



Semicircular canal system in early primates

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ABSTRACT

Mammals with more rapid and agile locomotion have larger semicircular canals relative to body mass than species that move more slowly. Measurements of semicircular canals in extant mammals with known locomotor behaviours can provide a basis for testing hypotheses about locomotion in fossil primates that is independent of postcranial remains, and a means of reconstructing locomotor behaviour in species known only from cranial material. Semicircular canal radii were measured using ultra high resolution X-ray CT data for 9 stem primates (“plesiadapiforms”; $n = 11$), 7 adapoids ($n = 12$), 4 omomyoids ($n = 5$), and the possible omomyoid *Rooneyia viejaensis* ($n = 1$). These were compared with a modern sample (210 species including 91 primates) with known locomotor behaviours. The predicted locomotor agilities for extinct primates generally follow expectations based on known postcrania for those taxa. “Plesiadapiforms” and adapoids have relatively small semicircular canals, suggesting they practiced less agile locomotion than other fossil primates in the sample, which is consistent with reconstructions of them as less specialized for leaping. The derived notharctid adapoids (excluding *Cantius*) and all omomyoids sampled have relatively larger semicircular canals, suggesting that they were more agile, with *Microchoerus* in particular being reconstructed as having had very jerky locomotion with relatively high magnitude accelerations of the head. *Rooneyia viejaensis* is reconstructed as having been similarly agile to omomyoids and derived notharctid adapoids, which suggests that when postcranial material is found for this species it will exhibit features for some leaping behaviour, or for a locomotor mode requiring a similar degree of agility.

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Introduction

The semicircular canal system is an ancient component of the vertebrate inner ear. In all gnathostomes (vertebrates with jaws) the bony component of the system includes 3 tubes in the otic capsule, the anterior, posterior, and lateral canals, which surround

membranous ducts that are part of the endolymph circuit. The canal system senses self-angular motion when an animal moves through the environment, and its sensory input, combined with otolithic, visual, and proprioceptive information, helps coordinate posture and body movements during locomotion. The best understood function of the canal system is its contribution to the stabilization of gaze. This is accomplished through the vestibuloocular and vestibulocollic reflexes that, when moving, involve the extraocular and neck muscles, respectively (Spoor and Zonneveld, 1998). Stabilization of vision is especially important in birds and arboreal

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and/or gliding mammals, such as most primates, dermopterans, and some scandentians, rodents, and marsupials, which rely on eyesight when moving quickly through the air or trees (Spoor and Zonneveld, 1998).

A recent experimental study has demonstrated the relationship between canal radius and the afferent sensitivity of the vestibular nerve (Yang and Hullar, 2007). The arc size of each of the three semicircular canals, expressing the length of the functionally important duct inside, scales with strong negative allometry (Spoor et al., 2007; Spoor and Thewissen, 2008). It has been shown that the residuals of canal size to body mass regressions are correlated with relative locomotor agility of a species. Most comprehensively, a recent study (Spoor et al., 2007) of semicircular canal radii in 210 extant mammal species found that primates (91 species) with locomotion characterized by frequent, high magnitude accelerations (e.g., leapers) typically have much larger canals for their body size than those whose locomotion is characterized by less frequent, smaller accelerations (e.g., arboreal quadrupeds that are not specialized leapers). Slow climbing animals (i.e., lorises and sloth lemurs) in particular have much smaller canals than would be expected for their body mass. These data allow for prediction of relative agility based on body mass and semicircular canal radii. It is therefore possible to use these variables to test hypotheses of locomotor behaviour based on postcrania for extinct animals using cranial data. This method can also provide the first locomotor information for species known only from cranial material. In combination with information on phylogeny and the functional morphology of closely related species, these data may also allow for some preliminary predictions about what the postcrania might look like when found. In this paper we apply these methods to a sample of primitive primates from the Paleocene and Eocene of North America and Europe.

Institutional abbreviations

AMNH, American Museum of Natural History (New York); BM(NH) M, Natural History Museum (London), fossil mammal collection; CM, Carnegie Museum of Natural History (Pittsburgh); MaPhQ, Montauban Muséum d'Histoire Naturelle (Montauban, France); MNHN, Muséum National d'Histoire Naturelle (Paris); MU-PRR, Montpellier University Perrière specimens (Montpellier); PLV, Leuven University (Belgium); PSU, Pennsylvania State University (State College); TMM, Texas Memorial Museum (Austin); UALVP, University of Alberta Laboratory of Vertebrate Paleontology (Edmonton); USNM, United States National Museum Department of Paleobiology (Smithsonian Institutions, Washington, D.C.); UM, University of Michigan Museum of Paleontology (Ann Arbor); UW, University of Wyoming (Laramie); YPM, Yale Peabody Museum (New Haven).

The fossil sample (Tables 1 and 3)

The fossil taxa studied in this paper fall into two general groups: stem primates (“plesiadapiforms”¹) and primitive crown primates (euprimates; Fig. 1). Representatives of five families of “plesiadapiforms” are included in the sample: Micromomyidae (*Dryomomys*, *Tinimomys*), Paromomyidae (*Ignacius*), Plesiadapidae (*Plesiadapis*, *Pronothodectes*), Carpolestidae (*Carpolestes*), and Microsypidae

Table 1

Body masses for “plesiadapiform” specimens used in this study. For body mass estimates derived from dental measurements, the 95% confidence interval is given in brackets.

	Specimen number	Body mass estimate
<i>Carpolestes simpsoni</i>	USNM 482354	100 ^a
<i>Carpolestes simpsoni</i>	UM 101963	100 ^a
<i>Dryomomys szalayi</i>	UM 41870	37 ^b
<i>Tinimomys graybulliensis</i>	UM 85176	38 ^c (26–54)
<i>Microsyps cf. latidens</i>	AMNH 55286	1243 ^d (1090–1416)
<i>Microsyps annectens</i>	UW 12362	2568 ^e (2336–2825)
<i>Ignacius graybullianus</i>	USNM 421608	375 ^e (306–460)
<i>Plesiadapis cookei</i>	UM 87990	2200 ^f
<i>Plesiadapis tricuspiciens</i>	MNHN isolated petrosal	2656 ^g (2418–2918)
<i>Pronothodectes gaoi</i>	UALVP 46685	777 ^b
<i>Pronothodectes gaoi</i>	UALVP 46687	777 ^b

^a Source: Bloch and Gingerich (1998).

^b Calculated from cranial and/or skeletal material for the present study.

^c Body mass estimates from measurements for a sample of this species ($n = 8$) from Szalay (1974), Beard and Houde (1989), and Rose et al. (1993) using Gingerich et al.'s (1982) equation for M¹.

^d Body mass estimated from the specimen using Gingerich et al.'s (1982) equation for M².

^e Body mass estimated from the specimen using Gingerich et al.'s (1982) equation for M¹.

^f Source: Gingerich and Gunnell (2005).

^g Body mass estimate from measurements of a sample of this species ($n = 5$) from Gingerich (1976) using Gingerich et al.'s (1982) equation for M¹.

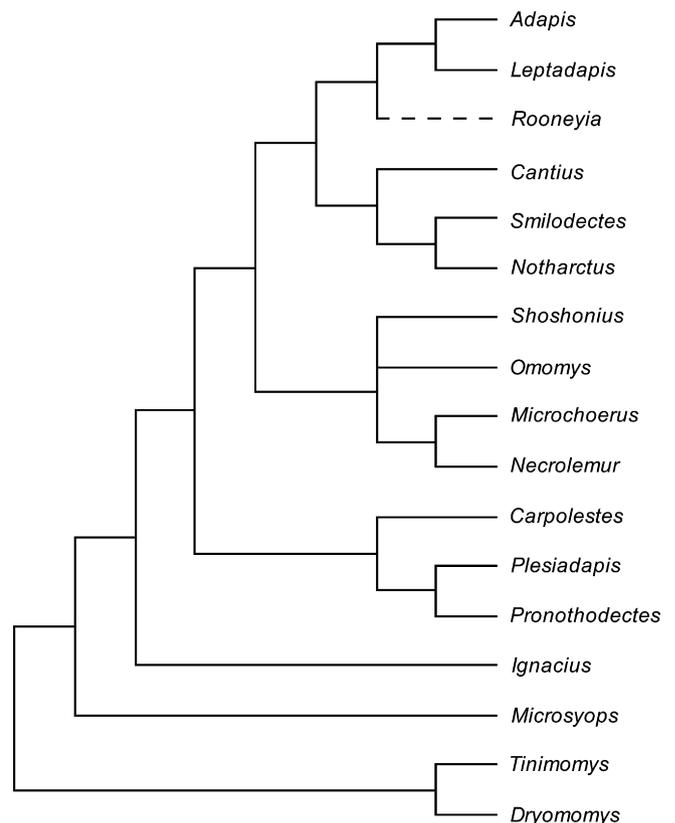


Fig. 1. Hypothesis of relationships for the fossil taxa included in this analysis based on Gingerich (1984) (for notharctids), Kay et al. (2004), and Bloch et al. (2007). The dotted line leading to *Rooneyia* reflects the uncertainty of its relationships. Its position here (from Kay et al., 2004) conflicts both with its traditional placement as an omomyoid (Szalay, 1976), and with recent hypotheses of it as a protoanthropoid (Rosenberger, 2006). This cladogram is included only to put the studied taxa in context, and was not used in the regression analyses (see text).

¹ “Plesiadapiforms” is included in quotation marks throughout the text because it refers to a likely non-monophyletic group (see Fig. 1). It is nonetheless a widely understood informal name and is used as such here. Based on the results of Silcox (2001) and Bloch et al. (2007) we are treating “plesiadapiforms” as stem primates in this paper. However, one author (MG) disagrees with this interpretation; he considers “plesiadapiforms” to pertain to a separate order of extinct arboreal mammals, more distantly related to living primates.

