ARTICLE

FIRST VIRTUAL ENDOCASTS OF A FOSSIL RODENT: *ISCHYROMYS TYPUS* (ISCHYROMYIDAE, OLIGOCENE) AND BRAIN EVOLUTION IN RODENTS

ORNELLA C. BERTRAND* and MARY T. SILCOX
Department of Anthropology, University of Toronto Scarborough, Toronto, Ontario, M1C 1A4, Canada, ornella.bertrand@mail.utoronto.ca; msilcox@utsc.utoronto.ca

ABSTRACT—The evolution of the brain in rodents has rarely been studied from the perspective of the fossil record. Here we describe the first virtual endocast of a fossil rodent, pertaining to *Ischyromys typus* (ROMV 1007; Orellan North American Land Mammal Age [NALMA], Nebraska), and form comparisons with partial and complete natural endocasts pertaining to the same genus, and with the virtual endocast of a closely related extant rodent (*Sciurus carolinensis*; AMNH 258346). These data allow us to formulate the first hypotheses informed by the fossil record concerning changes in brain size and shape through time in rodents, and to make comparisons with other euarchontoglirians, including Primates. *Ischyromys* exhibits several aspects of brain morphology that can be inferred to be primitive, in part based on their presence in plesiadapiform primates (e.g., exposed midbrain), although variation exists within the genus *Ischyromys* with respect to the visibility of the inferior colliculi. There is some evidence that neocorticalization occurred in rodents through time but to a lesser degree than in Primates. Arboreality might be linked to increases in the encephalization quotient and specializations related to vision in rodents, which contrasts with the situation in Primates. Finally, Oligocene rodents had smaller olfactory bulbs compared with plesiadapiform primates from the Eocene, meaning that olfaction might have been less critical in the early evolution of rodents. These results show that the evolution of the brain in mammals does not always follow the same evolutionary trajectories and demonstrates the importance of considering ecological factors when looking at brain size.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

Citation for this article: Bertrand, O. C., and M. T. Silcox. 2016. First virtual endocasts of a fossil rodent: *Ischyromys typus* (Ischyromyidae, Oligocene) and brain evolution in rodents. Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2016.1095762.

INTRODUCTION

Rodentia is the most diverse mammalian group today at both the taxonomic and ecological levels. Extant rodents include 2277 species divided into 33 families (Blanga-Kanfi et al., 2009). The classification by Wilson and Reeder (2005) is followed here, using the following suborders: Sciuromorpha (squirrels, mountain beavers); Castorimorpha (beavers, kangaroo rats); Myomorpha (rats, mice); and Anomaluromorpha (scaly-tailed squirrels, springhares) and Hystricomorpha with Old World (African porcupines, gundis) and New World (chinchillas, pacas) hystriognath rodents. The phylogenetic relationships between these suborders are not clear and differences exist between phylogenies based on molecular (Blanga-Kanfi et al., 2009; Churakov et al., 2010) and morphological (Wood, 1959; Meng, 1990) data. Rodents are part of Glires (Linnaeus, 1758) with Lagomorpha (rabbits). The monophyly of this group is now well established based on molecular (e.g., Murphy et al., 2001; Huchon et al., 2002; Poux et al., 2006) and morphological (e.g., Li et al., 1987; Meng et al., 2003; Marivaux et al., 2004; Meng, 2004) data. Glires is consistently recovered as part of a supraordinal grouping with Euarchonta (Primates, Scandentia, Dermoptera) in molecular analyses—this clade is referred to as Euarchontognires (Springer et al., 2004). Rodents occupy a broad array of different niches and vary along several lifestyle dimensions, including activity period (diurnal vs. nocturnal), habitat, and diet. Indeed, rodents can be arboreal, aerial, terrestrial, semiaquatic, burrowing, and even rock-dwelling (Krubitzer et al., 2011). The diet of rodents is also very diverse: some are herbivorous, others omnivorous (Landry, 1970), insectivorous (Pizzimenti and de Salle, 1980), and even fungivorous (Cork and Kenagy, 1989).

One aspect of rodent evolution that has been less thoroughly treated concerns changes in morphology and size of the brain. There have been some investigations of the form of the brain in living members of Glires. Lewis (1882) and Mann (1895) were the first authors to document the external morphology of the brain using rats and rabbits. Rodents were seen as having large olfactory bulbs and unconvoluted (smooth; lissencephalic) brains. In 1970, Brauer and Schober provided an atlas of brains for different taxonomic groups, including photos, illustrations, as well as brain and body masses for 42 species, from every suborder except Anomaluromorpha. Several subsequent authors considered aspects of the anatomy of the brain in specific subgroups of rodents (e.g., Crile and Quiring, 1940; Pilleri, 1959, 1960a, 1960b, 1961, 1963; Nikitenko, 1966; Sacher and Staffeldt, 1974; Pirlot and Kamiya, 1982), but it was Pilleri et al. (1984) who presented the first broad-reaching comparative study on brain anatomy with quantitative data. Pilleri and colleagues (1984) documented significant diversity in brain structure in rodents and demonstrated that the shape of the brain is not consistent within suborders, but rather that particular morphologies tend to characterize families or genera. Additionally, they tried to understand if the broad-reaching variability in ecology is reflected in the anatomy of the brain. Although providing a starting point to understand variation in the brain of modern rodents,

* Corresponding author.

Color versions of one or more of the figures in this article can be found online at www.tandfonline.com/UJVP.
none of these studies considered fossil taxa, limiting their relevance for understanding of how and why this diversity arose.

Because brains do not preserve in the fossil record, paleoneurologists only have access to the external morphology of the brain reflected in the interior of the cranium, as visualized in an endocast. Natural endocasts are produced by infilling of the cranial cavity with matrix during fossilization (Martin, 1990). A natural endocast is completely isolated from the skull by natural erosion or by preparing the skull away from the endocast. Latex endocasts can only be made from specimens that are not filled with matrix and are well enough preserved to withstand the process without breaking—as such, it is typically impossible to make them for small mammals. Only a few natural endocasts from the North American family Ischyromyidae (Scott and Osborn, 1887, 1890; Wood, 1937, 1974), Eocene European rodents (Dechaux, 1958), Miocene African philomorphs (Lavocat, 1973), and Miocene caviomorphs (Dozo, 1997a, 1997b, Dozo et al., 2004) have been described. No quantitative data have been produced for any of the published natural endocasts of rodents except by Dozo (1997a), and generally the provided descriptions are brief, with only very limited comparisons being made. What’s more, the taxa from which these endocasts derive are often well nested within modern suborders, limiting their relevance to broader questions of rodent or euarchontogliuran brain evolution. Perhaps within modern suborders, limiting their relevance to broader questions of rodent or euarchontogliuran brain evolution.

Perhaps within modern suborders, limiting their relevance to broader questions of rodent or euarchontogliuran brain evolution. What’s more, no quantitative data are available for them for small mammals. Only a few natural endocasts from the North American family Ischyromyidae (Scott and Osborn, 1887, 1890; Wood, 1937, 1974), Eocene European rodents (Dechaux, 1958), Miocene African philomorphs (Lavocat, 1973), and Miocene caviomorphs (Dozo, 1997a, 1997b, Dozo et al., 2004) have been described. No quantitative data have been produced for any of the published natural endocasts of rodents except by Dozo (1997a), and generally the provided descriptions are brief, with only very limited comparisons being made. What’s more, the taxa from which these endocasts derive are often well nested within modern suborders, limiting their relevance to broader questions of rodent or euarchontogliuran brain evolution. Perhaps the taxon most relevant to such questions that is known from natural endocasts is the primitive gliroid mammal Rhombomylus turpanensis (Meng et al., 2003), which provides a starting point for thinking about rodent brain evolution. Meng et al. (2003) describe R. turpanensis as having a small and unconvoluted cerebrum and cerebellum, as well as having large olfactory bulbs compared with rodents. However, no quantitative data are available for R. turpanensis.

Fortunately, with the increased accessibility of high-resolution X-ray computed tomography scanners, virtual endocasts from most fossilized crania can now be obtained. This paper presents the first virtual endocast of a fossil rodent, created from a cranium of Ischyromys typus (ROMV 1007) from the Early Oligocene of Nebraska (Orellan North American Land Mammal Age [NALMA]). Two other specimens were also examined: a natural endocast (AMNH 12252) and partial natural endocast (AMNH F:AM 144836) of Ischyromys typus, which were processed to generate digital versions to allow for quantification of aspects of their morphology in a manner that was comparable to that used for ROMV 1007. This species is a member of the Ischyromyidae, which is one of the oldest rodent families (late Paleocene to late Oligocene), either at the base of Rodentia (Matthew, 1910; Wilson, 1949; Wood, 1962) or the ancestor of modern Sciuromorpha (Harterberger, 1980; Dawson et al., 1984; Korth, 1984, 1994; Flynn et al., 1986). Consequently, studying the endocasts of members of this family is very relevant to understanding brain evolution in rodents.

The three endocasts of Ischyromys typus were compared with virtual endocasts from other known Tertiary Euarchontoglires (Gingerich and Gunnell, 2005; Koenigswald et al., 2009; Silcox et al., 2009, 2010a, 2011; Orliac et al., 2014) and a virtual endocast of a modern sciurid, in order to explore the changes occurring in brain size and morphology in Rodentia through time (Fig. 1).

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, NY, USA; AMNH F:AM, Frick collection: American Museum of Natural History, New York, NY, USA; CGM, Cairo Geological Museum, Cairo, Egypt; DPC, Duke University Primate Center, Durham, North Carolina, U.S.A.; MNHN CR, Museum National d'Histoire Naturel Cernay-le-Reims, Paris, France; NMB, Naturhistorisches Museum Basel, Basel, Switzerland; ROMV, Royal Ontario Museum Vertebrate Paleontology, Toronto, Canada; TMM, Texas Memorial Museum, Austin, Texas, U.S.A.; UF, University of Florida, Gainesville, Florida, U.S.A.; UM, University of Michigan, Ann Arbor, Michigan, U.S.A.; USNM, United States National Museum, Washington D.C., U.S.A.; UW, University of Wyoming, Laramie, Wyoming, U.S.A.

