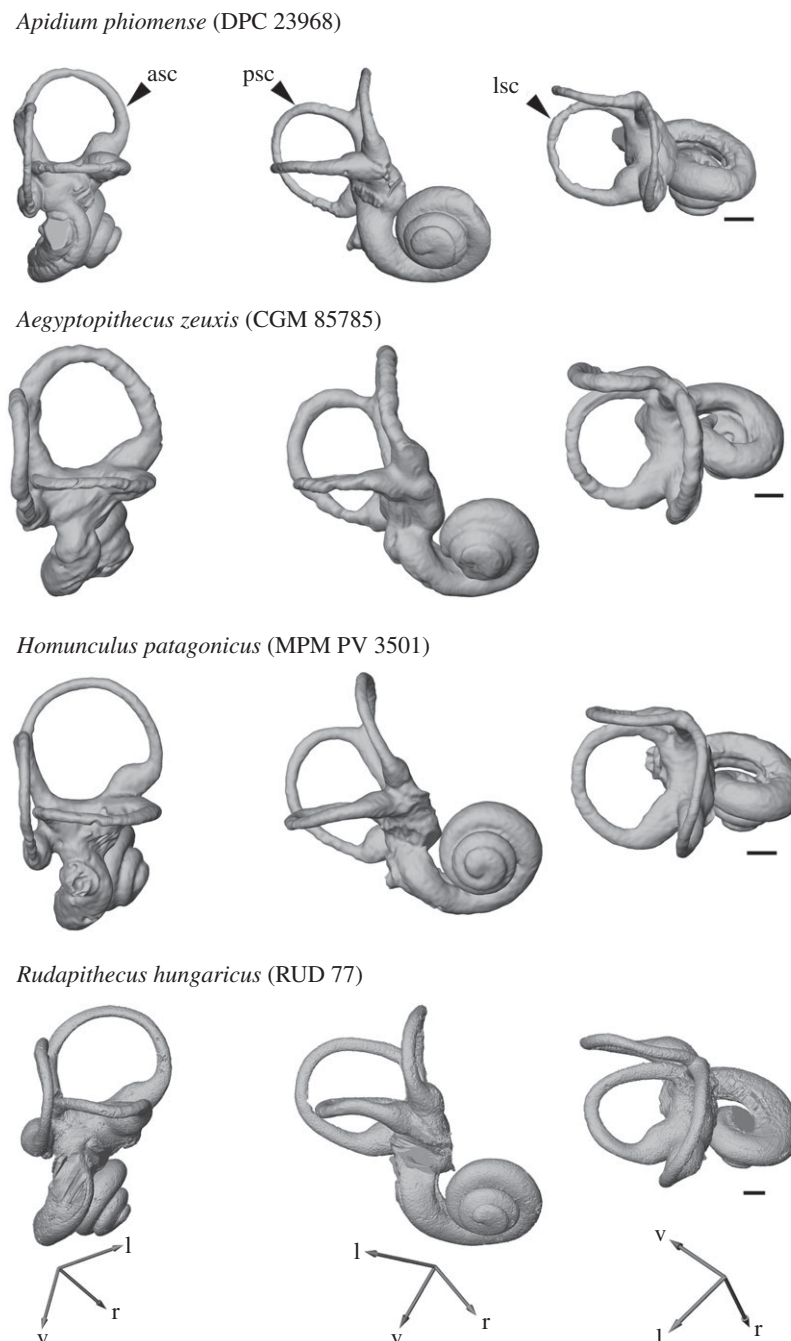


Figure 1. Three-dimensional reconstructions of bony labyrinths from several fossil specimens used in this study. Reconstructions are scaled for body mass (BM) based on the primate regression for the mean canal radius. Each view is perpendicular to the depicted canal, labelled as follows in the top row: asc, anterior semicircular canal; psc, posterior semicircular canal; lsc, lateral semicircular canal. Axes on bottom provide general anatomical orientation for each canal view: l, lateral; r, rostral; v, ventral. Note that reconstruction for *Apidium phiomense* is reversed for display.

using the PDTREE and PDDIST packages [22–25] and the custom code pGLS written in R [26].

