

ORIGINAL ARTICLE

ANATOMICAL
SOCIETY WILEY

Virtual brain endocasts of the palaeodont *Metacheiromys marshi* and the neurosensory evolution of early Pholidotamorpha

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Funding information

NSF, Grant/Award Number: BCS 1825129, DEB 1654952 and DEB 1654949; Marie Skłodowska-Curie Actions: Individual Fellowship, Grant/Award Number: H2020-MSCA-IF-2018-2020 and 792611; Agència de Gestió d'Ajuts Universitaris i de Recerca, Beatriu de Pinós Programme, Grant/Award Number: 2021 BP 00042; Ministerio de Ciencia, Innovación y Universidades y Agencia Estatal de Investigación, Grant/Award Number: RYC2023-042630-I; Ministerio de Universidades y Union Europea-NextGenerationEU; Fundación Margarita Salas; European Research Council, Grant/Award Number: 756226; European Union's Horizon 2020 Research and Innovation Programme; H2020 European Research Council; Leverhulme Trust; Philip Leverhulme Prize; Swedish Research Council, Grant/Award Number: 2021-02973; Generalitat de Catalunya/CERCA Programme; The Agència de Gestió d'Ajuts Universitaris i de Recerca, Generalitat de Catalunya, Grant/Award Number: 2021 SGR 00620; Agencia Estatal de

Abstract

Palaeodonts are extinct placental mammals exhibiting myrmecophagous and fossorial adaptations. They have been viewed as the sister group to Pholidota (pangolins), which is the sister-clade to Carnivora within Ferae. Palaeodonts display morphological features that are similar to those in pangolins and xenarthrans, which are likely related to their specialized ecological niche. Therefore, it has been challenging to decipher whether shared features are synapomorphies or convergences. Here, we describe in detail the brain virtual endocast anatomy of the middle Eocene palaeodont *Metacheiromys marshi* and make morphological and quantitative comparisons with two extant African pangolins, *Smutsia gigantea* and *Phataginus tricuspis*. We found several differences between the fossil and extant taxa including in the olfactory bulbs, the cerebellum, and the venous and arterial systems. However, we propose an anatomical feature as a possible synapomorphy uniting palaeodonts and pangolins in Pholidotamorpha: the presence of a well-developed orbital gyrus and a presylvian sulcus. These correlated features are present in some other groups but are likely derived traits acquired independently, for example in xenarthrans. In terms of the behavioural ecology of *M. marshi* and pangolins, we suggest that reduced olfaction and eye movement control is likely linked to fossoriality or slow arboreality as previously proposed for rodents. The expansion of the orbital gyrus of the neocortex is proposed to be related to the evolution of myrmecophagy and the emergence of a protrusile tongue in early Pholidotamorpha, acquired convergently in giant anteaters. Overall, this work provides a novel perspective on the evolution of palaeodonts and pangolins and

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Investigación de the Ministerio de Ciencia e Innovación: R + D + I project, Grant/Award Number: PID2020-117289GB-I00 and PID2024-160207NB-I00

presents new hypotheses related to the impact of ecological adaptations on the brain evolution of mammals.

KEYWORDS

myrmecophagy, neocortex, olfactory bulbs, orbital gyrus, petrosal lobules, Pholidota, presylvian sulcus, slow locomotion, tentorium

1 | INTRODUCTION

Palaeonodonta is an extinct clade of placental mammals with fossorial adaptations mainly known from the early Paleocene (Torrejonian) to the late Eocene (Chadronian) of North America and to a lesser degree from Eurasia (Rose, 2006, Kondrashov & Agadjanian, 2012). This group is composed of three families: Escavadodontidae, Epoicotheriidae, and Metacheiromyidae. 'Escavadodontidae' is likely basal and paraphyletic with the other two families that show more derived postcranial and dental features (Rose, 2008). Metacheiromyids display robust postcrania adapted to a fossorial lifestyle, although they are less derived in this regard than the Epoicotheriidae. A progressive reduction of the dentition is also present and was greater in Metacheiromyidae than in Epoicotheriidae (Rose, 2008). In metacheiromyids specifically, a grooved and rugose edge on the palate posterior to the cheek teeth suggests the presence of a protrusile tongue used for eating small invertebrates (Rose, 1978).

The phylogenetic position of Palaeonodonta has been a topic of debate for decades, with two main hypotheses. They have either been considered closely related to Xenarthra (anteaters, tree sloths, and armadillos) from the Americas (e.g., Gaudin, 2004; Patterson et al., 1992; Simpson, 1945; Szalay, 1977) or to Pholidota (pangolins) from Asia and sub-Saharan Africa today and from North America and Europe in the past (e.g., Alba et al., 2018; Emry, 1970; Gaudin et al., 2009, 2016, 2020; McKenna & Bell, 1997; Rose et al., 2005). More recently, the clade Palaeonodonta + Pholidota, referred as Pholidotomorpha (Gaudin et al., 2009), has received additional support from combined morphological and molecular phylogenetic analyses of placental mammals (O'Leary et al., 2013). Additionally, molecular phylogenies have recovered Pholidota as sister-clade to Carnivora (e.g., Delsuc et al., 2002; Foley et al., 2023; Meredith et al., 2011; Murphy et al., 2021; Murphy, Eizirik, Johnson, et al., 2001; Murphy, Eizirik, O'Brien, et al., 2001; O'Leary et al., 2013; Shoshani & McKenna, 1998). Past studies have found some potential morphological synapomorphies between Pholidota and Carnivora, including features in the cranium (ossified tentorium cerebelli) and in the wrist (fusion of the scaphoid and lunate bones). However, those characteristics are absent or reduced in the early members belonging to each group (Gaudin et al., 2020; Rose et al., 2005). To date, no molecular phylogenies have found Xenarthra + Pholidota as sister-clades, and at this point in the maturity of molecular analyses such a relationship would be highly unexpected (Gaudin et al., 2020).