(*Microsyops*; Table 1). All “plesiadapiforms” for which postcrania are known have features associated with arboreal behaviours. They possess, for example, a spherical capitulum on the humerus and a round radial head (allowing for extensive pronation and supination at the humeroradial joint), and long fingers with deep, narrow claws on most digits for grasping branches and clinging to tree trunks, respectively (Bloch et al., 2007). All known “plesiadapiforms” lack features for specialized euprimate-like leaping, however, such as hindlimbs that are much longer than the forelimbs (i.e., an intermembral index of lower than ~ 80) or elongate ankle elements (Simons, 1967; Szalay et al., 1975; Gebo, 1988; Beard, 1989; Godinot and Beard, 1991; Gingerich and Gunnell, 1992; Bloch and Boyer, 2002, 2007; Bloch et al., 2007). Suggestions that *Plesiadapis* may have been a ground-living form similar to a marmot (Gingerich, 1976) have been effectively refuted (Szalay and Decker, 1974; Szalay et al., 1975; Szalay and Dagosto, 1980; Beard, 1989; Godinot and Beard, 1991; Gingerich and Gunnell, 1992; Youlatos and Godinot, 2004; Bloch and Boyer, 2007; Bloch et al., 2007).

Although sharing these general similarities, there is also evidence of significant variability among the various “plesiadapiform” taxa in their locomotor modes. For instance, paromomyids and micromomyids have been reconstructed as dermopteran-like gliders (Beard, 1989, 1990, 1993). Revised functional interpretations and discovery of new fossils demonstrates that all supposed characteristic gliding features (e.g., elongate intermediate hand phalanges) are either not uniquely associated with gliding mammals or are absent in all “plesiadapiforms” for which the anatomy is known (Boyer et al., 2001; Bloch et al., 2003, 2007; Bloch and Boyer, 2007; Boyer and Bloch, 2008). Micromomyids are instead reconstructed as arborealists suited for large diameter supports, and particularly for the undersides of branches, similar to the most arboreal living tree shrew, *Ptilocercus lowii* (Bloch et al., 2003, 2007; Bloch and Boyer, 2007; Boyer and Bloch, 2008). Paromomyids are reconstructed as the most active and agile “plesiadapiforms” for which postcrania are known, practicing more bounding and scampering than the other species and bearing similarities in locomotor behaviours to extant callitrichines (Bloch and Boyer, 2007; Bloch et al., 2007; Boyer and Bloch, 2008). In contrast, certain plesiadapids appear to be the least active and agile “plesiadapiforms” known. *Plesiadapis cookei*, for example, has been reconstructed as a “rather slow and deliberate climber” (Gingerich and Gunnell, 1992: 2) whose impressive, hook-like claws may have limited its ability to locomote on small diameter substrates (Bloch and Boyer, 2007; Bloch et al., 2007), although Youlatos and Godinot (2004) suggested that *Plesiadapis tricuspiciens* might be analogized with *Ratufa* (giant squirrel), which can successfully navigate such substrates. The more primitive, smaller members of this family, such as *Nannodectes intermedius*, may have been more similar to paromomyids, exhibiting greater agility and making more extensive use of small diameter supports (Beard, 1989; Boyer et al., 2004; Bloch and Boyer, 2007). *Carpolestes simpsoni* shows special adaptations for effective use of small diameter supports similar to extant arboreal didelphid marsupials such as *Caluromys*, including the presence of a nail on the hallux (Bloch and Boyer, 2002, 2007; Sargis et al., 2007). Other aspects of its anatomy indicate that *Carpolestes simpsoni* was more agile than *Plesiadapis* and similar in this respect to more primitive plesiadapids such as *Nannodectes*. Of the five “plesiadapiform” families included in this study, microsyopids are the least well known postcranially. A distal humerus, partial proximal ulna, and proximal radius, found in direct association with dental material of *Microsyops*, have been mentioned in an abstract (Beard, 1991). There is also a distal humerus attributed to *Niptomomys doreanae* by Beard (1991), but without a direct dental association. These limited remains are suggestive of arboreal behaviour (e.g., *Microsyops* has a round radial head with a deeply

excavated, circular central fossa), but do not allow for a more detailed reconstruction of locomotor mode.

The euprimates include adapoids of the families Adapidae (*Adapis*, *Leptadapis*) and Notharctidae (*Cantius*, *Notharctus*, *Smilodectes*) and omomyoids of the families Omomyidae (*Omomys*, *Shoshonius*) and Microchoeridae (*Microchoerus*, *Necrolemur*; Fleagle, 1999; Table 3). Among adapoids, there is a clear divide between the two families represented here in terms of locomotor mode. The North American notharctids are generally considered to have been active arborealists who made use of at least some leaping (Gregory, 1920; Napier and Walker, 1967; Dagosto, 1983, 1993; Rose and Walker, 1985; Covert, 1985, 1986; Gebo, 1988; Fleagle and Anapol, 1992; Rose, 1995). The various taxa within Notharctidae may have differed, however, in how much leaping they practiced. In particular, it has been argued that *Cantius* was less specialized for leaping than *Notharctus* or *Smilodectes*, so that it is better analogized with lemurs that practice more above-branch quadrupedalism, such as *Eulemur*, than with more specialized leapers such as indriids (Covert, 1986; Gebo, 1987, 1988; Rose, 1995; Schmitt, 1996). It was nonetheless probably more of an active arborealist than the European adapids (Gebo, 1988), which have been reconstructed as either loris-like slow-climbers (Dagosto, 1983, 1993) or more agile but non-leaping, above branch arboreal quadrupeds (Godinot and Joffroy, 1984; Beard and Godinot, 1988; Godinot, 1991a, b, 1992; Godinot and Beard, 1991; Bacon and Godinot, 1998).

All the omomyoids included in this sample have been reconstructed as capable of some leaping behaviours (Schmid, 1979; Godinot and Dagosto, 1983; Dagosto, 1985; Gebo, 1988; Dagosto and Schmid, 1996; Dagosto et al., 1999; Anemone and Covert, 2000). However, North American omomyids are considered less specialized leapers than the European microchoerids (*Anemone* and Covert, 2000), with *Shoshonius* having been analogized to “prosimian taxa in which quadrupedalism and climbing are as important components of the locomotor repertoire as is leaping” (Dagosto et al., 1999: 175). *Omomys* may have been an even less active animal, with trabecular bone in its femoral head that is organized in a manner more comparable to lorises than galagos (Ryan and Ketcham, 2002). *Necrolemur*, in contrast, was a very specialized leaper, with features such as a fused tibiofibula, long ankle bones, and a very deep astragalar trochlea with steep sides, which would have limited motion at the ankle to flexion and extension (Godinot and Dagosto, 1983; Dagosto, 1985; Gebo, 1988). *Microchoerus* is less well known postcranially than *Necrolemur*, but is also generally held to have been an active leaper, although perhaps less specialized than *Necrolemur* (Schmid, 1979; Gebo, 1988; Dagosto and Schmid, 1996; Anemone and Covert, 2000).

From these locomotor reconstructions, some predictions can be made about how the fossil primates in this study might vary in terms of their relative semicircular canal radii. Since none of them

Table 2

Regression equations used to estimate body mass in kg from skull length using phylogenetic Generalized Least Squares (pGLS) and conventional least squares (LS). InML = natural log of Maximum Likelihood estimate; BL Trans = branch length transformation used in the phylogenetic Generalized Least Squares regression analysis; OU = the Ornstein-Uhlenbeck transformation (see text).

Method	df	slope	y int.	F	p	r ²	InML	BL Trans
Vertical								
LS	1,16	3.79	-6.85	196.51	<0.0001	0.92	7.60	
pGLS	1,16	2.70	-4.99	132.27	<0.0001	0.89	15.63	no trans.
Horizontal								
LS	1,19	3.81	-7.01	372.23	<0.0001	0.95	14.20	
pGLS	1,19	3.94	-7.22	234.17	<0.0001	0.92	15.50	OU = 0.242
Combined								
LS	1,37	3.79	-6.92	465.70	<0.0001	0.93	17.47	
pGLS	1,37	3.51	-6.43	255.27	<0.0001	0.87	23.92	OU = 0.586

Table 3
Body mass estimates for euprimate specimens used in this study. When both are present, underlined values (based on a conventional least squares equation) were used for [Supplementary Information Figs. 1 and 2](#), while the values in bold (based on the pGLS analysis) were used for [Figs. 3 and 4](#), and in all subsequent analyses. PI = prosthion-inion length; values in the M¹/PC column were either calculated from [Gingerich et al.'s \(1982\)](#) equation for M¹ from a measurement off the specimen unless otherwise noted, or (for *Omomys* and *Shoshonius*) from the postcranium (PC). Values in brackets are 95% confidence intervals.

