Endocranial morphology of Palaeocene Plesiadapis tricuspidens and evolution of the early primate brain

Maeva J. Orliac, Sandrine Ladeveze, Philip D. Gingerich, Renaud Lebrun and Thierry Smith

1. Introduction

Primates are generally recognized as having large brains relative to their body mass [1–3], and the evolution of the brain constitutes a key feature of primate evolution [2,4]. In primates, the brain fills the endocranial space, and cranial endocasts provide a good approximation of both brain size and brain shape [1]. This is true for fossil and living primates, providing a way to study primate brain evolution through time.

Palaeogene plesiadapoids, considered the closest relatives of Euprimates (or crown-group primates) [5,6], are crucial for understanding the earliest stages of primate brain evolution. Here, we use computed tomography (CT) to investigate the endocranial morphology of a key Palaeocene taxon: Plesiadapis tricuspidens from Berru (Late Palaeocene, Marne, France [7,8]). Advances have been made in understanding brain morphology in related plesiadapiforms [9–11], but good documentation of endocast morphology is limited to the Eocene megadephid Megadelphys undulatus [11] and Microspheny annectens [10], and to the Eocene paromomyid Ignacius graybullianus [9]. These specimens occur relatively late in the evolutionary history of plesiadapiforms. The only Palaeocene species studied previously, Plesiadapis cookei from the Late Palaeocene of North America, yielded a poorly preserved endocast [12]. The endocast of P. tricuspidens described here is both well preserved and the oldest documenting a possible ancestral primate brain. Investigation with micro-CT enables us to provide more precise quantification of the size of structures and to identify previously unappreciated anatomical

Expansion of the brain is a key feature of primate evolution. The fossil record, although incomplete, allows a partial reconstruction of changes in primate brain size and morphology through time. Palaeogene plesiadapoids, closest relatives of Euprimates (or crown-group primates), are crucial for understanding early evolution of the primate brain. However, brain morphology of this group remains poorly documented, and major questions remain regarding the initial phase of euprimate brain evolution. Micro-CT investigation of the endocranial morphology of Plesiadapis tricuspidens from the Late Palaeocene of Europe—the most complete plesiadapoid cranium known—shows that plesiadapoids retained a very small and simple brain. Plesiadapis has midbrain exposure, and minimal encephalization and neocorticalization, making it comparable with that of stem rodents and lagomorphs. However, Plesiadapis shares a domed neocortex and downwardly shifted olfactory-bulb axis with Euprimates. If accepted phylogenetic relationships are correct, then this implies that the euprimate brain underwent drastic reorganization during the Palaeocene, and some changes in brain structure preceded brain size increase and neocortex expansion during evolution of the primate brain.
2. Results

MNHN CR 125 is the most complete cranium of *P. tricuspidens* known to date. Detailed descriptions of the external features of this specimen were published previously, and several reconstructions of its undeformed aspect have been proposed [7,8,13,14]. The cranium is indeed compressed dorsoventrally, but lateral deformation is almost absent. Compared with other available endocasts of plesiadapiforms (e.g. *I. graybullianus* and *M. annectens*), and contrary to previous hypotheses [13,15], the braincase of *P. tricuspidens* is oblong in shape and small relative to skull dimensions (figure 1a,c and table 1).

Assuming that distortion results from dorsoventral compression only, we restored the endocranium of *P. tricuspidens* using landmarks based on the length/height ratios of the endocranial structures (for more details about the protocol, see the electronic supplementary material, text S1 and figure S6). The estimated endocranial volume of the ‘unflattened’ reconstruction of the endocranium of *P. tricuspidens* equals 5.213 cm³ (original endocranial volume 1 cm³). This value is smaller than previous estimates, which ranged between 12.00 and 18.70 cm³ [13,14], and smaller than the estimated brain weight of 14 g used in the literature [15]. Our interpolated endocranial volume estimate for *P. tricuspidens* is 5.10% for *I. graybullianus*; 5.10% for *M. annectens* [9,10] compared with Euprimates (e.g. 3% for *Adapis parisienis*; 3.4% for *Tetonius homunculus* [10]).