MATERIALS AND METHODS

The specimen ROMV 1007 includes a nearly complete cranium: one zygomatic arch is largely missing, whereas the other is partially detached. Matrix fills the cranium, forming a natural endocast (Fig. 2). Although the dorsal skull roof is missing, a high-density material covers the endocast so it is not visible from the exterior of the specimen. This specimen has not previously been described but can be identified as Ischyromys typus based on morphological characteristics used by Wood (1937) to identify specimens belonging to the same species: (1) the bullae are large and rounded; (2) no separation is present between the ecor- and entotympenic bones; (3) the mastoid (right side) has a bullate shape; (4) the foramen magnum is almost rectangular; (5) the palate ends at the level of the upper M2; and (6) the temporal crests join to form a long sagittal crest. Heaton (1993) reevaluated the taxonomy of this genus and suggested that only two species can be identified, which probably coexisted through the Oligocene; Ischyromys typus and I. parvidens. The specimen ROMV 1007 can be identified as I. typus rather than I. parvidens because the latter taxon is notably smaller. For example, I. parvidens has a much shorter tooth row (lower p4—m3: 12.16 mm for the holotype USNM 9134 in Wood, 1937) than I. typus (upper p4—m3: 17.37 mm; ROMV 1007). The specimen was found 9 miles northeast of Harrison, Sioux County, Nebraska, on a branch of Hat Creek. The Hat Creek Basin includes both early Chadronian (Ch2; late Eocene) and Orellan (early Oligocene) deposits (Janis et al., 2008). No remains of Ischyromys have been described from this basin for Ch2, whereas I. typus is known from the Orellan beds (Janis et al., 2008), suggesting that ROMV 1007 may come from the Oligocene deposits in this basin. In particular, the Orellan Brule Formation (White River Group) is known from the Hat Creek Basin. Although an origin from this formation for ROMV 1007 cannot be confirmed, such an origin is consistent with the records available and the known distribution of Ischyromys in the Basin. If correct, this would suggest an age between 33.7 and 32 Ma (Prothero and Ermy, 2004).

FIGURE 1. Relationships for Rodentia and other members of Euarchontoglires discussed in the text. Only groups represented by endocasts discussed here are included (i.e., Scandentia and Dermoptera are excluded because they are unknown from fossil skulls). The topology of the tree is based on Marivaux et al. (2004) and Silcox et al. (2010b).
on the slices containing the endocast, and a surface rendering of the endocast was obtained (Fig. 3). By loading and opening the skull and the endocast separately, two different labelfield modules were created to obtain an image showing the endocast inside a translucent cranium (Fig. 4A).

A natural endocast of *Ischyromys*, AMNH 12252 from the American Museum of Natural History, was used for comparison (Fig. 5). This specimen has not previously been described and is associated with a fragment of the cranium (mainly maxilla). This specimen was found in Sheep Mountain, West Pennington County, South Dakota; Database, AMNH). This locality is part of the Brule Formation and considered Orellan in age (early Oligocene; Janis et al., 2008). *Ischyromys typus* and *I. parvidens* have previously been described from the Sheep Mountain locality (Anderson, 2008). Based on dental morphology, this specimen has similarities with *Ischyromys typus* (Wood, 1937); M1 and M2 are longer mesiodistally than labiolingually, and the palate ends at the level of the M2. This specimen is closely comparable in size to ROMV 1007, so it clearly does not pertain to the smaller *Ischyromys parvidens* but instead probably to *I. typus*.

In order to allow for the gathering of quantitative data, the natural endocast (AMNH 12252) was also scanned to produce a virtual copy. It was scanned in June 2014 at the high-resolution X-ray computed tomography scanner at the SMIF at Duke University (North Carolina). It was scanned with a source-object distance of 90.67 mm and energy settings of 170 kV and 0.186 mA. A total of 1819 slices were reconstructed using 1700 views with an interslice spacing and interpixel distance of 0.023 mm (X = Y = Z), stored as 16-bit tiffs, resulting in a 4.02 GB data set. The data were cropped to 1047 columns × 800 rows using ImageJ and the endocast corresponds to 1745 slices. The vermis is damaged on the surface, the left paraflocculus is missing, and the olfactory bulbs are slightly broken ventrally. Nevertheless, the orbitotemporal canal and casts of foramina such as the optic canal are visible.

A partial natural endocast of *Ischyromys* sp. (AMNH F:AM 144836) was also used for comparison. The specimen is a cranium with a dorsally exposed endocast (Figs. 4B, 6A). Both zygomatic bones, the most anterior part of the rostrum, as well as the left M3, and both deciduous premolars are missing in AMNH F:AM 144836. No specimens of *Ischyromys* that include specifically diagnostic traits have been discovered from this locality; however, this specimen can be identified as *Ischyromys typus* in light of the morphological similarities that it shares with ROMV 1007 (i.e., large and rounded bullae, bullate-shaped mastoid, almost rectangular foramen magnum, etc. as well as a similar overall size.

The specimen, AMNH F:AM 144836, was found in Stark County, North Dakota. This locality is in the Brule Formation (White River Group) and is also considered Orellan in age (early Oligocene; Janis et al., 2008).

In order to allow for visualization of the full endocast, and gathering of quantitative data, AMNH F:AM 144836 was scanned at the AMNH microscopy and imaging facility in April 2015, with a source-object distance of 166.75 mm and energy settings of 170 kV and 0.220 mA. A total of 1796 slices were reconstructed using 1700 views with an interslice spacing and interpixel distance of 0.023 mm (X = Y = Z), stored as 16-bit tiffs, resulting in a data set of 1.93 GB. The data were cropped to 848 columns × 683 rows using ImageJ, and the endocast corresponds to 985 slices. A new labelfield module was created in the segmentation editor, and the endocast was selected by using the magic wand tool. The segmentation was done using a WACOM Cintiq 21UX tablet using Avizo 7.0.0 software (Visualization and Sciences Group, 1995—2011). Openings in the skull (e.g., foramina, fissures) were closed manually using straight lines to allow for the selection of just the endocranial cavity.

Finally, a virtual endocast of a modern sciuriform rodent, *Sciurus carolinensis* (AMNH 258346), was included for comparison (Fig. 7). The cranium of AMNH 258346 was complete and in good condition, and the endocranial cavity was manually segmented using a WACOM Cintiq 21UX tablet in ImageJ (Rasband, 1997—2014) and loaded into Avizo 7.0.0 software (Visualization and Sciences Group, 1995—2011). A new labelfield module was created based on the segmentation of the actual endocast (Fig. 8).
condition. This specimen was a female, and no body mass was associated with it. It was also scanned at Duke in June 2013, with a source-object distance of 187.80 mm and energy settings of 120 kV and 0.175 mA. A total of 1910 slices were reconstructed using 2100 views with an interslice spacing and interpixel distance of 0.032 mm (X = Y = Z), stored as 16-bit tiffs, resulting in a data set of 8.38 GB. The data were cropped to 1180 columns × 990 rows using ImageJ and the endocast corresponds to 1148 slices. The segmentation process was done using the Avizo 7.0 software (Visualization and Sciences Group, 1995—2011) and the WACOM Cintiq 21UX tablet. The same process used for AMNH F:AM 144836 was used to obtain the virtual endocast of AMNH 258346.

FIGURE 3. Virtual endocast of Ischyromys typus (ROMV 1007) in A, dorsal; B, ventral; C, right lateral; and D, left lateral views. Scale bar equals 10 mm.
Surface area was selected and the superior sagittal sinus was excluded, and the area of the hemisphere was doubled (NS1 × 2; Table 1; following Jerison, 2012; Long et al., 2015).

The left paraflocculus, sphenoidal fissure, optic nerves, brain stem, and postglenoid vein are not preserved in the natural endocast of Ischyromys typus (AMNH 12252). This means that the total surface area and volume of the endocast obtained for this specimen are not based on the same data compared with ROMV 1007. In order to evaluate the impact of these differences, we calculated what the endocranial volume and surface area of ROMV 1007 would be if the specimen lacked the same parts (see Results and Table S2). The total volume and surface area of the endocast of ROMV 1007 cropped to match the parts missing in AMNH 12252 represent 92.43% and 78.59% of the original values for ROMV 1007, respectively. The values for the total surface and volume of the endocast of AMNH 12252 were then estimated by assuming that the same percentage is missing from this specimen, i.e., that the regions lacking in AMNH 12252 would have accounted for the same proportion of the overall volume and surface area (see Table S2). This assumption leads to an increase in the total endocast volume and surface area of the endocast of AMNH 12252. The resulting estimated values for the total endocast surface area and the total endocast volume of AMNH 12252 were used in the calculation of the relative neocortical surface area, the percentage of the endocranial volume accounted for by the olfactory bulbs, and the encephalization quotient, as well as the ratio of the total endocast volume to body mass (Tables 1, 2). The surface renderings of the four endocasts are available on MorphoSource (www.morphosource.org) (Boyer et al., 2014).

In order to make comparisons of relative brain size, estimates of the encephalization quotient were calculated. The encephalization quotient (EQ = E/E*) was first proposed by Jerison (1973) and corresponds to the ratio between the actual brain size of a given species i (Ei) and the brain size expected for a hypothetical, ‘typical’ mammal of the same body mass (E∗; Martin, 1990). Body mass of each specimen was obtained based on skull length and cheek-tooth area for Ischyromys typus (ROMV 1007) and Sciurus carolinensis (AMNH 258346) and solely on cheek-tooth area for the natural endocasts of Ischyromys typus (AMNH 12252 and AMNH F:AM 144638) because the full skull length is not preserved. The body mass estimate for AMNH 12252 should be considered a minimum estimate because the M3 is missing and, consequently, CTL (cheek-tooth length) had to be estimated in this specimen. The regressions used to estimate body mass are from Bertrand et al. (2015; Table 2). In order to obtain the degree of relative encephalization, the cranial capacity or endocranial volume (mm³) was converted to brain mass (g) by dividing the endocranial volume by 1.05 (Hofman, 1983; Falk, 2007); the published EQs of apatemyids and plesiadapiforms had to be recalculated to be comparable to those calculated for I. typus and S. carolinensis because they were originally calculated based on volume (Silcox et al., 2009, 2010a, 2011). The encephalization quotient was determined for each specimen based on three different equations. The EQ was first calculated using Jerison’s original (1973) equation. However, this formulation has one major problem. In the equation \( E_i = 0.12(BM)^{0.67} \) (where BM = body mass), the intercept (0.12), based on scaling relationships in modern mammals, is too high for small mammals such as the majority of rodent species. Eisenberg (1981) took this factor into consideration and his equation \( E_i = 0.0553(BM)^{0.74} \) better encapsulates most of the body mass variation in Rodentia. However, the slope (0.74) is too steep for the relationship between brain and body mass in rodents specifically, and this results in overestimating the EQ of small species and underestimating the EQ of large species. Pilleri et al. (1984) proposed another equation adapted specifically.

One additional natural endocast of Ischyromys was used for comparison (Fig. 8B). This specimen is documented by a drawing in Wood (1937), identified as Ischyromys sp. (A. E. Wood no. 221) from the Oligocene of the White River Group. Unfortunately, this specimen could not be found, and Wood (1937) did not provide information on the locality from which it was discovered. He also does not specify whether or not any other elements were associated with it, making it impossible to assess its specific identity.