Taxon	Specimen	PI (mm)	Vertical LS	Body Mass estimate (g)				Combined pGLS	M ¹ /PC
				Vertical pGLS	Horizontal LS	Horizontal pGLS	Combined LS		
Adapoid euprimates									
<i>Adapis</i> sp.	MNHN QU 11064	69.3 ^a	1335 (588–3036)	928 (549–1570)	<u>996 (530–1873)</u>	1059 (584–1920)	1138 (524–2470)	1074 (556–2074)	1264 (1113–1435)
<i>Adapis</i> sp.	PLV 14	76.5 ^a	1942 (854–4415)	1212 (716–2050)	<u>1451 (772–2728)</u>	1562 (861–2834)	1655 (1137–5355)	1519 (787–2935)	2270 (2055–2507)
<i>Adapis parisiensis</i>	BM(NH) M 1345	85.0 ^a	2895.4 (1273–6582)	1609 (951–2723)	<u>2167 (1153–4075)</u>	2365 (1304–4291)	2468 (1137–5355)	2200 (1139–4248)	1775 (1590–1981)
<i>Adapis parisiensis</i>	MaPhQ 339	80.1 ^a	231 (1017–5256)	1371 (811–2320)	<u>1723 (919–3250)</u>	1872 (1032–3397)	1970 (908–4276)	1786 (924–3449)	2270 (2055–2507)
<i>Magnadapis quercyi</i>	MNHNQU 10875	106.1 ^a	6709 (295–15252)	2925 (1729–4949)	<u>5044 (2683–9482)</u>	5663 (3121–10274)	5718 (2635–12409)	4792 (2481–9256)	8054 (7314–8869)
<i>Magnadapis aff. intermedius</i>	MNHNQU 11035	136.0 ^b	17190 (7562–39080)	5711 (3376–9662)	<u>12985 (6907–24414)</u>	15050 (8295–27304)	14653 (6752–8327)	11460 (5933–22136)	9610 (87120–10723)
<i>Leptadapis leenhardti</i>	YPM 11481	95.5 ^a	4502 (1980–10235)	2203 (1302–3726)	<u>3378 (1796–6350)</u>	3742 (2062–6788)	3837 (1768–8327)	3311 (1714–6396)	6575 (6007–7198)
<i>Cantius nuniensis</i>	UM 103510	–	–	–	–	–	–	–	2274^d (2059–2511)
<i>Notharctus tenebrosus</i>	AMNH 127167	78.5 ^b	2141 (942–4869)	1299 (768–2197)	1601 (851–3009)	1729 (953–3138)	1825 (841–3961)	1663 (861–3212)	5273 (4835–5749)
<i>Notharctus tenebrosus</i>	AMNH 131764	82.0 ^b	<u>2526 (1111–5744)</u>	1461 (863–2471)	1890 (1005–3553)	2053 (1132–3725)	2154 (992–4673)	1933 (1004–3745)	5260 (4824–5736)
<i>Smilodectes gracilis</i>	AMNH 131762	71.5 ^b	<u>1503 (661–3418)</u>	1010 (597–1708)	1121 (597–2109)	1197 (660–2172)	1281 (590–2780)	1198 (620–2314)	2457 (2231–2706)
<i>Smilodectes gracilis</i>	UM 32773	60.0 ^c	<u>773 (340–1758)</u>	629 (372–1065)	575 (306–1081)	600 (331–1089)	659 (304–1430)	647 (335–1250)	2711 (2469–2976)
Omomyoid euprimates									
<i>Microchoerus</i> sp.	MUPRR 1771	49.5 ^b	<u>373 (164–848)</u>	375 (222–634)	276 (147–520)	282 (155–511)	318 (147–690)	329 (171–636)	1032 (898–1185)
<i>Necrolemur antiquus</i>	MNHNQU 11059	43.1 ^b	<u>220 (97–501)</u>	258 (152–436)	163 (87–306)	163 (90–295)	188 (87–407)	202 (105–390)	650 (550–769)
<i>Omomys carteri</i>	UCM 57459	–	–	–	–	–	–	–	230^e
<i>Omomys carteri</i>	UCM 57460	–	–	–	–	–	–	–	230^e
<i>Shoshonius cooperi</i>	sp mean	27.0 ^c	<u>38 (17–85)</u>	73 (43–124)	28 (15–52)	26 (14–47)	32 (15–69)	39 (20–76)	60–90 ^f
<i>Rooneyia viejaensis</i>	TMM 40 688–7	51.6 ^a	437 (192–993)	419 (248–709)	324 (172–609)	332 (183–601)	<u>372 (172–808)</u>	381 (197–736)	1821 (1633–2030)

^a Source: [Kay and Kirk \(2000\)](#).

^b PI measured for this study.

^c Source: [Bloch and Silcox \(2006\)](#).

^d Body mass estimated from measurements for a sample of this species ($n = 13$) provided by G.F. Gunnell using [Gingerich et al.'s \(1982\)](#) equation for M¹.

^e Body mass estimate based on postcrania taken from [Payseur et al. \(1999\)](#).

^f Body mass estimate based on postcrania taken from [Dagosto et al. \(1999\)](#).

are thought to be specialized euprimate-like leapers, “plesiadapiforms” are expected to have some of the smallest canals relative to their body masses for the fossil sample, with relatively slow-moving, derived plesiadapids perhaps having the smallest canals, and more agile paromomyids the largest. Among the euprimates, the European adapids, as non-leapers, are predicted to have canals scaled similarly to the “plesiadapiforms.” The canals are expected to be larger relative to body mass in the notharctids than in the adapids, with *Cantius* perhaps having the smallest canals among the three notharctids. Since all omomyoids are reconstructed as having done some leaping, it is to be expected that they will also have fairly large canals for their body mass, with the largest canals of all being predicted for the microchoerids.

Of the fossil primates included in this study, *Rooneyia* is the least well known in terms of both phylogeny and behaviour. Although it has traditionally been allied with the Omomyoidea (Szalay, 1976), it lacks distinctive omomyoid traits such as enlarged orbits, and possesses a number of derived traits not found in omomyoids such as fused frontal bones and very large hypocones (Gunnell and Rose, 2002). *Rooneyia* has generally not grouped with omomyoids in cladistic analyses; for example, in Kay et al.’s (2004) hypothesis of relationships it fell out within Adapoidea (Fig. 1). Rosenberger (2006) has recently suggested that it was a “protoanthropoid,” a surprising view in light of its North American location and late Eocene age. It seems fair to say that there is no current consensus on the systematic position of this genus. There are no postcrania known for *Rooneyia*, so the relative semicircular canal radii studied here provide the first basis upon which to form predictions about the locomotion of this taxon, and to test the hypothesis that it practiced omomyoid-like leaping behaviour, as its traditional taxonomic placement might suggest.

Methods

Semicircular canal radii were measured from ultra high resolution computed tomography (uHRCT) data, most of which were collected using the X-TEK x-ray subsystem on the OMNI-X HD-600 CT scanner at the Center for Quantitative Imaging (CQI), Pennsylvania State University. Cross-sectional slices were acquired for each specimen using 2400 views, 2 samples per view, and 41 slices per rotation. Voxel dimensions for the datasets studied here ranged from 0.015 mm to 0.130 mm. Between approximately 200 and 1200 slices were collected for each specimen depending on specimen and voxel size. The image data were reconstructed as 1024 × 1024 16 bit TIFF images.

The CT images were cropped to the maximum extents of the bony labyrinth. The scan data were initially viewed in Scion Image (Scion Corporation, 2002) to locate the area of the scans that contained useable data. The inner ear was cropped from the dataset and a stack was formed using cropvoi and strip2raw, DOS programs developed by Nathan Jeffery (University of Liverpool). A 2D image, showing the full extent of each semicircular canal, was generated by placing three points along the length of the canal and re-slicing the data in the resulting plane, using Voxblast for Unix (VayTek, Inc.; <http://www.vaytek.com/VBUnix.html>) on an SGI Octane 2 workstation. Arc height and width of the canals, as defined in Spoor and Zonneveld (1995; Figure 2), were then measured from the 2D images in Image J (Rasband, 1997–2007), and the radius of curvature was calculated as $R = 0.5 \times (\text{height} + \text{width})/2$.

The semicircular canal measurements from the fossil data were compared against a sample of 91 extant and recently extinct primates (subfossil lemurs; these are included as part of the modern strepsirrhine radiation) and 119 non-primate mammals (Supplementary Table 1; Spoor et al., 2007). Spoor et al. (2007) used both conventional and phylogenetically-informed multiple

regression analyses to study the relationship between canal size and agility of locomotion; this relationship was found to be statistically significant in both types of analyses. Agility scores were assigned to the modern taxa by Spoor et al. (2007) based on the field observations of J. Fleagle (Stony Brook University, Stony Brook, NY), S. McGraw (Ohio State University, Columbus, OH), and A.W., supplemented from the literature (Rowe, 1996; Fleagle, 1999) and video footage. Assignment of these scores was based on the typical angular accelerations of the head in locomotion, since this is the variable of greatest relevance to the semicircular canal system. The cladogram (with branch lengths) used in the phylogenetically-informed regressions by Spoor et al. (2007) is available at <http://www.pnas.org/content/104/26/10808/suppl/DC1>. For the current study, a \log_{10} transformed locomotor agility score was used as the dependent variable and \log_{10} body mass and \log_{10} semicircular canal radii were used as the independent variables in a phylogenetic Generalized Least Squares (pGLS) regression, also using this cladogram. Regression analyses were run using REGRESSIONv2.M program (available from A. R. Ives and T. Garland, Jr.) in Matlab vR2006a (Garland and Ives, 2000; Rohlf, 2001; Lavin et al., 2008). The pGLS regression analyses were run using the original branch lengths as well as after transforming the branch lengths using the maximum likelihood estimates for the Ornstein-Uhlenbeck (OU) transform (Blomberg et al., 2003; Garland et al., 2005), Grafen’s ρ (Grafen, 1989, 1992), and Pagel’s λ (Pagel, 1997, 1999), to determine the optimal regression model. Models were compared using the ln ML likelihood (natural log of Maximum Likelihood estimate) and the AIC (Akaike Information Criterion; Freckleton et al., 2002). Regression equations to predict agility were generated for both primate and mammalian samples for each canal using the results from the pGLS analyses with the highest likelihoods. Two independent sets of analyses were run for each canal – one using all 91 modern primate taxa and the other using the combined sample of 210 primate and non-primate mammal species. Regression equations were generated to predict locomotor agility for the fossil taxa based on their measured canal radii and estimated body masses using the pGLS approach (Garland and Ives, 2000; Walker et al., 2008),