The rhinal fissure marks the division between the palaeocortex (‘olfactory cortex’) and neocortex (isocortex). Its position is a key feature for assessing the expansion of the neocortex, which is the part of the brain responsible for major cognitive functions such as sensory perception, spatial reasoning and voluntary movement [22]. The location of the rhinal fissure was hypothetical in *P. cookei* [12], but it is clearly visible on both sides of the endocranial structures of *P. tricuspidens* (figure 1b; electronic supplementary material, figure S1). The rhinal fissure in *P. tricuspidens* is located more ventrally than that hypothesized for *P. cookei* [12], and it appears that the rhinal fissure is most probably not preserved in the specimen of *P. cookei* UM 87990, as previously proposed by Silcox et al. [10]. The neocortex of *P. tricuspidens* is convex dorsally and expanded well above the level of the olfactory bulbs (this is also observed in the undeformed endocranial endocranial of *P. cookei*; see electronic supplementary material, text S1 and figure S2). *Plesiadapis* differs from other plesiadapiforms in this character (figure 1c–e), but closely resembles modern dermopterans [12], scandentians (tree shrews) [23] and early Euprimates (e.g. the omomyid *Tetonius* [16]; figure 1f).

A small anterior neocortical lobe is recognizable, delimited laterally by inflection of the rhinal fissure and dorsally by shallow sulcus on the neocortex outer surface (figures 1b and 2a). The large inflection located in the first third of the hemisphere is here interpreted as a widely open sylvian fossa (figure 1b). As described for *Ignacius* and *Microsyops* [9,10], this depression is more similar to the sylvian fossa of...
The small anterior inflection of the rhinal fissure may represent the presylvia. The absence of a sylvian fissure, and, concurrently, of any demarcation of the temporal lobe, contrasts with the condition found in most Euprimates [2, 16, 20, 24], but is found in other living and fossil euarchontoglires and in all plesiadapiforms known from the relevant part of the endocast [9, 10].

The neocortical part of the cerebrum of *P. tricuspidens* is homogeneously smooth, except for a very slight inflection corresponding to the lateral sulcus, observed parallel to the sagittal sinus in the anterior half of the cerebral hemisphere (figure 2a). The ventral extension of the neocortex in the posterior half of the cerebrum cannot be precisely assessed owing to deformations. Its ventral location, however, might coincide with the orbitotemporal canal (figure 1b) interpreted as a landmark for the rhinal fissure in fossil primates [24, 25]. Little is preserved of the pyriform lobes, owing to dorsoventral compression, and their ventral extension cannot be determined.

The cerebrum of *P. tricuspidens* does not extend to the cerebellum, and the midbrain is widely exposed. As in *P. cookei* [12], the two slight swellings of the inferior colliculi are visible. Weak expansion and the low position of the inferior colliculi indicate that their exposure is due to weak expansion of the posterior cerebral hemisphere rather than any secondary sensory specialization like that seen in extinct and extant chiropterans (bats [26]) or dermopterans (flying lemurs [12, 27]). The size of the cerebellum of *P. tricuspidens* is reduced compared with other components of the brain (table 1). Its morphology is similar to that of other plesiadapiforms and most therian mammals: the paramedian fissures separate the lateral lobes of the cerebellum from the vermis [28]. *P. tricuspidens* shows broad round casts of the parafloccular lobes of the cerebellum, a morphology likely to be primitive for therians [28]. They are elongated, nearly cylindrical and protrude on the lateral sides of the endocast (figure 2a). This elongated shape differs from that of *I. graybullianus* and *M. annectens*, in which the parafloccular lobes are bigger and more rounded. Perfect preservation of both petrosals suggests that the shape of the parafloccular lobes (housed in the subarcuate fossae) is unlikely to have been affected by postmortem deformation.