Linear measurements of the endocasts (excepting the endocast illustrated by Wood, 1937) are presented in Tables 1 and S1 based on the dimensions illustrated in Figure 9. The measurements of ROMV 1007, AMNH 12252, AMNN F:AM 144638, and AMNH 258346 were made using Avizo 6.2.0 software (Visualization and Sciences Group, 1995—2010). In order to obtain the volume of the virtual endocast, a surface rendering was generated using unconstrained smoothing. Following Macrini et al. (2006), volumes were also calculated for specific anatomical portions of the endocast. The volume of the olfactory bulbs was obtained by isolating those structures and cropping out the rest of the endocast using the module ‘volume edit’ in Avizo 7.0.0. Both paraflocculi were resegmented on the XZ dimensions using a distinct labelfield module, then a surface rendering was generated for both the endocast and the paraflocculi. The surface area of the neocortex for each specimen was also calculated from the surface rendering of the full endocast in Avizo 7.0.0 software (Visualization and Sciences Group, 1995—2011). The neocortical surface area was estimated by selecting the area above the orbitotemporal canal and excluding the circular fissure and the confluence of sinuses. Three different ways of obtaining the neocortical surface area are included. First, the whole neocortical surface area was selected and the superior sagittal sinus was included (NS; Table 1). Second, the superior sagittal sinus was excluded from the surface area (NS2; Table 1; following Orliac et al., 2014). Third, only one side of the neocortex (the most complete hemisphere) was selected, the superior sagittal sinus was excluded, and the area of the hemisphere was doubled (NS1 x 2; Table 1; following Jerison, 2012; Long et al., 2015).

FIGURE 4. Virtual endocasts of A, I. typus (ROMV 1007); B, I. typus (AMNH F:AM 144638); and C, Sciurus carolinensis (AMNH 258346) inside a translucent rendering of the cranium, in right lateral view. Scale bar equals 10 mm.
FIGURE 5. Virtual rendering of a surface scan of the natural endocast of *I. typus* (AMNH 12252) in A, dorsal; B, ventral; C, right lateral; and D, left lateral views. Scale bar equals 10 mm.
FIGURE 6. Virtual rendering of a partial natural endocast of *I. typus* (AMNH F: AM 144638) in A, dorsal; B, ventral; C, right lateral; and D, left lateral views. Scale bar equals 10 mm.
to rodents with $E_q = 0.0997 \text{(BM)}^{0.6419}$. This equation has a slope that is substantively lower but a slightly higher intercept compared with the equation of Eisenberg (1981). In spite of these issues, it remains standard practice to report EQs based on both Jerison’s and Eisenberg’s equations to allow for comparison with other publications (e.g., Silcox et al., 2009, 2010a, 2011). The equations produced by Jerison (1973) and Eisenberg (1981) will be used to compare the EQs of our specimens with those calculated for members of other mammalian orders. Values for all three equations were calculated for the fossil endocasts and

FIGURE 7. Virtual endocast of *Sciurus carolinensis* (AMNH 258346) in A, dorsal; B, ventral; C, right lateral; and D, left lateral views. Scale bar equals 10 mm.
are included in Table 2. The EQ values for AMNH 12252 should be treated as estimates because of the uncertainty in the body mass and endocranial volume estimates.

Individual ratios between body mass and the different volumes obtained for the olfactory bulbs, paraflocculi, and endocast were calculated. The different volumes were converted to grams by dividing the endocranial volume by 1.05 and dividing by 1000 to convert them to cm³ (see Table 1).

No other linear measurement data are available for fossil or extant rodent endocasts; however, data on other early eutherians have been published, which allow for comparison with the rodent endocasts described in this paper. Gingerich and Gunnell (2005) published a reconstructed endocast of *Plesiadapis cooki*. Silcox and colleagues (2009, 2010a) provided data for two other endocasts of plesiadapiform primates (*Microsyops annectens*, *Ignacius graybullianus*). In 2011, Silcox et al. described the first virtual endocast of another plesiadapiform primate, *Plesiadapis tricuspidens*. Apatemyidae were recovered as the sister taxon to *Rhombomylos* by Silcox et al. (2010b), but this node was poorly supported, so Apatemyidae could alternatively be a primitive member of Euarchontoglires. These taxa help to provide a comparative context for the rodent endocasts described in this paper, and to provide some indication of what might be primitive for the larger taxonomic group to which rodents belong.

### Descriptions and Comparisons

#### Olfactory Bulbs

The olfactory bulbs account for 18% (ROMV 1007; AMNH F: AM 144836) and 15.2% (AMNH 12252) of the total endocast length (Table 1) in the various specimens of *Ischyromys typus*. The proportion is slightly lower in the specimen of *Sciurus carolinensis* (AMNH 258346), with the olfactory bulbs accounting for 14.7% of endocast length. The olfactory bulbs are longer in plesiadapiforms and apatemyids than in rodents. Indeed, they are between 19.4% (*Microsyops annectens*, UW 12352) and 23.8% (*Plesiadapis cookei*) in stem primates and correspond to 31% of the total length of the endocast in *Labidolemur kayi* (Table S1). Concerning the width of the olfactory bulbs, rodents (e.g., 30.2%, ROMV 1007; 37.42%, *S. carolinensis*) and *Labidolemur kayi* (31%) have a higher proportion for the relative width of the olfactory bulbs (OW/CRMW; Tables 1 and S1) compared with plesiadapiform Primates (e.g., 20.2%, *I. graybullianus*).

The olfactory bulbs account for 3.23% of the overall volume of the endocast in ROMV 1007, 3.68% in AMNH 12252, and 3.15% in AMNH F:AM 144836 (Table 1). The olfactory bulbs are similar in volume in *S. carolinensis* (AMNH 258346), accounting for 3.18% of the volume of the total endocast. The only other quantitative data on relative olfactory bulb size available for living rodents comes from Pirlot and Kamiya (1982), who estimated the volume of the olfactory bulbs for two sciuromorph taxa. The proportion for the olfactory bulbs is lower in those taxa compared with our specimen of *S. carolinensis* and represent 2.7% in *Glaucousmys* and 2.1% in *Iomys* (Tables 1 and S1). The olfactory bulbs of plesiadapiform primates generally account for about 5% of total endocast volume (4.9%, *Plesiadapis tricuspidens*; 5.53%, *Ignacius graybullianus*; 5.1%, *Microsyops annectens*; Silcox et al., 2009, 2010a; Orliac et al., 2014; Table S1), which is higher than for known Oligocene and extant rodents. In contrast, *Labidolemur* has larger olfactory bulbs, which represent approximately 13% of the total volume of the endocast (Silcox et al., 2011). The volume of the olfactory bulbs was also considered in relation to total body mass, representing a larger proportion in living rodents (0.04%, *S. carolinensis* AMNH 258346 and *Iomys*; Pirlot and Kamiya, 1982) compared with *I. typus* (0.01–0.02%; Tables 1 and S1).

Concerning the position of the olfactory bulbs, in *I. typus* (ROMV 1007; AMNH F:AM 144836) and *S. carolinensis* (AMNH 258346), they are located above the M1 (Fig. 4). This position differs from that observed in stem primates. For example, in the virtual endocast of *Microsyops annectens*, the olfactory bulbs are near the M3 (Silcox et al., 2010a). This difference is likely due to the presence of a long diastema in rodents that affects the position of the cheek-tooth row, so that the molars are more posteriorly positioned relative to the endocranial cavity.

#### Cerebrum and Midbrain

The virtual endocast ROMV 1007 has a longer circular fissure compared with AMNH 12252 and AMNH F:AM 144836 (Figs. 3, 5, 6). This could be due to the expansion of the cerebrum at the level of the circular fissure in AMNH 12252 and AMNH F:AM 144836 but not in ROMV 1007, or could reflect differences in preservation. The olfactory bulbs are not covered by the frontal lobes.
in any specimen of I. typus, meaning that only a limited expansion of the cerebellum rostrally is present in this early rodent. Uncovered olfactory bulbs also occur in *Rhombomylus turpanensis* and other Tertiary rodent natural endocasts such as *Pseudomys hians* (Scott and Osborn, 1890), *Adelomys vaillanti*, and *Treichomys bonduelli* (Dechaseaux, 1958). This observation has been made for plesiadapiforms as well (Silcox et al., 2009, 2010a; Orliac et al., 2014), and several Tertiary rodents (e.g., *Adelomys vaillanti*, *Pseudocylindrodon texanus* (Scott and Osborn, 1887, 1890; Dechaseaux, 1958; Wood, 1962, 1974; Meng et al., 2003; Silcox et al., 2009, 2010a; 2011). Additionnally, the cerebrum does not fully cover the midbrain in any of the fossils of *Ischyromys* described here, similar to the condition in other Tertiary rodents (Scott and Osborn, 1887, 1890; Dechaseaux, 1958; Wood, 1962, 1974), plesiadapiforms (Gingerich and Gunnell, 2005; Silcox et al., 2009, 2010a), and *R. turpae-*

### TABLE 1. Linear measurements, volumes, and surface areas for the different endocasts of *Ischyromys typus* (ROMV 1007; AMNH 12252; AMNH F: AM) and *Sciurus carolinensis* (AMNH 258346).

| Parameter | Abbreviation | Ischyromys typus ROMV 1007 | Ischyromys typus AMNH 12252 | Ischyromys typus AMNH F:AM | Sciurus carolinensis AMNH 258346 |
|-----------|--------------|---------------------------|---------------------------|---------------------------|-------------------------------|
| Measurements (mm) | | | | | |
| Total endocast length | TL | 40.55 | 39.51 | 40.43 | 36.91 |
| Olfactory bulbs length | OL | 2.74 | 5.99 | 7.14 | 5.41 |
| Olfactory bulbs width | OW | 7.12 | 7.29 | 7.73 | 9.77 |
| Olfactory bulbs height | OH | 5.75 | 6.43 | 6.72 | 7.87 |
| Cerebral maximal length | CRM | 20.96 | 18.77 | 20.43 | 26.80 |
| Cerebral maximal width | CRM | 23.58 | 20.06 | 23.72 | 26.11 |
| Cerebral maximal height | CRMH | 13.98 | 13.29 | 14.23 | 18.22 |
| Cerebellum width (without paraflocculi) | CLW | 19.98 | — | 21.44 | 19.90 |
| Cerebellum maximal length | CLML | 9.36 | 9.02 | 11.22 | 4.67 |
| Ratios linear measurements (%) | | | | | |
| OL/TL | 17.85 | 15.16 | 17.66 | 14.66 |
| CRML/TL | 51.69 | 47.51 | 50.53 | 72.61 |
| CLML/TL | 23.08 | 22.83 | 27.75 | 12.65 |
| CLW/CRMW | 35.64 | — | 36.05 | 49.10 |
| OL/CRMH | 60.43 | 45.07 | 50.18 | 29.69 |
| Surface areas (mm²) and volumes (mm³) | | | | | |
| Total endocast surface area | TS | 2727.54 | 3105.22 | 2673.32 | 2720.59 |
| Surface of the olfactory bulbs | OS | 176.40 | 188.82 | 206.49 | 193.01 |
| Total surface area without the olfactory bulbs | TS × OS | 2551.15 | 2916.39 | 2466.83 | 2527.58 |
| Neocortical surface area (all) | NS | 578.69 | 615.73 | 625.75 | 990.64 |
| Neocortical surface area (both sides) | NS2 | 560.58 | 597.95 | 609.84 | 969.85 |
| Neocortical surface area (one side doubled) | NS × 2 | 577.77 | 572.78 | 615.72 | 963.48 |
| Total endocast volume | TV | 5578.07 | 5934.55 | 7276.91 | 8052.59 |
| Olfactory bulbs volume | OV | 180.09 | 214.86 | 229.12 | 255.92 |
| Paraflocculus volume (right) | PVR | 45.57 | — | 57.28 | 81.91 |
| Paraflocculus volume (left) | PVL | 45.55 | — | 59.30 | 81.35 |
| Paraflocculus volume (both sides) | PV2 | 91.12 | — | 116.58 | 163.26 |
| Ratios surface areas and volumes (%) | | | | | |
| NS/TS | 21.22 | 19.83 | 23.41 | 36.41 |
| NS2/TS | 20.55 | 19.26 | 22.81 | 35.65 |
| NS1 × 2/TS | 21.18 | 18.45 | 23.03 | 35.41 |
| NS1 × 2/(TS − OS) | 22.65 | 19.64 | 24.96 | 38.12 |
| OV/TV | 3.23 | 3.68 | 3.15 | 3.18 |
| PV2/TV | 1.63 | — | 1.60 | 2.03 |
| Ratios body mass (g) | | | | | |
| (((OV/1.05)/1000)/(BM) × 100 | 0.01 | 0.02 | 0.02 | 0.04 |
| (((TV/1.05)/1000)/(BM) × 100 | 0.38 | 0.52 | 0.62 | 1.29 |
| (((PV2/1.05)/1000)/(BM) × 100 | 0.01 | — | 0.01 | 0.03 |