3. RESULTS

Semicircular canal measurements of each fossil specimen are listed in the electronic supplementary material, table S2 and three-dimensional reconstructions of four fossil specimens are shown in figure 1. Double logarithmic plots of canal size against BM in extant and fossil taxa reveal distinct patterns of variation in locomotor agility across fossil anthropoids (figure 2; electronic supplementary material, figure S1). The pGLS regression analyses of

$\log_{10}AGIL$ against both $\log_{10}BM$ and \log_{10} radius of curvature for the primate sample using Pagel's arbitrary branch lengths are highly significant for each canal and the mean canal radius (table 1). The ML estimates and the AIC obtained for each model indicate that correlations are strongest for the lateral canal (AIC: -163.4 ; see electronic supplementary material, table S3).

The fossil anthropoids analysed here clearly fall into the range of variation of modern primates, making agility reconstructions based on extant taxa relatively robust. Predicted agility scores based on the pGLS regression analyses for each canal radius are listed in table 2. Most of the agility patterns as predicted in the literature are

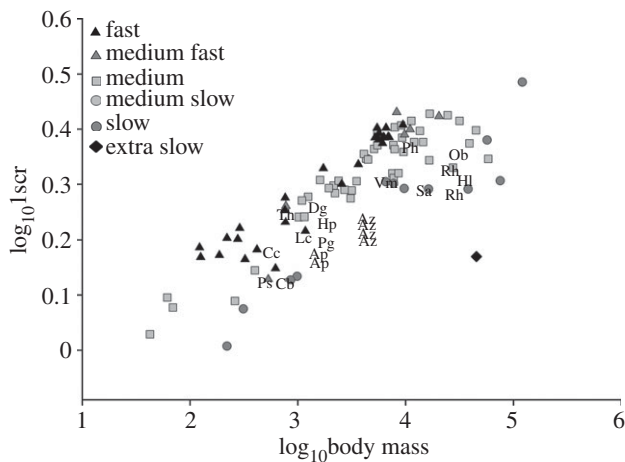


Figure 2. Relationship between lateral semicircular canal size, BM and agility in extant and extinct primates. Legend for extant taxa provided in the figure. Fossil taxa: Cb, *Catopithecus browni*; Ps, *Proteopithecus sylviae*; Ap, *Apidium phiomense*; Az, *Aegyptopithecus zeuxis*; Pg, *Parapithecus grangeri*; Dg, *Dolichocebus gaimanensis*; Hp, *Homunculus patagonicus*; Lc, *Lagonimico conclucatus*; Th, *Tremacebus harringtoni*; Cc, *Chilecebus carrascoensis*; Sa, *Saadanius hijazensis*; Vm, *Victoriapithecus macinnesi*; Ph, *Proconsul heseloni*; Ob, *Oreopithecus bambolii*; Hl, *Hispanopithecus laietanus*; Rb, *Rudapithecus hungaricus*.

supported by our reconstructions (table 2 and figure 3). This relatively high degree of correspondence with existing evidence for locomotor behaviours strongly suggests that the methods used here produce accurate reconstructions of locomotor agility.

The canal radius results suggest that the early anthropoids from the Fayum, Egypt, were generally medium slow to medium (table 2), with a relative lack of diversity in locomotor agility. The results for platyrrhines suggest that early members of this clade were adapted for more agile locomotor behaviours, although none appear to have been as fast as extant leaping primates. The results for *Ch. carrascoensis* generally confirm those of Ni *et al.* [73] who suggest that this taxon was similar to extant generalized quadrupeds, including other small-bodied platyrrhines such as *Leontopithecus rosalia*, *Saguinus oedipus* or *Callithrix jacchus*. Our predicted agility scores for *Ch. carrascoensis* similarly suggest a quadrupedal primate of medium speed, and in lateral semicircular canal radius, this taxon plots closest to *Le. rosalia*, *S. oedipus* and *Ca. jacchus* among the extant platyrrhines.

Among fossil catarrhine primates, *Aegyptopithecus* and *Saadanius* appear to retain the early anthropoid pattern of medium slow locomotion. The early cercopithecoid, *V. macinnesi*, as well as the basal hominoid, *P. heseloni*, are both reconstructed as relatively more agile than these earlier catarrhines. The apes of the later Miocene, *O. bambolii*, *R. hungaricus* and *Hi. laietanus*, all have relatively small canals for their BM, indicating slower, less agile locomotor behaviour.

