# Evolution of arboreality and fossoriality in squirrels and aplodontid rodents: Insights from the semicircular canals of fossil rodents

# Evolution of arboreality and fossoriality in squirrels and aplodontid rodents: insights from the semicircular canals of fossil rodents

**Short running page heading:** Semicircular canals of extant and extinct rodents

Raj Bhagat[1]*, Ornella C. Bertrand[2], Mary T. Silcox[1]

[1]Department of Anthropology, University of Toronto Scarborough, Toronto, ON M1C 1A4, Canada

[2]School of GeoSciences, University of Edinburgh, Grant Institute, Edinburgh, Scotland, UK

*Corresponding author

raj.bhagat@mail.utoronto.ca

**Short abstract:** Here we employ two methods of reconstructing locomotor agility from the semicircular canals (SCCs) of fossil rodents: radius of curvature dimensions and SCC orthogonality. Radius of curvature dimensions provide compelling evidence that arboreality was likely an ancestral trait for the Sciuroidea clade, and that early aplodontids were more arboreal than their burrowing descendants.

**Abstract –** Reconstructing locomotor behaviour for fossil animals is typically done with postcranial elements. However, for species only known from cranial material, locomotor behaviour is difficult to reconstruct. The semicircular canals (SCCs) in the inner ear provide insight into an animal's locomotor agility. A relationship exists between the size of the SCCs relative to body mass and the jerkiness of an animal's locomotion. Additionally, studies have also demonstrated a relationship between SCC orthogonality and angular head velocity. Here we employ two metrics for reconstructing locomotor agility, radius of curvature dimensions and SCC orthogonality, in a sample of twelve fossil rodents from the families Ischyromyidae, Sciuridae, and Aplodontidae. The method utilizing radius of curvature dimensions provided a reconstruction of fossil rodent locomotor behaviour that is more consistent with previous studies assessing fossil rodent locomotor behaviour compared to the method based on SCC orthogonality. Previous work on ischyromyids suggests that this group displayed a variety of locomotor modes. Members of Paramyinae and Ischyromyinae have relatively smaller SCCs and are reconstructed to be relatively slower compared to members of Reithroparamyinae. Early members of the Sciuroidea clade including the sciurid *Cedromus wilsoni* and the aplodontid *Prosciurus relictus* are reconstructed to be more agile than ischyromyids, in the range of extant arboreal squirrels. This reconstruction supports previous inferences that arboreality was likely an ancestral trait for this group. Derived members of Sciuridae and Aplodontidae vary in agility scores. The fossil squirrel *Protosciurus* cf. *rachelae* is inferred from postcranial material as arboreal, which is in agreement with its high agility, in the range of extant arboreal squirrels. In contrast, the fossil aplodontid *Mesogaulus paniensis* has a relatively low agility score, similar to the fossorial *Aplodontia rufa*, the only living aplodontid rodent. This result is in agreement with

its postcranial reconstruction as fossorial and with previous indications that early aplodontids were more arboreal than their burrowing descendants.

**Keywords:** inner ear, adaptation, Ischyromidae, Sciuroidea, locomotion, agility

## Introduction

The semicircular canals (SCCs) are housed in the petrosal bone (or petrous portion of the temporal) and are composed of three passageways (i.e., anterior, posterior and lateral SCCs) that are at approximately 90 degrees to one another (Spoor and Zonneveld, 1998). The SCCs are a part of the bony labyrinth which contains the soft tissue sacs and ducts that make up the membranous labyrinth (Lewis et al., 1985). The membranous ducts are filled with endolymph fluid, which, under inertial drag from movement, aid in detecting angular head accelerations and contribute to the stabilization of gaze during locomotion (Spoor and Zonneveld, 1998; Hullar, 2006; Berlin et al., 2013). Due to the concealed nature of the inner ear in the petrosal bone, studying its morphology proved to be difficult for early anatomists and required time-consuming and destructive techniques (as discussed in Spoor and Zonneveld, 1995). However, the increased use of X-ray computed tomography (CT) has provided an effective way to non-destructively measure and analyze inner ear morphology in extant and extinct specimens. Today, high resolution X-ray micro-computed tomography is commonly used to study SCC dimensions and morphology in detail (e.g., Spoor and Zonneveld 1995; Lebrun et al., 2010; Gunz et al., 2012; Malinzak et al., 2012; Berlin et al., 2013; Billet et al., 2015; Pfaff et al., 2015; Grohé et al., 2016; Mennecart and Costeur, 2016; Bernardi and Couette, 2017). Although CT data do not allow for characterization of the membranous labyrinth, the close relationship between the bony and membranous structures suggests that measurements of the bony labyrinth will mirror the functionally relevant parameters of the membranous structures. Using this approach also allows for the collection of data that is directly comparable to measurements of fossil specimens, in which the membranous labyrinth is not preserved.

Due to their relationship to vestibular sensitivity and angular head movements, the morphology of the SCCs is closely associated with an animal's locomotor behaviour (Spoor and Zonneveld, 1995, 1998; Yang and Hullar, 2007; Malinzak et al., 2012). Although in vertebrate paleontology, postcrania (e.g., long bones, pelvis, calcanei etc.) are typically used to reconstruct locomotor behaviour, many species are known only from cranial material. In particular, the petrosal bone preserves well in the fossil record because of its high density. Analyzing the relationship between SCC morphology and agility level (i.e., jerkiness of movement) or other aspects of locomotor behaviour in extant taxa can therefore help paleontologists make inferences about fossil species known from petrosals but not postcranial remains (e.g., Walker et al., 2008; Silcox et al., 2009; Orliac et al., 2012; Ryan et al., 2012; Billet et al., 2015; Ruf et al., 2016; Bernardi and Couette, 2017).

Three main methodologies have been proposed to relate data from the SCCs to aspects of locomotor behaviour in extant taxa (Table 1). To date, the largest and most diverse group of extant taxa has been assessed by Spoor et al. (2007). The authors ranked SCC sensitivity based on agility scores derived from field observations and video footage. Agility scores were ranked on a scale from 1-6 with 1 being extremely slow and 6 being fast. Their results show that animals with larger average SCC radii of curvature relative to body size have faster, jerkier locomotion compared to animals with smaller canals (Spoor et al., 2007). This relationship makes sense in light of work that has established a link between the relative size of the SCCs and their sensitivity (Spoor and Zonneveld, 1998; Yang and Hullar, 2007; Cox and Jeffery, 2010). The dataset provided by Spoor and collegues (2007) has frequently been used to reconstruct locomotor behaviour from fossils (e.g., primates [Walker et al., 2008; Silcox et al., 2009; Ryan et al., 2012; Bernardi and Couette, 2017], leptictids [Ruf et al., 2016], artiodactyls [Orliac et al.,

2012], xenarthrans [Billet et al., 2015], and early placental mammals [Cameron et al., 2019; Bertrand et al., 2020]). This is likely because of its large size and extensive taxonomic coverage (Table 1). Also, despite the rather qualitative approach to assessing agility, it relates the SCC radii to an aspect of behaviour that can be clearly understood with respect to a species' locomotor repertoire.

Pfaff et al. (2015) conducted a morphometric analysis of the SCCs using scaled data based on cranial measurements rather than body mass. Their sample included 50 taxa, mainly from the squirrel-related clade (Sciuridae, Gliridae, and Aplodontidae; Table 1). As opposed to using agility scores as a proxy for vestibular sensitivity, they calculated a measure of sensitivity based on SCC dimensions. They found substantial differences between subterranean, flying and gliding taxa. The vestibular sensitivity of the SCCs in fossorial sciurids was found to be higher relative to arboreal and gliding taxa, based largely on variation in the SCC diameters. They reasoned that the lessened sensory information flow during locomotion in flying and gliding taxa may be necessary to prevent over stimulation of the vestibular system (Schutz et al., 2014; Pfaff et al., 2015). The majority of their sample consisted of fossorial, arboreal and gliding taxa, therefore limiting inferences using this method of the vestibular sensitivity of taxa with less extreme locomotor behaviours (i.e., scansorial). Further investigation is still required to understand how SCC diameter influences sensitivity in other taxa beyond the squirrel-related clade. Additionally, measuring SCC diameter accurately is more challenging than measuring canal radii or angles. As a very small measurement, it will be more impacted, as a percentage of the measurement, by the threshold selected for the segmentation of the SCCs—this is a byproduct of partial volume averaging, which leads to changes in the apparent outer edge of the bone depending on the threshold used. Pfaff et al. (2015) acknowledge that they used different

threshold values in their manual segmentation process, but they did not consider the impact of varying thresholds on this measurement, which means that they did not account for the fact that different datasets would have different amounts of error introduced by partial voluming averaging. These authors also did not consider the degree to which their approach to scaling their measurements influenced their results.

As opposed to qualitatively assessing agility, Malinzak et al. (2012) directly measured angular velocity magnitude (AVM) of head rotations as a variable representing vestibular sensitivity in eleven strepsirrhine primates (Table 1). They found animals with more orthogonally positioned SCCs had higher angular head velocities than those with less orthogonal canals. Additionally, from analyzing angular head velocities with radii of curvature data from Spoor et al. (2007), they found no relationship between the two. However, Malinzak et al. (2012) had a small and not very diverse sample, either taxonomically, or in terms of the range of locomotor behaviours represented (Table 1). In contrast, results from Berlin et al. (2013) demonstrated that the radii of curvature (analyzed without angular velocity measurements) do in fact influence vestibular sensitivity in their larger and more diverse sample. In addition, studies using angular data to reconstruct locomotor behaviour in fossil taxa have shown a high degree of within-species variability, leading to the reconstruction of an implausible range of different behaviours for one species (Bernardi and Couette, 2017). This is in contrast to reconstructions using the radii of curvature, which yielded much more consistent agility estimates (Bernardi and Couette, 2017).

Here, we examine both the radii of curvature and degree of orthogonality of the SCCs for twelve fossil species of rodents from Ischyromyidae, and Sciuroidea (Sciuridae + Aplodontidae; Table 2). In spite of concerns about the applicability of the Malinzak et al. (2012) sample to

non-primate groups we included their approach, since it is the only dataset with quantatitive measures of angular velocity. The method from Pfaff et al. (2015) was not used for two reasons: 1. the lack of an error study demonstrating that small measurements such as the SCC diameter can be accurately measured in diverse microCT datasets across varying thresholds and 2. the lack of more behaviourly generalized rodents in their comparative sample, which is problematic when assessing locomotor behaviour in the range of fossil taxa considered here.

Sciuridae includes 58 extant genera and 285 species (Burgin et al., 2018). Squirrels are diverse in terms of locomotion, exhibiting terrestrial, scansorial, arboreal and gliding adaptations (Koprowski et al., 2016). The oldest sciurid known from postcranial material, the late Eocene *Douglassciurus jeffersoni* has been interpreted as arboreal (Emry and Thorington, 1982). During the Oligocene and Miocene, squirrels rapidly invaded their modern-day ecological niches (Mercer et al., 2003; Thorington et al., 2012). The sister-clade to Sciuridae, Aplodontidae, is only represented by a single species today, *Aplodontia rufa*. In the past, this group was more diverse, and was distributed across the Holarctic regions, being recovered from North America, Europe and Asia (Hopkins, 2008). Fossil Aplodontidae have been inferred to have exhibited a diverse array of behavioural locomotor types, with some specimens being reconstructed as fossorial (e.g. aplodontines and mylagaulines), as burrowing (meniscomyines), and even as having arboreal, squirrel-like adaptations (allomyines, prosciurines) based on postcranial and cranial data (Hopkins, 2005; 2008). The family's earliest members display squirrel-like adaptations, suggestive of arboreal and scansorial locomotor behaviour (Hopkins, 2005; 2008).

Ischyromyidae has been considered one of the most primitive rodent families (Korth, 1994) and has been discovered in North America (late Paleocene to early Eocene), Europe (early to late Eocene), and Asia (Early Oligocene; Korth, 1994; Anderson, 2008). There is uncertainty

about the relationships within Ischyromyidae and with other rodent families. A comprehensive analysis including representatives of all the various groups has yet to be published. Figure 1 illustrates the two most broadly supported hypotheses for the relationships among Ischyromyidae and Sciuroidea. The only difference stems from the position of Reithroparamyinae, which might either be more closely related to the Sciuroidea (Meng, 1990) or to Paramyinae (Asher et al., 2019). The positions of the fossil sciuroids in Figure 1 are based on different studies (Korth and Emry, 1991; Hopkins, 2008; Korth and Samuels, 2015), while the position of the extant squirrels, and their relationship to *Aplodontia rufa*, is based on molecular phylogenies (Mercer et al., 2003; Blanga-Kanfi et al., 2009; Churakov et al., 2010; Fabre et al., 2012).

Studies on postcranial anatomy reveal that Ischyromyidae had diverse lifestyles. The early Eocene paramyine, *Paramys,* may have been scansorial, spending some time in the trees and on the ground (Rose and Chinnery, 2004). Other members of this subfamily, *Pseudotomus* (Middle Eocene) was larger, and probably fossorial (Dunn and Rasmussen, 2007; Rose and Koenigswald, 2007). The ischyromyine, *Ischyromys* was also probably fossorial based on postcranial data (Wood, 1937). The Reithroparamyine, *Reithroparamys* was scansorial but may have potentially spent more time in the trees than *Paramys* (Wood, 1962, Rose and Chinnery, 2004). No postcrania have been recovered for *Rapamys* and *Titanotheriomys* and it remains unclear if these genera exhibited similar locomotor modes to their close relatives *Reithroparamys* and *Ischyromys* respectively. In contrast, a recent study found that some members of these three subfamilies (i.e. *Paramys, Reithroparamys, Rapamys* and *Ischyromys*) were terrestrial based on cranial dimensions (Bertrand et al., 2016a). This result may indicate that ischyromyids were more conservative in terms of cranial shape compared to squirrels, which show cranial adaptations based on locomotor mode (Luo et al., 2014). Our Sciuridae sample includes two

Oligocene fossils, the Sciurini *Protosciurus* considered arboreal based on postcranial data (Korth and Samuels, 2015), and *Cedromus* for which no postcranial data has been discovered to date. The postcrania of *Prosciurus* have previously been interpreted as squirrel-like, which suggest they it have been arboreal (Hopkins, 2007). The early Miocene *Mesogaulus* displays cranial adaptations for fossoriality, also present in other Mylagaulinae known for being fossorial (Hopkins, 2008).

From previous analyses of SCC dimensions (Spoor et al., 2007; Malinzak et al., 2012), we expect rodents with relatively faster locomotor behaviours to have relatively larger and more orthogonal SCCs in comparison to rodents with slower locomotor behaviours. Fossil rodents inferred to have had relatively agile locomotor behaviours (e.g., arboreal behaviour) including early Sciuroidea are expected to have relatively larger SCCs. In contrast, rodents that have been suggested to practice less agile locomotion (i.e., generalist, terrestrial or fossorial behaviours), including the fossorial *Pseudotomus*, and the aplodontid *Mesogaulus*, are expected to have relatively smaller and less orthogonally positioned SCCs. The current sample allows for consideration not only of individual species' locomotor behaviours, but patterns in change through time for the early phases of rodent evolution.

**Institutional abbreviations**

AMNH, American Museum of Natural History, New York, NY; AMNH F:AM, Frick collection: American Museum of Natural History, New York, NY; USNM, United State National Museum, Washington, D.C.; ROMV, Royal Ontario Museum Vertebrate Paleontology; YPM, Yale Peabody Museum, New Haven, CT.

# Materials and Methods

## Materials

High resolution microCT scans were obtained for fossil and extant rodent crania at the Shared Materials Instrumentation Facility (SMIF), Duke University, North Carolina or the Microscopy and Imaging Facilities (MIF) of the American Museum of Natural History, New York (Table S1). Semicircular canal dimensions were measured for twelve fossil rodent crania including eight ischyromyids, two sciurids, and two aplodontids (Table 2). The majority of the fossil rodents are from the early Eocene to Oligocene while *Mesogaulus paniensis* is from the early Miocene (Table 2). The fossil sample was chosen based on availability of well-preserved specimens in museum collections. The modern comparative dataset from Spoor and colleagues (2007) includes SCC dimensions for 210 mammals including thirty-eight extant rodents from various families including Anomaluridae, Bathyergidae, Castoridae, Caviidae, Chinchillidae, Dipodidae, Erethizontidae, Hydrochaeridae, Muridae, Myocastoridae, Pedetidae, Sciuridae, and Spalacidae. We measured SCC dimensions for an additional eighteen extant rodents to make the comparative sample more relevant to the fossils under study by expanding the taxonomic and ecological diversity in the sample. These include the only living aplodontid, *A. rufa* and seventeen species of Sciuridae (Table 3). We use one specimen for each species except for *Ischyromys typus*, for which two specimens were used (Table 2). Additional information regarding scanning acquisition can be found in Table S1.

## Methods

Semicircular canal dimensions were measured from the left inner ear of each specimen unless this side was not sufficiently well preserved. In such cases, measurements were taken from the right inner ear (indicated with an asterisk in Tables 2 and 3). On a WACOM Cintiq 21UX tablet, TIFF images of the CT data were visualized in ImageJ (Rasband, 1997-2014) and cropped around the bony labyrinth for each specimen to minimize the overall size of the dataset. Using AVIZO® 7.0.1 software (Visualization and Sciences Group, 1995-2012), the data were re-sliced so that each SCC could be visualized in a single plane following the approach of Spoor et al. (2007; see also Silcox et al., 2009). This was done by visualizing the dataset in orthogonal view using the Slice module and identifying each canal based on characteristic anatomical relationships (Fig. S1). The "fit to point" feature of the Slice module allows 3 points to be placed along the length of each SCC, to orient the slice in the resulting plane (Fig. 2). We measured arc height and width as outlined in Spoor et al. (2007) to calculate the average SCC radius (Fig. 2; Table S1). They are measured as the maximum length from one side to the other, taken from the center of the lumen (Fig. 2). Arc height and width has been previously described by Spoor and Zonneveld (1995) among other standardized measurements of the bony labyrinth in humans and other primates. The anterior SCC radius (ASR), posterior SCC radius (PSR) and lateral SCC radius (LSR) were calculated as follows:

$$R = 0.5\left(\frac{h + w}{2}\right)$$

Where R is the radius of each canal (i.e., ASR, PSR, and LSR), h is the height and w is the width. Furthermore, the average radius for all three SCCs (SCR) is calculated from ASR, PSR and LSR.

