Endocranial morphology of Labidolemur kayi (Apatemyidae, Apatotheria) and its relevance to the study of brain evolution in Euarchontoglires

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ENDOCRANIAL MORPHOLOGY OF LABIDOLEMUR KAYI (APATEMYIDAE, APATOTHERIA) AND ITS RELEVANCE TO THE STUDY OF BRAIN EVOLUTION IN EUARCHONTOGRISES

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ABSTRACT—Apatemyids are known from the Paleocene and Eocene of Europe, and the Paleocene to Oligocene of North America. We describe a new species, Labidolemur kayi, from the late Eocene of France. This new species exhibits a suite of dental and cranial features that suggest it had a diet similar to modern insectivores. The results of this study support previous suggestions that apatemyids are more closely related to modern Euarchontoglires than to other mammals such as Paleoryctidae. The cranial capacity of L. kayi is estimated at 0.5–0.6 cc, yielding an encephalization quotient (EQ) of 0.23–0.28 or 0.42–0.50 depending on the equation used. These values are much lower than estimates for C. sigei, suggesting significant increase occurred in brain size in Apatemyidae, perhaps related to elaborations in the family’s specialized manual extractive feeding regime. Similarities with primitive primates in EQ and the inferred position of the rhinal sulus may allow for inferences about encephalization and neocorticalization in the common ancestor of Euarchontoglires.
the potential relevance of \textit{L. kayi} and the later more dentally derived
native volume through comparisons between
generation of a set of estimates of volume for com-
tal or cranial specimens to generate an estimate (Gingerich and
Armstrong et al., 2011) derived from multiple postcranial ele-
ulated skeleton that allows for an estimate of body mass (74 g; 
data (microCT). One of these (USNM 530221) is part of an artic-
tial endocasts using high-resolution X-ray computed tomography
(USNM 530221, 530208) that are complete enough to yield par-
L. kayi
morphic morphology for Apatemyidae. 
of the group, so it may not form an accurate representation of the
tains to a relatively late occurring and dentally derived member
accurate because the cranium is almost entirely uncompressed. 
This specimen yielded a volume estimate that is likely to be very
rites du Quercy” (late Eocene, France; Koenigswald et al., 2009). The only endocranial
produced an excellent endocast, it was unfortunately lost by the
United States Postal Service in 1976 (W. E. Joyce, personal com-
munication as cited in Silcox et al., 2010b). The only endocranial
were made to a reconstruction of the endocast of
USNM 530208 is broken into rostral and caudal pieces (see
Silcox et al., 2010b:fig. 3). Only the caudal portion was
silcox et al., 2010b), including two
a nearly complete, articulated skeleton with a skull and dentaries
from UM locality SC-26 (Houde site 14), Clarks Fork Basin, 
northeastern Wyoming, Willwood Formation, early Wasatchian, 
lowermost \textit{Cardiolophus radinskyi} interval zone, early Eocene 
(between 54.92 and 54.70 Ma); and (2) USNM 530208, an associ-
ated rostrum and basiranium from UM locality SC-62 (Block 
Z), Clarks Fork Basin, northwestern Wyoming, lower Willwood 
Formation, middle Clarkforkian, uppermost \textit{Plesiadapis cookei}
range zone, late Paleocene (between 55.68 and 55.36 Ma; see 
Gingerich, 2003, for age model). Although the skull of USNM 530221 
is somewhat crushed, it preserves the rostral portion of the en-
docranial cavity fairly completely. While USNM 530208 is much 
less complete, its caudal portion is very well preserved, allowing 
for fine resolution of endocranial details.
Both specimens were prepared by P.H. by acid-etching them 
out of limestone. The limestone was dissolved by submersion 
in dilute, buffered 7% acetic acid for 2 days at a time. To pro-
tect fossils from acid-etching, a thin coating of PVA (polyvinyl 
acetate) was applied to the surface of all exposed bones. This 
mode of preparation is responsible in part for the fine surface 
detail on the virtual endocast of USNM 530208, because 
this specimen was almost entirely free of matrix. Comparisons 
were made to hemi-endocasts of \textit{Tupaia}, \textit{Sciurus}, and \textit{Saimiri}
(Carolina Biological Supply, Bobbitt Laboratory) housed in the 
University of Winnipeg Anthropology Museum. Comparisons 
were also made to \textit{Tupaia} and \textit{Sciurus}
were made to multiple postcranial elements, an approach that may be preferable to using only den-
tal or cranial specimens to generate an estimate (Gingerich and 
Gunnell, 2005). Together these specimens permit a fairly com-
plete characterization of the endocranial morphology of \textit{L. kayi}, 
and for the development of a set of estimates of volume for com-
posite endocasts produced using different assumption sets.
The aims of this study are twofold. First, we seek to consider 
evolutionary change in apatemyid endocranial anatomy and rel-
ative volume through comparisons between \textit{L. kayi}, the most 
primitive and oldest apatemyid for which an endocast is known, 
and the later more dentally derived \textit{C. sigei}. Second, we consider 
the potential relevance of \textit{L. kayi} to reconstructing primitive en-
docranial morphology for Apatemyidae, Euarchontoglires, and 
Primates.