4. DISCUSSION

The evidence from the semicircular canals suggests that the earliest anthropoids dating to the Late Eocene and Early Oligocene of Egypt were all medium to medium

slow in their locomotion. These predictions generally match the hypothesized locomotor behaviours based on postcranial fossil evidence for these Fayum taxa. *Catopithecus*, *Parapithecus* and *Aegyptopithecus*, all predicted to be slow or medium in agility based on postcranial evidence, are also reconstructed as medium to medium slow based on semicircular canal size. *Proteopithecus*, predicted to be an agile arborealist [27–30], is reconstructed as the fastest of the Fayum anthropoids based on the semicircular canal data. The extant taxon to which *Proteopithecus* appears most similar in the lateral canal plot is *Callimico goeldi*, a relatively agile, arboreal New World monkey. In contrast, the results for *Apidium* are somewhat surprising and contradict expectations. Postcranial remains of *Apidium* display adaptations to leaping [29,31–36], suggesting this taxon was an agile arborealist. The semicircular canal size data, however, suggest a slower animal more similar to other Fayum anthropoids such as *Catopithecus*, *Parapithecus* and *Aegyptopithecus*. In totality, these results suggest that the basal locomotor adaptation in anthropoids may have been relatively slow and deliberate rather than fast (figure 3). Perhaps as a result of a rapid radiation and diversification at the end of the Eocene, *Apidium*, along with many of the other Fayum taxa, retains a vestibular system reflective of this slow locomotor ancestry in spite of apparent adaptations to leaping in the postcranial skeleton.

In contrast to the earlier anthropoids of the Fayum, the fossil record for New World monkeys lacks significant postcranial remains. The semicircular canal results, therefore, represent the only available evidence for locomotor behaviour in many of these taxa. All five of the fossil species—*D. gaimanensis*, *Ho. patagonicus*, *La. conclucatus*, *T. harringtoni* and *Ch. carrascoensis*—are reconstructed as being relatively agile with scores of medium to medium fast. These results suggest that the common ancestor of these extinct platyrrhine taxa was an active and agile arboreal primate with locomotor behaviours most similar to those of the small-bodied callitrichids and cebids. On the basis of these semicircular canal data, we propose that basal platyrrhines underwent an early transition away from the relatively slow early anthropoid pattern to a more agile form of locomotion [30,74]. The subsequent radiation and diversification of platyrrhines in the New World may have begun from an agile, arboreal ancestor.

Locomotor abilities of early catarrhines are reconstructed here as predominantly medium to medium slow. A general similarity in relative canal size is evident among *Catopithecus*, *Aegyptopithecus* and *Saadanius*. In contrast to the platyrrhines, therefore, early members of the catarrhine clade retained the primitive anthropoid pattern of relatively slow to medium slow locomotion. Slow locomotor behaviours appear to be retained in most Miocene and recent hominids with the apparent exception of *P. heseloni*, which seems somewhat derived in canal size, especially compared with the similar-sized earlier catarrhine *Saadanius*. Relative canal size in *P. heseloni* is most similar to that of several species of medium-speed macaques (*Macaca tonkeana*, *Macaca fuscata*, *Macaca mulatta*), primarily quadrupedal taxa that engage in agile climbing and leaping at times [75].

This interpretation for *P. heseloni* differs from most locomotor reconstructions for the species based on postcranial fossil remains, which suggest it was a slow,

Table 1. Phylogenetic generalized least-squares regression results. ln ML, natural log maximum likelihood; AIC, Akaike Information Criterion; ASCR, anterior semicircular canal; PSCR, posterior semicircular canal; LSCR, lateral semicircular canal; SCR, mean semicircular canal; s.e., standard error.