Identification of foramina of the orbitotemporal region of *P. tricuspidens* has been subject to debate in recent decades and is still controversial (see [29] for review). Micro-CT images of MNHN CR 125, together with the observation of the basicranium fragment MNHN CR 965 (electronic supplementary material, figure S3), enable us to precisely identify the location of cranial nerves and several elements of the venous drainage system, especially in the basisphenoid/alisphenoid region (figures 1–3). On the ventral surface of the posterior cerebral hemisphere rather than any secondary sensory specialization like that seen in extinct and extant chiropterans (bats [26]) or dermopterans (flying lemurs [12, 27]).

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**Table 1.** Endocast measurements and EQ calculations for *Plesiadapis* and other plesiadapiforms. Lengths are given in millimetres, volumes in cubic millimetres. Maximum width of the cerebellum is given without the parafloccular lobes. EQ values estimated for *P. tricuspidens*, *M. annectens* and *I. graybullianus* correspond to different body mass estimates: cranial length generic primate equation [2]/upper molar area [17]/cranial length insectivore equation [18]. The last EQ value estimated for *P. tricuspidens* and the sole estimate for *P. cookei* correspond to long-bone body mass estimates.

<table>
<thead>
<tr>
<th></th>
<th><em>Plesiadapis tricuspidens</em></th>
<th><em>Plesiadapis cookei</em></th>
<th><em>Microsyops annectens</em></th>
<th><em>Ignacius graybullianus</em></th>
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<tr>
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<td>43.5</td>
<td>42/42</td>
<td>41.25</td>
<td>30.79</td>
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<td>cerebrum maximal length</td>
<td>18.2</td>
<td>22/19.1</td>
<td>22.26</td>
<td>15.8</td>
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<tr>
<td>cerebrum maximal width</td>
<td>22</td>
<td>22/20.6</td>
<td>24.00</td>
<td>19.44</td>
</tr>
<tr>
<td>olfactory bulbs length</td>
<td>9.7</td>
<td>10.9/2</td>
<td>8.00</td>
<td>6.28</td>
</tr>
<tr>
<td>olfactory bulbs maximum</td>
<td>—</td>
<td>5/5</td>
<td>5.00</td>
<td>3.94</td>
</tr>
<tr>
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<td>?/6.7</td>
<td>3.06</td>
<td>4.2</td>
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<tr>
<td>cerebellum maximal length</td>
<td>7.5</td>
<td>?/7.2</td>
<td>11.9</td>
<td>9.4</td>
</tr>
<tr>
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<td>19.6</td>
<td>?/20</td>
<td>23.9</td>
<td>15.6</td>
</tr>
<tr>
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<td>39%</td>
<td>52%</td>
<td>50%</td>
<td>66%</td>
</tr>
<tr>
<td>total endocast volume</td>
<td>278a, 521b</td>
<td>389*/500b</td>
<td>590</td>
<td>214</td>
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<tr>
<td>olfactory bulb volume</td>
<td>13.6</td>
<td>?/39</td>
<td>30</td>
<td>12</td>
</tr>
<tr>
<td>olfactory bulbs/endocast volume</td>
<td>4.9%</td>
<td>?/7.8%b</td>
<td>5.1%</td>
<td>5.5%</td>
</tr>
</tbody>
</table>

EQ Jerison [1]: 0.12/0.17/0.16/0.26 0.24 0.32/0.26/0.39 0.40/0.34/0.47

EQ Eisenberg [19]: 0.15/0.21/0.19/0.34 0.31 0.41/0.32/0.52 0.59/0.48/0.69

EQ Martin [2]: 0.11/0.17/0.15/0.27 0.24 0.33/0.26/0.42 0.49/0.40/0.58

*Deformed or partial endocast.

*Estimation after correcting deformation.
the endocast, just posterior to the circular fissure, casts of the optic chiasm and roots of the optic nerves (cranial nerve II) are present, allowing determination of the location of the optic foramen (figure 3b). Posterolateral to the optic chiasm is the cast of the sphenorbital fissure (pathway for the ophthalmic vein and cranial nerves III, IV, V1, V2 and VI). There is no trace of a separate course for V2 through a foramen rotundum (figure 3b; see electronic supplementary material, text S1 and figure S3). The confluence of the foramen rotundum and sphenorbital fissure (foramen orbitorotundum) contrasts with the interpretation for another plesiadapoid, Carpolestes [29], and contradicts the presence of a foramen rotundum as a character common to plesiadapoids and euprimates [5].