\textbf{Institutional Abbreviations—UM, University of Michigan Mu-
seum of Paleontology, Ann Arbor, Michigan; USNM, Department of Paleobiology, National Museum of Natural History, 
Smithsonian Institution, Washington, D.C.}

\section*{MATERIALS AND METHODS}

Two specimens were analyzed in detail in this study (see Silcox 
et al., 2010b, for detailed cranial descriptions): (1) USNM 530221, 
a nearly complete, articulated skeleton with a skull and dentaries
within the \textit{Apatemyidae}, \textit{Euarchontoglires}, and \textit{Primates}.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure1.png}
\caption{Hypothesis of relationships including \textit{Labidolemur kayi}, 
based on an analysis of 240 cranial, dental, and postcranial traits 
(Silcox et al., 2010b). Note that although the most parsimonious 
tree included a relationship between apatemyids and the basal member 
of Glires, \textit{Rhombobynthus turpensis}, this node was not well supported and 
a sister-group relationship with Euarchonta would require only five additional steps.}
\end{figure}
0.033 mm, the interslice distance was 0.036 mm, and the data set consisted of 361 images.

The images were initially cropped using crop16bit, a DOS program written by Nathan Jeffrey (University of Liverpool), to remove blank areas. The slices containing the braincase were manually segmented in ImageJ (Rasband, 1997–2008). In other words, the area that the brain would have occupied was filled with pure white to allow it to be selected independently of the specimen. When pieces of bone were missing, a straight line was drawn between the preserved edges. The segmented slices were loaded into ImageJ as an Image Sequence; the stack was converted to 8-bit, and was then loaded in Amira 3.1.1 (Visage Imaging). A labelfield module was attached, and using the Image Segmentation Editor each slice of the endocast was labeled. A surfacegen module was attached to the labels file and used to produce the surface rendering of the endocasts (Fig. 2A, D).

For USNM 530221, a portion of the skull is out of anatomical position on the left side; this was shifted into place using manual registration via landmarks. Two approaches were taken in Amira 3.1.1 to form a composite reconstruction. Both depend on selecting landmarks in the two surface reconstructions, and using those to allow the surfaces to be registered to one another. In the rigid warp approach, the landmarks are aligned but neither surface is altered (Fig. 2B). This has the advantage that it does not modify the original data sets, and works well when the two specimens being combined are of similar size and shape. However, in this case, USNM 530221 is clearly from a smaller individual than USNM 530208, so the composite generated using this approach is mis-proportioned, i.e., the rostral portion is too small, and the caudal portion too large. The second option, called a Bookstein warp, allows the surfaces to be registered to one another. In the rigid warp approach, the landmarks are aligned but neither surface is altered (Fig. 2B). This has the advantage that it does not modify the original data sets, and works well when the two specimens being combined are of similar size and shape. However, in this case, USNM 530221 is clearly from a smaller individual than USNM 530208, so the composite generated using this approach is mis-proportioned, i.e., the rostral portion is too small, and the caudal portion too large. The second option, called a Bookstein warp, allows the surfaces to be registered to one another. In this case, USNM 530208 was resized and warped to fit with USNM 530221.

The latter specimen was used as the reference because a reliable body mass estimate based on multiple postcranial elements was possible. The resulting composite (Fig. 2C) does not appear to be obviously mis-proportioned, and is probably a closer representation of the original size of the endocast of USNM 530221 than the composites produced using the rigid warp algorithm. The disadvantage to the technique is that details visible in the unaltered virtual endocast of USNM 530208 are lost in the process of combining the two reconstructions. For this reason, the composite is used to estimate volume (Table 1) and measurements such as total length (Table 2), whereas detailed morphology is assessed from the separate endocranial data sets. Volume estimates based on all assumption sets are provided in Table 1.

Linear measurements for the composite virtual endocast listed in Table 2 were done in Amira 3.1.1, and in all cases represent maximum values for a line fitted to the external surface of the endocast. For example, the maximum width represents the length of the longest line that could be fitted to the endocast perpendicular to the main rostrocaudal axis of the endocast, as defined by the superior sagittal sinus. Because these represent maximum values, particular landmarks were not employed in taking these measurements. All graphs were produced using SPSS version 12.0 for Windows.