Ratios based on the endocranial measurements are also presented in the table. Check-tooth area was used to estimate body mass. The total endocast surface area and total endocast volume of AMNH 12252 are estimated values (see Table S2). Abbreviation: BM, body mass.
The development of neocortical sulci has been shown to be related to the size of the brain, which is generally lissencephalic in species with brain weights of less than 5 g (Macrini et al., 2007a). Because the volume of the brain in _Ischyromys typus_ is just over 5 cm³ (ROMV 1007; Table 1) and over 7 cm³ (AMNH F: AM 144836; Table 1), it might be expected to exhibit some infolding, but the only indication of a neocortical sulcus is a weakly developed lateral sulcus in _I. typus_ (Figs. 3A, 5A, 6A). Similarly sized early Tertiary primates, including plesiadapiforms, have more marked sulci (see Silcox et al., 2010a; Orliac et al., 2014). The sylvian sulcus is a distinctive feature of the cerebrum in most Euprimates (but see Gazin, 1965), separating the frontal from the temporal lobe (Radinsky, 1970; Gurche, 1982; Martin, 1990), which is distinguishable in the largest living rodent, the capybara (Hydrochaeris hydrochaeris; Campos and Welker, 1976). A sylvian fossa is visible in _Ignacius graybullianus_, but a clear sulcus is not developed (Silcox et al., 2009), which is also true of _S. carolinensis_ (AMNH 258346; Fig. 7). The sulcus and fossa are both missing in _Microsyops annectens_ (Silcox et al., 2010a), _Plesiadapis tricuspidensis_ (Orliac et al., 2014), _Rhombomylus turpanensis_ (Meng et al., 2003), and _Ischyromys typus_ (ROMV 1007, AMNH 12252, and AMNH F: AM 144836). This suggests that the sylvian sulcus developed independently in Primates and Rodentia.

With respect to the cerebrum, the rhinal fissure, marking the separation between the paleocortex and the neocortex, is a key landmark, because it provides information on the degree of development of the latter (Jerison, 2012; Long et al., 2015). The orbitotemporal canal has been interpreted as representing a landmark for the rhinal fissure in fossils (Gurche, 1982; Novacek, 1982; Martin, 1990; Silcox et al., 2009, 2010a, 2011). The orbitotemporal canal can be visualized in three endocasts of _Ischyromys typus_ (ROMV 1007, Fig. 3; AMNH 12252, Fig. 5; AMNH F:AM 144836, Fig. 6), in which it clearly occupies a more dorsal position compared with _S. carolinensis_ (Fig. 7). Although obviously more data for both living and fossil rodents are needed, this contrast is suggestive of an expansion in the neocortex through time in rodents, as seen in primates (Jerison, 2012; Long et al., 2015). The position of this feature in _I. typus_ is similar to that described in other early Tertiary euarchontoglians in which it can be observed (i.e., _Microsyops annectens, Ignacius graybullianus, Labidolemur kawai, Plesiadapis tricuspidensis_; Silcox et al., 2009, 2010a, 2011; Orliac et al., 2014). In order to confirm these morphological interpretations, the neocortical surface area ratio using NSF (Neocortical surface area of the most complete hemisphere; Table 1) was calculated. Following Jerison (2012; see also Long et al., 2015), the ratio was also calculated without the olfactory bulbs (Tables 1 and S1). No neocortical surface areas have been published for rodents; consequently, the comparisons are made with other known Euarchontoglires with published data. The neocortical surface areas for _M. annectens_ (21.3%), _Ignacius graybullianus_ (USNM 421608, 19.7%; UF 26000, 21.4%), and _Plesiadapis tricuspidensis_ (19.9%) are in the range of the values found for _I. typus_ (ROMV 1007, 21.2%; AMNH 12252, 18.5%) and with AMNH F:AM 144836 (23.0%) having a slightly higher value. Our results also show that _S. carolinensis_ (AMNH 258346) has a higher proportion of the endocast devoted to the neocortex (35.4%) compared with _Ischyromys typus_.

**Cerebellum**

This region can be visualized most clearly in ROMV 1007 and AMNH F:AM 144836, because there are the only specimens of _Ischyromys typus_ that preserve both paraflocculi (AMNH 12252 only preserves one paraflocculus). As noted above, the cerebrum does not overlap onto the cerebellum, so the dorsal surface of the cerebellum is entirely exposed on the endocast (Figs. 3A, 5A, 6A), exhibiting a vermis that is clearly separated from the lateral lobes by paramedian fissures (see also Figs. 3, 5, 6, 8A), and rounded paraflocculi that are located at the level of the vermis. The cerebellum of _I. typus_ (e.g., ROMV 1007 and AMNH 12252) represents 23% of the total length of the endocast compared with a value of 17% for _Plesiadapis tricuspidensis_, calculated based on the reported measurements (Orliac et al., 2014: table 1)—however, damage to the caudal aspect of the cerebellum in the latter (i.e., see Orliac et al., 2014: fig. 2) makes it unclear to what degree this contrast is real. Other plesiadapiforms in which the proportions can be estimated ( _Microsyops annectens_, _Ignacius graybullianus_) exhibit higher values (29% and 30.5%, respectively, based on estimates in Orliac et al., 2014:table 1) than both _Ischyromys typus_ and _Plesiadapis tricuspidens_. It is difficult to assess the size of the cerebellum more generally, because it is often covered in whole or in part by the cerebrum (e.g., _Sciurus carolinensis_). So, for example, the cerebellum only accounts for 13% of the length of the endocast in _Sciurus carolinensis_ (Table 1), but this value is certainly an underestimate of its actual length because this part of the brain is partially covered by the cerebrum. We suspect that cranial flexure is not contributing significantly to the overlap of the cerebellum by the cerebrum because the specimens described have unflexed crania. Instead, expansion of the cerebrum onto the cerebellum is likely responsible for the observed overlap. Comparing widths of the cerebellum is also challenging because it is unclear what is appropriate as a standard of comparison. In the current study, total cerebellar width was calculated excluding the paraflocculi (see Fig. 9; Table 1). The cerebellum is wider than the cerebrum in _I. typus_ (ROMV 1007 and AMNH F:AM 144836) compared with _S. carolinensis_ (CLW/CRMW; Table 1); however, this may stem from relative expansion of the cerebrum in the latter rather than any kind of absolute decrease in the size of this region through time. More meaningful comparisons can be made for the paraflocculi specifically, because their volume can be calculated from the virtual data. The percentage of parafloccular volume relative to the volume of the total endocast is lower in _Ischyromys typus_ (1.60%, AMNH F:AM 144836; 1.63%, ROMV 1007) compared with _Sciurus carolinensis_ (2.03%; Table 1). Because the cerebrum in _S. carolinensis_ is clearly expanded (i.e., because it covers the midbrain and overlaps onto the cerebellum), this implies that the paraflocculi account for an even larger percentage of the non-cerebral part of the brain. The larger size of the paraflocculi relative to total body mass in _S. carolinensis_ (0.03%) than in _I. typus_ (0.01%) also suggests some expansion of this region of the brain through time (Table 1). The paraflocculi play a role in eye movement control (Rambold et al., 2002). This function may have been enhanced in squirrels such as _S. carolinensis_, suggesting a change in the relative importance of this sensory modality. However, more data are required to put this into a larger comparative context.

**Brainstem and Cranial Nerves**

The hypophyseal fossa for the pituitary gland is not visible in two specimens of _I. typus_, ROMV 1007 (Fig. 3B) and AMNH 12252 (Fig. 5B), in contrast to AMNH F:AM 144836 (Fig. 6B) and _S. carolinensis_ (AMNH 258346; Fig. 7B). This disparity likely stems from the presence of a complex of veins obscuring the relevant area in ROMV 1007 (Fig. 3B). There is no trace of this complex of veins in AMNH 12252.

Various casts of the openings for the cranial nerves can be seen on the ventral surface of ROMV 1007, AMNH 12252, and AMNH F:AM 144836 (Figs. 3B, 5B, 6B). The casts of the optic foramina for the optic nerves are visible in ROMV 1007 and AMNH F:AM 144836, whereas they are broken in AMNH 12252, but their roots are still visible. According to Wahlert
(1974), the foramen rotundum is confluent with the sphenobital fissure in most rodents. This condition is primitive for eutherians (Novacek, 1986) and is exhibited by many other mammalian orders (e.g., dermopterans, chiropterans, carnivores; see Novacek, 1986). Casts of the foramen rotundum (V2) and sphenobital fissure (passage for the ophthalmic veins, cranial nerves III, IV, V1, and VI) are distally separated and then fused rostrally in S. carolinensis (Fig. 7B). In contrast, I. typus (ROMV 1007 and AMNH F:AM 144836) lacks the foramen rotundum and in this regard is more similar to Ignacius graybullianus (Silcox et al., 2009:fig. 3B) and Pleiadapis tricuspidens (Orliac et al., 2014: fig. 2B). Consequently, the ophthalmalic veins and cranial nerves III, IV, V1, V2, and VI would have gone through the sphenobital fissure in I. typus ROMV 1007 and AMNH F:AM 144836 (Figs. 3B, 6B). Neither the sphenobital fissure nor the foramen rotundum is preserved in AMNH 12252 (Fig. 5B). According to Wahlert (1974), the mandibular nerve (V3) passes through the foramen ovale and then bends laterally and goes through the foramen ovale accessorius in Ischyromys. When looking at the computed tomography (CT) data of ROMV 1007 and AMNH F:AM 144836, the foramen ovale accessorius is not traceable, which suggests that our specimens lack this foramen or the quality of preservation does not allow for its identification. Nevertheless, ROMV 1007 and AMNH F:AM 144836 have a foramen ovale and V3 probably left the endocranial cavity by this foramen (Figs. 3B, 6B), which is also the case for pleiadapiforms (Silcox et al., 2009, 2010a; Orliac et al., 2014) and Labidolemur kayi (Silcox et al., 2011). In the specimen of S. carolinensis (AMNH 258346), the exit of the mandibular nerve V3 can also be identified. According to Wahlert (1974), two branches of V3 (the buccinator and masseteric nerves) exit the cranium by way of a united foramen in Marmota monax (MCZ B9911). The united cast of the foramen for the branches of V3 is present in S. carolinensis AMNH 258346 (Fig. 7B) but not in I. typus ROMV 1007 or AMNH F:AM 144836 (Figs. 3B, 6B).

