Evolution of locomotion in Anthropoidea: 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
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 sylvestris, 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 (Vicroripithecus macinnesi, Proconsul heseloni, Rudapithecus hungaricus, Hispanopithecus laetanus and Oreopithecus bambolii) the cercopithecoid–hominoïd 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 log10 agility (AGIL) against both log10 BM and log10 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, log10AGIL, 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:

\[ Y = X\beta + \epsilon, \]

where \( \beta \)'s are regression coefficients and \( \epsilon \)'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 in 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
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 log₁₀AGIL against both log₁₀BM and log₁₀ 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 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.](image-url)
or platyrrhines such as \cite{73} who suggest that this taxon was similar to extant gen-
for have been as fast as extant leaping primates. The results in locomotor agility. The results for platyrrhines suggest slow to medium (table 2), with a relative lack of diversity poids from the Fayum, Egypt, were generally medium to medium slow. A general similarity in relative canal size is evident among fossil catarrhine primates, \textit{Aegyptopithecus, Parapithecus} and \textit{Aepyopithecus}. Our predicted agility scores for these 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—\textit{D. gaimanensis, Ho. patagonicus, L. concinnus, T. harringtoni} and \textit{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 \cite{30,74}. The subsequent radiation and diversification of platyrrhines in the New World may have begun from an agile, arboreal ancestor.

Locomotor agilities of early catarrhines are reconstructed here as predominantly medium to medium slow. A general similarity in relative canal size is evident among \textit{Catopithecus, Aepyopithecus} and \textit{Saadanim}. 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 \textit{P. heseloni}, which seems somewhat derived in canal size, especially compared with the similar-sized earlier catarrhine \textit{Saadanim}. Relative canal size in \textit{P. heseloni} is most similar to that of several species of medium-speed macaques (\textit{Macaca tonkeana, Macaca fuscata, Macaca mulatta}), primarily quadrapedal taxa that engage in agile climbing and leaping at times \cite{79}.

This interpretation for \textit{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.

<table>
<thead>
<tr>
<th>canal</th>
<th>coefficient s.e.</th>
<th>T</th>
<th>p-value</th>
<th>ln ML</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>ASCR</td>
<td>(intercept)</td>
<td>1.080</td>
<td>0.120</td>
<td>9.025</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>logBM</td>
<td>−0.254</td>
<td>0.037</td>
<td>−6.916</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>logASCR</td>
<td>1.152</td>
<td>0.223</td>
<td>5.177</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>PSCR</td>
<td>(intercept)</td>
<td>1.112</td>
<td>0.122</td>
<td>9.095</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>logBM</td>
<td>−0.254</td>
<td>0.039</td>
<td>−6.506</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>logPSCR</td>
<td>1.191</td>
<td>0.256</td>
<td>4.647</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>LSCR</td>
<td>(intercept)</td>
<td>1.027</td>
<td>0.111</td>
<td>9.284</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>logBM</td>
<td>−0.231</td>
<td>0.030</td>
<td>−7.749</td>
<td>&lt;0.001</td>
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</tr>
<tr>
<td>logLSCR</td>
<td>1.356</td>
<td>0.203</td>
<td>6.698</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>SCR</td>
<td>(intercept)</td>
<td>1.083</td>
<td>0.113</td>
<td>9.617</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>logBM</td>
<td>−0.282</td>
<td>0.035</td>
<td>−8.010</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>logSCR</td>
<td>1.571</td>
<td>0.244</td>
<td>6.450</td>
<td>&lt;0.001</td>
<td></td>
</tr>
</tbody>
</table>

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. 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.