DESCRIPTION AND COMPARISONS

Olfactory Bulbs

Morphology of the olfactory bulbs is only observable in the virtual endocast derived from USNM 530221 (Fig. 3C, E, F). The olfactory bulbs are offset from the cerebrum by a circular fissure, but are nearly as broad caudally as the rostral end of the cerebrum, reflecting their relatively large size (Fig. 3C, E). The olfactory bulbs make up 12–15% of the total volume of the endocast, depending on the assumptions used in forming the composite (Table 1), and almost a third of the length of the composite produced using the Bookstein warp (Fig. 2C; Table 2). The volume of the olfactory bulbs relative to that of the overall endocast of Labidolemur kayi is in the range of ‘basal insectivores,’ small mammals with relatively primitive cerebral patterns (Stephan, 1972), Cretaceous eutherians such as Astoryctes, and the Oligocene leptictid Leptictis (Fig. 4). In contrast, all euarchontogliirans included in this study had relatively smaller olfactory bulbs. For example, although plesiadapiforms have relatively large olfactory bulbs for primates, the maximum percentage volume observed (5.53% for Ignacius graybullianus; Silcox et al., 2009, 2010a) is markedly lower than even the lowest estimate for L. kayi. Unfortunately quantitative data for the olfactory bulbs have not been published for two of the most relevant fossil taxa known from endocasts: the aptemeyid Carcinella sigei (Koenigswald et al., 2009) and the basal member of Glires Rhombomylus turpanensis (Meng et al., 2003). Nonetheless, it is clear that this region of the brain was also relatively voluminous in the former, based on the olfactory bulbs’ broad bases, and the fact that they account for more than a quarter of the total length of the endocast (Koenigswald et al., 2009:fig. 12). In R. turpanensis, on the other hand, the olfactory bulbs are relatively narrower, lacking the transverse expansion seen in the aptemeyids (Meng et al., 2003).
et al., 2003:fig. 50). They constitute only approximately a fifth of the total length of the endocast in *R. turpanensis*, a proportion similar to that observed for the plesiadapiforms *I. graybullianus* and *Microsyops annectens* (Silcox et al., 2009, 2010a). These observations suggest that voluminous olfactory bulbs were characteristic of apatemyids, who were distinct in this feature from euarchontoglians for which this morphology is known.

**Cerebrum**

The presence of a well-demarcated circular fissure suggests that the cerebrum would not have overlapped onto the...
TABLE 1.  Endocast and olfactory bulb volume estimates for *Labidolemur kayi* under different assumptions sets.

<table>
<thead>
<tr>
<th>Assumption set</th>
<th>Endocranial volume (mm³)</th>
<th>EQ (Jerison)</th>
<th>EQ (Eisenberg)</th>
<th>Olfactory bulb volume (mm³)</th>
<th>Olfactory bulb volume as a percentage of the total endocranial volume</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Rigid warp without altering USNM 530221</td>
<td>607.785</td>
<td>0.28</td>
<td>0.50</td>
<td>74.05</td>
<td>12.18</td>
</tr>
<tr>
<td>2. Rigid warp, with a portion of USNM 530221 shifted into anatomical position (Fig. 3B)</td>
<td>605.522</td>
<td>0.28</td>
<td>0.50</td>
<td>74.05</td>
<td>12.23</td>
</tr>
<tr>
<td>3. Composite with USNM 530208 resized but not warped, portion of USNM 530221 shifted into anatomical position</td>
<td>501.876</td>
<td>0.23</td>
<td>0.42</td>
<td>74.05</td>
<td>14.75</td>
</tr>
<tr>
<td>4. Bookstein warp of USNM 530221 and resized USNM 530208, with a portion of the former shifted into anatomical position (Fig. 3C)</td>
<td>524.127</td>
<td>0.24</td>
<td>0.43</td>
<td>68.22</td>
<td>13.02</td>
</tr>
</tbody>
</table>

*Assumption set 1 involves the least manipulation of the data, with the two endocasts being simply overlain on a series of landmarks. For set 2 a portion of the left side of the cranium that was out of place was moved into anatomical position, but neither reconstruction was resized. In set 3, USNM 530208 was resized down to fit better with USNM 530221, but no warping was imposed, whereas for set 4 a Bookstein warp was imposed to produce the best possible fit of the two surface reconstructions to one another. Encephalization Quotients (EQ) were calculated based on equations in Jerison, 1973 and Eisenberg, 1981 as indicated. An estimated body mass of 74 g (based on postcranial measurements; Armstrong et al., 2011) was used for calculating EQ.

olfactory bulbs in *L. kayi* (Fig. 3C, E). This is also true of other early Tertiary euarchontognathians, including even primitive euprimates (adapoids and omomyoids) that differ from extant euprimates in which the cerebrum does overlap onto the olfactory bulbs (Gurche, 1982; Meng et al., 2003; Silcox et al., 2009, 2010a). Both virtual endocasts of *L. kayi* show that the cerebrum had no neocortical sulci (Fig. 3A, E). Amongst modern groups, brains of less than 5 g typically do not exhibit these features (Macrini et al., 2007). Because the brain of *L. kayi* would have weighed significantly less than 5 g (see below), it would not be expected to have exhibited neocortical sulci. Notable, however, is the lack of a distinct sylvian sulcus (Fig. 3C), a feature of most living primates (except tarsiers and Daubentonia; Preuss, 2009) also present in most fossil euprimates (Le Gros Clark, 1945; Radinsky, 1967, 1970; Gurche, 1982; Martin, 1990; except Smilodectes; Gazin, 1965; see discussion in Silcox et al., 2010a), but missing in other living and fossil euarchontognathians, including *C. sigei* (see Koenigswald et al., 2009:pl. 2), *R. turpanensis* (see Meng et al., 2003;fig. 51), and all plesiadapiforms known from the relevant portion of the endocast (Silcox et al., 2009, 2010a). In contrast to all early Tertiary euprimates euprimates known from endocasts (including Smilodectes; Gazin, 1965; Silcox et al., 2010a), but in common with plesiadapiforms, *C. sigei*, *R. turpanensis*, and the Miocene rodent *Hypsosoteiromys* sp., *L. kayi* also lacks a well-developed temporal pole (Fig. 3C; D; Meng et al., 2003; Dozo et al., 2004; Koenigswald et al., 2009; Silcox et al., 2009, 2010a).