Using video footage and field observations, Spoor et al. (2007) assigned agility scores to extant mammals. Silcox et al. (2009) published regression equations to calculate agility scores for mammals using the Spoor et al. (2007) dataset. Because it may not be possible to recover all three SCCs for a particular specimen, depending on preservation and the quality of the data, they provided separate equations utilizing ASR, PSR, LSR as well as SCR. Here, we present agility scores utilizing the equation for SCR and LSR. The LSR has been found to be the best predictor of agility level (Silcox et al., 2009), likely because the lateral canal is the least constrained by the size and morphology of the petrosal lobule (Jeffery et al., 2008). For this reason, SCC dimensions are primarily analyzed using the LSR.

Although we calculate agility scores for the specimens in our sample (Table 3), in light of the qualitative approach used by Spoor et al. (2007) in assigning agility categories, we also examine the data directly through bivariate plots of $\log_{10}$LSR (logarithm of lateral SCC radius) vs. $\log_{10}$BM (logarithm of body mass) for our sample with the rodents from Spoor et al. (2007; Table S2), and with the full mammal dataset from Spoor et al. (2007; Table S3). Furthermore, we use residuals from the least squares regression of $\log_{10}$LSR and $\log_{10}$BM to analyze variation in relative LSR of our extant and fossil rodents relative to the dataset from Spoor et al. (2007) with extant rodents (Table S2) and all mammals (Table S3). Least squares regression analysis is used to remain consistent with methods from Spoor et al (2007) for analyzing the modern comparative dataset. The Kruskal-Wallis test is used to test for differences in the residuals from $\log_{10}$LSR and $\log_{10}$BM between different rodent groups. This non-parametric test allows for the statistical comparison of residuals based on sample medians between multiple groups and is ideal in situations of low sample size, as is the case for most of our groups (Madrigal, 1998). The Dunn's non-parametric post hoc test was used to assess where the significant differences between groups

lie. We present p-values with Bonferroni corrections. These tests were performed using PAST 3.16 (Hammer et al., 2001) to compare residuals for 1) all mammals from Spoor et al. (2007) grouped by agility with extant rodents as a separate group and 2) fossil rodents grouped by agility.

Manual segmentation of the bony labyrinth was also performed in AVIZO® 7.0.1 software (Visualization and Sciences Group, 1995-2012) using the Segmentation Editor (Fig. 3) for each specimen. The segmented bony labyrinth was used to obtain measurements of SCC orthogonality using the same side from which radii of curvature were measured. Following segmentation, an STL ascii surface file was generated and the Autoskeletonization feature in AVIZO was used to generate midline curves for each SCC. The midline curves represent the exact center of the lumen of each SCC. Measurements of orthogonality were obtained by defining the plane of each SCC, composed of 3 points on the midline curve. Angle measurements of the ipsilateral canal pairs were calculated between the resulting planes, including the angle between the anterior SCC and lateral SCC (ASC/LSC angle), posterior SCC and lateral SCC (PSC/LSC angle) and anterior SCC and posterior SCC (ASC/PSC angle; Tables 4, S4). $Log_{10}$AVM (logarithm of the angular velocity magnitude) was calculated for our sample, which provides an estimation of the head's rotational speed, modelled from a modern primate comparative sample (Table 4; see Malinzak et al., 2012). The following formula from Malinzak et al. (2012) was used to calculate $log_{10}$AVM:

$$\text{Log 10 (AVM)} = -0.51 \text{ x Log 10 (90VAR)} + 2.83$$

Here, 90VAR is the sum of the angular deviation from 90 degrees for all three SCC pairs. The calculated $log_{10}$AVM and 90 VAR for all rodents were compared to data from Malinzak et al. (2012) including 5 primates and 2 non-primate species, *Cynocephalus volans* and *Bradypus variegatus*. In order to obtain a more accurate idea of how 90VAR covaries with LSR in our

fossil and extant rodent sample, $log_{10}$90VAR values were plotted against residuals from the least squares regression of $log_{10}$LSR and $log_{10}$BM. Therefore, we were able to analyze 90VAR independently of AVM, which is calculated in part, using 90VAR.

Body mass is an important factor in this analysis, as previous work (Spoor et al., 2007) has shown that the strongest factor controlling SCC size is body size, so this variable must be controlled for when seeking a locomotor signal. Skeletal elements from which body mass can be estimated are quite limited for fossil rodents in this study since many are unknown from postcrania. Dental data from extant rodents have often been used to estimate body mass in fossil rodents (e.g., Legendre, 1986; Gagnon, 1996; Martin, 1996; Antoine et al., 2012). However, due to the derived nature of many extant rodent teeth, an accurate body mass estimation from dental measures is difficult to obtain (Bertrand et al., 2016a). Bertrand et al. (2016a) showed that cranial length was a reliable indicator of body mass for many of the fossil rodents in the current study. Therefore, this study utilized cranial length to estimate body mass of fossil rodents. In cases where cranial length was not available, cheek-tooth area was used, which is another reliable estimator of body mass (Bertrand et al., 2016a; Table S1).

# Results

## Radii of curvature of the semicircular canals

The relationship between body mass and LSC radius for the eighteen extant rodents measured in this study is shown in the broader context of the data for rodents from Spoor et al. (2007) in Figure 4 and for all mammals from Spoor et al. (2007) in Figure 5. Modern sciurids have large LSCs relative to body mass, plotting among the fast-moving rodents (Fig. 4) and fast-

moving mammals in general (Fig. 5). This result is consistent with expectations from their behavioural data, since they are mostly active arboreal/scansorial animals, with a few (i.e., *Rhinosciurus*, *Lariscus)* being terrestrial, but still fairly agile. As a result, this group has some of the highest residuals calculated from the least squares regression between $\log_{10}$LSR and $\log_{10}$BM and fall in the range of fast moving rodents (Fig. 4B) and fast moving mammals (Fig. 5B) from Spoor et al. (2007).

The Kruskal-Wallis test shows that a significant difference exists among the 6 mammalian agility groups and extant sciurids in terms of median residuals [H ($chi^2$) = 52.59; p = $1.42x10^{-9}$; Table 5]. The Dunn's post hoc test supports previous inferences (Spoor et al., 2007) that there are significant differences in relative SCC canal sizes among most of the agility groupings, with a few exceptions (Table 5). This test also shows that the median residuals of extant sciurids differ significantly from mammalian groups categorized as extremely slow, slow, medium slow, and medium (Table 5). The median of extant sciurids does not differ from the medians of the mammalian groups categorized as medium fast and fast (Table 5). On the other hand, *Aplodontia* has a relatively smaller LSC for its body mass, falling among the slowest modern rodents from Spoor et al. (2007; Fig. 4A) with a residual value that is much lower than modern squirrels and is in the range of relatively slower rodents from Spoor et al (2007; Fig. 4B). The agility score for *Aplodontia* is 4.0 (medium) based on LSR and 2.9 (medium-slow) based on SCR (Table 3).

The included fossil rodents have smaller LSCs relative to body mass (Fig. 4A), with residuals for this group calculated from $\log_{10}$BM and $\log_{10}$LSR being well below zero (Fig. 4B). They group with modern rodents from Spoor et al. (2007) categorized as medium to slow. In contrast, Reithroparamyinae (*Reithroparamys* and *Rapamys)* have relatively larger LSCs,

grouping among rodents categorized by Spoor et al. (2007) as having fast and medium agility (Fig. 4). Members of Ischyromyinae, however, show considerable variability in their agility scores (Table 6). The ischyromyine *Titanotheriomys* has a relatively larger LSC compared to *Ischyromys* and groups with rodents categorized by Spoor et al. (2007) as having fast and medium agility (Fig. 4). In contrast, *Ischyromys* groups with rodents categorized by Spoor et al. (2007) as slow and medium (Fig. 4). Hence, the residuals for *Reithroparamys, Rapamys* and *Titanotheriomys* are found to be greater than those calculated for *Paramys*, *Pseudotomus* and *Ischyromys* (Fig. 4).

Both fossil squirrels, *Cedromus* and *Protosciurus* have large SCCs relative to body mass, in the range of extant sciurids, resulting in much higher calculated residuals (Fig. 4). Both taxa group with rodents categorized by Spoor et al. (2007) as having fast locomotion (Fig. 4). In contrast, the two members of Aplodontidae vary considerably in LSC radius, with the early Oligocene *Prosciurus* having a larger LSC (and higher residual) compared to the early Miocene *Mesogaulus*, which has a much lower residual, close to the ischyromyids *Paramys* and *Ischyromys* (Fig. 4). *Prosciurus* groups with rodents from Spoor et al. (2007) categorized as having fast locomotion, while *Mesogaulus* is close to *Aplodontia* and rodents with relatively slower locomotion (Fig. 4).

The agility scores calculated using the all mammal predictive equations from Silcox et al. (2009) are presented in Table 6 for the LSR and average SCR, and these taxa are included in the bivariate plot of $\log_{10}$LSR vs. $\log_{10}$BM in Figure 5. The pattern of variation is similar to that described for the rodent sample, with notable variation in the residuals calculated from the least squares regression line among the fossil taxa. Indeed, these residuals can be used to divide the fossil rodent sample into three groups, which coincide with the ranges of their respective agility

scores (Fig. 6): 1) rodents with low residuals (median = -0.041) and medium slow to medium agility scores (*Paramys, Ischyromys,* and *Mesogaulus*); 2) rodents with intermediate residuals (median = 0.028) and medium to medium fast agility scores (*Reithroparamys, Rapamys,* and *Titanotheriomys*); and 3) rodents with high residuals (median = 0.097) and medium fast to fast agility scores (*Cedromus*, *Protosciurus,* and *Prosciurus*). A Kruskal Wallis test shows that there is a significant difference between the 3 groups and median residuals (p=0.0093). A Dunn's post hoc test reveals a significant difference between the groups with the highest and lowest residuals (p=0.0033). However, the median residuals for the intermediate fossil rodent group is not significantly different from the other two groups (Fig. 6).

## Semicircular canal orthogonality

Measurements of the angles between the SCCs are shown in Tables 4 and S4. Extant rodents have the greatest variation in 90 VAR for the ASC/LSC pair (variance = 17.7) compared to the ASC/PSC pair (variance = 7.1) and PSC/LSC pair (variance = 8.7; Table S4). This is consistent with previous findings from living and fossil primates where 90 VAR for the ASC/LSC angle showed the greatest variation (Malinzak et al. 2012; Berlin et al. 2013; Bernardi and Couette, 2017). In contrast, variation in 90 VAR for fossil rodents only differs slightly between the three canal pairs: ASC/LSC pair (variance = 8.6), ASC/PSC pair (variance = 8.5) and PSC/LSC pair (variance = 9.0; Table S4).

The angular velocity magnitude quantifies the rotational speed of the head. The average $\log_{10}$AVM value calculated for extant sciurids is 2.25 ±0.11 with values ranging from 2.1 to 2.45 (Table 4). The average $\log_{10}$AVM value for fossil rodents is 2.26 ±0.09 with values ranging from

2.11 to 2.43 (Table 4). All rodents have high $log_{10}$AVM values and relatively low $log_{10}$90VAR and group towards the top left of the distribution with the fastest moving primates from Malinzak et al. (2012; Fig. 7A). This result implies that rodent SCCs are relatively more orthogonal compared to slower moving primates. Rodent $log_{10}$AVM values encompass and extend beyond the range of two of the fastest primates from Malinzak et al (2012): 1) the leaper *Galago moholi* with the highest $log_{10}$AVM value for all primates and 2) the arboreal quadrupedal *Cheirogaleus medius*, with the second highest $log_{10}$AVM value (Fig. 7A). Consistent with results from Malinzak et al. (2012), the $log_{10}$AVM for the glider *Cynocephalus* (colugo) remains the highest calculated, while *Bradypus* (brown-throated sloth) remains the lowest (Fig. 7A). However, no discernible trends are apparent in the $log_{10}$AVM distribution for rodents. For example, the fast moving extant sciurids, that would be expected to have relatively more orthogonal SCCs, are found widely distributed along the $log_{10}$AVM and $log_{10}$90VAR scales (Fig. 7A). Furthermore, the slow-moving *Aplodontia* would be expected to have a relatively low $log_{10}$AVM, however, it plots much higher up, among fast moving sciurids. Fossil taxa fall within the range of variation of the extant sciurids, with the fastest moving non-rodent taxa. Ischyromyines might have been expected to have less orthogonal SCCs, but fall near both the top and bottom of the fossil rodent distribution, with both *Ischyromys* specimens showing the greatest difference (Fig. 7A). Similarly, no discernible trends are found in $log_{10}$90VAR for fossil and extant rodents when compared to residuals from LSR (slope = 0.085, intercept = -0.056, $R^2$ = 0.075; Fig. 7B). Fossil rodents that were found to have low residuals and medium slow to medium agility scores (*Paramys, Ischyromys,* and *Mesogaulus*) remain on the lower end of the residual distribution, but are quite spread apart with respect to the $log_{10}$90VAR scale (Fig. 7B).

# Discussion

## Semicircular canal radii of curvature dimensions and early rodent evolution

Ischyromyids are considered to be some of the most primitive rodents, with members of that group likely being ancestral to members of later occurring families such as Sciuridae and Aplodontidae (Korth, 1994). Based on postcranial data, *Paramys* has been reconstructed as being scansorial (Rose and Chinnery, 2004) compared to *Pseudotomus* (Dunn and Rasmussen, 2007) and *Ischyromys* (Wood, 1937), which both displayed more terrestrial to burrowing adaptations. Our results do not seem to match the differences observed in the postcrania of *Paramys* and *Ischyromys* as they both fall in the medium slow to medium locomotor category and had very similar agility scores. However, *Pseudotomus* had the lowest agility score of all ischyromyids, which is in accordance with postcranial data. In light of these results, *Ischyromys* may have been less specialized than *Pseudotomus.* However, it is possible that this discrepancy in agility for a similar style of locomotion could relate to body mass differences, with *Ischyromys* being much smaller than *Pseudotomus*. Additionally, if *Ischyromys* came from a reithroparamyine type ancestor that was more scansorial than *Paramys*, then a higher degree of agility than *Pseudotomus* could have been preserved in this taxon. The agility scores and residuals for members of Reithroparamyinae suggest they had medium to medium fast locomotion. This is consistent with previous inferences that *Reithroparamys* was squirrel-like based on the anatomy of its foot (Wood, 1962) and may suggest that this taxon may have spent more time in trees, or at least was more active than *Paramys*. The inferred more agile locomotion of reithroparamyines compared to paramyines and *Ischyromys* is consistent with the idea that they were moving in the direction of squirrel-like locomotion, and is also consistent with their inferred phylogenetic position as being closely related to the squirrel-related clade (Meng, 1990).

These categorizations are consistent with the residuals calculated from the least squares regression of $\log_{10}$LSR and $\log_{10}$BM where *Paramys*, *Pseudotomus* and *Ischyromys* have smaller residuals compared to the reithroparamines and *Titanotheriomys*, which are relatively higher (Fig. 6). However, the Dunn's post hoc test did not reveal a significant difference between the median residuals of these groups, which may be attributed to the low sample size (Fig. 6). Despite this fact, the groupings based on residuals as well as the reconstructed agility scores provide some insight on the locomotor mode of ischyromyids. The Oligocene *Ischyromys* has some of the lowest agility scores (3.8 and 4 for LSR) and fall in the smallest residual group (Fig. 6) while, taxa such as *Reithroparamys* and *Rapamys* have relatively higher scores (4.4 and 4.6 respectively for LSR) and fall in the intermediate residual group (Fig. 6).

The ancestor of Ischyromyidae was probably scansorial based on our results and on the inference that the most basal ischyromyid of our sample, *Paramys*, exhibited this behaviour. During the Eocene, *Pseudotomus* invaded a new type of ecological niche and become more fossorial, while other ischyromyids (i.e., *Reithroparamys, Rapamys* and *Titanotheriomys*) followed a different trajectory by becoming more agile, and were probably spending more time in trees as a result. During the Oligocene, *Ischyromys* became more fossorial departing from a hypothetical reithroparamyine scansorial ancestor, converging with the Eocene *Pseudotomus* in terms of locomotor behavior. Ultimately, ischyromyid agility reconstructions are in agreement with the idea that this group displayed a variety of locomotor modes. Those that were not exclusively arboreal, such as generalist, terrestrial or fossorial rodents, were found to have relatively smaller LSCs, while those with greater adaptations for arboreality were found to have relatively larger LSCs.

## Locomotor behavior in Sciuroidea

Making inferences regarding the locomotor behaviour of early sciurids is difficult as many specimens are unknown from postcranial material. Evidence from early fossil sciurids suggests that they were likely arboreal and that this locomotor behaviour was an ancestral trait for this group (Emry and Thorington, 1982). However, *Cedromus* is unknown from postcranial material and is placed outside of extant squirrels. Aspects of *Cedromus* endocranial anatomy (e.g., caudal expansion of the neocortex, large petrosal lobules) have led Bertrand et al. (2017) to interpret these features as indicative of improved vision, which may be consistent with arboreal locomotion. *Cedromus* has a LSR in the range of fast moving rodents such as the tree squirrel *Sciurus* (Fig. 5A). The fact that *Cedromus* falls in the highest residual group (Fig. 6) and has a high agility score in the fast agility range is consistent with an active and arboreal locomotor behaviour.