Casts of the internal auditory meatus, with passageways for cranial nerves VII (facial) and VIII (vestibulocochlear), are visible on both sides of ROMV 1007 and AMNH F:AM 144836 (Figs. 3, 6). They have the same position in Ischyromys typus (Figs. 3B, 6B), S. carolinensis (Fig. 7B), I. graybullianus (Silcox et al., 2009:fig. 3B), M. annectens (Silcox et al., 2010a:fig. 3B), P. tricuspidens (Orliac et al., 2014:fig. 2C), and L. kayi (Silcox et al., 2011:fig. 3B), located rostral to the paraflocculi. A cast of the jugular foramen, where the internal jugular vein and cranial nerves IX, X, and XI ran, is positioned ventral to the caudal end of the paraflocculi in ROMV 1007 and AMNH F:AM 144836 (Figs. 3, 6), in a position similar to that observed in S. carolinensis (Fig. 7), M. annectens, I. graybullianus, P. tricuspidens, and L. kayi (Silcox et al., 2009, 2010a, 2011; Orliac et al., 2014). Finally, in ROMV 1007 and AMNH F:AM 144836, the casts of two hypoglossal foramina are present on the brainstem (see Figs. 3B, 6B), which is similar to the condition described by Wahlert (1974) for another specimen of Ischyromys typus (CM 1123). This contrasts with the single opening in S. carolinensis (Fig. 7B) and in other early Tertiary euarchontoglians (Bloch and Silcox, 2006; Silcox et al., 2009, 2010a, 2011; Orliac et al., 2014).

Blood Vessels

The superior sagittal sinus is visible in AMNH 12252, A. E. Wood no. 221, ROMV 1007, and AMNH F: AM 144836 (Figs. 3A, 5A, 6A, 8), similar to M. annectens, I. graybullianus, P. tricuspidens, and L. kayi (Silcox 2009, 2010a, 2011; Orliac et al., 2014). In contrast, the superior sagittal sinus is less marked rostrally and not visible caudally in S. carolinensis (AMNH 258346; Fig. 7). This suggests that this sinus would have been located deep in the meninges (Macrini et al., 2007a). The intracranial dural sinus system of I. typus is typical of therian mammals (as described by Wible and Rougier, 2000). The superior sagittal sinus is continuous with the transverse and sigmoid sinuses; those sinuses are then continuous with the jugular foramen in the rodents (Figs. 3A, 5A, 6A, 7A), plesiadapiforms, and aptemyids (Silcox 2009, 2010a, 2011; Orliac et al., 2014). The jugular foramen is continuous with the cast of the inferior petrosal sinus in ROMV 1007, AMNH 12252, AMNH F:AM 144836 (Figs. 3B, 5B, 6B), and S. carolinensis (Fig. 7B). This sinus is not well marked as in I. graybullianus (Silcox, 2009:fig. 3B) and is not preserved in P. tricuspidens or L. kayi (Silcox et al., 2011; Orliac et al., 2014), but is well defined in the virtual endocast of M. annectens (Silcox et al., 2010a:fig. 3B). The postgonial foramen transmits the postgonial vein that branched off the external jugular vein (Novacek, 1986; Meng et al., 2003). The cast of the postgonial vein is identifiable in ROMV 1007 and AMNH F: AM 144836 (Figs. 3D, 6C) and has the same position as in S. carolinensis (Fig. 7C), plesiadapiforms, and L. kayi (Silcox et al., 2009, 2010a, 2011; Orliac et al., 2014). Finally, a cast of a vein continuous with the postgonial vein and the orbitotemporal canal that may be identified as an extension of the external jugular vein is visible on ROMV 1007 (Fig. 3D), AMNH F:AM 144836 (Fig. 6C), and S. carolinensis (Fig. 7B).

According to Wible (1987), the alisphenoid canal transmits the ramus infraorbitalis of the stapedial artery into the cranial cavity toward the sphenobital fissure in rodents. In ROMV 1007 and AMNH F:AM 144836, the alisphenoid canal is visible and merges with the sphenobital fissure (Figs. 3B, 6B). The transverse canal transmits veins that connect the two internal maxillary veins in Ischyromys (Wahlert, 1974). In ROMV 1007, the transverse canal enters the sphenoidal fissure medially from the alisphenoid canal (Fig. 3B); this contrasts with the condition in S. carolinensis (Fig. 7B). The transverse canal is not preserved in AMNH 12252 and AMNH F:AM 144836 (Figs. 5B, 6B). According to Wahlert (1974), Ischyromys lacks a stapedial foramen, which contrasts with Sciurus, which possesses a stapedial artery that branches off the internal carotid artery (Bugge, 1985).

Indeed, in ROMV 1007 and AMNH F:AM 144836, the cast of the stapedial artery is absent but is identifiable in S. carolinensis AMNH 258346 (Fig. 7D), as in L. kayi (Silcox et al., 2011: fig. 3B). This means that in Ischyromys typus, the irrigation of the rami infra- and supraorbitalis was presumably supplied by anastomosis arising from the external carotid artery as seen in Aploclonius (Bugge, 1985) and/or the internal carotid artery (Wahlert, 1974). The course of the internal carotid artery is visible in ROMV 1007 and AMNH F:AM 144638 where the vessel enters the endocranial cavity (Figs. 3B, 6B). In contrast, aptemyids (L. kayi; Silcox et al., 2011) and Microsyops present the primitive condition and have a promontorial artery visible on the surface of the endocast (Silcox et al., 2010a, 2011). Finally, modern sciurid rodents such as S. carolinensis do not have a promontorial artery (Wible, 1984; Wible et al., 2005), and the internal carotid is not present on the surface of the endocast of this specimen.

Brain Size and Encephalization Quotient

Endocranial volume can be measured for three specimens of Ischyromys typus (ROMV 1007 = 5.6 cc; AMNH 12252 = 5.8 cc; AMNH F:AM 144836 = 7.3 cc; Table 1). Body mass was estimated using skull length and cheek-tooth area, because they are the measures that give the best estimation for body mass in fossil rodents (Bertrand et al., 2015). The results are presented in Table 2. Using an estimate of body mass based on cheek-tooth area, ROMV 1007 has an EQ of 0.51, AMNH 12252 one of 0.62, and AMNH F:AM 144836 one of 0.77, based on the rodent-specific equation from Pilleri et al. (1984). They are markedly lower than our estimate for S. carolinensis using the same equation and cheek-tooth area
were available. (27 species); and Castorimorpha (33 species). The number of different rodent suborders is presented in Table S3. Each rodent body masses from the literature with species belonging to different rodents (>2640 specimens) with associated brain and cranial dimensions rather than cheek-tooth area). In spite of being notably younger, Ischyromys typus (ROMV 1007) is in the range of the fossil plesiadapiforms Microsyops annectens (middle Eocene) and Ignacius graybullianus (early Eocene) but has a higher EQ compared with Plesiadapis cookei and P. tricuspidens (both Paleocene; see Table 2) when comparing their EQ calculated using cranial length to estimate body mass.

DISCUSSION

Encephalization Quotient Evolution

Jerison (1973) suggested that mammalian groups generally show an increase in brain size through time, an idea that has been assessed in a number of mammalian groups (e.g., Perissodactyla [Radinsky, 1976]; Primates [e.g., Gurche, 1982; Silcox et al., 2010a]; Artiodactyla [Orliac and Gilissen, 2012]; Chiroptera [Yao et al., 2012]). However, the presence or absence of such a pattern has never been assessed for rodents, because of a

TABLE 3. Means of the encephalization quotients for the different rodent suborders (classification based on Wilson and Reeder, 2005).

| Suborder              | EQ Jerison (1973) | EQ Eisenberg (1981) | EQ Pilleri et al. (1984) |
|-----------------------|-------------------|---------------------|--------------------------|
| Myomorpha             | 0.59              | 0.97                | 0.80                     |
| Castorimorpha         | 0.57              | 0.82                | 0.82                     |
| Hystricomorpha        | 0.70              | 0.89                | 1.05                     |
| Sciuromorpha          | 0.87              | 1.27                | 1.22                     |

Three different formulae are used to estimate EQ (Jerison, 1973; Eisenberg, 1981; Pilleri et al., 1984). Individual EQ values are presented in Table S2.
lack of relevant data from fossil members of the order. Assessing the presence or absence of a temporal effect on brain size in Rodentia also requires an understanding of the range and pattern of relative brain size variation in living members of the order. Variations in EQ exist between the different suborders of living rodents (Table 3; Pilleri et al., 1984). For instance, the average EQ values for Myomorpha and Castorimorpha are below 1.0, whereas those for Hystrixcomorpha and Sciuromorpha are above 1.0 (assessed using the equation for EQ from Pilleri et al., 1984). Looking at the suborders individually, Myomorpha has the lowest and Sciuromorpha the highest EQ (Table 3).

Interestingly, the Oligocene *Ischyromys typus* has a higher EQ compared with some living forms belonging to the suborders Castorimorpha (*e.g.*, *Thomomys bottae*) and Myomorpha (*e.g.*, *Malacothrix typicus*). Each of those extant groups typically have an EQ below 0.50 (Table S3). If EQ increased through time for Rodentia as an Order, it is not clear why the Oligocene *I. typus* has a higher EQ compared with those extant taxa. However, because *I. typus* is considered to be only distantly related to those suborders, it is unclear to what extent this constitutes a relevant comparison—perhaps their ancestors had even smaller brains. Compared with the more closely related sciuriform rodents, two specimens of *Ischyromys typus* (*ROMV 1007* and *AMNH 12252*) have a lower EQ than found in living members of that suborder. Even though *AMNH F:AM 144836* has a higher EQ than some extant sciuriform individuals, this specimen is still at the very low end of the range of EQ variation for this suborder. More data are required to fully understand why EQ varies among rodents, but these data are suggestive of some temporal component to this variation.