canal	coefficient	s.e.	<i>T</i>	<i>p</i> -value	ln ML	AIC
ASCR					79.0	−150.0
(intercept)	1.080	0.120	9.025	<0.001		
logBM	−0.254	0.037	−6.916	<0.001		
logASCR	1.152	0.223	5.177	<0.001		
PSCR					76.9	−145.8
(intercept)	1.112	0.122	9.095	<0.001		
logBM	−0.254	0.039	−6.506	<0.001		
logPSCR	1.191	0.256	4.647	<0.001		
LSCR					85.7	−163.4
(intercept)	1.027	0.111	9.284	<0.001		
logBM	−0.231	0.030	−7.749	<0.001		
logLSCR	1.356	0.203	6.698	<0.001		
SCR					84.5	−161.1
(intercept)	1.083	0.113	9.617	<0.001		
logBM	−0.282	0.035	−8.010	<0.001		
logSCR	1.571	0.244	6.450	<0.001		

Table 2. Predicted agility measures based on semicircular canal radius using phylogenetic generalized least-squares models with Pagel's arbitrary branch length transformations. Agility measures are given on a six-point scale ranging from 1 (very slow) to 6 (fast). Agilities in brackets are hypothesized agilities based on postcranial remains taken from the literature.^a Colours indicate relative agility: blue, slow; yellow, medium; pink, fast. ASCR, anterior semicircular canal; PSCR, posterior semicircular canal; LSCR, lateral semicircular canal; SCR, mean semicircular canal.

taxon	ASCR	PSCR	LSCR	SCR	agility prediction (LSCR)
<i>Catopithecus browni</i>	—	3.0	3.3	—	medium slow (slow)
<i>Proteopithecus sylviae</i>	—	3.6	3.7	—	medium (fast)
<i>Apidium phiomense</i>	3.1	3.3	3.2	3.0	medium slow (fast)
<i>Parapithecus grangeri</i>	3.4	3.7	3.4	3.3	medium slow (medium)
<i>Aegyptopithecus zeuxis</i> (4400 g) ^b	3.2	3.1	3.0	3.0	medium slow (slow)
<i>Aegyptopithecus zeuxis</i> (2866 g) ^b	3.6	3.4	3.3	3.4	medium slow (slow)
<i>Dolichocebus gaimanensis</i>	4.5	4.5	4.3	4.4	medium
<i>Homunculus patagonicus</i>	5.0	4.5	4.1	4.5	medium fast (fast (46)—medium (48))
<i>Lagonimico conclucatus</i>	4.4	4.6	3.7	4.2	medium
<i>Tremacebus harringtoni</i>	4.5	5.4	4.8	4.9	medium fast
<i>Chilecebus carrascoensis</i>	4.2	4.2	4.1	3.9	medium
<i>Saadanius hijazensis</i>	2.6	3.0	2.9	2.8	medium slow
<i>Victoriapithecus macinnesi</i>	3.0	3.1	3.5	3.1	medium (medium)
<i>Proconsul heseloni</i>	2.9	2.9	3.8	3.2	medium (slow)
<i>Oreopithecus bambolii</i>	2.3	3.1	3.0	2.7	medium slow (slow)
<i>Hispanopithecus laietanus</i>	2.0	2.5	2.5	2.2	slow (slow)
<i>Rudapithecus hungaricus</i>	2.1	2.6	2.4	2.2	slow (slow)

^a*Catopithecus browni* [27–29], *Proteopithecus sylviae* [27–30], *Apidium phiomense* [29,31–36], *Parapithecus grangeri* [32,35,37,38], *Aegyptopithecus zeuxis* [28,32,35,39–41], *Dolichocebus gaimanensis* [35,42], *Homunculus patagonicus* [43–48], *Victoriapithecus macinnesi* [49–55], *Proconsul heseloni* [56–59], *Oreopithecus bambolii* [53,60–68], *Hispanopithecus laietanus* and *Rudapithecus hungaricus* [53,63,64,69–72].

^bAgility predictions for *Aegyptopithecus* including the isolated YPM 25972 petrosal are shown in parentheses.

deliberate arboreal quadruped [56–59]. In contrast, however, analyses of humeral and femoral diaphyseal strength suggest that *P. heseloni* had forelimb to hind limb strength proportions most similar to those of extant colobines [76]. Ruff [76] considered this limb bone diaphyseal pattern, with stronger femora than humeri, indicative of at least some leaping in *P. heseloni*, a locomotor reconstruction also partially supported by morphological features of the pedal phalanges [69]. On the basis of semicircular canal size and the various lines of postcranial evidence, we hypothesize that *P. heseloni* was an arboreal quadruped that at times engaged in some leaping, as seen in many cercopithecoids.