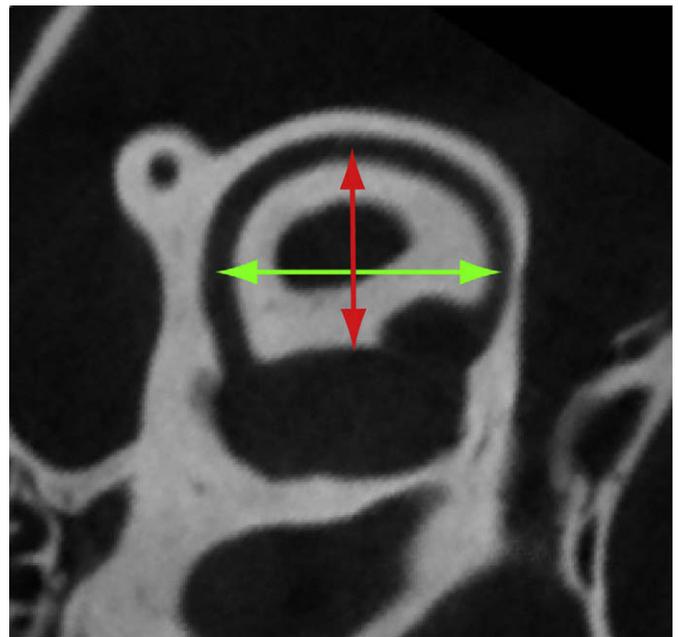


Fig. 2. Lateral semicircular canal of *Peridicticus potto* (uncatalogued PSU specimen) with arrows indicating the height (red) and width (green) of the canal. This image was obtained by re-slicing the dataset in the plane of the canal in Voxblast. Measurements were taken at the maximum height and width of the canal, to the midpoint of the lumen.

which also made use of this cladogram. The resulting predictive equations are given below:

Primate Predictive Equations: (AGIL = agility; BM = body mass; ASCR = anterior semicircular canal radius; PSCR = posterior semicircular canal radius; LSCR = lateral semicircular canal radius; SCR = average semicircular radius.)

$$\text{ASCR} : \log_{10}\text{AGIL} = 1.089 - 0.260 (\log_{10}\text{BM}) + 0.985 (\log_{10}\text{ASCR})$$

$$\text{PSCR} : \log_{10}\text{AGIL} = 1.131 - 0.284 (\log_{10}\text{BM}) + 1.282 (\log_{10}\text{PSCR})$$

$$\text{LSCR} : \log_{10}\text{AGIL} = 1.069 - 0.261 (\log_{10}\text{BM}) + 1.453 (\log_{10}\text{LSCR})$$

$$\text{SCR} : \log_{10}\text{AGIL} = 1.114 - 0.302 (\log_{10}\text{BM}) + 1.522 (\log_{10}\text{SCR})$$

All Mammals Predictive Equations:

$$\text{ASCR} : \log_{10}\text{AGIL} = 0.850 - 0.153 (\log_{10}\text{BM}) + 0.706 (\log_{10}\text{ASCR})$$

$$\text{PSCR} : \log_{10}\text{AGIL} = 0.881 - 0.151 (\log_{10}\text{BM}) + 0.677 (\log_{10}\text{PSCR})$$

$$\text{LSCR} : \log_{10}\text{AGIL} = 0.959 - 0.1670 (\log_{10}\text{BM}) + 0.854 (\log_{10}\text{LSCR})$$

$$\text{SCR} : \log_{10}\text{AGIL} = 0.948 - 0.188 (\log_{10}\text{BM}) + 0.962 (\log_{10}\text{SCR})$$

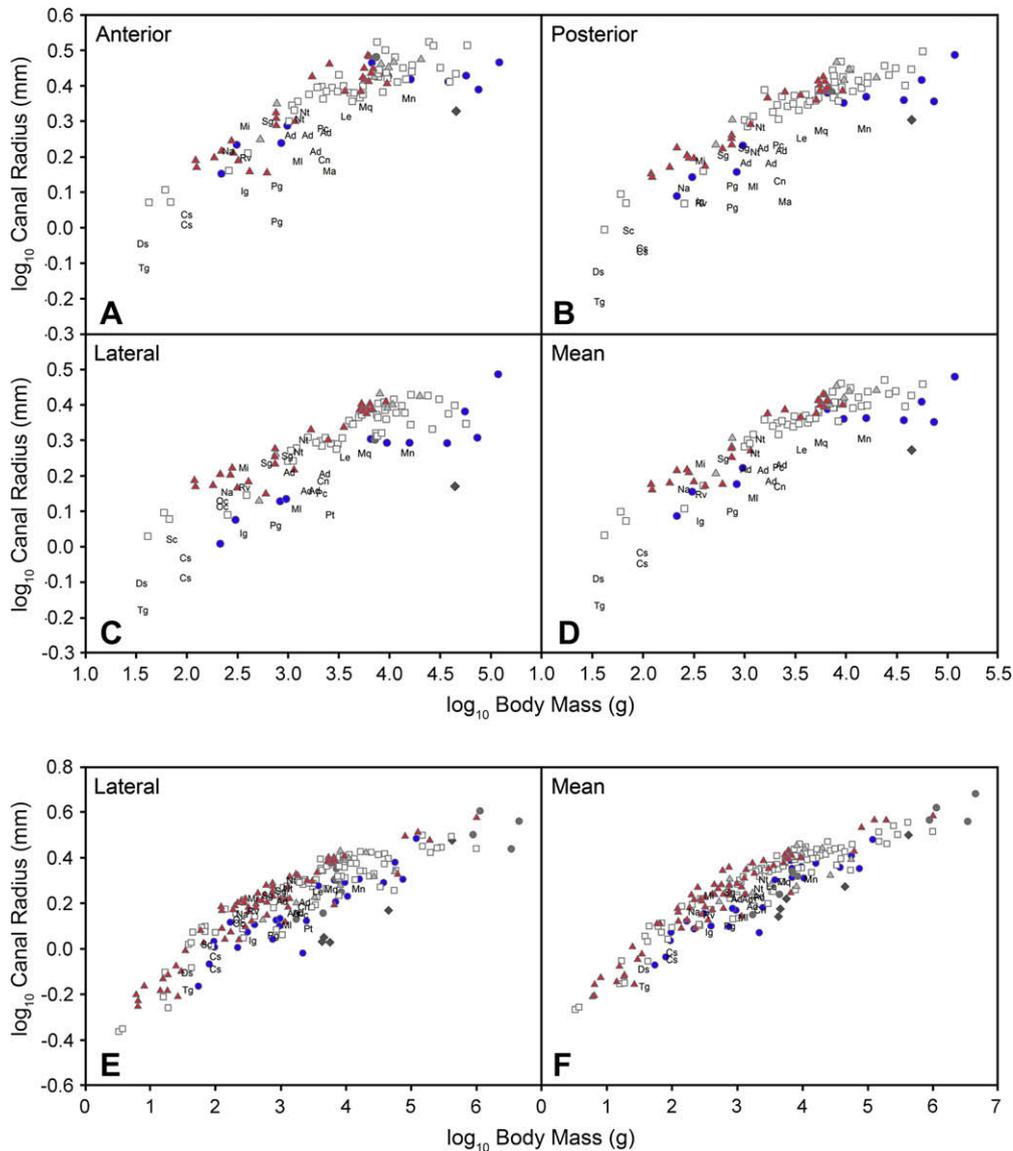


Fig. 3. Double logarithmic plots of semicircular canal radius on body mass for individual extant primates, extant mammals, and fossil specimens. Body mass estimates for adapoids and omomyoids were calculated using pGLS (bold values in Table 3). Modern taxa are plotted as symbols depending on their locomotor agility: fast = red triangle; medium fast = grey square; medium slow = grey circle; slow = blue circle; extra slow = grey diamond. Fossils are plotted as characters for their taxonomic name as follows: Ad = *Adapis* sp.; Cn = *Cantius nuniensis*; Cs = *Carpolestes simpsoni*; Ds = *Dryomomys szalayi*; Ig = *Ignacius graybullianus*; Le = *Leptadapis leenhardtii*; Mi = *Microchoerus* sp.; Ma = *Microsypops annectens*; Ml = *Microsypops cf. latidens*; Mn = *Magnadapis aff. intermedius*; Mq = *Magnadapis quercyi*; Na = *Necrolemur antiquus*; Nt = *Notharctus tenebrosus*; Oc = *Omomyomys carteri*; Pc = *Plesiadapis cookei*; Pt = *Plesiadapis tricuspidens*; Pg = *Prionothodectes gaoi*; Rv = *Rooneyia viejaensis*; Sc = *Shoshonius cooperi*; Sg = *Smilodectes gracilis*; Tg = *Tinimomys graybullianus*. A) Anterior semicircular canal radius, primates; B) posterior semicircular canal radius, primates; C) lateral semicircular canal radius, primates; D) mean semicircular canal radius, primates; E) lateral semicircular canal radius, all mammals; F) mean semicircular canal radius, all mammals.

Although Garland and Ives (2000) outline a method to predict unknown values for a species on a phylogenetic tree using phylogenetic regression methods, this method was not used here because it has yet to be validated for multiple regressions using pGLS. Therefore, the hypothesis of relationships given in Fig. 1 was not incorporated into the statistical analyses, and branch lengths were not calculated for this particular cladogram.

A recent study examining the correlation between semicircular canal size and subarcuate fossa development in primates has found that, of the three canals, the lateral one is likely to predict locomotor agility most reliably (Jeffery et al., 2008). This is because the size of the anterior canal, and to a lesser extent the posterior canal, may be spatially influenced by the fossa and its contents, the petrosal lobule of the cerebellar paraflocculus. The lateral canal also performed the best at recovering the agilities of modern taxa using the predictive equations (Supplementary Information Table 1). Hence, for the present study we analysed all three canals, but paid particular attention to the predictions derived from the lateral canal.