A clearly defined orbitotemporal canal (sometimes referred to as a ‘sinus canal,’ but see discussion in Wible and Gaudin, 2004; Wible, 2008) can be identified in USNM 530208 (Fig. 3D). This structure has a close relationship with the rhinal sulcus in extant lemuroiforms (Martin, 1990), and has been interpreted as a landmark for the sulcus in the endocasts of primitive primates (Gazin, 1965; Gurche, 1982; Martin, 1990; Silcox et al., 2009, 2010a), and in the Oligocene lepidiodontid *Lepticid* (Novacek, 1982). The rhinal sulcus (or fissure) is the external marker of the division between the neo- or iso-cortex and the paleocortex (Jerison, 1973, 1991), making its position a coarse indicator of the degree of neocorticalization. The orbitotemporal canal is located between a half and two thirds of the way down the lateral aspect of the cerebrum in *L. kayi* (Fig. 3D), a position broadly similar to that observed in *I. graybullianus* and *M. annectens* (Silcox et al., 2009, 2010a). This contrasts with the more dorsal position suggested for the rhinal fissure in *Plesiadapis cooki* by Gingerich and Gunnell (2005). However, the indentation that these authors identify as the rhinal fissure may in fact represent a lateral sulcus, based on the presence of a sulcus identified as such in a similar position in *M. annectens* (Silcox et al., 2010a). In contrast to that of *L. kayi* and plesiadapiforms, when it can be observed the orbitotemporal canal or rhinal sulcus is generally more ventrally located in fossil and living euprimates (e.g., see Gurche 1982:fig. 5). In many living primates the rhinal sulcus is no longer identifiable, because of overgrowth of the neocortex (Martin, 1990).

No trace of either the orbitotemporal canal or a separate sulcus is identifiable in the endocasts of either *R. turpanensis* or *C. sigei*. In the latter case, this is likely a product of the difficulty of visualizing structures on the surface of the reconstructed endocast (see Koenigswald et al., 2009:fig. 12). Meng et al. (2003) interpreted the absence of the rhinal sulcus in *R. turpanensis* as a primitive feature. However, Macrini et al. (2007) note that the rhinal sulcus may be absent on the endocast of mammals with small brains, even if the feature is present on the brain, and Silcox et al. (2010a) suggested that its absence on the endocast of *R. turpanensis* was likely a product of the poor quality of preservation of the endocast surface. Dozo et al. (2004) similarly suggested that poor preservation could explain the absence of this feature in an endocast of *Hypsosoteiromys*. The identification of the rhinal sulcus on the endocasts of Cretaceous eutherians by Kielen-Jaworowska (1984) would make it surprising if it were truly absent in *R. turpanensis*, although Macrini et al. (2007:table 3, character 6) apparently disagree with this identification. In any case, it is

TABLE 2. Measurements from the composite endocast for *Labidolemur kayi*, produced using a Bookstein Warp (assumption set 4; Fig. 2C).

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total length</td>
<td>17.51</td>
</tr>
<tr>
<td>Maximum width</td>
<td>10.47</td>
</tr>
<tr>
<td>Maximum depth</td>
<td>8.41</td>
</tr>
<tr>
<td>Olfactory bulb length</td>
<td>5.42</td>
</tr>
<tr>
<td>Olfactory bulb length/total length</td>
<td>0.31</td>
</tr>
<tr>
<td>Ratio of olfactory bulb length to the length of rest of the brain</td>
<td>1.23</td>
</tr>
<tr>
<td>Olfactory bulb width</td>
<td>3.25</td>
</tr>
<tr>
<td>Endocast width/length ratio</td>
<td>0.60</td>
</tr>
<tr>
<td>Endocast height/length ratio</td>
<td>0.48</td>
</tr>
<tr>
<td>Endocast height/width ratio</td>
<td>0.80</td>
</tr>
<tr>
<td>Right optic nerve cross-sectional area</td>
<td>0.48</td>
</tr>
<tr>
<td>Left optic nerve cross-sectional area</td>
<td>0.36</td>
</tr>
<tr>
<td>Average optic nerve cross-sectional area</td>
<td>0.42</td>
</tr>
</tbody>
</table>