*Aplodontia* predominantly displays fossorial locomotor behaviour (Carraway and Verts, 1993) and its low agility score inferred from its relatively small LSC (Figs. 4 and 5), reflects the fact that fossorial animals are likely to experience smaller degrees of angular accelerations of the head than animals that are actively locomoting through the trees or hopping on the ground. As such, this result is more consistent with expectations from behaviour than the results for fossorial rodents in Pfaff (2015). In contrast, early aplodontids show squirrel-like adaptations, suggesting they had arboreal and scansorial locomotor behaviours (Hopkins, 2005; 2008). The early aplodontid *Prosciurus* has a relatively larger LSC and groups with fast moving taxa such as the flying squirrel *Glaucomys* (Fig. 5A) and falls in the high residual group (Fig. 6). Furthermore, *Prosciurus* yielded the highest agility score (6.1 from the LSC) out of all fossil rodents and can be reconstructed as having fast, agile locomotor behaviour. This is in line with previous

interpretations of its postcrania by Hopkins (2007), who found that it had squirrel-like adaptations and may have been arboreal. Furthermore, Bertrand et al. (2018) found similarities in the endocranial anatomy (i.e., expanded neocortex, and petrosal lobules) in *Prosciurus,* which resembled arboreal squirrels. The high agility reconstructed for early Oligocene members of both Sciuridae and Aplodontidae is consistent with the inference that arboreality was likely an ancestral trait for Sciuroidea. This group was more adapted to arboreal lifestyle and were more agile than their ischyromyid ancestors.

More derived members of Sciuroidea in our sample include the late Oligocene sciurid *Protosciurus* and the early Miocene aplodontid *Mesogaulus*. *Protosciurus* is known from postcrania and has been considered arboreal (Korth and Samuels, 2015). Its high agility score and placement in the high residual group (Fig. 6) is consistent with this behavioural reconstruction. This finding suggests that this taxon had fast, agile locomotion comparable to extant tree squirrels (Fig. 5A). On the other hand, *Mesogaulus* has a relatively lower agility score (Table 6) and falls in the low residual group (Fig. 6). This suggests that this species displayed medium slow to medium locomotion, similar *Aplodontia* and some ischyromyids (i.e., *Paramys* and *Ischyromys*). *Mesogaulus* also has relatively smaller SCCs compared to *Prosciurus* (Figs. 4 and 5), which is consistent with its postcranial reconstruction indicating that it was a specialized burrower (Hopkins, 2008). *Mesogaulus* and *Aplodontia* can be inferred to have had similar locomotor adaptations, because of their relatively similar LSC sizes (Figs. 4 and 5) and agility scores. The relatively slower locomotor reconstruction of *Mesogaulus* is in line with inferences that derived aplodontids became more fossorial through time compared to their arboreal ancestors (Hopkins, 2007). Bertrand et al. (2018) found that *Mesogaulus* had a smaller neocortex

and petrosal lobules, which might indicate that this taxon was spending more time underground and required less vision to survive.

## Semicircular canal orthogonality and rodent locomotor behaviour

The second method used, which analyzes the angles between the SCCs, relies on the relationship between SCC orthogonality (90VAR) and angular velocity magnitude (AVM). Animals with more orthogonal SCCs (lower 90VAR) are expected to have greater angular head velocities compared to animals with less orthogonal SCCs (higher 90VAR). Semicircular canal orthogonality is used to calculate angular velocity magnitude (AVM) based on the primate dataset and equation from Malinzak et al. (2012). The $\log_{10}$AVM values for primates range from 1.82 for slow moving species and 2.36 for fast moving species. Rodents have $\log_{10}$AVM values and SCCs that are generally more orthogonal (lower $\log_{10}$90VAR values) than primates, however there is some overlap with the two most agile primates (Fig. 7A). Within the rodent sample, $\log_{10}$AVM scores did not follow patterns of locomotor behaviour. For example, the extant sciurids, who exhibit agile, arboreal locomotion, were found widely distributed along the $\log_{10}$AVM and $\log_{10}$90VAR scales (Fig. 7A). Additonally, *Aplodontia rufa* was found to have a much higher $\log_{10}$AVM value and more orthogonal SCCs (Fig. 7A) than would be expected based on its less agile, fossorial adaptations. These results suggest that the comparative dataset from Malinzak et al. (2012) may not be applicable to non-primate groups such as rodents. This is further exemplified in the comparison of $\log_{10}$90VAR and residuals from LSR, which has a relatively weak $R^2$ value of 0.075. The applicability of this method to primate groups beyond strepsirrhines has also been questioned and a recent study showed an unexpectedly broad range

of $log_{10}$AVM values for multiple specimens of the fossil primate *Adapis parisiensis*, which ranged the entire primate $log_{10}$AVM scale (Bernardi and Couette, 2017).

The fact that this method does not factor in any element of body size may be one reason for the broad range of $log_{10}$AVM scores. A recent study analyzing intraspecific variation in primates using SCC dimensions (i.e., radii of curvature and canal angles), demonstrates the importance of body size in such analyses. For both strepsirrhine and platyrrhine primate groups, functional differences in SCC morphology, driven partly by variation in orthogonality, were only distinguishable when body size was accounted for (Gonzales et al., 2018). Another reason for the broad range of $log_{10}$AVM scores may have to do with the way SCC shape varies based on function between taxa. Gonzales et al. (2018) highlighted the idea that vertebrates may employ more than one morphological strategy in detecting the environment through angular head rotations. In fact, divergent adaptations of the vestibular system have been documented in fossorial ceacilians (Maddin and Sherratt, 2014) and snakes (Yi and Norell, 2015). In this respect, rodents may have developed a different SCC shape based on function, which relies less on orthogonality and more on SCC size compared to other groups.

## Limitations to using SCC radii of curvature dimensions

Limitations exist when using the Spoor et al. (2007) method with respect to the agility scores that are calculated. Since the designation of agility level in the modern comparative dataset was performed in a qualitative manner (Spoor et al., 2007), it is fair to raise questions regarding the information content of the reconstructed agility scores for fossil rodents. Also, in modern mammals, considerable overlap exists between different agility categories (Fig. 5). For

example, in terms of the relative size of the LSR, some mammals in the fast category are found to range as low as mammals in the slow category, while mammals grouped in the medium category vary extensively, with their range covering mammals categorized as slow, medium slow, medium, medium fast and fast (Fig. 5). Unfortunately, besides the dataset from Malinzak et al. (2012) which uses direct measurements of angular head velocity, no other comparative datasets exist that have assessed agility in a more quantitative methodology. The Spoor et al. (2007) dataset remains the largest and most diverse sample for which an agility assessment is available. Within the context of the current analysis, the results from the SCC radii data (considered using either residuals or agility scores) are consistent with the locomotor data that are available for some of the taxa in the sample, and in fact seem to tell a compelling story of increasing agility with adaptations for arboreality in some lineages, and decreasing agility in groups that become more fossorial. In contrast, the data from the orthogonality analysis do not seem to show any clear relationship to previously inferred patterns of locomotor behaviour.

## Conclusions

The SCCs serve as an independent source of data to infer locomotor behaviour of fossil species that are unknown from postcranial material. This study is the first to use SCC dimensions to reconstruct locomotor agility for fossil rodents. The variability in relative LSC size and agility scores among Ischyromyidae supports previous interpretations that they had diverse locomotor behaviours (e.g., Wood, 1937; Rose and Chinnery, 2004; Dunn and Rasmussen, 2007;). Some taxa such as *Paramys, Pseudotomus* and *Ischyromys* had relatively lower inferred agility compared to the faster moving reithroparamyines. The fast locomotor agility reconstructions for

early sciuroids, suggests they were fast and highly agile animals and supports previous findings suggesting that the common ancestor for this group was most likely arboreal (Emry and Thorington, 1982; Hopkins, 2005; 2008). The low agility of *Ischyromys* might be a derived condition, while the higher agility exhibited in *Reithroparamys* might show a transition from scansorial ischyromyid to highly arboreal early sciuroids. In later aplodontids, a decrease in inferred agility level is observed, which is consistent with previous work suggesting that these later members displayed terrestrial to fossorial adaptations (Hopkins, 2008).

All considered, fossil rodent agility reconstructions speak to our understanding of major evolutionary transitions in rodents. Viewed from another perspective, the impressive consistency between the inferences previously made based on postcranial and endocranial data for shifts in locomotor type in rodent evolution, and the patterns in SCC size observed here, serve to validate the value of these dimensions to understanding broad-scale patterns of locomotor evolution through time. In contrast, the lack of such agreement with calculated orthogonality measures suggests that variation in this parameter is not informative with respect to locomotor behaviour in rodents.



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## Author Contributions

RB, OCB and MTS all contributed to the conception and design of the study and the analysis and interpretation of the data. For each specimen, OCB acquired the CT data, RB collected measurements and reconstructed agility. RB drafted the article and OCB and MTS revised it critically. All authors gave final approval before submission.

## Data Availability Statement

The surface renderings of the bony labyrinth endocasts described in this paper are available on MorphoSource (www.morphosource.org; Boyer et al. 2014) at https://www.morphosource.org/MyProjects/Dashboard/dashboard/select_project_id/1030

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Additional information for each specimen including location and date of scanning, source-object distance, energy settings, number of views, interslice spacing/interpixel distance, raw data used to calculate semicircular canal dimensions (see legend), body mass calculations, and locomotor behaviour with references. Under body mass calculations, red indicates specimens for which cheek-tooth area was used instead of skull length. Asterisks indicate specimens for which the right semicircular canals were measured. AMNH, American Museum of Natural

History. SMIF, Shared Materials Instrumentation Facility. LSH, Lateral SCC Height. LSW, Lateral SCC Width. PSH, Posterior SCC Height. PSW, Posterior SCC Width. ASH, Anterior SCC Height. ASW, Anterior SCC Width. LSR, Lateral SCC Radius. PSR, Posterior SCC Radius. ASR, Anterior SCC Radius.

**Table S2.** Data from Figure 4 including log10LSR, log10BM and residuals from the regression of log10LSR and log10BM. Specimens with agility category designations originate from Spoor et al. 2007. Specimens without an agility designation include the extant and fossil rodents examined in this study. Abbreviations: F, fast. M, medium. S, slow.

**Table S3.** Data from Figure 5 including log10LSR, log10BM and residuals from the regression of log10LSR and log10BM. Specimens with agility category designations originate from Spoor et al. 2007. Specimens without an agility designation include the extant and fossil rodents examined in this study. Abbreviations: F, fast. MF, medium fast. M, medium. MS, medium slow. S, slow. ES, extremely slow.

**Table S4.** Additional information for each specimen including the angle between the anterior and lateral semicircular canals (ASC/LSC), anterior and posterior semicircular canals (ASC/PSC), and the posterior and lateral semicircular canals (PSC/LSC). The deviation from 90 degrees for each angle pair is given as A/L 90VAR for the anterior and lateral semicircular canals, A/P 90VAR for the anterior and posterior semicircular canals, and P/L 90VAR for the posterior and lateral semicircular canals. The average deviation from 90 degrees for all three

794 semicircular canal pairs is given as 90VAR. The logarithm of the angular velocity magnitude
795 logAVM is calculated using the formula from Malinzak et al. 2012.

796

797 **Fig. S1.** Coronal slices from the CT scan data of the right cranium of *Tamiascuirus hudsonicus*
798 (USNM 549146) depicts cochlea, anterior semicircular canal (ASC), lateral semicircular canal
799 (LSC) and posterior semicircular canal (PSC).

800

801 ## Table legends

802 **Table 1.** Studies of semicircular canal (SCC) dimensions and vestibular sensitivity in extant
803 taxa. Studies that have analyzed semicircular canal dimensions and vestibular sensitivity in
804 extant taxa are given under Study. Semicircular canal dimensions are the aspect of the SCCs
805 measured in each study in order to determine vestibular sensitivity. The predictive factor is the
806 way in which vestibular sensitivity is quantified as a result of the varying SCC dimensions. The
807 order of the taxa is given under Extant Taxa as well as the number of species used in each order
808 given under Number of Taxa for Spoor et al. (2007) and Pfaff et al. (2015). The species is given
809 for Malinzak et al. (2012) under Extant Taxa.

810

811 **Table 2.** Fossil specimens of eight ischyromyid, two sciurid and two aplodontid rodents used in
812 this study. Fossil rodent specimens including family, subfamily, catalogue number and epoch.
813 Asterisks indicate specimens for which the right semicircular canals were measured.

814

**Table 3.** Eighteen additional extant sciurid and aplodontid rodents included in this study with family/subfamily, catalogue number, predicted agility scores from the average semicircular canal radius (SCR) and lateral semicircular canal radius (LSR), and locomotor behaviour. Agility scores are calculated from the all mammal predictive equations from Silcox et al. (2009). The seventeen sciurids span the subfamilies Sciurini, Xerinae, Pteromyini, and Callosciurinae. Asterisks indicate specimens for which the right semicircular canals were measured. References for locomotor behaviour can be found in Table S1. Abbreviations: F, fast. MF, medium fast. M, medium. MS, medium slow.

**Table 4.** Measurements of semicircular canal angles between each of the ipsilateral canal pairs for fossil and extant rodents with catalogue number. The angle between the anterior and lateral semicircular canals is represented by ASC/LSC, the angle between the anterior and posterior semicircular canals is represented by ASC/PSC, and the angle between the posterior and lateral semicircular canals is represented by PSC/LSC. 90VAR represents the sum of the deviation from 90 degrees for all three ipsilateral canal pairs. The logarithm of the angular velocity magnitude ($\log_{10}$AVM) provides an estimate of angular head velocity and is calculated using the formula from Malinzak et al. 2012.

**Table 5.** Dunn's post-hoc test analyzing the differences in median residuals between the 6 agility groups of mammals and extant sciurids. P-values are presented in the upper right half of the table and z statistics are given in the lower left half. Significant differences are highlighted in bold for p-values.

838 **Table 6.** Fossil rodent agility scores calculated from average and lateral semicircular canal
839 radius. Agility scores calculated from average semicircular canal radius (SCR) and lateral
840 semicircular canal radius (LSR) for fossil rodents with family, subfamily and catalogue number
841 for each specimen. Agility Category reflects where the specimen falls on the agility scale, ranked
842 by Spoor et al. (2007). Abbreviations: F, fast. MF, medium fast. M, medium. MS, medium slow.
843
844 **Figure legends**

845 **Fig. 1.** Cladogram representing the relationship among the taxa discussed in the text following
846 different studies (Korth and Emry 1991, Mercer and Roth 2003, Hopkins 2008). **A.** Topology
847 based on Meng (1990) and **B.** Section of the cladogram differing based on Asher et al. (2019).
848 The symbol † indicates extinct taxa.
849
850 **Fig. 2.** The anterior semicircular canal of *Heliosciurus rufobrachium* (USNM 378091) after re-
851 slicing of the data in the plane of the canal using the "fit to points" tool in the Slice module of
852 AVIZO 7.0.1. Height and width are shown by the blue and orange arrows respectively. They
853 represent the maximum span of the canal, measured at the center of the lumen. Scale bar = 1mm.
854
855 **Fig. 3.** Bony labyrinth reconstructions for rodents including the extant sciurid *Sciurus*
856 *carolinensis* (AMNH 258346), the extant aplodontid *Aplodontia rufa* (AMNH 42389), two
857 ischyromyids *Paramys delicatus* (AMNH 12506) and *Reithroparamys delicatissimus* (AMNH
858 12561), the fossil sciurid *Cedromus wilsoni* (USNM 256584), and the fossil aplodontid
859 *Prosciurus relictus* (USNM 437793). Each semicircular canal is shown in its respective plane,

including the anterior semicircular canal (left), posterior semicircular canal (middle), and the lateral semicircular canal (right). Scale bars represent 1 mm.

**Fig. 4.** Relationship between body mass (BM) and lateral semicircular canal radius (LSR; A) and the residuals from the least squares regression of $\log_{10}$BM and $\log_{10}$LSR (B) for fossil and extant rodents in the context of extant rodents from Spoor et al. (2007). The regression line in Part A is calculated using modern specimens and has the following parameters: slope = 0.1595, intercept = -0.24696, and $R^2 = 0.71377$. Modern rodents from Spoor et al. (2007) fall into the fast (e.g., *Glaucomys volans*; agility score = 6), medium (e.g., *Hydrochaeris hydrochaeris*; agility score = 3) and slow (e.g., *Erethizon dorsatum*; agility score = 2) categories. *Aplodontia rufa* generally has small SCCs relative to body mass and groups with rodent taxa in the medium agility category. Convex hulls represent the position of rodents categorized as fast from Spoor et al. (2007; blue) relative to extant sciurids (orange).

**Fig. 5.** Relationship between body mass (BM) and lateral semicircular canal radius (LSR; A) and the residuals from the least squares regression of $\log_{10}$BM and $\log_{10}$LSR (B) for fossil and extant rodents in the context of all mammals from Spoor et al. (2007). The regression line in Part A is calculated using modern specimens and has the following parameters: slope = 0.13208, intercept = -0.20602, and $R^2 = 0.71377$. The taxa indicated in Part A include *Sciurus carolinensis* and *Sciurus granatensis,* taxa that group near the fossil sciurids, *Glaucomys volans* which groups near the early fossil aplodontid *Prosciurus relictus*, and *Aplodontia rufa* which groups in a

881 similar agility range to *Mesogaulus paniensis*. The orange convex hull in Part B represents the
882 position of the residuals for extant sciurids.