Body mass (Tables 1 and 3)

Estimating body mass is a central concern to this study, because the strong relationship between body mass and semicircular canal size implies that the former must be accounted for before any reconstruction of locomotor mode can be made. Reconstructing body mass for extinct forms is difficult, as can be seen by the wide range of estimates available for some species. For example, Dagosto and Terranova (1992) reported body mass estimates for *Necrolemur antiquus* that ranged from 4 g to 419 g, depending on the model and body part measured. When more than one skeletal element is available for a given individual it is possible to consider multiple estimates from different parts of the skeleton, and to produce a consensus estimate that is most consistent with all of the skeletal elements available (e.g., see Gingerich and Gunnell, 2005). We consider such estimates as more reliable than ones based on only a single region, as they allow for an assessment of the relative scaling of the parts of the body to one another. This means, for example, that it is possible to determine if an animal was megadont, or had unusually long hindlimbs for the size of its skull, and to adjust the body mass estimate accordingly. Species for which such solid estimates are available include *Carpolestes simpsoni*, *Dryomomys szalayii*, *Plesiadapis cookei*, *Pronothodectes gaoi*, and *Omomys carteri* (Bloch and Gingerich, 1998; Payseur et al., 1999; Gingerich and Gunnell, 2005; and this study). In some cases these well-supported estimates can be used to constrain the likely values for a given taxon. For example, it would appear that body mass estimates for *Plesiadapis tricuspis* based on the skull (10.5 kg; Martin, 1990) are too high since they substantially exceed the well-supported estimate for the similarly sized species *Plesiadapis cookei* derived from multiple postcranial remains (2.2 kg; Gingerich and Gunnell, 2005). This overestimation of body mass from cranial remains using a primate regression is not surprising since “plesiadapiform” skulls tend to be long relative to those of extant primates. For these reasons, a molar-based estimate was used for *P. tricuspis*.

If such well-supported, species-level body mass estimates were not available, an estimate was calculated from measurements of M^1 (or M^2 if M^1 was missing) if the scanned specimen included teeth. Deriving estimates directly from the scanned specimens, whenever possible, helps to deal with problems of intra-specific variability and uncertain species attribution. The length and width of M^1 or M^2 were measured either from 3D reconstructions made in Amira 3.1.1 (Visage Imaging, Carlsbad, CA; <http://www.amiravis.com/>), or using digital callipers or a reticle on the specimen themselves, and a body mass estimate was calculated from Gingerich et al.’s (1982)

equations ($\ln \text{ body weight} = 1.62[\ln M^1 \text{ area}] + 2.72$, or $\ln \text{ body weight} = 1.37[\ln M^2 \text{ area}] + 3.49$; where M^1 or M^2 area was calculated as length \times width). A few of the specimens scanned were isolated petrosals; in these cases, body mass estimates were calculated from a sample of M^1 for the species using the M^1 equation (*Cantius nuniensis*, *Plesiadapis tricuspis*, *Tinimomys graybulliensis*).

Body masses were also estimated for adapoid and omomyoid specimens that were sufficiently well preserved using a regression of \log_{10} body mass against \log_{10} skull length (Table 2). A sample of 39 extant primates comprised of strepsirrhines and tarsiers was used. Tarsiers and many strepsirrhines (e.g., indriids, some galagids, *Lepilemur*) prefer vertical resting postures while others (e.g., most lemurids, cheirogaleids, lorises, some galagids) prefer horizontal ones (Rowe, 1996). Skull length increases in all groups with increasing body mass, but those species with vertical resting postures have relatively shorter skulls. For this reason, the modern sample was divided into vertical and horizontal postural groups depending on their preferred behaviour, and these two postural groupings, as well as a combined group, were used in three independent regression analyses (Table 2). Both conventional least squares and pGLS analyses were used following the same procedure with branch length transformations in the REGRESSIONv2.M package within Matlab vR2006a. If the extinct species had skeletal evidence suggesting that one or the other resting posture was used in life, then that estimate was preferred; otherwise, the combined estimate was used. Skull lengths for fossils were either taken from the literature, measured from uhrCT data in Amira 3.1.1, or were

Table 4

Radius of curvature (R) for the anterior (ASC), posterior (PSC), lateral (LSC), and mean (SC) semicircular canals for the fossil specimens included in this study. All measurements are in mm.

	Specimen number	ASC-R	PSC-R	LSC-R	SC-R
“Plesiadapiforms”					
<i>Carpolestes simpsoni</i> ^a	USNM 482354	1.0	0.9	0.8	0.9
<i>Carpolestes simpsoni</i>	UM 101963	1.1	0.9	0.9	1.0
<i>Dryomomys szalayii</i>	UM 41870	0.9	0.8	0.8	0.8
<i>Tinimomys graybulliensis</i>	UM 85176	0.8	0.6	0.7	0.7
<i>Microsypops cf. latidens</i> ^a	AMNH 55286	1.5	1.3	1.3	1.4
<i>Microsypops annectens</i>	UW 12362	1.4	1.2		
<i>Ignaciuss graybullianus</i>	USNM 421608	1.3	1.2	1.1	1.2
<i>Plesiadapis cookei</i>	UM 87990	1.9	1.7	1.4	1.7
<i>Plesiadapis tricuspis</i>	MNHN isolated petrosal			1.2	
<i>Pronothodectes gaoi</i>	UALVP 46685	1.3	1.3	1.1	1.3
<i>Pronothodectes gaoi</i>	UALVP 46687	1.0	1.1		
Adapoid euprimates					
<i>Adapis sp.</i>	MNHN QU 11064	1.8	1.5	1.6	1.7
<i>Adapis sp.</i>	PLV14	1.8	1.7	1.4	1.6
<i>Adapis parisiensis</i>	BM(NH) M 1345	1.9	1.7	1.6	1.7
<i>Adapis parisiensis</i>	MaPhQ 339	1.6	1.5	1.4	1.5
<i>Magnadapis quercyi</i>	MNHN-QU10875	2.2	1.9	1.8	2.0
<i>Magnadapis aff. intermedius</i>	MNHN-QU11035	2.3	1.9	1.8	2.0
<i>Leptadapis leenhardtii</i>	YPM11481	2.1	1.8	1.8	1.9
<i>Cantius nuniensis</i>	UM 103510	1.5	1.4	1.5	1.5
<i>Notharctus tenebrosus</i>	AMNH 127167	2.0	1.6	1.8	1.8
<i>Notharctus tenebrosus</i>	AMNH 131764	2.1	1.9	2.0	2.0
<i>Smilodectes gracilis</i>	AMNH 131762		1.7	1.8	
<i>Smilodectes gracilis</i>	UM 32773	2.0	1.6	1.7	1.8
Omomyoid euprimates					
<i>Omomys carteri</i>	UCM 57459			1.3	
<i>Omomys carteri</i>	UCM 57460			1.3	
<i>Shoshonius cooperi</i>	CM 60492		1.0	1.0	
<i>Microchoerus sp.</i>	MU-PRR 1771	1.9	1.5	1.7	1.7
<i>Necrolemur antiquus</i>	MNHN-QU 11059b	1.6	1.30	1.4	1.5
<i>Rooneyia viejaensis</i>	TMM 40 688-7	1.6	1.2	1.5	1.4

^a calculated as an average from the right and left sides of the specimen.

measured directly on the specimens with callipers. Skull lengths and body masses for the extant taxa were taken from Kay and Kirk (2000). It is important to note that the semicircular canals sense angular motion and are inactive when an animal is still, so using posture does not constitute a false premise in this case.

In contrast to “plesiadapiforms,” skull length seems to provide a better estimate of body mass than tooth area for euprimates. For example, Dagosto et al. (1999) found that estimates of body mass from tooth area for *Shoshonius* were substantially larger (103–155 g; Conroy, 1987; Fleagle, 1988) than the estimate derived from a sample of postcranial elements (60–90 g), suggesting that this taxon was megadont. Our equation for body mass in an animal with a vertical body position from the pGLS analysis produced an estimate (73 g; 95% confidence interval 43–124 g) within the range of the postcranial estimates, suggesting that this equation performed better than the dental regression. For this reason, body mass estimates based on skull length were used for the fossil euprimates when available. Although there are good reasons to prefer a phylogenetically-based least squares approach for this sample, using this approach produced estimates for some forms (e.g., *Magnadapis aff. intermedius*) that seem implausibly high—this is because at higher body masses, horizontal forms are predicted to have larger body masses than vertical forms in the pGLS analysis, which is contrary to expectations. For this reason, plots of \log_{10} body mass vs. \log_{10} canal size were generated using body mass estimates from both types of equations (Figs. 2 and 3; Supplementary Figs. 1 and 2), to allow the study of the effect of the phylogenetic correction on the interpretation of the results. Only the estimates derived from the pGLS equations were used in subsequent analyses, since the two

regressions produced the same basic interpretations about the relative agilities of the fossil primates. Since skull length appears to substantially over-estimate body mass in “plesiadapiforms” (as discussed above), the body masses of these taxa were based on dental measurements when postcrania were unavailable.

Results

Measurements of the semicircular canals that could be taken from the fossil specimens are given in Table 4. This information, along with body mass, was entered into predictive equations for locomotor agility based on both the primate (Table 5) and overall mammal (Table 6) modern samples (Supplementary Table 1; Spoor et al., 2007). The same relationships hold when the agility scores are not logged.