Measurements in mm or mm².
FIGURE 4. Bivariate plots of ln olfactory bulb volume versus A, ln intracranial volume, and B, ln body mass for an array of living and fossil mammals. Range of values for *Labidolemur kayi* (indicated by the arrow) in A represents different assumption sets for the estimation of intracranial volume (see Table 1). Range of values presented for *Ignacius graybullianus* and *Microsyops annectens* in B reflect varying body mass estimates, including confidence intervals (Silcox et al., 2009, 2010a). Data from Stephan et al. (1970, 1981), Gurche (1982), Novacek (1982), Pirlot and Kamiya (1982), Kielan-Jaworowska (1984), Martin (1990), Silcox et al. (2009, 2010a), and the current study (see Supplementary Table 1). The lines plotted represent least squares regression lines. Designation of taxa as ‘basal’ vs. ‘progressive’ insectivores follows Stephan (1972), who indicated that the ‘basal’ forms had relatively primitive cerebral patterns, whereas the ‘progressive’ forms “reveal distinct marks of higher development” (p. 156).
not possible to compare the location of the orbitotemporal canal in *L. kayi* to any corresponding feature of the endocast of *R. turpanensis*.

**Midbrain**

The caudal end of the cerebrum is well preserved in USNM 530208 and ends too far rostrally to cover the caudal colliculi (Fig. 3A). Exposure of these midbrain structures is also observed in many early Tertiary euarchontoglians (i.e., *P. cookei, I. graybullianus, M. cf. elegans, one specimen of M. annectens, R. turpanensis; Ischyromys* sp.; Wood, 1937; Meng et al., 2003; Silcox et al., 2009, 2010a) but not in *C. sigei*, a different specimen of *M. annectens*, *Megadellhus lundeliusi*, the fossil rodent described by Moodie (1922; species unknown), or any known euprimate (Szalay, 1969; Koenigswald et al., 2009, 2010a). This suggests that exposed caudal colliculi might have been primitive for Euarchontoglires (also supported by their exposure in Cretaceous eutherians including *Asioryctes*, *Kielan-Jaworowska*, 1984), with expansion of the cerebrum caudally to cover them occurring independently within Apatemyidae, Glires, Microsyopidae, and Euprimates. Exposure of the midbrain also occurs in living dermopterans, but this has been argued to be a product of an expansion of the colliculi, rather than representing a primitive feature (Gingerich and Gunnell, 2005); indeed, it has been suggested that midbrain exposure can appear as a derived feature, rather than a primitive one (Edinger, 1964), so caution is necessary in interpreting its significance.

**Cerebellum**

Morphology of the cerebellum is well preserved in the virtual endocast of USNM 530208. In this specimen, it is possible to identify the vermis and left lateral lobe of the cerebellum (Fig. 3A), separated by a paramedian fissure, as is typical of therians generally (Macrini et al., 2007). The portion of the cranium that would have housed the right lateral lobe and paramedian fissure is missing. Although there is no established method for estimating the size of the cerebellum from an endocast independent of the mass of the brain, in taxa in which the brain is not significantly flexed, some coarse indication of its size can be gleaned from the percentage that it contributes to the total length of the endocast. Silcox et al. (2010a) estimated that the cerebellum constituted about a quarter of the total length in *M. annectens*, *R. turpanensis, I. graybullianus, and Adapis parisienensis*. In contrast, the cerebellum is much shorter in *C. sigei*, constituting approximately 13% of the total length of the endocast, and this region also appears to have been quite short in *L. kayi*. Although there is some damage to the relevant part of USNM 530208, it is clear that on the left side the caudal extent of the occipital bone is preserved (Fig. 6), implying that in the intact cranium there would not have been space caudally for a much more extensive cerebellum. It is perhaps surprising that a region of the brain generally understood to be related to motor control would be so short in a family thought to have engaged in complex extractive foraging behaviors (Koenigswald and Schierning, 1987).

The fissura prima cannot be identified on the surface of the cerebellum in either virtual endocast of *L. kayi*. As observed in
nerve V₂, is identifiable on the virtual endocast of USNM 530208, located just caudal to the alisphenoid canal (Figs. 3B, 5A). Both virtual endocasts exhibit clear casts of the internal auditory meatus, with distinct casts for nerves VII and VIII (Figs. 3B, F, 5B), just medial and ventral to the rostral end of the paraflocculus. In the virtual endocast of USNM 530208, the cast of the single jugular (posterior lacerate) foramen (which presumably housed nerves IX, X, and XI, in addition to the sigmoid sinus) is evident ventral to the caudal end of the cast of the paraflocculus (Figs. 3B, D, 5C). The cast of the single hypoglossal foramen for cranial nerve XII is only identifiable on the left side of the cast of the brainstem in the virtual endocast of USNM 530208 (Figs. 3B, 5D).