883

884

885 **Fig. 6.** Boxplot of fossil rodent residuals calculated from the least squares regression of $\log_{10}$BM
886 and $\log_{10}$LSR. Fossil rodents fall into three residual categories: 1. low residuals (median = -
887 0.041) and yielding medium slow to medium agility scores, 2. intermediate residuals (median =
888 0.028) yielding medium to medium fast agility scores, and 3. high residuals (median = 0.098)
889 yielding medium fast to fast agility scores.

890

891 **Fig. 7.** A. Relationship between $\log_{10}$90VAR and $\log_{10}$AVM for fossil and extant rodents in the
892 context of primates and two non-primate species from Malinzak et al. (2012); B. Relationship
893 between $\log_{10}$90VAR and the residuals from the least squares regression of $\log_{10}$LSR and
894 $\log_{10}$BM for fossil and extant rodents.

**Table 1.** Studies of semicircular canal (SCC) dimensions and vestibular sensitivity in extant taxa. Studies that have analyzed semicircular canal dimensions and vestibular sensitivity in extant taxa are given under Study. Semicircular canal dimensions are the aspect of the SCCs measured in each study in order to determine vestibular sensitivity. The predictive factor is the way in which vestibular sensitivity is quantified as a result of the varying SCC dimensions. The order of the taxa is given under Extant Taxa as well as the number of species used in each order given under Number of Taxa for Spoor et al. (2007) and Pfaff et al. (2015). The species is given for Malinzak et al. (2012) under Extant Taxa.

| Study | SSC dimensions | Predictive factors | Extant taxa | Number of taxa |
|---|---|---|---|---|
| Spoor et al. 2007 | Radii of curvature | Agility score | Artiodactyla | 8 |
| | | | Carnivora | 19 |
| | | | Chiroptera | 7 |
| | | | Dasyuromorphia | 3 |
| | | | Dermoptera | 2 |
| | | | Didelphimorphia | 1 |
| | | | Diprotodontia | 15 |
| | | | Eulipotyphla | 6 |
| | | | Lagomorpha | 2 |
| | | | Monotremata | 1 |
| | | | Notoryctemorphia | 1 |
| | | | Peramelemorphia | 1 |
| | | | Perissodactyla | 2 |
| | | | Primates | 91 |
| | | | Proboscidae | 2 |
| | | | Rodentia | 38 |
| | | | Scandentia | 6 |
| | | | Sirenia | 1 |
| | | | Xenarthra | 4 |
| Pfaff et al. 2015 | Multiple dimensions including SSC diameter | SSC sensitivity equation | Chiroptera | 3 |
| | | | Diprotodontia | 1 |
| | | | Eulipotyphla | 1 |
| | | | Notoryctemorphia | 1 |
| | | | Rodentia | 43 |

| | | | | |
|---|---|---|---|---|
| | | | Scandentia | 1 |
| Malinzak et al. 2012 | SSC orthogonality; variance from 90 degrees (90var) | Angular velocity magnitude | *Cheirogaleus medius* | 1 |
| | | | *Daubentonia madagascariensis* | 1 |
| | | | *Eulemur fulvus* | 1 |
| | | | *Eulemur mongoz* | 1 |
| | | | *Galago moholi* | 1 |
| | | | *Hapalemur griseus* | 1 |
| | | | *Lemur catta* | 1 |
| | | | *Microcebus murinus* | 1 |
| | | | *Nycticebus pygmaeus* | 1 |
| | | | *Propithecus verreauxi* | 1 |
| | | | *Varecia variegata* | 1 |

9

**Table 2.** Fossil specimens of eight ischyromyid, two sciurid and two aplodontid rodents used in this study. Fossil rodent specimens including family, subfamily, catalogue number and epoch. Asterisks indicate specimens for which the right semicircular canals were measured.

| Family | Subfamily | Species | Catalogue Number | Epoch |
|---|---|---|---|---|
| Ischyromyidae | Paramyinae | *Paramys copei* * | AMNH 4756 | Early Eocene |
| | Paramyinae | *Paramys delicatus* | AMNH 12506 | Middle Eocene |
| | Paramyinae | *Pseudotomus oweni* * | USNM 17161 | Middle Eocene |
| | Reithroparamyinae | *Reithroparamys delicatissimus* | AMNH 12561 | Middle Eocene |
| | Reithroparamyinae | *Rapamys atramontis* | AMNH 128704 | Middle Eocene |
| | Ischyromyinae | *Ischyromys typus* | AMNH F:AM 144638 | Early Oligocene |
| | Ischyromyinae | *Ischyromys typus* | ROMV 1007 | Early Oligocene |
| | Ischyromyinae | *Titanotheriomys veterior* | AMNH 79314 | Late Eocene |
| Sciuridae | Cedromurinae | *Cedromus wilsoni* | USNM 256584 | Early Oligocene |
| | Sciurinae | *Protosciurus* cf. *rachelae* | YPM 14736 | Late Oligocene |
| Aplodontidae | Prosciurinae | *Prosciurus relictus* | USNM 437793 | Early Oligocene |
| | Mesogaulinae | *Mesogaulus paniensis* | AMNH F:AM 65511 | Early Miocene |

**Table 3.** Eighteen additional extant sciurid and aplodontid rodents included in this study with family/subfamily/tribe, catalogue number, predicted agility scores from the average semicircular canal radius (SCR) and lateral semicircular canal radius (LSR), and locomotor behaviour. The seventeen sciurids span the subfamilies Sciurini, Xerinae, Pteromyini, and Callosciurinae. Asterisks indicate specimens for which the right semicircular canals were measured. References for locomotor behaviour can be found in Table S1. Abbreviations: F, fast. MF, medium fast. M, medium. MS, medium slow.

| Family/Subfamily/Tribe | Species | Catalogue Number | Agility score from SCR | Agility score from LSR | Agility Category | Locomotor Behaviour |
|---|---|---|---|---|---|---|
| Aplodontidae | *Aplodontia rufa* | AMNH 42389 | 2.9 | 4 | MS - M | Fossorial |
| Sciurini | *Sciurus carolinensis* | AMNH 258346 | 5.2 | 4.7 | MF | Arboreal |
| Sciurini | *Tamiasciurus hudsonicus* | USNM 549146 | 5.4 | 5.7 | MF-F | Arboreal |
| Xerinae | *Funisciurus pyrropus* | USNM 294865 | 5.1 | 5.6 | MF-F | Scansorial |
| Xerinae | *Heliosciurus rufobrachium* | USNM 378091 | 5.5 | 5.4 | MF | Arboreal |
| Xerinae | *Paraxerus cepapi* | USNM 367956 | 4.9 | 5.1 | MF | Scansorial |
| Xerinae | *Protoxerus stangeri* | USNM 435027 | 5.1 | 5.2 | MF | Arboreal |
| Pteromyini | *Aeromys tephromelas* | USNM 481190 | 4.9 | 4.7 | MF | Glider |
| Pteromyini | *Glaucomys volans* | AMNH 240290 | 5.6 | 5.6 | F | Glider |
| Pteromyini | *Petaurista petaurista* | USNM 589079 | 5.2 | 5 | MF | Glider |
| Pteromyini | *Hylopetes spadiceus* | USNM 488639 | 4.6 | 4.7 | MF | Glider |
| Pteromyini | *Petinomys setosus* | USNM 488674 | 4.9 | 4.7 | MF | Glider |
| Pteromyini | *Pteromyscus pulverulentus* | USNM 481178 | 5.4 | 5 | MF | Glider |
| Pteromyini | *Pteromys buechneri* | USNM 172622 | 5.2 | 5.3 | MF | Glider |
| Callosciurinae | *Rhinosciurus laticaudatus* | USNM 488511 | 4.4 | 4.5 | M-MF | Terrestrial |
| Callosciurinae | *Callosciurus caniceps* | USNM 294865 | 5.2 | 6.1 | MF-F | Arboreal |
| Callosciurinae | *Lariscus insignis* * | USNM 488570 | 4.9 | 4.8 | MF | Terrestrial |
| Callosciurinae | *Dremomys rufigenis* * | USNM 488602 | 4.6 | 4.6 | MF | Scansorial |

6

**Table 4.** Measurements of semicircular canal angles between each of the ipsilateral canal pairs for fossil and extant rodents with catalogue number. The angle between the anterior and lateral semicircular canals is represented by ASC/LSC, the angle between the anterior and posterior semicircular canals is represented by ASC/PSC, and the angle between the posterior and lateral semicircular canals is represented by PSC/LSC. 90VAR represents the sum of the deviation from 90 degrees for all three ipsilateral canal pairs. The logarithm of the angular velocity magnitude ($log_{10}$AVM) provides an estimate of angular head velocity and is calculated using the formula from Malinzak et al. 2012.

| Fossil/Extant | Species | Catalogue Number | ASC/LSC | ASC/PSC | PSC/LSC | 90VAR | $log_{10}$AVM |
|---|---|---|---|---|---|---|---|
| Extant | *Aplodontia rufa* | AMNH 42389 | 88 | 86.2 | 87.2 | 8.6 | 2.35 |
| | *Sciurus carolinensis* | AMNH 258346 | 85.3 | 82.7 | 85.8 | 16.2 | 2.21 |
| | *Tamiasciurus hudsonicus* | USNM 549146 | 84.6 | 83.2 | 79.5 | 22.7 | 2.14 |
| | *Funisciurus pyrropus* | USNM 294865 | 79 | 82.6 | 84.7 | 23.7 | 2.13 |
| | *Heliosciurus rufobrachium* | USNM 378091 | 88.4 | 83.5 | 88.3 | 9.8 | 2.32 |
| | *Paraxerus cepapi* | USNM 367956 | 87.5 | 87 | 90 | 5.5 | 2.45 |
| | *Protoxerus stangeri* | USNM 435027 | 76.3 | 81.8 | 88.1 | 23.8 | 2.13 |
| | *Aeromys tephromelas* | USNM 481190 | 89 | 81.7 | 83.7 | 15.6 | 2.22 |
| | *Glaucomys volans* | AMNH 240290 | 78.9 | 86.4 | 89.6 | 15.1 | 2.23 |
| | *Petaurista petaurista* | USNM 589079 | 80.4 | 85.4 | 87.8 | 16.4 | 2.21 |
| | *Hylopetes spadiceus* | USNM 488639 | 82 | 82.5 | 96.4 | 21.9 | 2.15 |
| | *Petinomys setosus* | USNM 488674 | 88.8 | 85.1 | 88.6 | 7.5 | 2.38 |
| | *Pteromyscus pulverulentus* | USNM 481178 | 87.2 | 86.8 | 88.5 | 7.5 | 2.38 |
| | *Pteromys buechneri* | USNM 172622 | 80.7 | 79.5 | 97.4 | 27.2 | 2.10 |
| | *Rhinosciurus laticaudatus* | USNM 488511 | 80.3 | 88 | 89.4 | 12.3 | 2.27 |
| | *Callosciurus caniceps* | USNM 294865 | 81 | 80.3 | 93.7 | 22.4 | 2.14 |
| | *Lariscus insignis* | USNM 488570 | 89.5 | 81.8 | 89.4 | 9.3 | 2.34 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | *Dremomys rufigenis* | USNM 488602 | 85 | 88.3 | 90.4 | 7.1 | 2.40 |
| Fossil | *Paramys copei* | AMNH 4756 | 88.1 | 96.3 | 86.5 | 11.7 | 2.29 |
| | *Pseudotomus oweni* | USNM 17161 | 77.3 | 90.7 | 84.1 | 19.3 | 2.17 |
| | *Paramys delicatus* | AMNH 12506 | 86.6 | 92.6 | 86 | 10 | 2.32 |
| | *Reithroparamys delicatissimus* | AMNH 12561 | 86.7 | 89.1 | 91.9 | 6.1 | 2.43 |
| | *Rapamys atramontis* | AMNH 128704 | 85.7 | 85.6 | 90.5 | 9.2 | 2.34 |
| | *Titanotheriomys veterior* | AMNH 79314 | 95.6 | 97.4 | 90.7 | 13.7 | 2.25 |
| | *Ischyromys typus* | AMNH F:AM 144638 | 83.1 | 82.8 | 78.6 | 25.5 | 2.11 |
| | *Ischyromys typus* | ROMV 1007 | 83.6 | 89.7 | 88.8 | 7.9 | 2.37 |
| | *Cedromus wilsoni* | USNM 256584 | 87.1 | 82.3 | 87.8 | 12.8 | 2.27 |
| | *Protosciurus* cf. *rachelae* | YPM 14736 | 83.6 | 83.6 | 84.9 | 17.9 | 2.19 |
| | *Prosciurus relictus* | USNM 437793 | 81.8 | 83.8 | 87.3 | 17.1 | 2.20 |
| | *Mesogaulus paniensis* | AMNH F:AM 65511 | 94.1 | 97.8 | 85.6 | 16.3 | 2.21 |

**Table 5.** Dunn's post-hoc test analyzing the differences in median residuals between the 6 agility groups of mammals and extant sciurids. P-values are presented in the upper right half of the table and z statistics are given in the lower left half. Significant differences are highlighted in bold for p-values.

| | Extremely Slow | Slow | Medium Slow | Medium | Medium Fast | Fast | Extant Sciuridae |
|---|---|---|---|---|---|---|---|
| **Extremely Slow** | | 0.1801 | 0.1589 | **0.00102** | **0.001105** | **$5.536 \times 10^{-05}$** | **$1.414 \times 10^{-05}$** |
| **Slow** | 1.341 | | 0.7588 | **0.0001696** | **0.001528** | **$2.226 \times 10^{-07}$** | **$6.498 \times 10^{-07}$** |
| **Medium Slow** | 1.409 | 0.3071 | | **0.02687** | **0.02561** | **0.001206** | **0.000308** |
| **Medium** | 3.285 | 3.76 | 2.213 | | 0.5562 | **0.02782** | **0.008347** |
| **Medium Fast** | 3.262 | 3.169 | 2.232 | 0.5885 | | 0.4789 | 0.1276 |
| **Fast** | 4.032 | 5.179 | 3.238 | 2.2 | 0.7081 | | 0.2178 |
| **Extant Sciuridae** | 4.342 | 4.976 | 3.608 | 2.638 | 1.523 | 1.233 | |

**Table 6.** Fossil rodent agility scores calculated from average and lateral semicircular canal radius. Agility scores calculated from average semicircular canal radius (SCR) and lateral semicircular canal radius (LSR) for fossil rodents with family, subfamily and catalogue number for each specimen. Agility Category reflects where the specimen falls on the agility scale, ranked by Spoor et al. (2007). Abbreviations: F, fast. MF, medium fast. M, medium. MS, medium slow.

| Family | Subfamily | Species | Catalogue Number | Agility Score from SCR | Agility Score from LSR | Agility Category |
|---|---|---|---|---|---|---|
| Ischyromyidae | Paramyinae | *Paramys copei* | AMNH 4756 | 3.6 | 3.9 | MS - M |
| | Paramyinae | *Paramys delicatus* | AMNH 12506 | 3.4 | 3.5 | MS - M |
| | Paramyinae | *Pseudotomus oweni* | USNM 17161 | 3.1 | 3.2 | MS |
| | Reithroparamyinae | *Reithroparamys delicatissimus* | AMNH 12561 | 4.5 | 4.4 | M - MF |
| | Reithroparamyinae | *Rapamys atramontis* | AMNH 128704 | 4.6 | 4.6 | M - MF |
| | Ischyromyinae | *Titanotheriomys veterior* | AMNH 79314 | 4.6 | 4.6 | M - MF |
| | Ischyromyinae | *Ischyromys typus* | ROMV 1007 | 3.4 | 3.8 | MS - M |
| | Ischyromyinae | *Ischyromys typus* | AMNH F:AM 144638 | 4 | 4 | M |
| Sciuridae | Cedromurinae | *Cedromus wilsoni* | USNM 256584 | 5.5 | 5.3 | MF - F |
| | Sciurinae | *Protosciurus* cf. *rachelae* | YPM 14736 | 5.7 | 5.4 | MF - F |
| Aplodontidae | Prosciurinae | *Prosciurus relictus* | USNM 437793 | 6.1 | 6.1 | F |
| | Mesogaulinae | *Mesogaulus paniensis* | AMNH F:AM 65511 | 4.2 | 4.1 | M |

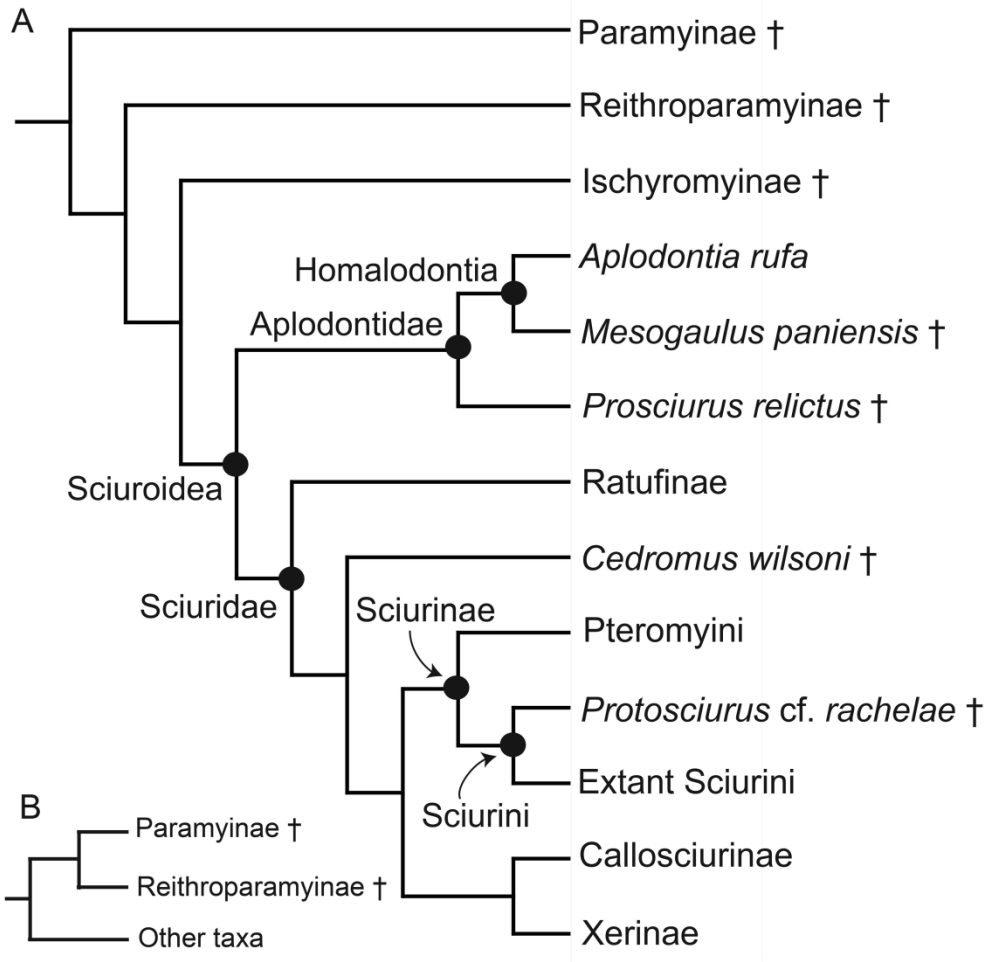


**Figure 1**. Cladogram representing the relationship among the taxa discussed in the text following different studies (Korth and Emry 1991, Mercer and Roth 2003, Hopkins 2008). A. Topology based on Meng (1990) and B. Section of the cladogram differing based on Asher et al. (2019). The symbol † indicates extinct taxa.