In general, “plesiadapiforms” have relatively smaller semicircular canals than most of the euprimates. In an overall plot of their \log_{10} semicircular canal radii vs. \log_{10} body mass (Fig. 4, Supplementary Fig. 2), the “plesiadapiform” distribution generally lies below the fossil eupimate distribution, with the exception of the adapid adapoids and the most primitive notharctid in the sample, *Cantius nuniensis*. This distinction can be clearly seen in the plots of \log_{10} lateral semicircular canal radius (LSCR) vs. \log_{10} body mass (Fig. 4B), which, as noted above, is the canal most sensitive to changes in locomotor behaviour. *Shoshonius cooperi* has an absolutely larger lateral semicircular canal than either specimen of *Carpolestes simpsoni*, even though its reconstructed body mass is somewhat lower. Similarly, *Omomyx* has an absolutely larger lateral canal than *Ignaciux graybullianus*, even though it was a somewhat smaller animal. This

Table 5
Predictions for locomotor agility for fossil taxa based on a predictive equation for primates calculated from the values in Table 1, and the values in bold in Table 3. Values are on a six-point agility scale (1 = extremely slow, 2 = slow [e.g., *Loris*], 3 = medium slow, 4 = medium [e.g., *Cebus*, *Cheirogaleus*], 5 = medium fast, 6 = fast [e.g., *Galago*, *Saimiri*]; see Spoor et al., 2007). Values in brackets represent the predictions calculated from the 95% confidence intervals given for the body mass estimates in Tables 1 and 3.

Taxon	Specimen number	Primate Prediction			
		ASCR	PSCR	LSCR	SCR
“Plesiadapiforms”					
<i>Carpolestes simpsoni</i>	USNM 482354	3.8	3.0	2.6	2.7
<i>Carpolestes simpsoni</i>	UM 101963	4.0	3.1	3.1	3.0
<i>Dryomomys szalayi</i>	UM 41870	4.3	3.4	3.2	3.2
<i>Tinimomys graybullianus</i>	UM 85176	3.7 (3.3–4.0)	2.6 (2.3–2.9)	2.5 (2.3–2.7)	2.4 (2.2–2.7)
<i>Microsypops cf. latidens</i>	AMNH 55286	2.9 (2.8–3.0)	2.5 (2.4–2.6)	2.6 (2.5–2.7)	2.4 (2.3–2.5)
<i>Microsypops annectens</i>	UW 12362	2.3 (2.2–2.3)	1.8 (1.8–1.9)		
<i>Ignaciux graybullianus</i>	USNM 421608	3.3 (3.1–3.5)	3.1 (3.0–3.3)	2.8 (2.7–3.0)	2.8 (2.6–3.0)
<i>Plesiadapis cookei</i>	UM 87990	3.1	3.0	2.6	2.8
<i>Plesiadapis tricuspidens</i>	MNHN isolated petrosal			2.0 (2.0–2.1)	
<i>Pronothodectes gaoi</i>	UALVP 46685	2.8	2.9	2.5	2.5
<i>Pronothodectes gaoi</i>	UALVP 46687	2.3	2.4		
Adapoid euprimates					
<i>Adapis sp.</i>	MNHN QU 11064	3.6 (3.1–4.2)	3.2 (2.7–3.8)	3.8 (3.3–4.4)	3.4 (2.8–4.1)
<i>Adapis sp.</i>	PLV 14	3.3(2.8–3.8)	3.2 (2.7–3.8)	2.9 (2.5–3.4)	3.0 (2.5–3.6)
<i>Adapis parisiensis</i>	BM(NH) M 1345	3.0 (2.6–3.5)	2.8 (2.4–3.3)	3.0 (2.6–3.6)	2.8 (2.3–3.3)
<i>Adapis parisiensis</i>	MaPhQ 339	2.8 (2.4–3.3)	2.7 (2.3–3.2)	2.8 (2.4–3.2)	2.5 (2.1–3.1)
<i>Magnadapis quercyi</i>	MNHNQU 10875	2.8 (2.4–3.3)	2.6 (2.2–3.1)	2.9 (2.5–3.4)	2.7 (2.2–3.2)
<i>Magnadapis aff. intermedius</i>	MNHNQU 11035	2.3 (2.0–2.7)	2.0 (1.7–2.4)	2.3 (2.0–2.7)	2.1 (1.7–2.5)
<i>Leptadapis leenhardtii</i>	YPM11481	2.9 (2.5–3.4)	2.8 (2.3–3.3)	3.2 (2.7–3.7)	2.8 (2.4–3.4)
<i>Cantius nuniensis</i>	UM 103510	2.5 (2.5–2.6)	2.2 (2.2–2.3)	2.9 (2.8–2.9)	2.3 (2.2–2.3)
<i>Notharctus tenebrosus</i>	AMNH 127167	3.8 (3.3–4.4)	3.3 (2.8–3.8)	4.4 (3.8–5.0)	3.7 (3.2–4.4)
<i>Notharctus tenebrosus</i>	AMNH 131764	3.9 (3.4–4.4)	3.9 (3.4–4.6)	4.7 (4.1–5.4)	4.2 (3.5–4.9)
<i>Smilodectes gracilis</i>	AMNH 131762		3.7 (3.2–4.3)	4.5 (3.9–5.2)	
<i>Smilodectes gracilis</i>	UM 32773	4.5 (3.9–5.2)	4.0 (3.4–4.6)	4.8 (4.1–5.5)	4.4 (3.8–5.2)
Omomyoid euprimates					
<i>Omomyx carteri</i>	UCM 57459			4.3	
<i>Omomyx carteri</i>	UCM 57460			4.1	
<i>Shoshonius cooperi</i>	CM 60492		3.9 (3.4–4.5)	4.1 (3.5–4.7)	
<i>Microchoerus</i>	MUPRR 1771	5.0 (4.4–5.8)	4.4 (3.8–5.1)	5.2 (4.5–6.0)	4.9 (4.2–5.8)
<i>Necrolemur antiquus</i>	MNHNQU 11059	4.7 (4.1–5.4)	3.9 (3.3–4.5)	4.6 (4.0–5.2)	4.3 (3.7–5.0)
<i>Rooneyia viejaensis</i>	TMM 40 688-7	4.1 (3.8–4.8)	3.1 (2.5–3.7)	4.3 (3.6–5.1)	3.6 (3.0–4.4)

Table 6

Predictions for locomotor agility for fossil taxa based on a predictive equation for all mammals calculated from the values in Table 1, and the values in bold in Table 3. Values are on a six-point agility scale (1 = extremely slow, 2 = slow [e.g., *Loris*], 3 = medium slow, 4 = medium [e.g., *Cebus*, *Cheirogaleus*], 5 = medium fast, 6 = fast [e.g., *Galago*, *Saimiri*]; see Spoor et al., 2007). Values in brackets represent the predictions calculated from the 95% confidence intervals given for the body mass estimates in Tables 1 and 3.

Taxon	Specimen number	Mammal Prediction			
		ASCR	PSCR	LSCR	SCR
“Plesiadapiforms”					
<i>Carpolestes simpsoni</i>	USNM 482354	3.1	3.4	3.5	3.4
<i>Carpolestes simpsoni</i>	UM 101963	3.2	3.5	3.9	3.6
<i>Dryomomys szalayi</i>	UM 41870	3.3	3.6	4	3.7
<i>Tinimomys graybulliensis</i>	UM 85176	2.9 (2.7–3.1)	3.2 (3.0–3.4)	3.4 (3.2–3.7)	3.1 (2.9–3.3)
<i>Microsypops cf. latidens</i>	AMNH 55286	2.9 (2.8–2.9)	3.1 (3.1–3.2)	3.3 (3.3–3.4)	3.1 (3.1–3.2)
<i>Microsypops annectens</i>	UW 12362	2.4 (2.4–2.4)	2.6 (2.6–2.7)		
<i>Ignacius graybullianus</i>	USNM 421608	3.2 (3.1–3.3)	3.5 (3.4–3.6)	3.6 (3.5–3.7)	3.4 (3.3–3.5)
<i>Plesiadapis cookei</i>	UM 87990	3.2	3.4	3.3	3.4
<i>Plesiadapis tricuspidens</i>	MNHN isolated petrosal			2.8 (2.6–2.9)	
<i>Pronothodectes gaoi</i>	UALVP 46685	3.1	3.4	3.3	3.2
<i>Pronothodectes gaoi</i>	UALVP 46687	2.8	3.1		
Adapoid euprimates					
<i>Adapis</i> sp.	MNHN QU 11064	3.7 (3.4–4.1)	3.5 (3.2–3.9)	4.2 (3.8–4.7)	3.9 (3.5–4.3)
<i>Adapis</i> sp.	PLV 14	3.5 (3.2–3.8)	3.6 (3.3–3.9)	3.6 (3.2–3.9)	3.6 (3.2–4.0)
<i>Adapis parisiensis</i>	BM(NH) M 1345	3.3 (3.0–3.7)	3.3 (3.0–3.6)	3.6 (3.3–4.0)	3.4 (3.1–3.8)
<i>Adapis parisiensis</i>	MaPhQ 339	3.2 (2.9–3.5)	3.2 (3.0–3.5)	3.5 (3.1–3.8)	3.2 (2.9–3.6)
<i>Magnadapis quercyi</i>	MNHNQU 10875	3.3 (3.0–3.6)	3.2 (2.9–3.5)	3.5 (3.2–3.9)	3.3 (3.0–3.7)
<i>Magnadapis aff. intermedius</i>	MNHNQU 11035	2.9 (2.7–3.2)	2.8 (2.5–3.0)	3.0 (2.7–3.3)	2.8 (2.5–3.2)
<i>Leptadapis leenhardtii</i>	YPM 11481	3.3 (3.1–3.7)	3.3 (3.0–3.6)	3.7 (3.3–4.1)	3.5 (3.1–3.9)
<i>Cantius nuniensis</i>	UM 103510	3.0 (2.9–3.0)	2.9 (2.9–3.0)	3.5 (3.5–3.6)	3.0 (3.0–3.1)
<i>Notharctus tenebrosus</i>	AMNH 127167	3.9 (3.6–4.2)	3.6 (3.3–3.9)	4.5 (4.2–5.0)	4.1 (3.7–4.6)
<i>Notharctus tenebrosus</i>	AMNH 131764	3.9 (3.6–4.3)	3.9 (3.6–4.3)	4.8 (4.4–5.2)	4.4 (4.0–4.9)
<i>Smilodectes gracilis</i>	AMNH 131762		3.8 (3.5–4.1)	4.6 (4.3–5.1)	
<i>Smilodectes gracilis</i>	UM 32773	4.3 (4.0–4.7)	4.0 (3.7–4.3)	4.8 (4.4–5.3)	4.6 (4.1–5.0)
Omomyoid euprimates					
<i>Omomys carteri</i>	UCM 57459			4.7	
<i>Omomys carteri</i>	UCM 57460			4.5	
<i>Shoshonius cooperi</i>	CM 60492		3.9 (3.6–4.3)	4.6 (4.2–5.0)	
<i>Microchoerus</i> sp.	MUPRR 1771	4.5 (4.2–4.9)	4.2 (3.9–4.5)	5.1 (4.7–5.6)	4.9 (4.4–5.4)
<i>Necrolemur antiquus</i>	MNHNQU 11059	4.3 (4.0–4.7)	3.9 (3.6–4.2)	4.8 (4.4–5.2)	4.5 (4.0–4.9)
<i>Rooneyia viejaensis</i>	TMM 40 688-7	3.9 (3.6–4.3)	3.5 (3.1–3.8)	4.6 (4.1–5.1)	4.0 (3.5–4.5)