Besides increase in EQ occurring through time, differences in the timing of the increase in brain size have also been observed between groups. Primates have a progressive increase in relative brain size, with living species having higher EQs compared with Oligocene taxa (Radinsky, 1974; Simons, 1993), which have higher values compared with Eocene Euprimates, which generally have higher EQs than Paleocene-Eocene fossil stem Primates (*plesiadapiforms*; Radinsky, 1977; Jerison, 1979; Gurche, 1982; Gingerich and Gunnell, 2005; Silcox et al., 2009, 2010a; Orliac et al., 2014). Artiodactyls are similar because they also exhibit an increase in EQ, but it happened later in time, during the Pliocene-Pleistocene (Orliac and Gilissen, 2012). In Perissodactyla, EQ increases between the Eocene and Oligocene epochs (Radinsky, 1976), earlier than the observed increases in EQ in artiodactyls (Orliac and Gilissen, 2012). Finally, bats show an increase in EQ between the Oligocene and Miocene epochs (Yao et al., 2012). The increase in EQ can also vary its intensity. Shultz and Dunbar (2010) showed that a general relative brain size increase occurred through time in many mammalian orders, but variation from small to large changes can be observed. For example, Primates and Artiodactyls both experienced increase in relative brain size, but the changes were more marked in Primates (Shultz and Dunbar, 2010). There is less evidence for decreases in EQ within mammalian orders. According to Finarell and Flynn (2009), EQ decreases in carnivores in response to reduced predation (Palombo et al., 2007) or domestication (Kruska, 1988). They suggested that brain volume may decrease when cognitive demands are minimized. Because the EQ of *Ischyromys* is low compared with that calculated for most sciuriforms, time could be a factor, but obviously more data are needed for both earlier and later fossil rodents to ascertain whether Oligocene *Ischyromys* had a large (or small) brain relative to the ancestral condition, and when the increase in brain size evident in most living sciuriforms occurred.

Other factors could potentially influence brain size changes. Ecological factors may also have an impact on brain size variation in Rodentia (*e.g.*, Mace et al., 1981; Pilleri et al., 1984). Indeed, social behavior, locomotion, and activity period may influence EQ (Pilleri et al., 1984). According to Pilleri et al. (1984), rodents with higher EQ are arboreal, taxa with medium EQ are terrestrial or semiaquatic, whereas fossorial species have a lower EQ. Indeed, the fossorial species *Malacothrix typicus* has the lowest EQ and the arboreal *Tamiasciurus hudsonicus* the highest EQ in our sample (see Table S3). Concerning *Ischyromys* typus, this species has been considered terrestrial (Bertrand et al., 2015) to fossorial (Wood, 1937). Even for a terrestrial rodent, *I. typus* has an EQ at or below the range documented for extant Sciuromorpha exhibiting similar locomotor habits (*e.g.*, *Aplodontia rufa, Marmota marmota*; Table S3). This may indicate that in mammals such as rodents that are extremely diverse taxonomically and ecologically, temporal effects may be tempered by ecological factors in mediating variation in EQ.

### Brain Size in Rodentia in the Context of Euarchontoglires

Knowing how relative brain size changed through time in each mammalian order is critical to understanding the primitive condition for the common ancestor of Euarchontoglires. Non-primate euarchontan groups (Dermoptera or Scandentia) are not known from preserved cranial fossil material, limiting the usefulness of these orders for establishing what is primitive for Euarchontoglires. To date, the only available EQ data for fossil Euarchontoglires belong to Primates and Apatemyidae (Gurche, 1982; Martin, 1990; Gingerich and Gunnell, 2005; Koenigswald et al., 2009; Silcox et al., 2009, 2010a, 2011; Orliac et al., 2014). Because Rodentia has the best fossil record available for any members of Euarchontoglires (including Lagomorpha), this group is then extremely relevant to investigating character polarity in the clade. *Ischyromys* typus has an EQ in the range of Eocene plesiadapiforms but higher than Paleocene primates and *Labidolemur* (see Table 2). However, it is worth noting that it postdates all of these taxa. In terms of more temporally relevant comparisons, the omomyoid primate *Rooneyvia viejaensis* (TMM 40688-7) from the early Oligocene has a higher EQ (0.81 [Gurche, 1982] or 1.07, calculated using the data from Kirk et al., 2014) compared with *I. typus* (0.35–0.53; Table 2) using Jerison’s calculation. Furthermore, the encephalization quotients for two early anthropoid primates also from the Oligocene have been calculated. *Aegyptopithecus zeuxis* (CGM 40237) and *Parapithecus grangeri* (DPC 18651) have EQs of 0.75 and 0.91, respectively (Bush et al., 2004; Martin 1990) using Jerison’s equation, so those early anthropoids also have a higher EQ compared with *I. typus* from the same epoch. Therefore, Oligocene omomyoid and anthropoid primates already had a larger brain relative to their body mass compared with rodents of that epoch. This suggests that if brain size increase occurred in Rodentia (or even just in Sciuromorpha), it was delayed in comparison with Primates. To the extent that these data are relevant for estimating what was primitive for Euarchontoglires, and therefore for rodents, it appears as though little brain size change occurred in the early evolution of Rodentia. Nevertheless, more data from fossil rodents of the Eocene epoch are necessary to see if brain size increased (or decreased) between the Eocene and the Oligocene.

### Change in the Relative Proportions of Parts of the Brain through Time

The EQ offers only a coarse indication of the relative size of the brain. In order to put those data into a more biologically meaningful context, differences in the proportional sizes of the various functional components of the brain can be considered, to the extent that is possible from endocasts. For example, compared with body mass, olfactory bulb size may have remained stable during the early radiation of Primates and some other parts of the brain (*i.e.*, neocortex) may have increased in proportion in early Euprimates (Martin, 1990; Silcox et al., 2010a, 2011;
Long et al., 2015). Consequently, high EQ may be mainly due to the expansion of the neocortex in living Primates. In rodents, neocortical surface area accounts for a larger proportion relative to the total surface area in the endocast of *S. carolinensis* compared with *I. typus*, suggesting that neocortical expansion also occurred at some point in rodent (or at least sciuromorph) evolution after the Oligocene. Knowing that *I. typus*, *M. annectens*, *I. graybullianus*, and *P. tricuspidens* have a similar proportion of neocortical surface area relative to total endocast surface area suggests that neocortical expansion probably happened independently in Primates and Rodentia. The high EQ of *S. carolinensis* is actually due to both neocortical and parafloccular expansion. The paraflocculi and the neocortex represent a higher percentage of the brain compared with those of *I. typus* (ROMV 1007; AMNH F: AM 144836), meaning that both of those structures are enlarged compared with the other parts of the brain. This is also reflected in the fact that they represent a higher percentage of brain mass relative to body mass in *S. carolinensis* (see Table 1).

Concerning the condition for the common ancestor of rodents, the ubiquity of exposure of the midbrain in early euarchontogliresans as well as in the Oligocene *I. typus* suggests that this is likely to be the primitive condition for the group. *Rhombomylus turpanensis* (Eocene Glires) had a very broadly exposed midbrain (see Meng et al., 2003:fig. 50) compared with all known Tertiary rodent endocasts (see Scott and Osborn, 1887, 1890; Dechaseaux, 1958; Wood, 1962, 1974; Figs. 3, 5, 6). This may suggest that a first neocortical expansion occurred at the base of Rodentia (i.e., after *Rhombomylus*), with another expansion taking place in more recent groups such as Sciuromophra.

Within Euarchontoglires, midbrain coverage by the cerebrum is absent in primitive members of both Primates and Rodentia, and this feature seems to vary in the brain of living rodents (see Brauer and Schober, 1970). Unfortunately, apart from the endocast of *S. carolinensis* documented here, no endocasts of extant rodents have been published. As shown by Macrini et al. (2007b), there may be a discrepancy between the external morphology of the brain and the form of the endocast in this region, so it remains unclear to what extent the inferior colliculi are visible on the endocast versus the brain in living rodents. Nevertheless, the brains of living primates are similar to those of some extant rodents in which the cerebrum not only covers the midbrain but overlaps to some degree onto the cerebellum, suggesting that expansion of the cerebrum happened independently in the two orders. The Oligocene rodent *I. typus* had a similar position for the orbitotemporal canal compared with other primitive euarchontogliresans, and the expansion in neocortex size in rodents probably occurred later than the Oligocene. Because Eocene Euprimates already show a more ventrally located orbital bar; Silcox et al., 2010a), this suggests that neocortical increase was initiated earlier in Primates than in Rodentia. More data are needed from both modern and fossil taxa to characterize the nature and timing of this process (Bertrand et al., 2016).

The percentage of olfactory bulb volume relative to total endocranial volume for *I. typus* (ROMV 1007 and AMNH F: AM 144836) is similar to that of *S. carolinensis*, but the only two other extant taxa for which data are known (Glaucomys and Iomys; Pirlot and Kamiya, 1982) both have a lower percentage of olfactory bulb volume. More data are needed to fully understand changes in olfactory bulb size through time in Rodentia, and how this pattern relates to other euarchontogliresans. The contrast in size between the larger olfactory bulbs in *Labidolemur kayi* and plesiadapiforms with the relatively smaller bulbs in Oligocene rodents suggests that some reduction in this part of the brain may have occurred early in rodent evolution, but data are needed for more primitive rodents to determine the pattern of change in the group.

### Vision and Arboreality in Euarchontoglires

The neocortex is where the integration of sensory and motor information takes place (Martin, 1990). It would be ideal to be able to look at functional areas within the context of the neocortex to determine which parts of the neocortex have expanded. Krubitzer et al. (2011) built a map of the neocortex in different rodents, including *Sciuurus carolinensis*. One aspect of their work was to compare arboreal and terrestrial habits in different rodent species. For example, in arboreal squirrels (*S. carolinensis*), additional visual fields have developed relatively the neocortex compared with subterranean species (*Heterocephalus glaber*) (Krubitzer et al., 2011). However, no identifiable anatomical landmarks separating these functional areas are visible on the endocranial surface. One indicator that has been interpreted as relevant in determining changes in functional areas is the degree of caudal expansion of the neocortex, where the visual processing areas are located. For instance, plesiadapiform primates lack this caudal expansion (*I. graybullianus*, *M. elegans*, *M. annectens* UW 14559, *P. cookei*, and *P. tricuspidens*; Gingerich and Gunnell, 2005; Silcox et al., 2009, 2010a; Oriolà et al., 2014), which has been interpreted as indicating that visual specialization had not yet developed in stem forms (but see Silcox et al., 2010a). In contrast, in arboreal squirrels (*S. carolinensis*), there is a greater level of coverage of the midbrain by the neocortex, reflecting expansion in the number of their visual fields. This view has been supported by the lack of other traits related to vision (e.g., postorbital bar; Silcox et al., 2010a). Interestingly, this is true of forms that were arboreal, contradicting the idea that improvements to vision and conversion in size increase occurred with the initial transition to arboreality in primates (Falk, 2007).