Investigation of CT scans confirms the presence of a suboptic foramen (carrying a vein communicating between the ophthalmic veins in the two orbits [30]; figure 3b) located anterior and slightly ventral to the very small optic foramen in P. tricuspidens (figure 3). Lateral to the partial cast of the hypophyseal fossa is the cast of the foramen ovale (cranial nerve V3). As observed in I. graybullianus [9], a wide canal received the postglenoid vein. This communicates dorsally with a parietal foramen, which probably transmitted the capsuloparietal emissary vein [31]. Just ventral to the parafloccular lobe, casts of the internal auditory meatus (cranial nerves VII and VIII) are preserved. On the caudal aspect of the endocast, the jugular foramen most probably transmitted cranial nerves IX, X and XI, as well as the internal jugular vein [9]. The cast of the hypoglossal foramen (cranial nerve XII) is visible on the brainstem.

**Figure 2.** Labelled endocast and sphenoidal sinuses of Plesiadapis tricuspidens (MNHN CR 125) in (a) dorsal and (b,c) ventral views (scale bar, 1 cm). (d–g) Schematic dorsal views showing the expansion of the neocortex (red), olfactory bulbs (blue), midbrain (violet) and cerebellum of (d) P. tricuspidens, (e) Microsyops annectens (after [10]), (f) Ignacius graybullianus (after [9]), (g) Adapis parisiensis (after [20]). al, anterior lobe; bs, brain stem; ic, inferior colliculi; jv, jugular vein; llc, lateral lobe of the cerebellum; p, pituitary; pmf, paramedian fissure; s, sulcus; ss, sagittal sinus; ts, transverse sinus; other abbreviations as in figure 1.

**Figure 3.** Identification of orbitosphenoid foramina of Plesiadapis tricuspidens (MNHN CR 125), after in situ reconstruction of pathways of cranial nerves (red) and veins (blue), (a) viewed through a translucent rendering of the skull; (b) corresponding location in the cranium (scale bar, 1 cm). fj, foramen jugulare; fo, foramen ovale; hf, hypoglossal foramen; of, optic foramen; pf, postglenoid foramen; sf, sphenorbital fissure; sof, suboptic foramen; other abbreviations as in figure 1.
One of the most striking features revealed by virtual three-dimensional reconstruction of the endocranial cast of *P. tricuspidens* is the presence of two symmetrical cavities floored by the sphenoid bone and located ventral to the braincase (figures 1a,b and 2c; electronic supplementary material, figures S4 and S5). They expand from the posterior margin of the optic chiasm anteriorly to the hypothesized location of the sphenoid fossa posteriorly. Pneumatization of the sphenoid is widespread in primitive mammals and occurs in several living euprimates [32]. However, unlike most extant primates [32], the large sinuses observed in *P. tricuspidens* are separated from the nasal cavity anteriorly by a small distinct presphenoid sinus (figures 1b and 2c). Their posterior location in the endocranium and the absence of a connection with the nasal cavity preclude identification as paranasal features. We interpret these sinuses as basi-sphenoid paratympanic sinuses similar to the basisphenoid sinuses that communicate with the tympanic cavity in macroscelideans, chrysochlorids and talpids [33]. Most of the tympanic cavity of MNHN CR 125 is broken away, but its putative anterior extension, delimited anterolaterally by the foramen ovale and medially by some remnants of the bulla (electronic supplementary material, figure S4), indicates that a communication of posterior parts of the basisphenoid paratympanic sinus with the tympanic cavity was almost certain. A similar structure was interpreted in *Carpolesistes* as anterior and posterior chambers of the auditory bulla [29, fig. 16]; for further discussion, see electronic supplementary material, text S1 and figure S5). The role of this potential accessory auditory cavity is unclear; it could have served as a resonating chamber, or it could have been involved in low-frequency hearing [34]. This paratympanic sinus, so far not reported in non-plesiadapoid plesiadapiforms, could also represent a primitive condition of the auditory bulla structure in Euprimateformes.