distinction is also clear in the reconstructions of the inner ear system (Fig. 5) in which the “plesiadapiforms” have notably relatively small canals compared with many of the euprimates.

Within “plesiadapiforms” relative semicircular canal radii do not reflect the fine scale differences in locomotion that have been proposed based on the postcranium. For example, *Plesiadapis cookei* is predicted by the equations to have the same degree of agility as *Ignacius graybullianus* (Tables 5 and 6), even though analysis of postcranial material suggests that *P. cookei* was a somewhat slower moving animal than paromomyids like *Ignacius*. Predictions for locomotor agility in “plesiadapiforms” are generally in the range of 2–3 (slow-medium slow) based on the primate equation, and in the range of 3–4 (medium slow-medium) based on the all mammal equation. The predicted agility values for the microsypops (poorly known from postcranials) suggest that *Microsypops latidens* practiced medium slow locomotion and was similarly agile to *Tinimomys*, and that *Microsypops annectens* was a somewhat slower moving form.

While there is a strong offset between the “plesiadapiforms” and some of the euprimates in relative semicircular canal radii, this contrast is not as apparent with the adapid adapoids (Figs. 4 and 5), which is in keeping with reconstructions of adapids as being less agile than other primitive euprimates. For example, *Leptadapis* and *Magnadapis* have notably small canals—they have similarly sized or smaller lateral semicircular canals than *Smilodectes* and *Notharctus*, but larger body masses (Fig. 4B). This observation must be tempered, however, with concerns over the body mass estimates used for the various specimens of *Leptadapis* and *Magnadapis*. These forms bear large nuchal crests, which add to the measured

cranial length, and may artificially inflate the estimated body mass. There is also a substantial range of variability amongst these forms, which reflects the fact that they represent a broader diversity of species and genera than had traditionally been recognized (Godinot and Couette, 2008). However, if the lower body mass estimates derived from the upper molar measurements are used, the locomotor predictions are not substantially changed. For example, if the degree of agility for *Magnadapis aff. intermedius* (MNHN-QU11035) is predicted from the molar estimate (9,669.6 g) the result is still in the slow-medium slow range (2.6 for the lateral canal based on the primate equation). In short, even if somewhat lower body mass estimates are used, predicted agility scores for the adapids based on the primate equation range from slow to medium, which are generally in line with reconstructions of their locomotion from postcranial material.

The primitive notharctid *Cantius nuniensis* has a predicted agility score of only 2.9 (medium slow, based on the lateral canal, primate model). In contrast, the more derived notharctid adapoids *Smilodectes* and *Notharctus* have predicted agility scores in the medium-medium fast range. This is in keeping with reconstructions that they were active arborealists that did some leaping, although likely less than very specialized modern leapers such as indriids (assigned agility scores of 6, fast). While the small size of the canals of *C. nuniensis* relative to those of *Smilodectes* and *Notharctus* is consistent with reconstructions of this genus as being less specialized for leaping than other notharctids, postcranial material for other species of *Cantius* indicates some leaping behaviour, which might lead one to expect a higher agility score (Rose and Walker, 1985; see discussion below).

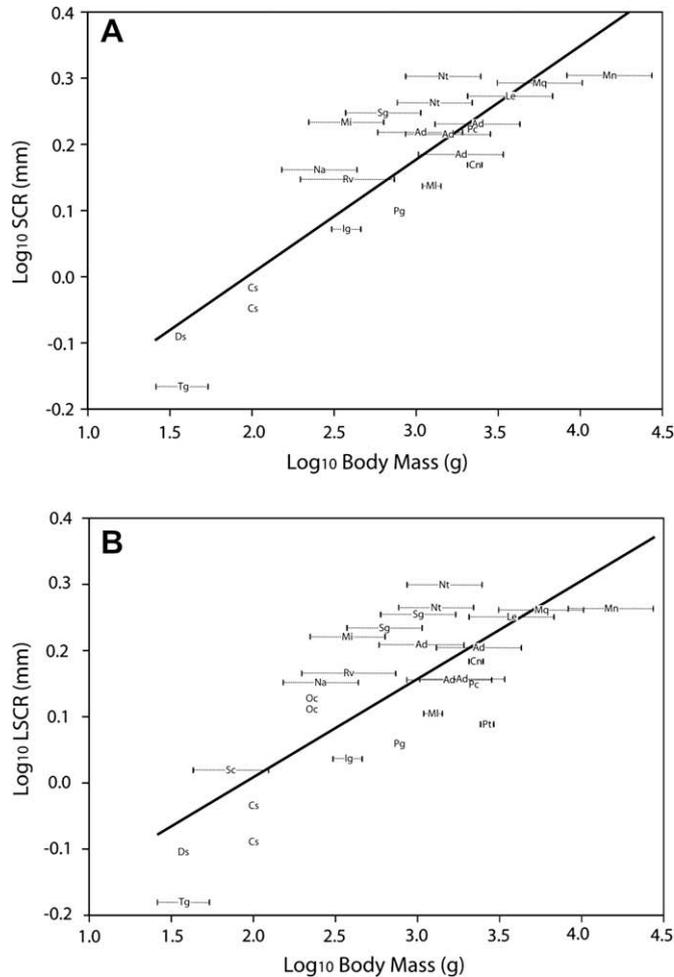


Fig. 4. Double logarithmic plots of body mass vs. A) average semicircular canal radius (SCR) and B) lateral semicircular canal radius (LSCR) for the fossil specimens studied here. See Fig. 3 for abbreviations. Body mass (BM) estimates were calculated for the adapoids and omomyoids using pGLS equations (values in bold in Table 3). The lines represent least squares regression lines: A) $\log_{10}\text{SCR} = 0.172(\log_{10}\text{BM}) - 0.338$, $r^2 = 0.766$; B) $\log_{10}\text{LSCR} = 0.148(\log_{10}\text{BM}) - 0.288$, $r^2 = 0.619$.

The smaller North American omomyoids, as noted above, are clearly distinctive from similarly sized “plesiadapiforms,” which is consistent with a locomotor mode that includes some specialized leaping. Predicted agility scores for *Omomys* and *Shoshonius* are in the medium–medium fast range, similar to the slower, more quadrupedal galagids (e.g., *Otolemur crassicaudatus*). The microchoerids were also reconstructed as being in the medium fast range, with *Microchoerus* (Fig. 5) in particular plotting with fast-moving modern primates; this is consistent with the inferred specializations for leaping in these taxa. *Rooneyia* has predicted agility scores that suggest it practiced medium-medium fast locomotion, similar to an omomyid omomyoid or a derived notharctid adapoid.

Discussion

The general concordance between locomotor reconstructions based on the postcranium and agility reconstructions presented here confirms the utility of the semicircular canal radii in reconstructing locomotor modes in fossil primates back to the Paleocene. This allows us to provide the first reconstructions of locomotion for taxa known only from craniodental remains, or those that are poorly known from the postcranium, such as microsypoids and

Rooneyia. The microsypoids are predicted to have been slow–medium slow animals. As such, it might be predicted that when more postcranial material is recovered they will lack evidence of specialized euprimate-like leaping. *Rooneyia*, on the other hand, may have practiced some leaping (or a locomotor mode requiring a similar degree of agility), although it would not be predicted that its postcranium would exhibit the high degree of specialization for leaping seen in fossil microchoerids, modern tarsiers, or indriids.