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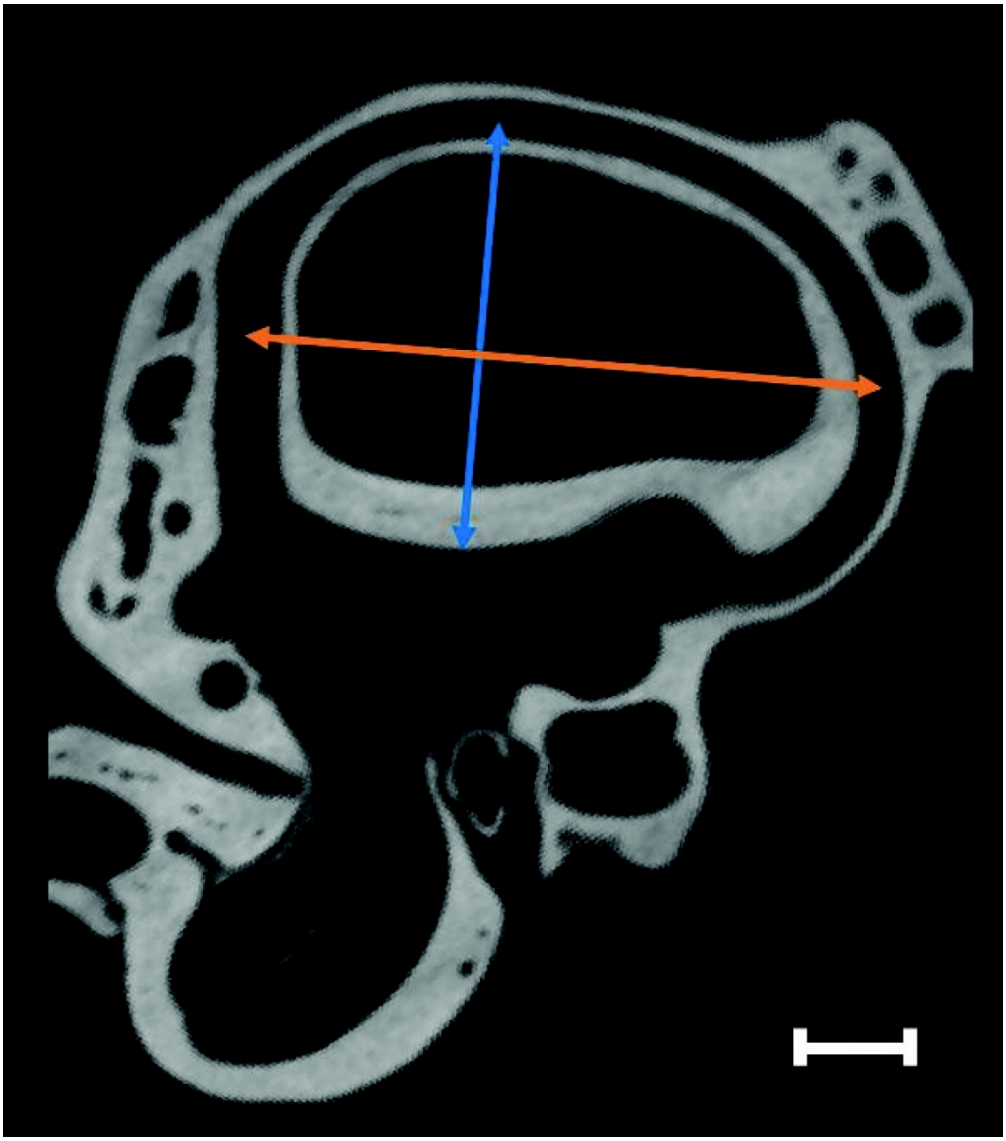

**Figure 2**. The anterior semicircular canal of *Heliosciurus rufobrachium* (USNM 378091) after re-slicing of the data in the plane of the canal using the "fit to points" tool in the Slice module of AVIZO 7.0.1. Height and width are shown by the blue and orange arrows respectively. Scale bar = 1mm.

158x179mm (600 x 600 DPI)

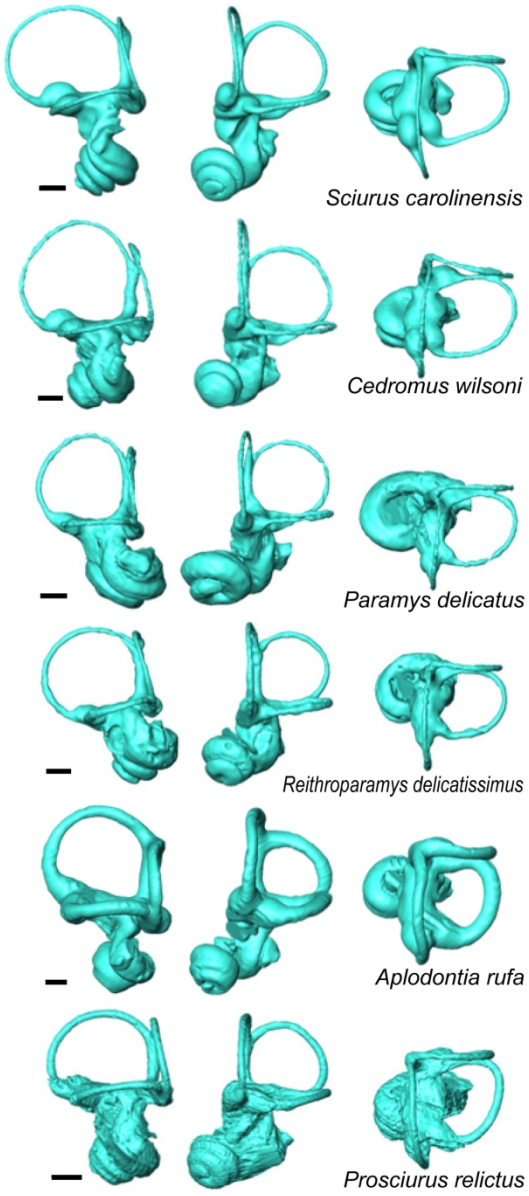


**Figure 3**. Bony labyrinth reconstructions for rodents including the extant sciurid *Sciurus carolinensis* (AMNH 258346), the extant aplodontid *Aplodontia rufa* (AMNH 42389), two ischyromyids *Paramys delicatus* (AMNH 12506) and *Reithroparamys delicatissimus* (AMNH 12561), the fossil sciurid *Cedromus wilsoni* (USNM 256584), and the fossil aplodontid *Prosciurus relictus* (USNM 437793). Each semicircular canal is shown in its respective plane, including the anterior semicircular canal (left), posterior semicircular canal (middle), and the lateral semicircular canal (right). Scale bars represent 1 mm.

111x254mm (600 x 600 DPI)

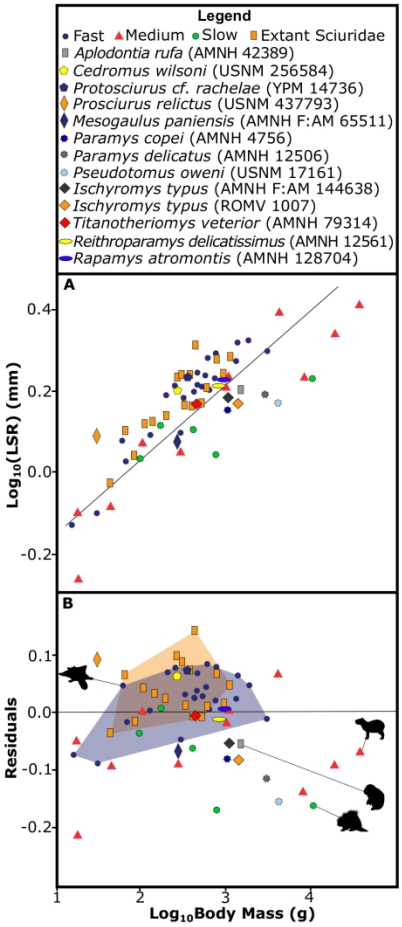


**Figure 4**. Relationship between body mass (BM) and lateral semicircular canal radius (LSR; A) and the residuals from the least squares regression of $\log_{10}$BM and $\log_{10}$LSR (B) for fossil and extant rodents in the context of extant rodents from Spoor et al. (2007). The regression line in Part A is calculated using modern specimens and has the following parameters: slope = 0.1595, intercept = -0.24696, and $R^2$ = 0.71377. Modern rodents from Spoor et al. (2007) fall into the fast (e.g., *Glaucomys volans*; agility score = 6), medium (e.g., *Hydrochaeris hydrochaeris*; agility score = 3) and slow (e.g., *Erethizon dorsatum*; agility score = 2) categories. *Aplodontia rufa* generally has small SCCs relative to body mass and groups with rodent taxa in the medium agility category. Convex hulls represent the position of rodents categorized as fast from Spoor et al. (2007; blue) relative to extant sciurids (orange).

215x279mm (600 x 600 DPI)

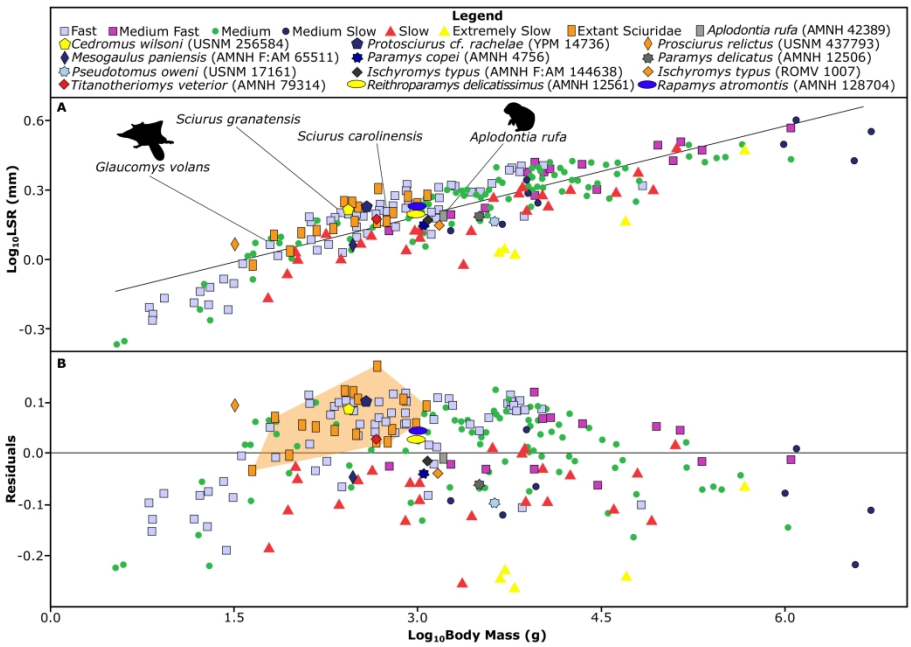


**Figure 5**. Relationship between body mass (BM) and lateral semicircular canal radius (LSR; A) and the residuals from the least squares regression of $\log_{10}$BM and $\log_{10}$LSR (B) for fossil and extant rodents in the context of all mammals from Spoor et al. (2007). The regression line in Part A is calculated using modern specimens and has the following parameters: slope = 0.13208, intercept = -0.20602, and $R^2$ = 0.71377. The taxa indicated in Part A include *Sciurus carolinensis* and *Sciurus granatensis*, taxa that group near the fossil sciurids, *Glaucomys volans* which groups near the early fossil aplodontid *Prosciurus relictus*, and *Aplodontia rufa* which groups in a similar agility range to *Mesogaulus paniensis*. The orange convex hull in Part B represents the position of the residuals for extant sciurids.

279x215mm (600 x 600 DPI)

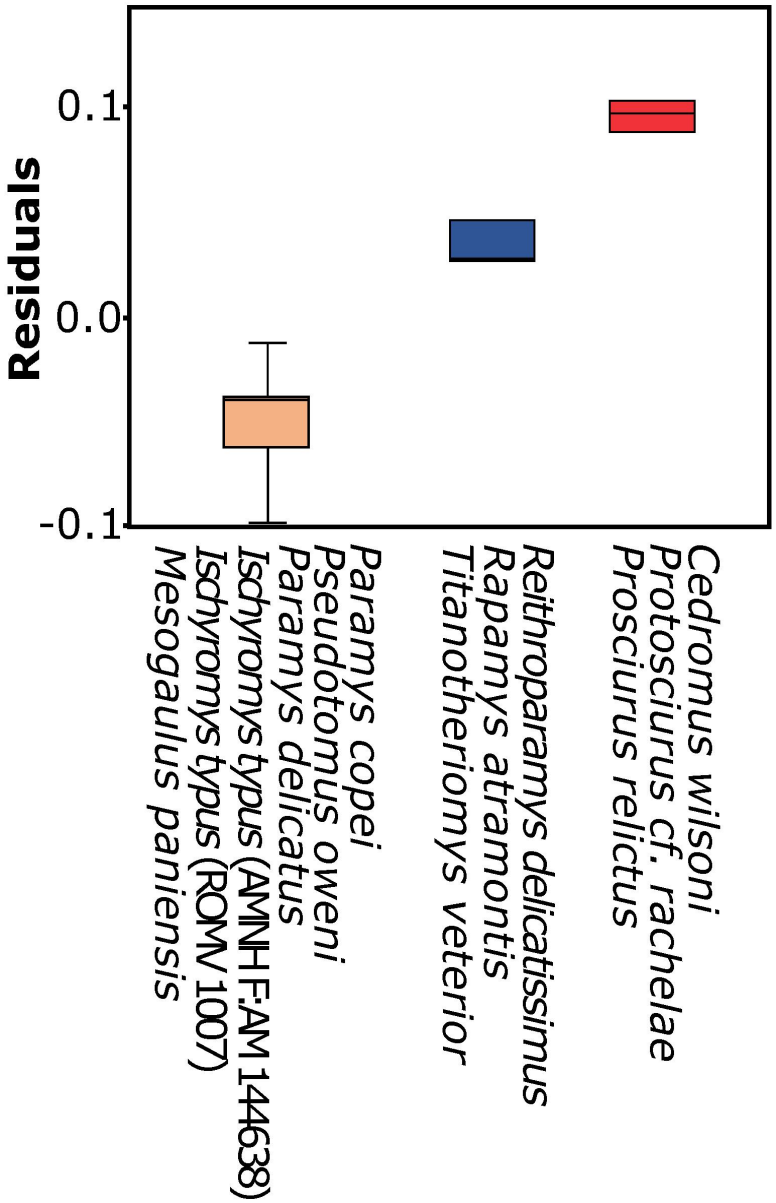


**Figure 6**. Boxplot of fossil rodent residuals calculated from the least squares regression of $log_{10}$BM and $log_{10}$LSR. Fossil rodents fall into three residual categories: 1. low residuals (median = -0.041) and yielding medium slow to medium agility scores, 2. intermediate residuals (median = 0.028) yielding medium to medium fast agility scores, and 3. high residuals (median = 0.098) yielding medium fast to fast agility scores.