Blood Vessels

Several elements of the system of sinuses and veins draining blood from the brain are evident on the endocast of USNM 530208, including the caudal portion of the superior sagittal sinus, transverse sinus, postglenoid vein, and sigmoid sinus (in the cast of the jugular foramen; Figs. 3B, D, 5C). This suggests that L. kayi would have had a fairly typical pattern of blood flow from the brain, similar to that observed in I. graybullianus, M. annectens, and most other members of Euarchontoglires (except dermopterans, which lack the postglenoid vein). The superior sagittal sinus is less pronounced rostrally (Fig. 3A, E), suggesting that it may have been located deep within the meninges (Macrini et al., 2007); a similar morphology was observed in the endocasts of microsyopsids (Silcox et al., 2010a). Casts of the sigmoid and inferior petrosal sinuses are not clearly evident on either virtual endocast, but this is likely influenced by poor preservation in the relevant regions. There are no casts of foramina for rami temporales or emissary veins passing through the parietal, or along the parietal-squamosal suture in the virtual endocasts of L. kayi. As noted by Silcox et al. (2010b), the absence of these foramina contrasts with other apatemyids known from the cranium. Although Silcox et al. (2010b) identified several landmarks of a transpromontorial internal carotid artery in the basicranium of USNM 530208, only a few parts of the path of arterial blood flow to the brain are evident on the virtual endocasts, including the orbitotemporal canal (presumably for the ramus superior of the stapedial artery, in addition to one or more veins; Wible, 1987), and the alisphenoidal canal (presumably for the ramus superior of the stapedial artery, Fig. 3B, D). No cast of the anterior carotid foramen for the promontory artery is evident on either of the virtual endocasts—this likely reflects the poor preservation of the relevant region in both specimens (Silcox et al., 2010b).

Brain Size and EQ

Obtaining an accurate estimate of cranial capacity is complicated by the fact that neither endocast for L. kayi is complete, and by the evident difference in size between the two individuals to which they pertained (i.e., the area of M1 in USNM 530221 is 86% that of USNM 530208; based on data from Silcox et al., 2010b). Although it is generally preferable to minimize manipulation of the data for well-preserved specimens, in this case a straight overlaying of the two endocasts on one another using a rigid warp algorithm produces a result that is clearly poorly proportioned (Fig. 2B), and the volume estimate derived from it is probably too large for the individual represented by USNM 530221 and too small for the individual represented by USNM 530208. The result of the Bookstein warp (Fig. 2C) appears to be a more reasonable representation of the size and proportions of the endocast of USNM 530221, but in the absence of any external source of validation this reconstruction must be treated with caution. To be maximally conservative, we have included estimates of volume based on four levels of manipulation of the data in Table 1. These different assumptions sets produce a range of cranial

Brainstem and Cranial Nerves

The hypophyseal fossa can be observed on both virtual endocasts (Fig. 3B, F), but is only well enough preserved to be measured in USNM 530208, in which it is wider (width = 2.6 mm) than long (length = 1.7 mm), and reasonably deep (depth ~ 1.8 mm). These proportions differ from those observed in both M. annectens, in which the fossa is longer than wide and very shallow (Silcox et al., 2010a), and in I. graybullianus, in which it is relatively deep, but more nearly circular (Silcox et al., 2009). Although Macrini et al. (2007) scored characters related to the proportions of the hypophyseal fossa, this wide range of morphologies in a group of fairly closely related taxa suggests that the size and shape of this fossa may be a feature of relatively low phylogenetic valence. This inference should perhaps not be surprising because the hypophyseal fossa’s form is apparently a poor predictor of the form of the pituitary gland in mammals (Edinger, 1942).

Although the optic chiasm is not preserved, casts of cranial nerve II are identifiable in the virtual endocast of USNM 530221 rostral to the hypophyseal fossa (Fig. 3F). Lateral to the hypophyseal fossa in the virtual endocast of USNM 530221 is an undifferentiated bulge that likely corresponds to the trigeminal ganglion, and the passageway of cranial nerves III, IV, V₁, and V₂ and the ophthalmic vein to the sphenorbital fissure (Fig. 3F). Silcox et al. (2010b) suggested that there was no distinct foramen rotundum in Labidolemur kayi, so all of these vessels and nerves presumably passed through this opening. This area is obstructed in ventral view in the virtual endocast of USNM 530208 by the cast of the alisphenoid canal (Fig. 3B), which is inferred to have housed the ramus infraorbitalis of the ramus inferior of the stapedial artery (Silcox et al., 2010b). The cast of the foramen ovale, for cranial
capacity estimates that extends from approximately 0.5 to 0.6 cc. An estimate of the mass of the brain can be calculated by assuming that brain tissue has a density similar to liquid water (Gingerich and Gunnell, 2005), which has a specific gravity of 1 g/cm³. Using this assumption, the brain of *L. kayi* would have been approximately 0.5–0.6 g (mass = volume/specific gravity).