The agility scores generally follow expectations based on the known postcranial material. For example, the “plesiadapiforms” fall below the range of variation and computed regression lines for most euprimates as expected based on their lack of specializations for euprimate-like leaping. However, their predicted agility scores from the primate equation are lower than anticipated based on postcranial analysis and, unexpectedly, are somewhat lower than those computed for the adapoid adapoids. Based on functional analysis of the postcrania, all of the sampled “plesiadapiforms,” with exception of *Plesiadapis*, were likely relatively agile and active animals. Although not specialized for euprimate-like leaping, the more active “plesiadapiforms” (e.g., paromomyids) would nonetheless have been capable of active locomotion similar to callitrichine primates and arboreal sciurids. This seems at odds with reconstructed agilities as low as 2.8 (slow-medium slow) for *Ignacius graybullianus* for the lateral canal from the primate predictive equation. The predictions from the all mammal equation are generally more in line with the predictions based on the known postcranial data for “plesiadapiforms.” For example, *Dryomomys szalayii*, with a predicted agility of 4.0 (based on the lateral canal) from the all mammal equation has been analogized with *Ptilocercus lowii*, which was assigned an agility score of 4 (medium). The all mammal equation is based in part on non-primate members of Euarchoptoglires (2 species of dermopterans, 6 species of tree shrews, 2 species of lagomorphs, and 38 species of rodents—see Supplementary Information Table 1); consequently, it more effectively brackets the “plesiadapiforms” phylogenetically than the primate equation, which is likely one reason why it seems to perform better at predicting their agility. It is interesting to note, however, that “plesiadapiforms” generally plot below the modern tree shrews (Fig. 3), which have somewhat larger canals than would be expected based on their assigned agility scores (Supplementary Information Table 1), suggesting that “plesiadapiforms” may have been somewhat less agile.

The low predicted agility scores for *Cantius nuniensis* are also surprising, in light of the presence of some features for leaping in other members of this genus (Rose and Walker, 1985). While it was expected that it would be reconstructed as less agile than the more derived notharctids, it is surprising that its scores from the primate predictive equation are in the slow-medium slow range. One possibility is that the body mass estimate for this taxon may be incorrect. This is the only euprimate for which a molar-based estimate was used; the estimates for the other euprimates in the sample suggest that upper molar size may significantly over-estimate body mass. Since postcranial material for this particular species of *Cantius* is unknown, it is also possible that it diverged from the general notharctid pattern and practiced a less-agile form of locomotion.

A possible criticism of the methods of this study is that the apparent offset in relative semicircular canal radii between “plesiadapiforms” and most euprimates simply stems from different bases for body mass estimation, and, in particular, the use of dental estimates for several of the “plesiadapiforms,” not locomotor differences. It is important to note, however, that this contrast holds between forms whose body mass was estimated using multiple indicators. This can be seen, for example, in the contrast between *Shoshonius* and *Carpolestes* (Fig. 4B). In the case of *Shoshonius*, while we did use a cranium-based body mass estimate in our analysis, the

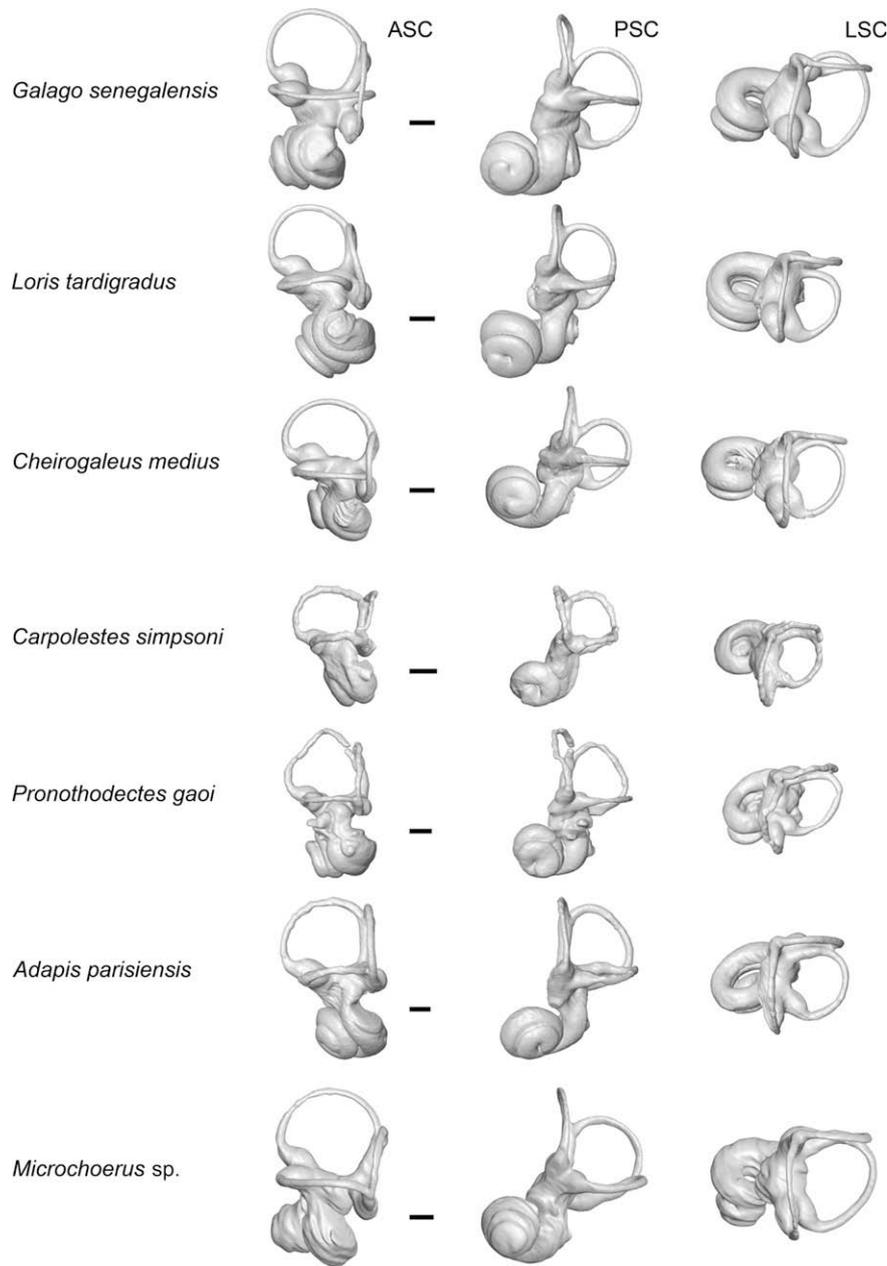


Fig. 5. Reconstructed left bony labyrinths for selected extant and fossil species. Reconstructions are scaled for body mass based on the primate regression for the mean canal radius. ASC = anterior semicircular canal; PSC = posterior semicircular canal; LSC = lateral semicircular canal. Scale bar for each is 1 mm. There is a clear difference in the radii of the canals amongst the three modern forms, with it being largest in the relatively agile galago, and smallest in the slower moving loris. Amongst the fossils, the smallest canals are found in the “plesiadapiforms” (*Carpolestes* and *Pronothodectes*), while the largest canals are found in *Microchoerus*, who can be reconstructed as having been an agile, rapidly moving arborealist.

value derived from the pGLS equation is consistent with the estimate from postcrania (Dagosto et al., 1999), which makes us confident that it is correct.

While the relatively small semi-circular canal radii of the “plesiadapiforms” are consistent with independently derived locomotor reconstructions of them as not being specialized leapers (Simons, 1967; Szalay et al., 1975; Gebo, 1988; Beard, 1989; Godinot and Beard, 1991; Gingerich and Gunnell, 1992; Bloch and Boyer, 2002, 2007; Bloch et al., 2007), the predictions are not met in terms of fine-scale differences amongst the various species. This likely reflects the degree of sensitivity of the semicircular canal system for locomotor reconstruction—while it is clearly possible to differentiate between major differences in locomotor mode (e.g., specialized leaping vs. lacking traits for specialized leaping), smaller scale

contrasts may be difficult to recover. In part, this may be the consequence of small samples inadequately representing intraspecific variation in canal size, combined with the use of species means for body mass for some of the “plesiadapiforms,” both of which could be obfuscating average differences that may actually exist between the sampled species. However, it is worth noting that the prediction equations were only able to recover the agility scores of the modern taxa to an average of within approximately 1 unit (Supplementary Information Table 1), which suggests that the semicircular canal system is not sufficiently sensitive to uncover fine scale locomotor differences.

One caveat to the interpretation of these data must be made. Body mass is a critical variable to the reconstruction of locomotor mode from semicircular canal radii. If body mass estimates using

dental dimensions are employed for the euprimates, for example, they are all reconstructed as having less agile locomotion, and the distribution of fossil primates shifts down into or below the range of modern slow-moving forms. We consider the cranium-based body mass estimates for the euprimates used here to be more reliable than estimates based on the upper molars; when used, these lower body mass estimates effectively eliminate this discrepancy. This emphasizes, however, the fact that the conclusions of this paper are only as good as the body mass estimates upon which they were based. One test for the inferences made here will be the development of better body mass estimates based on associated crania and postcranials for more species of early primates, resulting in measurements of semicircular canal radii that can be matched with more confidence to estimates of body mass.

Conclusions

Reconstructions of locomotor agility for Paleocene and Eocene fossil primates from relative semicircular canal radii generally conformed to expectations based on available postcranial material. “Plesiadapiforms,” as non-leaping arborealists, had relatively smaller semicircular canal radii than most extant euprimates, omomyoids, and derived notharctids. Within “plesiadapiforms,” relative canal radii did not reflect fine scale locomotor differences inferred from the postcranial remains. Amongst euprimates, a clear distinction is present in the relative size of the semicircular canals between adapid adapoids—reconstructed as having been non-leaping arborealists and possessing relatively small canals—and the derived notharctid adapoids and omomyoids, who have been considered at least occasional leapers and whose canals are larger relative to body mass. The relative canal radii of microsypoid “plesiadapiforms” (poorly known from the postcranium) suggest that they were arborealists not capable of specialized euprimate-like leaping, with *Microsypops annectens* in particular being a rather slow-moving form. *Rooneyia viejaensis* (known only from the skull) was likely an occasional leaper, similar to known omomyid omomyoids or notharctid adapoids; therefore, it can be predicted that when its postcranial remains are found they will show specializations for some specialized euprimate-like leaping, similar to *Omomys*.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at [10.1016/j.jhevol.2008.10.007](https://doi.org/10.1016/j.jhevol.2008.10.007)

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