64x100mm (600 x 600 DPI)

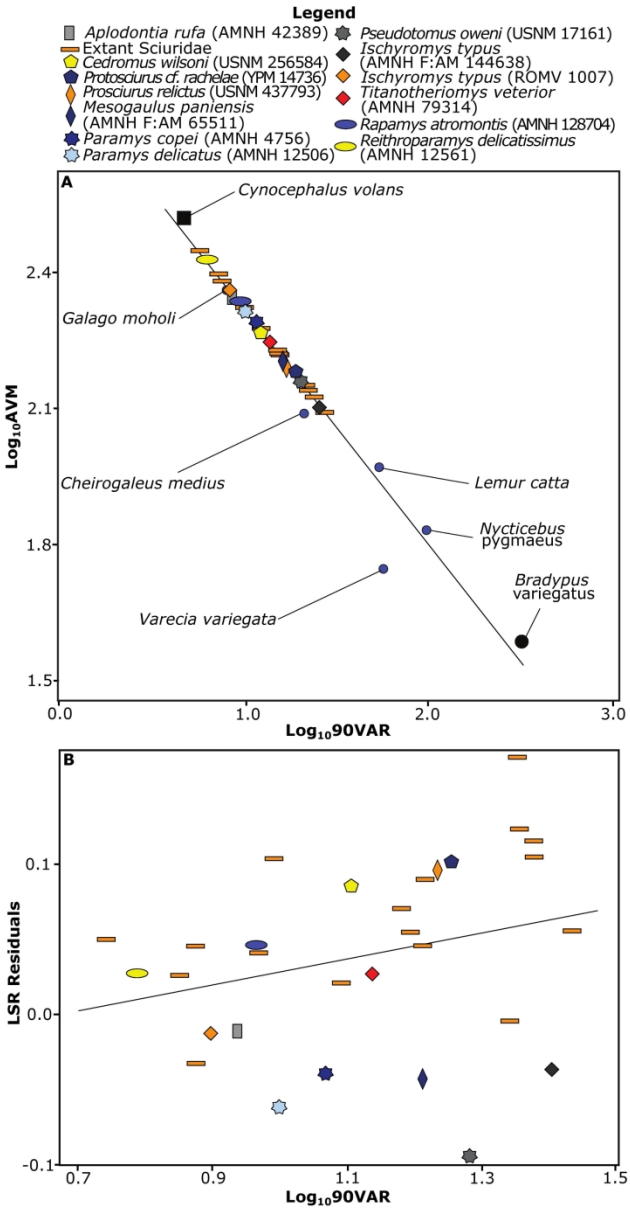


**Figure 7**. A. Relationship between $\log_{10}$90VAR and $\log_{10}$AVM for fossil and extant rodents in the context of primates and two non-primate species from Malinzak et al. (2012); B. Relationship between $\log_{10}$90VAR and the residuals from the least squares regression of $\log_{10}$LSR and $\log_{10}$BM for fossil and extant rodents.

141x268mm (300 x 300 DPI)

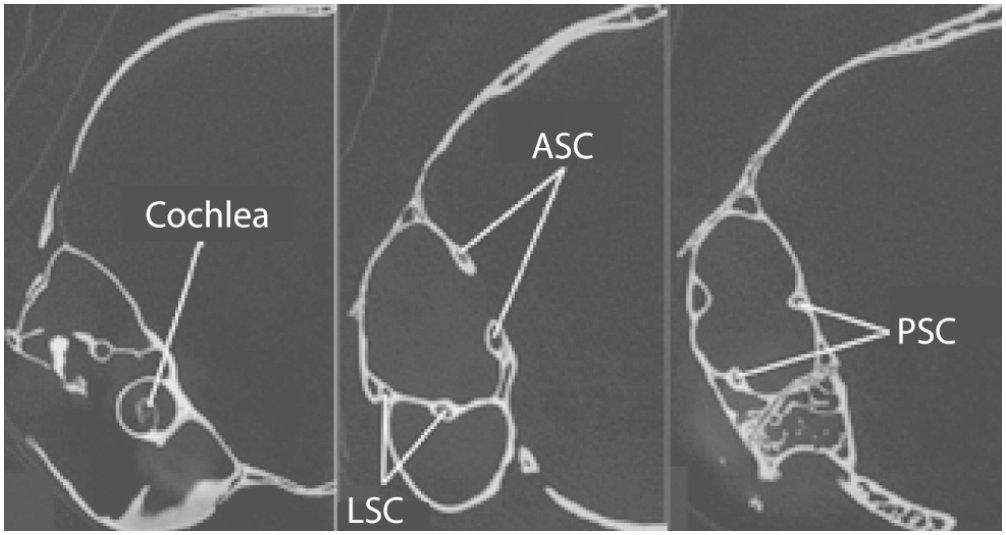


**Figure S1**. Coronal slices from the CT scan data of the right cranium of *Tamiascuirus hudsonicus* (USNM 549146) depicts cochlea, anterior semicircular canal (ASC), lateral semicircular canal (LSC) and posterior semicircular canal (PSC).

113x59mm (220 x 220 DPI)

# Evolution of arboreality a

[1]Department of Anthr
[2]School of Geo

Journal of Anatomy

## SUPPORTING TABLES

# nd fossoriality in squirrels and aplodontid rodents: insi semicircular canals of fossil rodents

Raj Bhagat[1], Ornella C. Bertrand[2], Mary T. Silcox[1]

Corresponding author: raj.bhagat@mail.utoronto.ca

opology, University of Toronto Scarborough, Toronto, ON M1C 1A4, Ca
Sciences, University of Edinburgh, Grant Institute, Edinburgh, Scotland,

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**Table S1.** Additional information for each specimen including location and date of scanning, so area was used instead of skull length. Asterisks indicate specimens for which the right semicircu Radius. PSR, Posterior SSC Radius. ASR, Anterior SSC Radius.

| | Specimen | Catalogue Number | Location and Date of Scanning |
|---|---|---|---|
| Fossil | *Paramys copei* * | AMNH 4756 | AMNH - 2013 |
| | *Paramys delicatus* | AMNH 12506 | AMNH - 2013 |
| | *Pseudotomus oweni* * | USNM 17161 | SMIF - 2014 |
| | *Reithroparamys delicatissimus* | AMNH 12561 | AMNH - 2013 |
| | *Rapamys atramontis* | AMNH 128704 | AMNH - 2013 |
| | *Ischyromys typus* | AMNH F:AM 144638 | AMNH - 2015 |
| | *Ischyromys typus* | ROMV 1007 | SMIF - 2013 |
| | *Titanotheriomys veterior* | AMNH 79314 | AMNH - 79314 |
| | *Cedromus wilsoni* | USNM 256584 | SMIF - 2014 |
| | *Protosciurus* cf. *rachelae* | YPM 14736 | SMIF - 2014 |
| | *Prosciurus relictus* | USNM 437793 | SMIF - 2014 |
| | *Mesogaulus paniensis* | AMNH F:AM 65511 | AMNH - 2015 |
| | *Aplodontia rufa* | AMNH 42389 | SMIF - 2013 |
| | *Sciurus carolinensis* | AMNH 258346 | SMIF -2013 |
| | *Tamiasciurus hudsonicus* | USNM 549146 | SMIF - 2014 |
| | *Funisciurus pyrropus* | USNM 294865 | SMIF - 2014 |
| | *Heliosciurus rufobrachium* | USNM 378091 | SMIF - 2014 |
| | *Paraxerus cepapi* | USNM 367956 | SMIF - 2014 |
| | *Protoxerus stangeri* | USNM 435027 | SMIF - 2014 |
| | *Aeromys tephromelas* | USNM 481190 | SMIF - 2014 |
| Extant | *Glaucomys volans* | AMNH 240290 | SMIF -2013 |
| | *Petaurista petaurista* | USNM 589079 | SMIF - 2014 |
| | *Hylopetes spadiceus* | USNM 488639 | SMIF - 2014 |
| | *Petinomys setosus* | USNM 488674 | SMIF - 2014 |
| | *Pteromyscus pulverulentus* | USNM 481178 | SMIF - 2014 |
| | *Pteromys buechneri* | USNM 172622 | SMIF - 2014 |
| | *Rhinosciurus laticaudatus* | USNM 488511 | SMIF - 2014 |
| | *Callosciurus caniceps* | USNM 294865 | SMIF - 2014 |
| | *Lariscus insignis* * | USNM 488570 | SMIF - 2014 |
| | *Dremomys rufigenis* * | USNM 488602 | SMIF - 2014 |

ɔurce-object distance, energy settings, number of views, interslice spacing/interpixel distance, raw da
ılar canals were measured. AMNH, American Museum of Natural History. SMIF, Shared Materials I

| Source-object Distance (mm) | Energy settings mA | kv | Number of views | Interslice spacing/interpixel distance (mm) |
|---|---|---|---|---|
| 158.79 | 170 | 180 | 1500 | 0.039046 |
| 144.74 | 170 | 180 | 2150 | 0.035591 |
| 265.08 | 165 | 88 | 1650 | 0.056952 |
| 176.94 | 180 | 240 | 1500 | 0.043510 |
| 175.87 | 170 | 180 | 1580 | 0.043247 |
| 166.75 | 170 | 220 | 1500 | 0.041057 |
| 229.08 | 155 | 186 | 2300 | 0.039463 |
| - | - | - | - | 0.035560 |
| 113.87 | 165 | 88 | 1600 | 0.026133 |
| 111.98 | 170 | 100 | 1800 | 0.028292 |
| 77.34 | 165 | 98 | 1650 | 0.016195 |
| 196.29 | 220 | 150 | 1500 | 0.048330 |
| 239.82 | 145 | 160 | 2700 | 0.041313 |
| 187.80 | 120 | 175 | 2100 | 0.032352 |
| 119.96 | 150 | 98 | 1700 | 0.025826 |
| 122.09 | 255 | 55 | 1800 | 0.026453 |
| 130.89 | 225 | 55 | 1800 | 0.028359 |
| 102.24 | 150 | 98 | 1700 | 0.022011 |
| 158.79 | 225 | 55 | 1800 | 0.034404 |
| 170.24 | 225 | 55 | 1800 | 0.036885 |
| 107.46 | 105 | 165 | 2775 | 0.018512 |
| 170.24 | 225 | 55 | 1800 | 0.036885 |
| 93.89 | 160 | 119 | 1700 | 0.020213 |
| 82.87 | 150 | 98 | 1700 | 0.017841 |
| 113.53 | 150 | 98 | 1700 | 0.024442 |
| 96.69 | 160 | 119 | 1700 | 0.020816 |
| 143.25 | 150 | 98 | 1700 | 0.030840 |
| 144.07 | 150 | 98 | 1700 | 0.031016 |
| 132.25 | 150 | 980 | 1700 | 0.028471 |
| 140.03 | 150 | 98 | 1700 | 0.030147 |

ta used to calculate semicircular canal dimensions (see legend), body mass calculations, and locomot
Instrumentation Facility. LSH, Lateral SSC Height. LSW, Lateral SSC Width. PSH, Posterior SSC H

| LSH | LSW | PSH | PSW | ASH | ASW | LSR | PSR | ASR | SCR |
|---|---|---|---|---|---|---|---|---|---|
| 3.027 | 2.659 | 3.03 | 2.88 | 3.391 | 3.543 | 1.4215 | 1.4575 | 1.7335 | 1.5375 |
| 2.951 | 3.264 | 3.314 | 3.543 | 3.88 | 4.317 | 1.55375 | 1.71425 | 2.04925 | 1.77242 |
| 2.842 | 3.086 | 3.311 | 3.453 | 3.464 | 4.017 | 1.482 | 1.691 | 1.87025 | 1.68108 |
| 3.176 | 3.283 | 3.379 | 3.26 | 4.082 | 4.698 | 1.61475 | 1.65975 | 2.195 | 1.82317 |
| 3.779 | 3.038 | 3.446 | 3.703 | 4.302 | 4.544 | 1.70425 | 1.78725 | 2.2115 | 1.901 |
| 2.546 | 3.559 | 3.25 | 2.976 | 3.472 | 4.655 | 1.52625 | 1.5565 | 2.03175 | 1.70483 |
| 2.601 | 3.311 | 2.91 | 2.228 | 2.979 | 3.856 | 1.478 | 1.2845 | 1.70875 | 1.49042 |
| 2.855 | 3.061 | 2.802 | 3.427 | 3.253 | 4.333 | 1.479 | 1.55725 | 1.8965 | 1.64425 |
| 3.311 | 3.06 | 3.24 | 3.402 | 4.155 | 4.736 | 1.59275 | 1.6605 | 2.22275 | 1.8253 |
| 3.658 | 3.176 | 3.847 | 3.768 | 4.518 | 4.632 | 1.7085 | 1.90375 | 2.2875 | 1.96658 |
| 2.272 | 2.602 | 2.427 | 2.582 | 2.386 | 3.449 | 1.2185 | 1.25225 | 1.45875 | 1.30983 |
| 2.68 | 2.483 | 2.125 | 2.588 | 2.926 | 3.451 | 1.17825 | 1.29075 | 1.59425 | 1.3544 |
| 1.877 | 2.633 | 2.14 | 2.81 | 2.77 | 3.605 | 1.59375 | 1.2375 | 1.1275 | 1.319583 |
| 4.652 | 3.412 | 3.27 | 3.17 | 4.005 | 5.485 | 1.6115 | 2.016 | 2.3725 | 2 |
| 3.087 | 3.792 | 2.772 | 3.225 | 3.566 | 4.855 | 1.71975 | 1.49925 | 2.10525 | 1.77475 |
| 3.176 | 3.727 | 2.983 | 3.16 | 3.437 | 4.224 | 1.72575 | 1.53575 | 1.91525 | 1.725583 |
| 2.968 | 3.898 | 3.727 | 4.191 | 3.456 | 4.847 | 1.7165 | 1.9795 | 2.07575 | 1.923917 |
| 2.411 | 2.949 | 2.376 | 2.655 | 2.881 | 3.548 | 1.34 | 1.25775 | 1.60725 | 1.401667 |
| 3.755 | 3.876 | 3.865 | 3.886 | 4.32 | 5.212 | 1.90775 | 1.93775 | 2.383 | 2.076167 |
| 3.455 | 3.488 | 3.569 | 4.057 | 4.553 | 5.423 | 1.73575 | 1.9065 | 2.494 | 2.045417 |
| 2.411 | 2.663 | 2.556 | 2.621 | 2.757 | 3.603 | 1.2685 | 1.29425 | 1.59 | 1.38425 |
| 3.657 | 4.073 | 4.22 | 4.558 | 4.827 | 5.777 | 1.9325 | 2.1945 | 2.651 | 2.259333 |
| 1.848 | 2.581 | 2.005 | 2.157 | 2.455 | 3.35 | 1.10725 | 1.0405 | 1.45125 | 1.199667 |
| 1.733 | 2.047 | 2.016 | 2.21 | 2.58 | 2.93 | 0.945 | 1.0565 | 1.3775 | 1.126333 |
| 2.589 | 2.962 | 3.452 | 4.149 | 3.381 | 3.64 | 1.38775 | 1.90025 | 1.75525 | 1.681083 |
| 2.432 | 2.816 | 2.755 | 3.128 | 2.616 | 3.419 | 1.312 | 1.47075 | 1.50875 | 1.4305 |
| 2.78 | 3.175 | 2.849 | 3.212 | 3.401 | 4.328 | 1.48875 | 1.51525 | 1.93225 | 1.645417 |
| 3.51 | 4.743 | 3.017 | 3.353 | 3.265 | 4.572 | 2.06325 | 1.5925 | 1.95925 | 1.871667 |
| 2.656 | 3.219 | 3.379 | 3.297 | 3.372 | 4.308 | 1.46875 | 1.669 | 1.92 | 1.685917 |
| 2.824 | 3.05 | 2.96 | 3.253 | 3.436 | 4.101 | 1.4685 | 1.55325 | 1.88425 | 1.635333 |

:or behaviour with
leight. PSW, Poste

| Body Mass (g) |
|---|
| 1029.89 |
| 2913.82 |
| 3911.71 |
| 856 |
| 918.932649 |
| 1109.01 |
| 1342.23 |
| 434.263 |
| 268.89 |
| 349.616 |
| 30.075 |
| 266.48 |
| 1475.86 |
| 592.55 |
| 256.61 |
| 301.15 |
| 354.98 |
| 138.13 |
| 767.23 |
| 904.59 |
| 63.97 |
| 1096.65 |
| 84.22 |
| 41.86 |
| 195.44 |
| 106.37 |
| 507.38 |
| 437.35 |
| 324.71 |
| 418.43 |

references. Under body mass calculations, red indicates specimens for which cheek-tooth
erior SSC Width. ASH, Anterior SSC Height. ASW, Anterior SSC Width. LSR, Lateral SSC

| Locomotor Behaviour |
| --- |
| Scansorial (Rose and Chinnery, 2004) |
| Scansorial (Rose and Chinnery, 2004) |
| Fossorial (Dunn and Rasmussen, 2007) |
| Arboreal (Wood, 1962) |
| Terrestiral (Bertrand et al., 2016) |
| Fossorial (Wood, 1937) |
| Fossorial (Wood, 1937) |
| Terrestrial (Bertrand et al., 2016a) |
| Arboreal (Hypothesized; see Bertrand et al., 2017) |
| Arboreal (Korth and Samuels, 2015) |
| Arboreal (Hopkins, 2005; 2008) |
| Fossorial (Hopkins, 2005; 2008) |
| Fossorial (Hopkins, 2005; 2008) |
| Arboreal (Reid, 2006) |
| Arboreal (Reid, 2006) |
| Scansorial (Kingdon, 1974) |
| Arboreal (Kingdon, 1974) |
| Scansorial (Kingdon, 1974) |
| Arboreal (Kingdon, 1974; Thorington et al., 2012) |
| Glider (Thorington et al., 2012) |
| Glider (Reid, 2006) |
| Glider (Francis, 2008; Smith and Xie, 2013; Thorington et al., 2012) |
| Glider (Nowak, 1999) |
| Glider (Thorington et al., 2012) |
| Glider (Nowak, 1999) |
| Glider (Thorington et al., 2012) |
| Terrestrial (Nowak, 1999; Francis, 2008) |
| Arboreal (Nowak, 1999) |
| Terrestrial (Francis, 2008; Thorington et al., 2012) |
| Scansorial (Francis, 2008; Nowak, 1999) |