<table>
<thead>
<tr>
<th>taxon</th>
<th>ASCR</th>
<th>PSCR</th>
<th>LSCR</th>
<th>SCR</th>
<th>agility prediction (LSCR)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Catopithecus browni</td>
<td>—</td>
<td>3.0</td>
<td>3.3</td>
<td>—</td>
<td>medium slow (slow)</td>
</tr>
<tr>
<td>Proteopithecus sylociae</td>
<td>—</td>
<td>3.6</td>
<td>3.7</td>
<td>—</td>
<td>medium (fast)</td>
</tr>
<tr>
<td>Apidium phionense</td>
<td>3.1</td>
<td>3.3</td>
<td>3.2</td>
<td>3.0</td>
<td>medium slow (slow)</td>
</tr>
<tr>
<td>Parapithecus grangeri</td>
<td>3.4</td>
<td>3.7</td>
<td>3.4</td>
<td>3.3</td>
<td>medium slow (medium)</td>
</tr>
<tr>
<td>Aegyptopithecus zeuxis (4400 g)b</td>
<td>3.2</td>
<td>3.1</td>
<td>3.0</td>
<td>3.0</td>
<td>medium slow (slow)</td>
</tr>
<tr>
<td>Aegyptopithecus zeuxis (2866 g)b</td>
<td>3.6</td>
<td>3.4</td>
<td>3.3</td>
<td>3.4</td>
<td>medium slow (slow)</td>
</tr>
<tr>
<td>Dolichocebus gaimanensis</td>
<td>4.5</td>
<td>4.5</td>
<td>4.3</td>
<td>4.4</td>
<td>medium</td>
</tr>
<tr>
<td>Homunculus patagonicus</td>
<td>5.0</td>
<td>4.5</td>
<td>4.1</td>
<td>4.5</td>
<td>medium fast (fast (46)—medium (48))</td>
</tr>
<tr>
<td>Lagominus concavia(us)</td>
<td>4.4</td>
<td>4.6</td>
<td>3.7</td>
<td>4.2</td>
<td>medium</td>
</tr>
<tr>
<td>Tremacebus harringtoni</td>
<td>4.5</td>
<td>5.4</td>
<td>4.8</td>
<td>4.9</td>
<td>medium fast</td>
</tr>
<tr>
<td>Chilcebus caramasconesi</td>
<td>4.2</td>
<td>4.2</td>
<td>4.1</td>
<td>3.9</td>
<td>medium</td>
</tr>
<tr>
<td>Saadanius hijazensis</td>
<td>2.6</td>
<td>3.0</td>
<td>2.9</td>
<td>2.8</td>
<td>medium slow</td>
</tr>
<tr>
<td>Victoriapithecus macinnesi</td>
<td>3.0</td>
<td>3.1</td>
<td>3.5</td>
<td>3.1</td>
<td>medium (medium)</td>
</tr>
<tr>
<td>Proconsul heseloni</td>
<td>2.9</td>
<td>2.9</td>
<td>3.8</td>
<td>3.2</td>
<td>medium (slow)</td>
</tr>
<tr>
<td>Oreopithecus bambolii</td>
<td>2.3</td>
<td>3.1</td>
<td>3.0</td>
<td>2.7</td>
<td>medium slow (slow)</td>
</tr>
<tr>
<td>Hispanopithecus laetanus</td>
<td>2.0</td>
<td>2.5</td>
<td>2.5</td>
<td>2.2</td>
<td>slow (slow)</td>
</tr>
<tr>
<td>Rudapithecus hungaricus</td>
<td>2.1</td>
<td>2.6</td>
<td>2.4</td>
<td>2.2</td>
<td>slow (slow)</td>
</tr>
</tbody>
</table>

*Catopithecus browni* [27–29], *Proteopithecus sylociae* [27–30], *Apidium phionense* [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 laetanus* and *Rudapithecus hungaricus* [53,63,64,69–72].

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

Table 1 shows the results of phylogenetic generalized least-squares regression analysis for semicircular canal size and postcranial features. The results 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 more agile behaviour than earlier catarrhines. Cercopithecoids largely retain a 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 more agile behaviour than earlier catarrhines. Cercopithecoids largely retain a
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*, 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 *Saadanius*. 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 Caenozoic 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].

REFERENCES