3. Discussion

(a) Brain size and neocorticalization of early Euprimateformes

Depending of the equation used, and with different craniodental body mass estimates, the estimated encephalization quotient (EQ = brain size expressed as a function of body mass [1]) of *P. tricuspidens* ranges between 0.12 and 0.21 (EQ Jerison [1] range = 0.12–0.17; EQ Eisenberg [19] range = 0.15–0.21; EQ Martin [2] range = 0.11–0.17; table 1). With a body mass estimate of 2039 g based on long-bone dimensions [35,36], the EQ of *P. tricuspidens* ranges between 0.26 and 0.34 (EQ Jerison [1] = 0.26; EQ Eisenberg [19] = 0.34; EQ Martin [2] = 0.27; see electronic supplementary material, table S1). These values are very close to that calculated for *P. cooki* (0.24–0.31, long-bone body mass estimate of 2200 g [12]; table 1). The different EQ estimates calculated for *Plesiadapis* are generally below those of living primates and scandentians, and below those of other plesiadapiforms (EQ estimates for *P. tricuspidens* calculated from a body mass based on long-bone dimensions overlap *M. annectens* EQ estimates calculated from a body mass based on cranio-dental measurements) and fossil euprimates [9,10] (table 1).

Among Primates, Plesiadoipoidea, found to be a sister taxon to Euprimates in recent analyses (Euprimateformes clade) [5,6], comprises species with the smallest EQ [9,10,12]. Small brain size is plesiomorphic compared with Euprimates, in which the increase of brain volume is principally due to
expansion of the neocortex [37]. In addition to a low EQ value, *P. tricuspidens* retains a number of plesiomorphic endocranial features that differ markedly from Euprimates. These include the posterior position of the braincase within the cranium, and the relative proportions of brain components. The total surface area of the neocortex of the ‘unflattened’ model of *P. tricuspidens* endocranial represents 22% of the entire endocranial surface area reduced by olfactory bulbs (neocorticalization ratio [38, p. 386]; electronic supplementary material, text S1 and figure S7), which is inferior to fossil Euprimates such as *Adapis* (51% [38]) and corresponds to the expected surface area of the brain devoted to neocortex of the average mammals around 55 Ma [38, fig. 6]. The neocortex of *P. tricuspidens* shows a primitive evolutionary stage of expansion when compared with other plesiadapiforms (Microsyopsidae and Paromomyidae; figure 2d versus figure 2e–g).

*Plesiadapis tricuspidens* is closer morphologically to the Early Eocene stem gliroid *Rhombomylus* [39] in terms of cerebral expansion than it is to other known plesiadapiforms or to Euprimates. This implies (i) that expansion of the neocortex is not a feature that evolved in early Euprimateformes, (ii) that *Microsops* and *Ignacius*, two plesiadapiforms more recent than *Plesiadapis* in time but more basal in the primate tree, experienced an increase of their brain volume independently (figure 4). This crucial event that also occurred independently in Euprimates is probably associated with evolution of the visual system [9].

Measurements of the optic foramen are relevant to assessing activity period [40,41]. Identification of the optic nerve foramen for *P. tricuspidens* allows us to calculate the optic foramen index (OFI = 0.69) and optic foramen quotient (OFQ = –66.57; see electronic supplementary material, text S1 and figure S8 for more details) for this taxon. Together with the small size of the orbit (also observed in *Carpoleses* [29]), these small OFI and OFQ values (lower than most primates and closer to dermopterans [9]) indicate a non-visually directed nocturnal mammal similar to *Carpoleses* [29]. In Euprimates, a close relationship exists between the relative endocranial volume and the optic foramen area [42]. Similarly, *P. tricuspidens* has a very small optic foramen area and a low relative endocranial volume. This supports the idea that small brain size in early Euprimateformes may be correlated to a weakly developed visual system [10].