**Table S2.** Data from Figure 4 including log10LSR, log10BM and residuals from the regr
Specimens with agility category designations originate from Spoor et al. 2007. Specimen
the extant and fossil rodents examined in this study. Abbreviations: F, fast. M, medium. S

| Species | log10BM | log10LSR |
|---|---|---|
| *Anomalurus derbianus* | 2.656 | 0.215 |
| *Castor canadensis* | 4.271 | 0.343 |
| *Cavia porcellus* | 3 | 0.216 |
| *Chinchilla laniger* | 2.653 | 0.245 |
| *Cryptomys hottentotus natalensis* | 1.978 | 0.033 |
| *Cryptomys mechowi* | 2.602 | 0.107 |
| *Dipus sagitta* | 1.82 | 0.026 |
| *Erethizon dorsatum* | 4.026 | 0.232 |
| *Glaucomys volans* | 1.774 | 0.081 |
| *Hydrochaeris hydrochaeris (Hydrochoerus capybara)* | 4.597 | 0.419 |
| *Idiurus macrotis* | 1.477 | -0.098 |
| *Idiurus zenkeri* | 1.197 | -0.13 |
| *Lophiomys imhausi* | 2.878 | 0.043 |
| *Marmota monax* | 3.61 | 0.396 |
| *Meriones unguiculatus* | 2 | 0.074 |
| *Microtus pennsylvanicus* | 1.633 | -0.081 |
| *Mus musculus* | 1.276 | -0.257 |
| *Myocastor coypus* | 3.895 | 0.235 |
| *Ondatra zibethicus* | 2.998 | 0.235 |
| *Pedetes capensis* | 3.484 | 0.298 |
| *Peromyscus maniculatus* | 1.229 | -0.101 |
| *Petaurista petaurista* | 3.267 | 0.322 |
| *Rattus norvegicus* | 2.431 | 0.05 |
| *Ratufa bicolor* | 3.138 | 0.317 |
| *Ratufa macroura* | 3.112 | 0.273 |
| *Sciurus aberti* | 2.78 | 0.28 |
| *Sciurus carolinensis* | 2.711 | 0.213 |
| *Sciurus granatensis* | 2.398 | 0.213 |
| *Sciurus niger* | 2.877 | 0.289 |
| *Sciurus richmondi* | 2.301 | 0.19 |
| *Sciurus vulgaris* | 2.507 | 0.183 |
| *Spalax ehrenbergi* | 2.23 | 0.117 |
| *Spermophilus beecheyi* | 2.791 | 0.205 |
| *Spermophilus parryi* | 2.872 | 0.231 |
| *Spermophilus richardsoni* | 2.461 | 0.098 |
| *Spermophilus tridecemlineatus* | 2.1 | 0.091 |
| *Xerus erythropus* | 2.76 | 0.238 |
| *Xerus rutilus* | 2.623 | 0.197 |
| *Aplodontia rufa* | 3.169 | 0.20242 |
| *Sciurus carolinensis* | 2.7727 | 0.20723 |
| *Tamiasciurus hudsonicus* | 2.4093 | 0.23547 |
| *Funisciurus pyrropus* | 2.4788 | 0.23698 |
| *Heliosciurus rufobrachium* | 2.5502 | 0.23464 |

| | | |
|---|---|---|
| *Paraxerus cepapi* | 2.1403 | 0.1271 |
| *Protoxerus stangeri* | 2.8849 | 0.28052 |
| *Aeromys tephromelas* | 2.9565 | 0.23949 |
| *Glaucomys volans* | 1.806 | 0.10329 |
| *Petaurista petaurista* | 3.0401 | 0.28612 |
| *Hylopetes spadiceus* | 1.9254 | 0.044246 |
| *Petinomys setosus* | 1.6218 | -0.024568 |
| *Pteromyscus pulverulentus* | 2.291 | 0.14231 |
| *Pteromys buechneri* | 2.0268 | 0.11793 |
| *Rhinosciurus laticaudatus* | 2.7053 | 0.17282 |
| *Callosciurus caniceps* | 2.6408 | 0.31455 |
| *Lariscus insignis* | 2.5115 | 0.16695 |
| *Dremomys rufigenis* | 2.6216 | 0.16687 |
| *Paramys copei* | 3.0128 | 0.15275 |
| *Paramys delicatus* | 3.4645 | 0.19138 |
| *Pseudotomus oweni* | 3.5924 | 0.17085 |
| *Reithroparamys delicatissimus* | 2.9325 | 0.20811 |
| *Rapamys atramontis* | 2.9633 | 0.23153 |
| *Ischyromys typus* ROMV 1007 | 3.0449 | 0.18363 |
| *Ischyromys typus* AMNH F:AM 144638 | 3.1278 | 0.16967 |
| *Titanotheriomys veterior* | 2.6378 | 0.16997 |
| *Cedromus wilsoni* | 2.4296 | 0.20215 |
| *Protosciurus cf. rachelae* | 2.5436 | 0.23261 |
| *Prosciurus relictus* | 1.4782 | 0.085826 |
| *Mesogaulus paniensis* | 2.4257 | 0.071237 |

ression of log10LSR and log10BM.
ıs without an agility designation include
S, slow.

| Agility Category | Residual |
|---|---|
| F | 0.038324 |
| M | -0.091269 |
| M | -0.015544 |
| F | 0.068803 |
| S | -0.035534 |
| S | -0.061063 |
| F | -0.017333 |
| S | -0.16319 |
| F | 0.045004 |
| M | -0.067267 |
| F | -0.086624 |
| F | -0.073964 |
| S | -0.16908 |
| M | 0.067161 |
| M | 0.0019567 |
| M | -0.094507 |
| M | -0.21356 |
| M | -0.1393 |
| M | 0.003775 |
| F | -0.010742 |
| M | -0.050068 |
| F | 0.047869 |
| M | -0.090788 |
| F | 0.063445 |
| F | 0.023592 |
| F | 0.083546 |
| F | 0.027552 |
| F | 0.077475 |
| F | 0.077075 |
| F | 0.069947 |
| F | 0.03009 |
| S | 0.0082715 |
| F | 0.0067916 |
| F | 0.019872 |
| F | -0.047573 |
| F | 0.0030066 |
| F | 0.044736 |
| F | 0.025588 |
| - | -0.056087 |
| - | 0.011937 |
| - | 0.098143 |
| - | 0.088568 |
| - | 0.074843 |

| | |
|---|---|
| - | 0.032685 |
| - | 0.067332 |
| - | 0.014889 |
| - | 0.062194 |
| - | 0.048185 |
| - | -0.015901 |
| - | -0.036288 |
| - | 0.023851 |
| - | 0.041613 |
| - | -0.011723 |
| - | 0.1403 |
| - | 0.013321 |
| - | -0.0043187 |
| - | -0.0808316 |
| - | -0.11424775 |
| - | -0.1551778 |
| - | -0.01266375 |
| - | 0.00584365 |
| - | -0.05507155 |
| - | -0.0822541 |
| - | -0.0037991 |
| - | 0.0615888 |
| - | 0.0738658 |
| - | 0.0970131 |
| - | -0.06870215 |

**Table S3.** Data from Figure 5 including log10LSR, log10BM and residuals from the regression of log
log10BM. Specimens with agility category designations originate from Spoor et al. 2007. Specimens
designation include the extant and fossil rodents examined in this study. Abbreviations: F, fast. MF, n
medium. MS, medium slow. S, slow. ES, extremely slow.

| Species | log10BM | log10LSR | Agility Category |
|---|---|---|---|
| *Bos taurus* | 5.462 | 0.447 | M |
| *Camelus dromedarius* | 5.618 | 0.495 | M |
| *Gazella bennetti* | 4.362 | 0.321 | M |
| *Giraffa camelopardalis* | 5.952 | 0.502 | MS |
| *Hippopotamus amphibius* | 6.057 | 0.606 | MS |
| *Oryx beisa (gazella)* | 5.298 | 0.424 | M |
| *Ovis aries* | 4.528 | 0.273 | M |
| *Sus scrofa* | 4.74 | 0.258 | M |
| *Canis familiaris* | 4.141 | 0.305 | M |
| *Enhydra lutris* | 4.432 | 0.318 | MF |
| *Felis catus* | 3.556 | 0.228 | M |
| *Felis concolor* | 4.751 | 0.34 | MF |
| *Herpestes ichneumon (griseus)* | 3.474 | 0.185 | M |
| *Lutra lutra* | 3.912 | 0.28 | MF |
| *Lynx rufus* | 3.989 | 0.314 | M |
| *Mustela nivalis (Putorius vulgaris)* | 1.94 | 0.013 | M |
| *Nyctereutes procyonoideus viverrinus* | 3.653 | 0.158 | MS |
| *Panthera leo* | 5.172 | 0.5 | M |
| *Panthera tigris* | 5.176 | 0.451 | M |
| *Procyon cancrivorus* | 3.845 | 0.308 | MS |
| *Proteles cristatus* | 3.932 | 0.251 | MS |
| *Taxidea taxus* | 3.857 | 0.352 | MS |
| *Vulpes vulpes* | 3.699 | 0.267 | M |
| *Halichoerus grypus* | 5.288 | 0.477 | MF |
| *Odobenus rosmarus* | 6.006 | 0.577 | MF |
| *Phoca groenlandica (Pagophilus groenlandicus)* | 5.106 | 0.512 | MF |
| *Phoca vitulina* | 4.91 | 0.495 | MF |
| *Eptesicus fuscus* | 1.274 | -0.113 | F |
| *Myotis lucifugus* | 0.91 | -0.162 | F |
| *Myotis macrodactylus* | 0.813 | -0.251 | F |
| *Nyctalus lasiopterus aviator* | 1.542 | -0.007 | F |
| *Pipistrelles pipistrelles* | 0.816 | -0.226 | F |
| *Pteropus giganteus* | 3.07 | 0.118 | F |
| *Rhinolophus cornutus cornutus* | 0.785 | -0.2 | F |
| *Phascogale tapoatafa (Phascologale penicillata)* | 2.236 | 0.075 | F |
| *Sminthopsis laniger (Antechinomys lanigera)* | 1.398 | -0.074 | F |
| *Sminthopsis macroura (S. larapinta)* | 1.266 | -0.183 | F |
| *Cynocephalus variegatus* | 3.138 | 0.222 | F |
| *Cynocephalus volans* | 3 | 0.221 | F |
| *Didelphis virginiana* | 3.341 | -0.018 | S |
| *Acrobates pygmaeus* | 1.157 | -0.182 | F |
| *Ailurops ursinus* | 3.845 | 0.207 | S |

| | | | |
|---|---|---|---|
| *Cercartetus nanus* | 1.425 | -0.209 | F |
| *Dactylopsila trivirgata* | 2.556 | 0.122 | F |
| *Hemibelideus lemuroides* | 2.985 | 0.102 | S |
| *Macropus fuliginosus (melanops)* | 4.797 | 0.327 | F |
| *Petauroides volans* | 3.114 | 0.184 | F |
| *Petaurus breviceps* | 2.146 | 0.043 | F |
| *Petaurus norfolcensis* | 2.362 | 0.041 | F |
| *Petrogale penicillata* | 3.823 | 0.194 | F |
| *Phalanger orientalis* | 3.398 | 0.124 | S |
| *Phascolarctos cinereus* | 3.842 | 0.309 | S |
| *Pseudocheirus peregrinus* | 2.893 | 0.182 | M |
| *Spilocuscus maculatus* | 3.581 | 0.277 | S |
| *Trichosurus vulpecula* | 3.533 | 0.194 | M |
| *Blarina brevicauda* | 1.201 | -0.209 | M |
| *Erinaceus europaeus* | 2.934 | 0.086 | M |
| *Scalopus aquaticus* | 1.908 | -0.066 | S |
| *Sorex cinereus* | 0.577 | -0.349 | M |
| *Sorex hoyi* | 0.519 | -0.362 | M |
| *Talpa europaea* | 1.989 | 0.009 | S |
| *Lepus europaeus* | 3.522 | 0.227 | MF |
| *Oryctolagus cuniculus* | 3.241 | 0.202 | MF |
| *Ornithorhynchus anatinus* | 3.243 | 0.157 | M |
| *Notoryctes typhlops* | 1.74 | -0.163 | S |
| *Isoodon obesulus (Perameles obesula)* | 3.025 | 0.063 | M |
| *Diceros bicornis* | 6 | 0.441 | M |
| *Equus caballus* | 5.398 | 0.444 | M |
| *Alouatta seniculus* | 3.826 | 0.303 | S |
| *Aotus trivirgatus* | 2.889 | 0.261 | MF |
| *Arctocebus calabarensis* | 2.494 | 0.075 | S |
| *Ateles geoffroyi* | 3.877 | 0.32 | M |
| *Avahi laniger* | 3.07 | 0.216 | F |
| *Cacajao calvus* | 3.5 | 0.289 | M |
| *Cacajao melanocephalus* | 3.433 | 0.29 | M |
| *Callicebus moloch* | 3.009 | 0.241 | M |
| *Callicebus torquatus* | 3.095 | 0.277 | M |
| *Callimico goeldi* | 2.727 | 0.128 | MF |
| *Callithrix jacchus* | 2.51 | 0.165 | F |
| *Cebus apella* | 3.489 | 0.275 | M |
| *Cercocebus torquatus atys* | 3.792 | 0.386 | F |
| *Cercopithecus cephus* | 3.632 | 0.347 | M |
| *Cercopithecus diana* | 3.716 | 0.385 | F |
| *Cercopithecus mitis* | 3.899 | 0.403 | M |
| *Cercopithecus mona* | 3.708 | 0.364 | M |
| *Cercopithecus nictitans* | 3.738 | 0.392 | M |
| *Cheirogaleus major* | 2.602 | 0.145 | M |
| *Cheirogaleus medius* | 2.416 | 0.089 | M |
| *Chlorocebus aethiops* | 3.613 | 0.355 | M |
| *Colobus guereza* | 3.99 | 0.39 | MF |
| *Colobus polykomos* | 3.959 | 0.407 | M |

| | | | |
|---|---|---|---|
| *Daubentonia madagascariensis* | 3.407 | 0.3 | F |
| *Erythrocebus patas* | 3.975 | 0.408 | F |
| *Eulemur fulvus ssp.* | 3.332 | 0.298 | M |
| *Eulemur macaco* | 3.378 | 0.306 | M |
| *Eulemur mongoz* | 3.206 | 0.308 | M |
| *Galago elegantulus* | 2.46 | 0.221 | F |
| *Galago moholi* | 2.272 | 0.172 | F |
| *Galago senegalensis* | 2.342 | 0.203 | F |
| *Galagoides alleni* | 2.442 | 0.202 | F |
| *Galagoides demidoff* | 1.789 | 0.096 | M |
| *Gorilla gorilla* | 5.083 | 0.485 | S |
| *Hapalemur griseus* | 3.038 | 0.271 | M |
| *Hapalemur simus* | 3.237 | 0.329 | F |
| *Homo sapiens* | 4.766 | 0.346 | M |
| *Hylobates hoolock* | 3.838 | 0.386 | F |
| *Hylobates klossii* | 3.754 | 0.392 | F |
| *Hylobates lar* | 3.75 | 0.381 | F |
| *Hylobates moloch* | 3.818 | 0.402 | F |
| *Hylobates pileatus* | 3.736 | 0.402 | F |
| *Hylobates syndactylus* | 4.053 | 0.415 | M |
| *Indri indri* | 3.802 | 0.384 | F |
| *Lagothrix lagotricha* | 3.867 | 0.301 | MS |
| *Lemur catta* | 3.344 | 0.284 | M |
| *Leontopithecus rosalia* | 2.792 | 0.148 | F |
| *Lepilemur sp.* | 2.883 | 0.233 | F |
| *Lophocebus albigena* | 3.916 | 0.431 | MF |
| *Loris tardigradus* | 2.342 | 0.007 | S |
| *Macaca cyclopis* | 3.738 | 0.371 | M |
| *Macaca fascicularis* | 3.651 | 0.345 | M |
| *Macaca fuscata* | 3.978 | 0.359 | M |
| *Macaca mulatta* | 3.968 | 0.385 | M |
| *Macaca nemestrina* | 3.89 | 0.312 | M |
| *Macaca nigra* | 3.885 | 0.371 | M |
| *Macaca sylvanus* | 4.132 | 0.397 | M |
| *Macaca tonkeana* | 4.077 | 0.377 | M |
| *Mandrillus sphinx* | 4.5 | 0.415 | M |
| *Microcebus murinus* | 1.841 | 0.077 | M |
| *Microcebus rufus* | 1.628 | 0.029 | M |
| *Nasalis larvatus* | 4.31 | 0.423 | MF |
| *Nycticebus coucang* | 2.933 | 0.127 | S |
| *Otolemur crassicaudatus* | 3.061 | 0.241 | M |
| *Otolemur garnetti* | 2.883 | 0.276 | F |
| *Pan paniscus* | 4.592 | 0.374 | M |
| *Pan troglodytes* | 4.653 | 0.398 | M |
| *Papio hamadryas z* | 4.223 | 0.428 | M |
| *Perodicticus potto* | 2.993 | 0.134 | S |
| *Pithecia pithecia* | 3.288 | 0.293 | M |
| *Pongo pygmaeus* | 4.755 | 0.38 | S |
| *Procolobus badius* | 3.934 | 0.32 | M |