Encephalization quotient (EQ) estimates calculated from all four estimates, based on the body mass estimate for USNM 530221 (74 g; Armstrong et al., 2011), are included in Table 1 and Figure 7. These EQ estimates lie within the range calculated for plesiadapiforms, and near the top part of the range of estimates for ‘archaic’ non-primates from the Late Cretaceous and early Tertiary. However, they are markedly lower than EQ estimates for *C. sigei* calculated by Koenigswald et al. (2009; 0.81 using Jerison’s 1973 equation). Although this may stem in part from the different bases for body mass estimation (teeth in *C. sigei*; postcra-

FIGURE 7. Box plot of encephalization quotients of living non-primate eutherians, living and fossil non-hominin eurytarsids, archaic non-primate mammals, plesiadapiforms, *Labidolemur kayi*, and *Carcinella sigei* using Eisenberg’s (1981) equation. Note that the range of values for Rodentia represents only two data points (Pirlot and Kamiya, 1982), and is therefore unlikely to be representative of the full range of variation for the order. The archaic non-primate mammals include a variety of late Cretaceous and early Tertiary taxa (see Supplementary Table 2). The range of estimates portrayed for *L. kayi* represents varying estimates of cranial capacity based on different assumption sets (see Table 1), whereas the range provided for *C. sigei* reflects the prediction limits for the body mass estimate calculated by Koenigswald et al. (2009). Data from Stephan et al., 1970; Szalay and Berzi, 1973; Radinsky, 1978; Pirlot and Kamiya, 1982; Conroy, 1987 (just for *Oreopithecus* body mass estimate); Martin, 1990; Simons and Rasmussen, 1996; Bush et al., 2004; Gingerich and Gunnell, 2005; Sears et al., 2008; Koenigswald et al., 2009; Silcox et al., 2009, 2010a; and the current study.

The most notable contrast between the endocast of *Labidolemur kayi*, and those of non-apatemyids, early Tertiary eucharontoglorians, is in the size of the olfactory bulbs (Fig. 4). Jerison (1973) argued that large olfactory bulbs represent the primitive condition for mammals. This inference is supported by the relatively large size of this region of the brain in Cretaceous eutherians (Kielan-Jaworowska, 1984; Supplementary Table 1; supplementary materials available online at www.vertepaloo.org/jvp/JVPcontents.html), and by Macrini et al.’s (2007) character analysis. Macrini et al. (2007) used a cutoff of 6% for percentage of the endocast composed of the olfactory bulb casts to differentiate between ‘large’ and ‘small.’ Based on this cutoff, all living and fossil euarchontans known from endocasts, including plesiadapiforms, would fall into the ‘small’ size range (Supplementary Table 1; based on data from Stephan et al., 1970, 1981; Gurche, 1982; Martin, 1990). There are much fewer published data for members of Glires, but Pirlot and Kamiya (1982) provide volumes for two genera of gliding rodents (*Iomys* and *Glaucomys*), which both also fall well below 6% (Supplementary Table 1), and both living and fossil erethizontid rodents have tiny olfactory bulbs (Dozo et al., 2004). In contrast, the two apatemyids, *Carcinella sigei* and *L. kayi*, appear to share relatively large olfactory bulbs, with all estimates for *L. kayi* substantially exceeding the 6% cutoff (Table 1). This suggests that apatemyids may have been primitive relative to other eucharontoglorians in retaining relatively large olfactory bulbs. Assuming the hypothesis of relationships provided in Figure 1 is correct, it is possible that reduction of this region occurred independently in euarchontans and glians.

One caveat to this interpretation is the recognition that some taxa may evolve relatively larger olfactory bulbs in association with specializations to the sense of smell—for example, Novaeeck (1982) suggested this for certain eutherpinyalans. It has been suggested that apatemyids were similar in their ecology to extant extractive foragers such as *Daubentonia madagascarensis* and the four species of petaurid marsupial *Dactylopsila* (Koenigswald and Schierning, 1987). Living aye-ayes have an exceptionally complex nasal skeleton compared to other strepsirrhines (Maier, 1993; Ruf, 2008), and even though their olfactory bulbs account for only approximately 1.6% of their total endocranial volume (Stephan et al., 1970), these structures are relatively enlarged compared to those of other euprimates, whereas areas of the brain associated with vision are reduced (Kaufman et al., 2005). Therefore, it is possible that the large size of the olfactory bulbs in apatemyids reflect, at least in part, similar specializations related to extractive foraging.

The similarity in the inferred position of the rhinal sulcus in *Ignacius graybullianus*, *Microstomum connectens*, and *L. kayi* suggests that this state may be primitive for Eucharontoglorines, although in the absence of other additional relevant data (e.g., from primitive scandentians, dermopterans, or members of Glires) this conclusion remains tentative. This position is more ventral than that
observed in Cretaceous eutherians (Kielen-Jaworowska, 1984; but see Macrini et al., 2007) and living insectivorans that have been considered to have relatively primitive cerebral patterns such as Solenodon (see Allen, 1910; pl. 6; e.g., ‘basal insectivores’ of Stephan et al., 1970; Stephan, 1972), suggesting some neocorticalization may have occurred in the early evolution of Euarchontognires.

The virtual endocasts of L. kayi share a number of characteristics with those published for plesiadapiforms (Fig. 3). In addition to the approximate position of the orbitotemporal canal, these include exposed caudal colliculi (missing in some derived members of Microsyopidae, but inferred to be primitive for the family; Silcox et al., 2010a; the midbrain is also exposed in Rhombomylus—see Meng et al., 2003:fig. 50) and an overlapping range of EQ estimates. Although it would be beneficial to assess these features in a wider range of early Tertiary euarchontognires, if they were available, the distribution of these similarities nonetheless suggests that they may have characterized the common ancestor of Euarchontognires.