The results of the current analysis indicate that basal Old World monkeys (represented by *V. macinnesi*) and basal hominoids (represented by *P. heseloni*) were both relatively derived in vestibular morphology compared with earlier catarrhines pre-dating the ape–Old World monkey split (e.g. *Aegyptopithecus*, *Saadanius*). This derived condition in early members of both extant catarrhine lineages implies either that early OWMs and hominoids independently derived this behaviour from a less agile common ancestor, or that the last common ancestor of crown catarrhines may have been an active arboreal quadruped with relatively more agile behaviour than earlier catarrhines. Cercopithecoids largely retain a

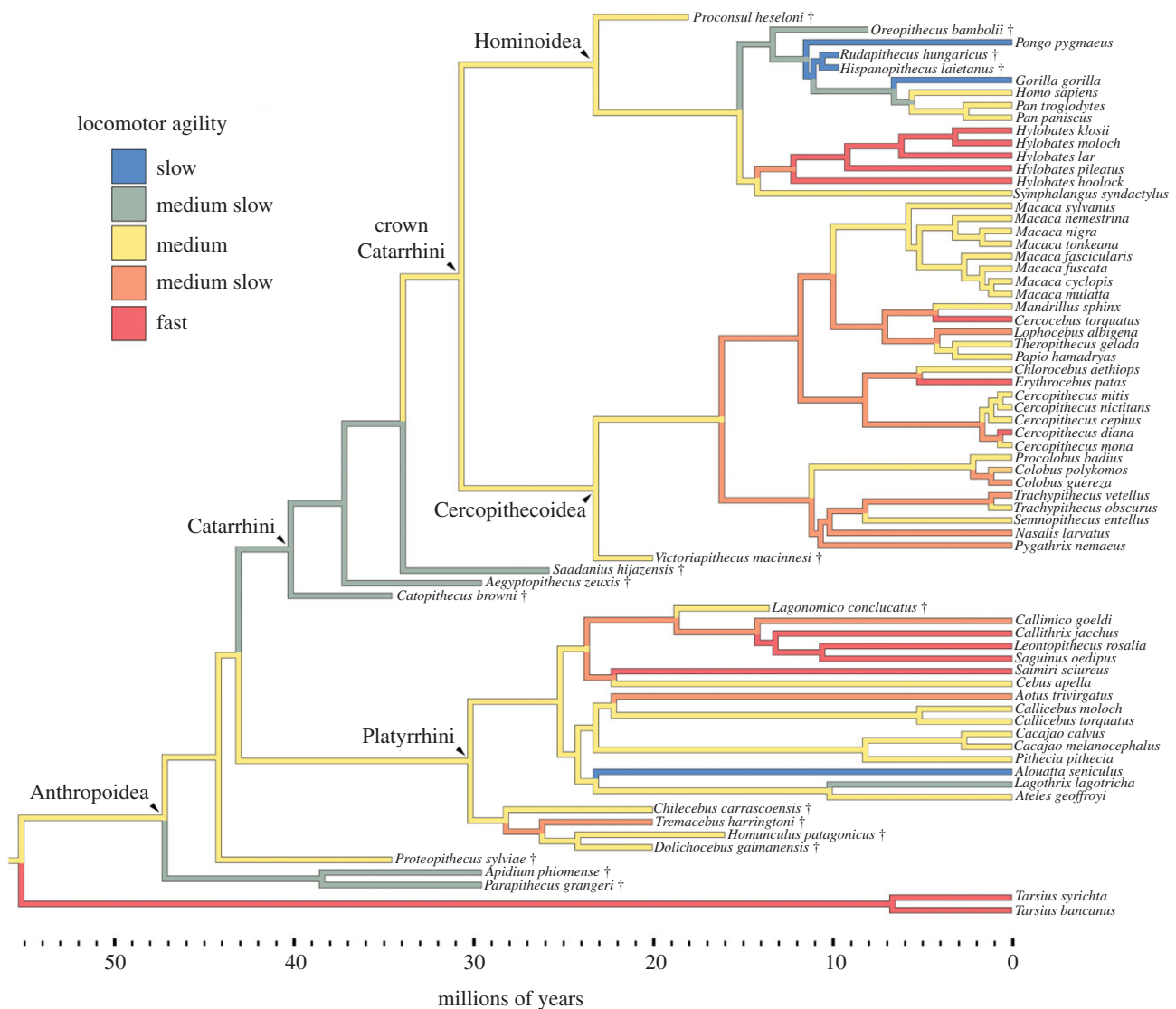


Figure 3. Cladogram of extant and extinct haplorhine taxa with agility scores mapped onto the branches using the same colour scheme as in table 2. Major clades discussed in the text are noted. Note that strepsirrhines were included in the pGLS analyses, but are not displayed here owing to space. Ancestral agility predictions at nodes and along branches are estimated based on parsimony reconstruction method using MESQUITE v. 2.75. Co-author M.L.M. disagrees with the tree as depicted and prefers alternative placement of certain fossil taxa.

relatively agile locomotor pattern with a few derived, even faster, taxa evolving more recently, mostly among the colobines.

Contrasting with the relatively agile locomotor reconstruction for *P. heseloni* and cercopithecoids, diversification of apes during the later Miocene through the present was characterized by species with slower, more deliberate arboreal locomotion (*Hispanopithecus*, *Rudapithecus*, *Oreopithecus* and the extant great apes), except in the case of the agile hylobatids. It seems most reasonable that the basal ape, and perhaps basal crown catarrhine, locomotor mode was slow, representing a retention of the primitive catarrhine condition seen in *Saadianius*. This primitive locomotor pattern was retained by most hominoid taxa throughout the Neogene with the exception of a few lineages that independently derived more agile locomotion, including *Proconsul* and the hylobatids. If the last common ancestor of apes and OWM was relatively fast, then the pattern of slow, deliberate locomotion seen in living apes and large-bodied apes of