| | | | |
|---|---|---|---|
| *Propithecus diadema* | 3.785 | 0.375 | F |
| *Propithecus verreauxi* | 3.561 | 0.336 | F |
| *Pygathrix nemaeus* | 4.041 | 0.399 | MF |
| *Saguinus oedipus* | 2.621 | 0.182 | F |
| *Saimiri sciureus* | 2.88 | 0.253 | F |
| *Semnopithecus entellus* | 4.162 | 0.377 | M |
| *Tarsius bancanus* | 2.088 | 0.186 | F |
| *Tarsius syrichta* | 2.099 | 0.169 | F |
| *Theropithecus gelada* | 4.219 | 0.344 | M |
| *Trachypithecus obscurus* | 3.898 | 0.364 | M |
| *Trachypithecus vetellus* | 3.847 | 0.385 | MF |
| *Varecia variegata* | 3.545 | 0.306 | M |
| *Archaeolemur edwardsi* | 4.389 | 0.425 | M |
| *Babakotia radofilai* | 4.21 | 0.307 | S |
| *Hadropithecus stenognathus* | 4.433 | 0.331 | M |
| *Megaladapis cf madagascariensis* | 4.58 | 0.291 | S |
| *Megaladapis edwardsi* | 4.877 | 0.306 | S |
| *Mesopropithecus pithecoides* | 3.987 | 0.292 | S |
| *Palaeopropithecus ingens* | 4.657 | 0.17 | ES |
| *Elephas maximus* | 6.538 | 0.439 | MS |
| *Loxodonta africana* | 6.657 | 0.562 | MS |
| *Dendrogale murina* | 1.653 | 0.075 | M |
| *Ptilocercus lowii* | 1.588 | 0.021 | M |
| *Tupaia glis* | 2.152 | 0.176 | M |
| *Tupaia minor* | 1.845 | 0.1 | M |
| *Tupaia tana* | 2.312 | 0.157 | M |
| *Urogale everetti* | 2.439 | 0.217 | M |
| *Dugong dugon (Halicore australis)* | 5.628 | 0.477 | ES |
| *Bradypus tridactylus* | 3.665 | 0.051 | ES |
| *Bradypus variegates* | 3.637 | 0.033 | ES |
| *Choloepus hoffmanni* | 3.757 | 0.03 | ES |
| *Zaedyus pichiy* | 3.241 | 0.131 | MS |
| *Anomalurus derbianus* | 2.656 | 0.215 | F |
| *Castor canadensis* | 4.271 | 0.343 | M |
| *Cavia porcellus* | 3 | 0.216 | M |
| *Chinchilla laniger* | 2.653 | 0.245 | F |
| *Cryptomys hottentotus natalensis* | 1.978 | 0.033 | S |
| *Cryptomys mechowi* | 2.602 | 0.107 | S |
| *Dipus sagitta* | 1.82 | 0.026 | F |
| *Erethizon dorsatum* | 4.026 | 0.232 | S |
| *Glaucomys volans* | 1.774 | 0.081 | F |
| *Hydrochaeris hydrochaeris (Hydrochoerus capybara)* | 4.597 | 0.419 | M |
| *Idiurus macrotis* | 1.477 | -0.098 | F |
| *Idiurus zenkeri* | 1.197 | -0.13 | F |
| *Lophiomys imhausi* | 2.878 | 0.043 | S |
| *Marmota monax* | 3.61 | 0.396 | M |
| *Meriones unguiculatus* | 2 | 0.074 | M |
| *Microtus pennsylvanicus* | 1.633 | -0.081 | M |
| *Mus musculus* | 1.276 | -0.257 | M |

| | | | |
|---|---|---|---|
| *Myocastor coypus* | 3.895 | 0.235 | M |
| *Ondatra zibethicus* | 2.998 | 0.235 | M |
| *Pedetes capensis* | 3.484 | 0.298 | F |
| *Peromyscus maniculatus* | 1.229 | -0.101 | M |
| *Petaurista petaurista* | 3.267 | 0.322 | F |
| *Rattus norvegicus* | 2.431 | 0.05 | M |
| *Ratufa bicolor* | 3.138 | 0.317 | F |
| *Ratufa macroura* | 3.112 | 0.273 | F |
| *Sciurus aberti* | 2.78 | 0.28 | F |
| *Sciurus carolinensis* | 2.711 | 0.213 | F |
| *Sciurus granatensis* | 2.398 | 0.213 | F |
| *Sciurus niger* | 2.877 | 0.289 | F |
| *Sciurus richmondi* | 2.301 | 0.19 | F |
| *Sciurus vulgaris* | 2.507 | 0.183 | F |
| *Spalax ehrenbergi* | 2.23 | 0.117 | S |
| *Spermophilus beecheyi* | 2.791 | 0.205 | F |
| *Spermophilus parryi* | 2.872 | 0.231 | F |
| *Spermophilus richardsoni* | 2.461 | 0.098 | F |
| *Spermophilus tridecemlineatus* | 2.1 | 0.091 | F |
| *Xerus erythropus* | 2.76 | 0.238 | F |
| *Xerus rutilus* | 2.623 | 0.197 | F |
| *Aplodontia rufa* | 3.1690452 | 0.2024202 | - |
| *Sciurus carolinensis* | 2.772725 | 0.2072303 | - |
| *Tamiasciurus hudsonicus* | 2.4092736 | 0.2354653 | - |
| *Funisciurus pyrropus* | 2.4787829 | 0.2369779 | - |
| *Heliosciurus rufobrachium* | 2.5502039 | 0.2346438 | - |
| *Paraxerus cepapi* | 2.140288 | 0.1271048 | - |
| *Protoxerus stangeri* | 2.8849256 | 0.2805215 | - |
| *Aeromys tephromelas* | 2.9564518 | 0.2394872 | - |
| *Glaucomys volans* | 1.8059764 | 0.1032905 | - |
| *Petaurista petaurista* | 3.040068 | 0.2861195 | - |
| *Hylopetes spadiceus* | 1.9254152 | 0.0442457 | - |
| *Petinomys setosus* | 1.6217992 | -0.024568 | - |
| *Pteromyscus pulverulentus* | 2.2910135 | 0.1423112 | - |
| *Pteromys buechneri* | 2.0268192 | 0.1179338 | - |
| *Rhinosciurus laticaudatus* | 2.7053333 | 0.1728218 | - |
| *Callosciurus caniceps* | 2.6408291 | 0.3145519 | - |
| *Lariscus insignis* | 2.5114957 | 0.1669479 | - |
| *Dremomys rufigenis* | 2.6216228 | 0.166874 | - |
| *Paramys copei* | 3.0127908 | 0.1527469 | - |
| *Paramys delicatus* | 3.4644627 | 0.1913811 | - |
| *Pseudotomus oweni* | 3.5923667 | 0.1708482 | - |
| *Reithroparamys delicatissimus* | 2.9324738 | 0.2081053 | - |
| *Rapamys atramontis* | 2.9632837 | 0.2315333 | - |
| *Ischyromys typus* ROMV 1007 | 3.0449355 | 0.1836257 | - |
| *Ischyromys typus* AMNH F:AM 144638 | 3.1278269 | 0.1696744 | - |
| *Titanotheriomys veterior* | 2.6377528 | 0.1699682 | - |
| *Cedromus wilsoni* | 2.4295747 | 0.2021476 | - |
| *Protosciurus cf. rachelae* | 2.5435913 | 0.232615 | - |

| | | | |
|---|---|---|---|
| *Prosciurus relictus* | 1.4782056 | 0.0858255 | - |
| *Mesogaulus paniensis* | 2.4256646 | 0.0712374 | - |

g10LSR and
without an agility
nedium fast. M,

| Residual |
|---|
| -0.068402 |
| -0.041007 |
| -0.049114 |
| -0.078122 |
| 0.01201 |
| -0.069741 |
| -0.11904 |
| -0.16204 |
| -0.035924 |
| -0.061359 |
| -0.035656 |
| -0.081493 |
| -0.067826 |
| -0.030677 |
| -0.0068474 |
| -0.037214 |
| -0.11847 |
| 0.022901 |
| -0.026627 |
| 0.0061722 |
| -0.062319 |
| 0.048587 |
| -0.015544 |
| -0.01542 |
| -0.010254 |
| 0.043618 |
| 0.052506 |
| -0.075248 |
| -0.076171 |
| -0.15236 |
| -0.0046459 |
| -0.12776 |
| -0.081465 |
| -0.097661 |
| -0.01431 |
| -0.052626 |
| -0.14419 |
| 0.013553 |
| 0.03078 |
| -0.25326 |
| -0.12879 |
| -0.094828 |

-0.19119
-0.0095758
-0.086238
-0.10057
-0.021277
-0.034423
-0.064952
-0.10492
-0.11879
0.0075684
0.005913
0.010041
-0.066619
-0.16161
-0.095502
-0.11199
-0.21919
-0.22453
-0.047686
-0.032166
-0.020051
-0.065315
-0.1868
-0.13052
-0.14546
-0.062949
0.0036817
0.085441
-0.048387
0.013946
0.016535
0.03274
0.042589
0.049592
0.074233
-0.026162
0.0395
0.020193
0.091172
0.073305
0.10021
0.09404
0.080267
0.1043
0.0073485
-0.024084
0.083815
0.06902
0.090115

0.056024
0.089002
0.06393
0.065854
0.090572
0.1021
0.077935
0.09969
0.085481
0.06573
0.019656
0.075761
0.10748
-0.077474
0.085097
0.10219
0.09172
0.10374
0.11457
0.085699
0.087852
-0.0037336
0.048345
-0.014747
0.058234
0.11979
-0.09631
0.083305
0.068796
0.039605
0.066926
0.0042286
0.063889
0.057265
0.044529
0.026659
0.039862
0.019995
0.059755
-0.05437
0.042723
0.10123
-0.026492
-0.010549
0.076246
-0.055295
0.064741
-0.042021
0.006417

0.081097
0.071683
0.071284
0.041839
0.07863
0.033303
0.11624
0.097785
-0.007226
0.055172
0.082908
0.043796
0.05132
-0.043037
-0.048491
-0.10791
-0.13214
-0.028583
-0.23908
-0.21852
-0.11124
0.062693
0.017278
0.097785
0.062334
0.057652
0.10088
-0.060328
-0.22705
-0.24136
-0.2602
-0.091051
0.070216
-0.015094
0.02578
0.10061
-0.022233
-0.030651
-0.0083643
-0.093734
0.052711
0.017847
-0.087061
-0.082078
-0.13111
0.12521
0.015861
-0.090665
-0.21951

-0.073432
0.045045
0.043853
-0.057305
0.096515
-0.065066
0.10855
0.067987
0.11884
0.060952
0.10229
0.11503
0.092105
0.057896
0.028483
0.042385
0.057687
-0.021028
0.019653
0.07948
0.056575
-0.010127
0.047029
0.12327
0.1156
0.10383
0.050437
0.1055
0.055019
0.070778
0.090608
-0.004042
-0.032754
0.045735
0.056253
0.021522
0.17177
0.04125
0.026631
-0.03916255
-0.060185094
-0.097611583
0.026804158
0.046162794
-0.012529399
-0.037428948
0.02759378
0.087269394
0.102677444

0.096604134
-0.043124335

**Table S4.** Additional information for each specimen including the angle between the anterior and la
and the posterior and lateral semicircular canals (PSC/LSC). The deviation from 90 degrees for eacl
90VAR for the anterior and posterior semicircular canals, and P/L 90VAR for the posterior and late
pairs is given as 90VAR. The logarithm of the angular velocity magnitude logAVM is calculated us

| | Specimen | Catalogue Number | ASC/LSC | ASC/PSC |
|---|---|---|---|---|
| Fossil | *Paramys copei* | AMNH 4756 | 88.1 | 96.3 |
| | *Paramys delicatus* | AMNH 12506 | 86.6 | 92.6 |
| | *Pseudotomus oweni* | USNM 17161 | 77.3 | 90.7 |
| | *Reithroparamys delicatissimus* | AMNH 12561 | 86.7 | 89.1 |
| | *Rapamys atramontis* | AMNH 128704 | 85.7 | 85.6 |
| | *Ischyromys typus* | AMNH F:AM 144638 | 83.1 | 82.8 |
| | *Ischyromys typus* | ROMV 1007 | 83.6 | 89.7 |
| | *Titanotheriomys veterior* | AMNH 79314 | 95.6 | 97.4 |
| | *Cedromus wilsoni* | USNM 256584 | 87.1 | 82.3 |
| | *Protosciurus* cf. *rachelae* | YPM 14736 | 83.6 | 83.6 |
| | *Prosciurus relictus* | USNM 437793 | 81.8 | 83.8 |
| | *Mesogaulus paniensis* | AMNH F:AM 65511 | 94.1 | 97.8 |
| Extant | *Aplodontia rufa* | AMNH 42389 | 88 | 86.2 |
| | *Sciurus carolinensis* | AMNH 258346 | 85.3 | 82.7 |
| | *Tamiasciurus hudsonicus* | USNM 549146 | 84.6 | 83.2 |
| | *Funisciurus pyrropus* | USNM 294865 | 79 | 82.6 |
| | *Heliosciurus rufobrachium* | USNM 378091 | 88.4 | 83.5 |
| | *Paraxerus cepapi* | USNM 367956 | 87.5 | 87 |
| | *Protoxerus stangeri* | USNM 435027 | 76.3 | 81.8 |
| | *Aeromys tephromelas* | USNM 481190 | 89 | 81.7 |
| | *Glaucomys volans* | AMNH 240290 | 78.9 | 86.4 |
| | *Petaurista petaurista* | USNM 589079 | 80.4 | 85.4 |
| | *Hylopetes spadiceus* | USNM 488639 | 82 | 82.5 |
| | *Petinomys setosus* | USNM 488674 | 88.8 | 85.1 |
| | *Pteromyscus pulverulentus* | USNM 481178 | 87.2 | 86.8 |
| | *Pteromys buechneri* | USNM 172622 | 80.7 | 79.5 |
| | *Rhinosciurus laticaudatus* | USNM 488511 | 80.3 | 88 |
| | *Callosciurus caniceps* | USNM 294865 | 81 | 80.3 |
| | *Lariscus insignis* | USNM 488570 | 89.5 | 81.8 |
| | *Dremomys rufigenis* | USNM 488602 | 85 | 88.3 |

ateral semicircular canals (ASC/LSC), anterior and posterior semicircular canals (ASC/PSC), h angle pair is given as A/L 90VAR for the anterior and lateral semicircular canals, A/P eral semicircular canals. The average deviation from 90 degrees for all three semicircular canal sing the formula from Malinzak et al. 2012.

| PSC/LSC | A/L 90VAR | A/P 90VAR | P/L 90VAR | 90VAR | log90VAR | logAVM |
|---|---|---|---|---|---|---|
| 86.5 | 1.9 | 6.3 | 3.5 | 11.7 | 1.068185862 | 2.285225211 |
| 86 | 3.4 | 2.6 | 4 | 10 | 1 | 2.32 |
| 84.1 | 12.7 | 0.7 | 5.9 | 19.3 | 1.285557309 | 2.174365772 |
| 91.9 | 3.3 | 0.9 | 1.9 | 6.1 | 0.785329835 | 2.429481784 |
| 90.5 | 4.3 | 4.4 | 0.5 | 9.2 | 0.963787827 | 2.338468208 |
| 78.6 | 6.9 | 7.2 | 11.4 | 25.5 | 1.40654018 | 2.112664508 |
| 88.8 | 6.4 | 0.3 | 1.2 | 7.9 | 0.897627091 | 2.372210183 |
| 90.7 | 5.6 | 7.4 | 0.7 | 13.7 | 1.136720567 | 2.250272511 |
| 87.8 | 2.9 | 7.7 | 2.2 | 12.8 | 1.10720997 | 2.265322915 |
| 84.9 | 6.4 | 6.4 | 5.1 | 17.9 | 1.252853031 | 2.191044954 |
| 87.3 | 8.2 | 6.2 | 2.7 | 17.1 | 1.23299611 | 2.201171984 |
| 85.6 | 4.1 | 7.8 | 4.4 | 16.3 | 1.212187604 | 2.211784322 |
| 87.2 | 2 | 3.8 | 2.8 | 8.6 | 0.934498451 | 2.35340579 |
| 85.8 | 4.7 | 7.3 | 4.2 | 16.2 | 1.209515015 | 2.213147343 |
| 79.5 | 5.4 | 6.8 | 10.5 | 22.7 | 1.356025857 | 2.138426813 |
| 84.7 | 11 | 7.4 | 5.3 | 23.7 | 1.374748346 | 2.128878344 |
| 88.3 | 1.6 | 6.5 | 1.7 | 9.8 | 0.991226076 | 2.324474701 |
| 90 | 2.5 | 3 | 0 | 5.5 | 0.740362689 | 2.452415028 |
| 88.1 | 13.7 | 8.2 | 1.9 | 23.8 | 1.376576957 | 2.127945752 |
| 83.7 | 1 | 8.3 | 6.3 | 15.6 | 1.193124598 | 2.221506455 |
| 89.6 | 11.1 | 3.6 | 0.4 | 15.1 | 1.178976947 | 2.228721757 |
| 87.8 | 9.6 | 4.6 | 2.2 | 16.4 | 1.214843848 | 2.210429637 |
| 96.4 | 8 | 7.5 | 6.4 | 21.9 | 1.340444115 | 2.146373501 |
| 88.6 | 1.2 | 4.9 | 1.4 | 7.5 | 0.875061263 | 2.383718756 |
| 88.5 | 2.8 | 3.2 | 1.5 | 7.5 | 0.875061263 | 2.383718756 |
| 97.4 | 9.3 | 10.5 | 7.4 | 27.2 | 1.434568904 | 2.098369859 |
| 89.4 | 9.7 | 2 | 0.6 | 12.3 | 1.089905111 | 2.274148393 |
| 93.7 | 9 | 9.7 | 3.7 | 22.4 | 1.350248018 | 2.141373511 |
| 89.4 | 0.5 | 8.2 | 0.6 | 9.3 | 0.968482949 | 2.336073696 |
| 90.4 | 5 | 1.7 | 0.4 | 7.1 | 0.851258349 | 2.395858242 |

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