Features observed in fossil euprimate endocasts that are missing in both L. kayi and in plesiadapiforms include the sylvian sulcus (missing in Smilodectes; Gazin, 1965), caudal expansion of the cerebrum to cover the midbrain, and a well-developed temporal pole. The absence of these features in an additional group with possible links to Euarchonta supports the inference that they could be euprimate synapomorphies (Silcox et al., 2010a). Even though more has been written about the evolution of the brain in Primates than in any other order, one of the problems that remains in answering questions about early primate brain evolution is the absence of closely related fossil outgroups to Primates sensu lato (i.e., including plesiadapiforms), to establish what is primitive for the group as a whole. Although extant treeshrews have often been used as stand-ins for primitive primates (e.g., Le Gros Clark, 1924, 1959, Kaas 2008), contrasts between the form of the brain in tupaiid scandentians and the endocasts of plesiadapiforms suggest that the brain of Tupaia, at least, makes a poor model for the primitive morphology of the brain in Euprimates (Silcox et al., 2009, 2010a). This viewpoint is supported by analyses that suggest that specializations of the brain associated with diurnal visual processing may have evolved independently in the two orders (Campbell, 1966, 1980; Allman, 1977), with Tupaia actually having a visual system more similar to that of living sciurid rodents than to primates in some features (Kaas, 2002; but see Lyon, 2009). Contrasts in the form of the brain between Tupaia and Pilocercus, including, for example, the relatively smaller rostral (superior) colliculi in the latter (Le Gros Clark, 1926), also support the inference that many of the specializations of the visual system of diurnal treeshrews occurred within Scandentia. Another frequently adopted approach uses eulipotyphlan as stand-ins for primitive primates (e.g., Stephan et al., 1970, 1982; Martin, 1990:fig. 8.17). An obvious problem with this approach is the great phylogenetic distance between eulipotyphlan and primates in current, broadly held hypotheses of mammalian interrelationships (e.g., see Springer et al., 2004).

Extinct apatemyids, in particular L. kayi, may form a more appropriate basis for comparison with primates than these extinct taxa. For example, the similarity in the position of the orbitotemporal canal in L. kayi and plesiadapiforms suggests that this position might be primitive for Euarchontognires. If this structure is associated with the rhinal fissure in these forms, then this would represent a more ventral position for this critical dividing line between the neo- and paleo-cortices than observed in primitive eulipotyphlan, implying a more ancient history for at least some measure of neocorticalization. One thing worthy of note, however, is that the relatively larger olfactory bulbs in a species with a similar EQ to those calculated for plesiadapiforms implies that the rest of the brain was relatively smaller in L. kayi than in primitive primates, suggesting perhaps a relatively larger neocortex was present in plesiadapiforms.

In terms of the very small size of the olfactory bulbs observed in modern euprimates, the contrast between the large bulbs of apatemyids, and the smaller bulbs of other non-euprimate euarchontognires, suggests that the acquisition of Euprimate's relatively diminutive olfactory bulbs may have occurred in a multi-step process, with some reduction in the size of this region (or expansion to other parts of this brain) pre-dating the euprimate node. This further emphasizes the inappropriateness of using living eulipotyphlan, with their larger olfactory bulbs, as primitive models for the brain in early primates.

The endocasts of L. kayi are also relevant for considering evolution of the brain within Apatemyidae. The relative brain size of C. sigei is large compared not only to L. kayi, but to other ‘archaic’ mammals (Fig. 7). Some authors (e.g., Gibson, 1986) have suggested that complex extractive feeding behaviors may have played a role in the evolution of primate intelligence, and indeed Daubentonia is the most encephalized of the lemurs (Barrickman and Lin, 2010), with an enlarged frontal cortex (Kaufman et al., 2005). Perhaps the increase in relative brain size that seems to have occurred in Apatemyidae might also be tied to elaborations in foraging behavior. Koenigswald et al. (2005a) documented more specialized hand proportions in middle Eocene Heterohyxus manus than observed in early Eocene Apatemys charadi or L. kayi, which is consistent with the idea that apatemyids became more specialized for manual extractive foraging through time. This hypothesis would require the discovery of postcranial material for C. sigei to be tested.

CONCLUSIONS

The endocranial anatomy of Labidolemur kayi is interesting both from the perspective of its potential importance to understanding euarchontogniran brain evolution, and to informing our understanding of evolution within the Apatemyidae. Features shared with other early Tertiary euarchontognirans that may be primitive for the group include exposed caudal colliculi, a similarly located orbitotemporal canal (that may reflect the location of the rhinal sulcus) on the lateral surface of the cerebrum, and an overlapping range of EQ estimates. The large size of the olfactory bulbs contrasts with the condition in other early Tertiary euarchontognirans, excepting the only other apatemyid known from an endocast, Carcinella sigei. However, the endocast of L. kayi contrasts markedly with that of C. sigei in being much smaller, both absolutely, and relative to body mass. This suggests significant increase occurred in brain size in Apatemyidae over the course of the Eocene, which might be related to elaborations in the family’s specialized manual extractive feeding regime.

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