Recent analyses of *Plesiadapis* postcranial elements support the conclusion that this genus was capable of both quadrupedal walking and arboreal locomotion, with probable claw clinging [43,44], and potential suspensory behaviours [45]. In terms of diet, *Plesiadapis* has been suggested to be folivorous, with *P. cookei* more specialized to a folivorous diet and *P. tricuspidens* more omnivorous [46]. The reconstruction of *Plesiadapis* ecology therefore indicates that it was not highly specialized in terms of vision, locomotion nor diet; its endocranial cast morphology probably partly reflects this lack of specialization.

(b) Euprimate brain bauplan

Reconstruction of the plesiomorphic condition of the primate brain and the derived characters shared by Euprimates is crucial for defining the euprimate brain bauplan. In order to test the impact of endocranial morphology on primate relationships and to follow the evolutionary history of brain characters, we included 11 new endocranial characters in a simplified version of the morphological matrix of reference [5] (character list, character distribution and data matrix are provided in the electronic supplementary material, text S1 and dataset S1). Results are congruent with the relationships supported by Bloch et al. [5]. The endocranial of *Plesiadapis*—and by extension the ancestral brain of Euprimates—exhibits a pair of derived features in spite of its overall primitive morphology. Plesiadapoids and Euprimates share a low position of the olfactory bulbs relative to the cranial roof and a demarcation of an anterior lobe of the neocortex (both convergently observed in Scandentia + Dermoptera), whereas Euprimates are diagnosed by (i) demarcation of the temporal lobe, (ii) lack of exposure of the midbrain, (iii) a posterior location of the optic chiasma (convergently observed in Scandentia + Dermoptera) and (iv) the presence of a sylvian fissure (although lacking in the basal adapoid euprimate *Smilodectes* [24]). Modification of the anterior-most region of the cerebrum, together with ventral displacement of the olfactory bulbs, may therefore constitute the very first phase of neocortical expansion towards the Euprimates brain bauplan, before expansion of the sylvian complex and demarcation of the temporal lobe.

4. Conclusion

The virtual endocranial of *Plesiadapis* shows a more primitive picture of the substrate from which the euprimate brain arose than is suggested from the anatomy of other plesiadapiforms. The endocranial morphology of *P. tricuspidens* is very close to that of *Plesiadapis cookei* and differs markedly from both other plesiadapiforms and Euprimates. The small EQ and weak neocortex expansion in *Plesiadapis* indicates a primitive evolutionary stage of the brain when compared with other known plesiadapiforms (Microsyopsidae and Paromomyidae), which can be correlated with the lack of strong specialization in terms of vision, locomotion and diet. The current phylogenetic framework, including plesiadapoids as the closest relatives of Euprimates, implies that the euprimate brain evolved from a broadly plesiomorphic bauplan with unexpectedly limited encephalization and neocorticalization. Given what we know from *Plesiadapis* and other mammalian brains in the Palaeocene, the euprimate brain was profoundly modified in proportions and structure during the Palaeocene or earliest Eocene. In primates, changes in brain structure preceded both brain size increase and neocortex expansion. Modification of the anterior-most region of the cerebrum, together with ventral displacement of the olfactory bulbs, may constitute the very first phase of neocortical expansion towards the Euprimates brain bauplan, before expansion of the sylvian complex and demarcation of the temporal lobe.

Acknowledgements. We thank S. Lourian (University of Brussels) for the CT scan of *Plesiadapis cookei*, and T. Ryan and A. Walker (University Center for Quantitative X-ray Imaging, Penn State) and F. Goussard (3D plateform UMR 7207 CR2P) for the micro-CT scan and data managing of *P. tricuspidens*. Thanks are due to C. Argot and C. Sagne (MNHN) for the loan of *Plesiadapis cookei* specimens. We are grateful to M. T. Silcox and two anonymous reviewers for their enriching comments on earlier versions of the manuscript.

Funding statement. This study is a contribution to projects MO/36/020 and BR/121/A3/PALEURAFRICA supported by the Federal Science Policy Office of Belgium (to T.S. and S.L.). Research has been partly supported by the ANR Palasiafrica and the ATM MNHN ‘Etat et structure phylogénétique de la biodiversité actuelle et fossile’. This is ISE-M publication no. 2014-012.