The contrast between *S. carolinensis*, an arboreal taxon, and the semi-fossil or terrestrial fossil species *I. typus* in the caudal extent of the cerebrum could in part relate to the development of arboreal habits in the evolution of the former, particularly because EQ is related to arboreality in rodents (Pil-leri et al., 1984). In order to test this hypothesis, the ideal approach would be to look at arboreal fossil rodents. Unfortunately, no well-preserved cranium of a specimen associated with postcranial evidence that indicate arboreality has yet been described. Another approach would be to compare *S. carolinensis* with extant semi-fossil taxa to examine variation in neocortical coverage. Indeed, many semi-fossil myomorphs (e.g., Acidomys cahuitensis, Microtus americana, and Crinicus crinitus; Christensen and Evans, 1979) have a relatively lower EQ (<0.75; Pil-leri et al.’s equation) and lack caudal expansion of the neocortex (see Brauer and Schober, 1970). This means that variation in neocortical expansion in rodents might be linked to habitats as well as to temporal effects. However, it is worth noting that the brain of extant semi-fossil taxa also have exposed inferior colliculi. Unfortunately, this feature cannot be verified on endocasts because they have not been described for those species yet. Christensen and Evans (1979) have described the inferior colliculi as being associated with acoustic reflexes. Edinger (1964) cautioned against viewing exposed inferior colliculi as a primitive trait and has suggested that ‘extensive’ midbrain exposure (with visible inferior colliculi) could be a derived feature linked to increase in auditory acuity (Wood, 1974). As seen in two of the endocasts of *Ischyromys typus* (AMNH F: AM 144638) and *Ischyromys* sp. (A. E. Wood no. 221; Wood, 1937), the inferior colliculi are exposed. Although this may reflect a lack of neocortical expansion, it is also possible that the colliculi are visible because this particular part of the brain is enlarged. Strong acoustic reflexes may be critical in semi-fossil species, for instance, to avoid predators or when visibility is reduced in burrows (Begall et al., 2007). Tenrecemorpha (tenrecs) living in subterranean environments or exhibiting nocturnal habits echorlocate (Gould, 1965) and have exposed inferior colliculi.
the increase started earlier and was ultimately more pronounced in Primates. However, in light of the low EQs in some rodent suborders (e.g., Myomorpha; see Fig. 10), not all rodent clades may have experienced significant brain size increase through time. Fossil specimens for a wider diversity of rodents will be needed to assess the full pattern.

Another factor playing a role in EQ variation is locomotor habit. Pilleri et al. (1984) found that arboreal squirrels have a higher EQ compared with terrestrial rodents belonging to the same suborder. Consequently, arboreality might be linked to high EQ in Sciuromorpha—this contrasts with the situation in primates in which arboreality preceded significant brain size increase (Silcox et al., 2009, 2010a). The inferred terrestrial (Bertrand et al., 2015) or semi-fossorial (Wood, 1937) habits of Ischyromys typus may also partly explain its relatively low EQ.

Concerning the neocortex, Oligocene rodents have similar features seen in Paleocene and Eocene stem primates but are different from Eocene and Oligocene euprimates that already have expanded neocortices. The midbrain is exposed in all stem primates as well as in Rhombomylus, early rodents, and the most primitive apatemyids, suggesting that this condition is primitive. However, interpreting the exposure of the midbrain is complicated. Expansion of the neocortex to cover the midbrain may reflect specializations in neocortical functions such as vision. However, it may also be the case that the midbrain is exposed because the inferior colliculi are expanded. Those structures are also observable in semi-fossorial rodents (Brauer and Schober, 1970), which may reflect auditory specialization. In Ischyromys typus, the small relative area of the neocortex compared with the one modern sciuromorph for which there are relevant data (Sciurus carolinensis) would suggest that its exposed midbrain was reflective of a lack of neocortical expansion. However, if _I_. _typus_ was semi-fossorial, it is also possible that the emergence of the inferior colliculi in some specimens represents a degree of specialization of those structures.

Ultimately, the first virtual endocast of a fossil rodent, _Ischyromys typus_, sheds light on rodent brain evolution by providing the first quantitative data for any relatively primitive member of the order, allowing for preliminary ideas about the pattern of evolution of the size and form of the brain in rodents. In light of the excellent fossil record for rodents, future work documenting endocranial form in other members of the order will allow for testing of these ideas and for refinements to our understanding of the pattern of change through time in this very diverse clade.

ACKNOWLEDGMENTS

We thank the Paleontology departments of the Royal Ontario Museum (ROM) and the American Museum of Natural History (AMNH) for providing access to the specimens to be scanned. We also thank the Shared Materials Instrumentation Facility (SMIF) at Duke University as well as the AMNH microscopy and imaging facility for scanning the specimens. We also thank E. Charles for the segmentation of _Sciurus carolinensis_, E. Westwig and J. Galkin for their help in the AMNH collections, and K. Seymour in the ROM collections. We thank T. E. Macrini and M. Orlac for their useful feedback and suggestions. This research was supported by an NSERC Discovery Grant to M.T. S., and an AMNH Collection Study Grant and Pilot Research Funding from the Department of Anthropology of the University of Toronto to O.C.B.

LITERATURE CITED

Anderson, D. 2008. Ischyromyidae; pp. 311–325 in C. M. Janis, G. F. Gunnell, and M. D. Uhen (eds.), Evolution of Tertiary Mammals of North America, Volume 2, Small Mammals, Xenarthrans, and Marine Mammals. Cambridge University Press, Cambridge, UK.
Armstrong, S. D., J. I. Bloch, P. Houde, and M. T. Silcox. 2011. Cochlear labyrinth volume in euarchontoglires: implications for the evolution of hearing in Primates. Anatomical Record 294:263–266.

Begall, S., H. Burda, and C. E. Schleich (eds.). 2007. Subterranean Rodents: News from Underground. Springer, Heidelberg, Germany.

Bertrand, O. C., F. Amarod-Mughal, and M. T. Silcox. 2016. Virtual endocasts of Eocene Paramys (Paramyinae): oldest endocast record for Rodentia and early brain evolution in Euarchontoglires. Proceedings of the Royal Society B: Biological Sciences 283:20152316.

Bertrand, O. C., M. A. Schillaci, and M. T. Silcox. 2015. Cranial dimensions as estimators of body mass and locomotor habits in extant and fossil rodents. Journal of Vertebrate Paleontology, e1014905, doi: 10.1080/02724634.2015.1014905.

Blanga-Kanfi, S., H. Miranda, O. Penn, T. Pupko, R. W. DeBry, and D. Huchon. 2009. Rodent phylogeny revised: analysis of six nuclear genes from all major rodent clades. BMC Evolutionary Biology 9(71).

Bloch, J. I., and M. T. Silcox. 2006. Cranial anatomy of Paleocene “plesiapiadiform” Carpolesistes simpsoni (Mammalia, Primates) using ultra high-resolution X-ray computed tomography, and the relationships of Carpolesistiforms to Euprimates. Journal of Human Evolution 51:3–35.

Boyer, D. M. S. Kaufman, G. F. Gunnell, A. L. Rosenberger, and E. Delson. 2014. Managing 3D digital data sets of morphology: morphosource is a new project-based data archiving and distribution tool. American Journal of Physical Anthropology 153(Supplement):34.

Brauer, K., and W. Schober. 1970. Katalog der Säugetiergehirne. Catalogue of Mammalian Brains. Gustav Fischer Verlag, Jena, Germany 40 pp.

Bugge, J. 1985. Systematic value of the carotid arterial pattern in rodents; pp. 355–379 in W. P. Luckett and J.-L. Hartenberger (eds.), Evolutionary Relationships among Rodents, A Multidisciplinary Approach. Plenum Press, New York, New York.

Bush, E. C., E. L. Simons, D. J. Dubowitz, J. M. Allman. 2004. Endocranial volume and optic foramen size in Parapithecus granger: pp. 603–614 in C. F. Ross and R. F. Kay (eds.), Anthropoid Origins: New Visions. Kluwer, Boston, Massachusetts.

Campos, G. B., and W. I. Welker. 1976. Comparisons between brains of a large and a small hystricomorph rodent: capybara, Hydrochaeris and guinea pig, Cavia—neocortical projection regions and measurements of brain subdivisions. Brain, Behavior and Evolution 13:243–266.

Cork, S. J., and G. J. Kenagy. 1989. Nutritional value of hypogeous fun-}

Carnivora. Proceedings of the National Academy of Sciences 106:9345–9349.

Flynn, L. J., L. L. Jacobs, and I. U. Cheema. 1986. Baluchimyinae, a new cetadactyloid rodent subfamily from the Miocene of Baluchistan. American Museum Novitates 2841:1–58.

Gazin, C. L. 1965. An endocast cranial of the Bridger middle Eocene primate Smilodectes gracilis. Smithsonian Miscellaneous Collections 149:1–14.

Gingerich, P. D., and G. F. Gunnell. 2005. Brain of Plesiadapis cookei (Mammalia, Primate: Cercopithecidae) and comparison with the brains of the same: a modern synthesis of cortical organization. Brain, Behavior and Evolution 122:102–117.

Huchon, D., O. Madsen, M. J. J. B. Sibbald, K. Ament, M. Sanhope, F. Catzzells, W. W. de Jong, and E. J. P. Douzery. 2002. Rodent phylogeny and a timescale for the evolution of Gliridae: evidence from an extensive taxon sampling using three nuclear genes. Molecular Biology and Evolution 19:1053–1065.

Janis, C. M., G. F. Gunnell, and M. D. Uhen (eds.). 2008. Evolution of Tertiary Mammals of North America, Volume 2, Small Mammals, Xenarthrans, and Marine Mammals. Cambridge University Press, Cambridge, UK., 802 pp.

Jernigan, H. J. 1973. Evolution of the Brain and Intelligence. Academic Press, New York, New York, 482 pp.

Jernigan, H. J. 1979. Brain, body and encephalization in early primates. Journal of Human Evolution 8:615–635.

Jernigan, H. J. 2012. Digitized fossil brains: neocorticalization. Biolin- gualis 6:383–392.

Kirk, E. C., P. Daghighi, T. E. Macrini, B.-A. S. Bhullar, and T. B. Rowe. 2014. Cranial anatomy of the Duchesnean primate, Parapithecus granger, a Colhuehuapian erethi- zontid rodent from the Miocene of Buenos Aires, Argentina. American Journal of Physical Anthropology 153:88–118.

Kruska, D. C. T. 1988. Mammalian domestication and its effect on brain size. Indian Journal of Experimental Biology 26:1315–1326.

Kruiska, D. C. T. 1988. Evidence for echolocation in the Tenrecidae of Mad-agascar. C. R. Acad. Sc. Paris 306:417–420.

Kuenen, L. J., L. L. Jacobs, and I. U. Cheema. 1986. Baluchimyinae, a new cetadactyloid rodent subfamily from the Miocene of Baluchistan. American Museum Novitates 2841:1–58.

Landry, S. O., Jr. 1970. The Rodentia as omnivores. Quarterly Review of Biology 45:351–372.

Lavocat, R. 1973. Les rongeurs du Miocène d’Afrique Orientale. Mio- cène inférieur. Mémoires et Travaux de L’Institut de Montpel-lier de l’école Pratique des Hautes Etudes 1:1–284.
Lewis, W. B. 1882. On the comparative structure of the brain in rodents. Philosophical Transactions of the Royal Society of London 173:699–746.

Li, C.-K., R. W. Wilson, M. R. Dawson, and L. Krishntalka. 1987. The origin of rodents and lagomorphs; pp. 97–108 in H. H. Genoways (ed.), Current Mammalogy. Plenum Press, New York, New York.

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis, Volume 1: Regnum Animale. Editio decima, reformata. Laurentii Salvii, Stockholm, Sweden, 824 pp.

Long, A., J. I. Bloch, and M. T. Silcox. 2015. Quantification of neocortical ratios in stem primates. American Journal of Physical Anthropology 157:337–373.

Mace, G. M., P. H. Harvey, and T. H. Clutton-Brock. 1981. Brain size and ecology in small mammals. Journal of Zoology 193:333–354.