the later Miocene would have been secondarily derived from a relatively agile ancestral state.

At present, the evidence from the semicircular canals does not specifically favour one of these alternative scenarios. Beyond recovering new fossils, our understanding of anthropoid locomotor evolution during the Cenozoic will also benefit from further analyses of the canal system, including the introduction of more sophisticated morphometric methods [77,78]. Such an approach will allow for an integrated assessment of functionally relevant aspects, including planar orientation of the canals, which, like arc size, is now known to affect their sensitivity, and may correlate well with locomotor repertoire [8,79,80].

We thank the following for giving access to specimens for scanning or access to CT scans: L. Aiello, C. Beard, H. Chatterjee, M. Dawson, J. Dines, K. Doyle, A. Grader, L. Godfrey, L. Gordon, G. Gunnell, P. Halleck, G. Höck, J. J. Hublin, T. Holmes, W. Jungers, H. Kafka, D. Lieberman, R. Martin, E. Mbua, P. Morris, S. McLaren, J. Mead, T. Rasmussen, J. Rossie, D. Rothrock, H. Temming,

J. Thewissen, J. Wible and G. Weber. We thank R. Kay who kindly provided CT scan data for platyrrhine fossil material, supported by National Science Foundation (BCS-0851272, 0824546) and National Geographic grants. Mark Coleman and one anonymous reviewer provided helpful comments that improved the manuscript. The following institutions lent specimens or allowed scanning: The Carnegie Museum of Natural History, Duke Lemur Center Division of Fossil Primates, National Museums of Kenya, Field Museum of Natural History, Grant Museum of Zoology and Napier Collection, University College London, National Museum of Natural History, Smithsonian Institution, Natural History Museum of Los Angeles County, Pratt Museum, Amherst College, Royal College of Surgeons, London, University of Kansas Natural History Museum, University of Michigan Museum of Paleontology, Natural History Museum of Vienna. This work is Duke Primate Center publication no. 1223. This research was supported by National Science Foundation award BCS-0003920 to A.W. and F.S. and an NSERC discovery grant to M.T.S.

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