Macrini, T. E., G. W. Rougier, and T. Rowe. 2007a. Description of a cranial endocast from the fossil mammal Vencelettes neuguenianus (Theriiformes) and its relevance to the evolution of endocranial characters in therians. Anatomical Record 290:875–892.

Macrini, T. E., T. Rowe, and M. Archer. 2006. Description of a cranial endocast from a fossil platypus, Obothrodon dicksoni (Monotremata, Ornithorhynchidae), and the relevance of endocranial characters to monotreme monophyly. Journal of Morphology 267:1000–1015.

Macrini, T. E., T. Rowe, and J. L. VandeBerg. 2007b. Cranial endocasts from a growth series of Monodelphis domestica (Didelphidae, Marsupialia): a study of individual and ontogenetic variation. Journal of Morphology 268:844–865.

Mann, G. 1895. Homoplasy of the brain of rodents, insectivores, and carnivores. Journal of Anatomy and Physiology 30(5):1–36.

Marrivaux, L., M. Vianey-Liaud, and J.-J. Jaeger. 2004. High-level phylogeny of early Tertiary rodents: dental evidence. Zoological Journal of the Linnean Society 142:105–134.

Martin, R. D. 1990. Primate Origins and Evolution: A Phylogenetic Reconstruction. Chapman and Hall, London, U.K., 804 pp.

Matthew, W. D. 1910. On the osteology and relationships of Paramys and the affinities of the Ischyromyidae. Bulletin of the American Museum of Natural History 183(1):1–112.

Meng, J. 1990. The auditory region of Reithroparamys delicatissimus (Mammalia, Rodentia) and its systematic implications. American Museum Novitates 2972:1–35.

Meng, J. 2004. Phylogeny and divergence of basal Gliridae. Bulletin of the American Museum of Natural History 285:93–109.

Meng, J., Y. Hu, and C. Li. 2003. The osteology of Rhombomys (Mammalia, Gliridae) implicates for phylogeny and evolution. Bulletin of the American Museum of Natural History 275:1–247.

Murphy, W. J., E. Eizirik, W. E. Johnsson, Y. P. Zhang, O. A. Ryder, and S. J. O’Brien. 2001. Molecular phylogenetics and the origins of placental mammals. Nature 409:614–618.

Nikitenko, M. F. 1966. On the brain structure of the beaver in relation to physiological and psychological life and evolution. Zoologicheski Zhurnal 45:261–274.

Novacek, M. J. 1982. The brain of Leptictis dakotensis, an Oligocene leporid, Eutheria, Mammalia, from North America. Journal of Paleontology 56:1177–1186.

Novacek, M. J. 1986. The skull of Myotragus balearicus (Artiodactyla, Mammalia, Primates) and brain evolution in Mediterranean Islands. Quaternary International 160:186–193.

Pilleri, G. 1959a. Beitrag zur vergleichenden Morphologie des Nagetiergehirnes. L. Beitrag: Sciuromorpha. Acta Anatomica, Suplementum 38:1–42.

Pilleri, G. 1960a. Zentralnervensystem, Körporgange und stammesgeschichtliche Verwandtschaft der Aplodontia rufa Rafinesques (Rodentia, Aplodontioidea). Acta Anatomica, Suplementum 41:5–35.

Pilleri, G. 1960b. Vergleichend-morphologische Untersuchungen über das Zentralnervensystem nearktischer Sciuromorpha und Bemerkung zum Problem Hirnform und Taxonomie. Acta Anatomica 11:26–68.

Pilleri, G. 1961. Das Gehirn der Macrotarsomyss (Rodentia, Nesomyinae). Revue Suisse de Zoologie 68:433–442.

Pilleri, G. 1963. Über das Gehirn von Castor fiber und vergleichend-anatomische Betrachtungen mit dem Gehirn von Castor canadensis (Rodentia). Journal für Hirnforschung 6:55–70.

Pilleri, G. M. Gibr, and C. Kraus. 1984. Cephalization in rodents with particular reference to the Canadian beaver (Castor canadensis); pp. 11–12 in G. Pilleri (ed.), Investigations on Beavers. Brain Anatomy Institute, Berne, Switzerland.

Pirlot, P., and T. Kamiya. 1982. Relative size of brain and brain components in three gliding placentals (Dermoptera; Rodentia). Canadian Journal of Zoology 60:565–572.

Pizzimenti, J. J., and R. Salle. 1980. Dietary and morphometric variation in some Peruvian rodent communities: the effect of feeding strategy on evolution. Biological Journal of the Linnean Society 13:263–285.

Poux, C., P. Chevret, D. Huchon, W. W. de Jong, and E. J. P. Douzery. 2006. Arrival and diversification of caviomorph rodents and platyrhine primates in South America. Systematic Biology 55:229–244.

Prothero, D. R., and R. J. Ermy. 2004. The Chadronian, Orellan, and Whitneyan North American Land Mammal Ages; pp. 156–168 in M. O. Woodburne (ed.), Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology. Columbia University Press, New York, New York.

Radinsky, L. B. 1970. The fossil evidence of prosimian brain evolution; pp. 209–224 in C. R. Novack and W. Montagna (eds.), The Primate Brain: Advances in Primatology, Volume 1. Appleton Century Crofts, New York, New York.

Radinsky, L. B. 1974. The fossil evidence of anthropoid brain evolution. American Journal of Physical Anthropology 41:15–28.

Radinsky, L. B. 1976. Oldest horse brains: more advanced than previously realized. Science 194:626–627.

Radinsky, L. B. 1977. Early primate brains: facts and fiction. Journal of Human Evolution 6:79–86.

Rambold, H., A. Churchill, Y. Selig, L. Jasmin, and S. G. Lisberger. 2002. Partial ablation of the flocculus and ventral paraflocculus in monkeys cause linked deficits in smooth pursuit eye movements and adaptive modification of the VOR. Journal of Neurophysiology 87:912–924.

Rasband, W. S. 1997–2014. ImageJ. U.S. National Institutes of Health, Bethesda, Maryland. Available at http://imagej.nih.gov/ij/. Accessed June 10, 2013.

Sacher, G. A., and E. F. Staffeldt. 1974. Relation of gestation time to brain weight for placental mammals: implications for the theory of vertebrate growth. American Naturalist 108:593–615.

Scott, W. B., and H. F. Osborn. 1887. Preliminary report on the vertebrate fossils of the Uinta formation, collected by the Princeton Expedition of 1886. Proceedings of the American Philosophical Society 24:255–264.

Scott, W. B., and H. F. Osborn. 1890. The Mammalia of the Uinta formation. Transactions of the American Philosophical Society 16:461–572.

Silcox, M. T., A. E. Benham, and J. I. Bloch. 2010a. Endocasts of Microsyops (Microsyopidae, Primates) and the evolution of the brain in primitive primates. Journal of Human Evolution 58:505–521.

Silcox, M. T., C. K. Dalmy, and J. I. Bloch. 2009. Virtual endocast of Ignacinus graywallibullians (Palaeomyidae, Primates) and brain evolution in early Primates. Proceedings of the National Academy of Sciences of the United States of America 106:10987–10992.

Silcox, M. T., J. I. Bloch, D. M. Boyer, and P. Houde. 2010b. Cranial anatomy of Palaeocene and Eocene Labidolemur kayi (Mammalia: Apatotheria) and the relationships of the Apatemyidae to other mammals. Zoological Journal of the Linnean Society 160:773–825.

Silcox, M. T., C. K. Dalmy, A. Hrenchuk, J. I. Bloch, D. M. Boyer, and P. Houde. 2011. Endocranial morphology of Labidolemur kayi (Apatemyidae, Apatotheria) and its relevance to the study of brain evolution in Euarichtognires. Journal of Vertebrate Paleontology 31:1314–1325.
Simons, E. L. 1993. New endocasts of *Aegyptopithecus*: oldest well-preserved record of the brain in Anthropoidea. American Journal of Science 293:383–390.

Shultz, S., and R. Dunbar. 2010. Encephalization is not a universal macroevolutionary phenomenon in mammals but is associated with sociality. Proceedings of the National Academy of Sciences 107:21582–21586.

Springer, M. S., M. J. Stanhope, O. Madsen, and W. W. de Jong. 2004. Molecules consolidate the placental mammal tree. Trends in Ecology and Evolution 19:430–438.

Stephan H., G. Baron, and H. D. Frahm. 1991. Insectivora: With a Stereotaxic Atlas of the Hedgehog Brain. Comparative Brain Research in Mammals, Volume I. Springer, New York, New York, 573 pp.

Visualization Sciences Group. 1995–2010. Avizo/6.2.0. Konrad-Zuse-Zentrum für Informationstechnik, Berlin, Germany.

Visualization Sciences Group. 1995–2011. Avizo/7.0.0. Konrad-Zuse-Zentrum für Informationstechnik, Berlin, Germany.

Wahlert, J. H. 1974. The cranial foramina of protrogomorphous rodents; an anatomical and phylogenetic study. Bulletin of the Museum of Comparative Zoology 146:363–410.

Wible, J. R. 1984. The ontogeny and phylogeny of the mammalian cranial arterial pattern. Ph.D. dissertation, Duke University, Durham, North Carolina, 704 pp.

Wible, J. R. 1987. The eutherian stapedial artery: character analysis and implications for superordinal relationships. Zoological Journal of the Linnean Society 91:107–135.

Wible, J. R., and G. W. Rougier. 2000. Cranial anatomy of *Kryptobaatar dashevegi* (Mammalia, Multituberculata), and its bearing on the evolution of mammalian characters. Bulletin of the American Museum of Natural History 247:1–120.

Wible, J. R., Y. Wang, C. Li, and M. R. Dawson. 2005. Cranial anatomy and relationships of a new ctenodactyloid (Mammalia, Rodentia) from the early Eocene of Hubei Province, China. Annals of Carnegie Museum 74:91–150.

Wilson, D. E., and D. M. Reeder (eds.). 2005. Mammal Species of the World: A Taxonomic and Geographic Reference, third edition. John Hopkins University Press, Baltimore, Maryland, 2122 pp.

Wilson, R. W. 1949. Additional Eocene rodent material from Southern California. Carnegie Institute of Washington Publication 584:1–25.

Wood, A. E. 1937. The mammalian fauna of the White River Oligocene. Part II. Rodentia. Transactions of the American Philosophical Society 28:157–269.

Wood, A. E. 1959. Eocene radiation and phylogeny of the rodents. Evolution 13:354–361.

Wood, A. E. 1962. The early Tertiary rodents of the family Paramyidae. Transactions of the American Philosophical Society 52(1):1–261.

Wood, A. E. 1974. Early Tertiary vertebrate faunas Vieja Group Trans-Pecos Texas: Rodentia. Bulletin of the Texas Memorial Museum 21:1–112.

Yao, L., J. P. Brown, M. Stampanoni, F. Marone, K. Isler, and R. D. Martin. 2012. Evolutionary change in the brain size of bats. Brain, Behavior and Evolution 80:15–25.

Submitted May 26, 2015; revisions received August 23, 2015; accepted September 11, 2015.

Handling editor: Guillermo Rougier.