The reason that a link between Xenarthra and Pholidota persisted in the literature is because of the presence of shared morphological features related to a convergent lifestyle including diet (e.g., reduction of the dentition) and fossoriality (e.g., sacro-innominate fusion in the vertebral column), but also cranial similarities (e.g., shallow subarcuate fossa, palatine confined to the ventral orbital wall, mandibular symphyseal spout, squamosal epitympanic sinus) reported by several studies (Gaudin, 2004; Novacek, 1986, 1992; Novacek & Wyss, 1986). It is worth noting that the morphological analysis of O'Leary et al. (2013) recovered the group 'Edentata' including Pholidota + Xenarthra + Tubulidentata (the armadillos from Africa), which was first proposed by Cuvier (1798). Later, Weber (1904) proposed to classify pangolins and armadillos in their own orders as Pholidota and Tubulidentata. Regarding the phylogenetic position of Palaeonodonta, this group displays derived features that are present in both xenarthrans and pangolins, including fossorial adaptations and reduced dentition suggesting a myrmecophagous diet (Gaudin et al., 2020; Rose, 2006). The grouping of Palaeonodonta with pangolins and xenarthrans was originally proposed by Matthew (1918) and supported by Novacek (1986), but later was abandoned (Gaudin et al., 1996; Rose et al., 2005; Rose & Emry, 1993). Additionally, Palaeonodonta, and specifically the taxon *Metacheiromys*, share morphological features of the auditory region with both Xenarthra and Pholidota (Gaudin et al., 2019), most of which are likely derived characters (O'Leary et al., 2013).

The fossil record of Pholidota is relatively incomplete, which may in part explain the difficulties of finding shared morphological features between Pholidota and Carnivora. Today, there are eight recognized species of pangolins belonging to three genera, including *Manis* from Asia and *Phataginus* and *Smutsia* from Africa (Gaubert et al., 2011, 2020). However, it is likely that the number of species is underestimated based on recent molecular data (Gu et al., 2023; Heighton et al., 2023; Wangmo et al., 2025). There is also a significant ghost lineage for Pholidota as the oldest fossil is dated to the middle Eocene, while the oldest Carnivoramorpha and Palaeonodonta are Paleocene in age (Gaudin et al., 2016, 2020; O'Leary et al., 2013). Eocene pangolins are already relatively derived, sharing morphological features with Palaeonodonta, including postcranial fossorial adaptations in the scapula, humerus, metapodials, and unguals (see Gaudin et al., 2009, 2020; Rose et al., 2005; Storch, 2003). More specifically, the Eocene pangolin *Eomanis* was already clearly adapted to a fossorial lifestyle and likely had a myrmecophagous diet (e.g., it was edentulous; Gaudin et al., 2020). Another taxon, *Patriomanis* is a late

Eocene pangolin from North America that is also edentulous, but shows a mix of fossorial and arboreal adaptations with a prehensile tail (Gaudin et al., 2016, 2020).

Internal cranial anatomy has had an important role supporting the close relationship between Pholidota and Carnivora because the presence of an ossified tentorium has been one of the very few derived morphological characters linking both clades. Most mammals have a membranous tentorium that separates the cerebrum and cerebellum, but Pholidota and Carnivora have a bony lamina within the membranous tentorium (Gaudin et al., 2016). In Pholidota, the ossified tentorium extends from the anteroventral border of the petrosal to the dorsal part of the cranial cavity and includes components from the parietal and squamosal (Gaudin et al., 2016). Carnivora also has a tentorial process of the parietal but not of the squamosal (Nojima, 1990). To study endocranial anatomy in fossil pangolins, the sediment inside the holotype cranium of the latest Eocene taxon *Patriomanis americana* (AMNH F:AM 78999) was removed. Its endocranial anatomy was briefly described by Emry (1970), who found that this specimen had a less developed bony tentorium in comparison to extant pangolins. More recently, the use of micro-computed tomography (micro-CT) scanning has revolutionized our understanding of the internal anatomy of extinct species by serving as a non-invasive technique that reveals endocranial anatomy while preventing the destruction of the fossils themselves (Bertrand et al., 2025; Dozo et al., 2023 and references therein). For example, a study of the auditory region of *Metacheiromys* using CT data provided substantial new information regarding potential shared morphological features among Palaeaeodonta, Xenarthra, and Pholidota (Gaudin et al., 2019). An ossified tentorium was found to be absent in *Metacheiromys*, with only a sharp crista petrosa present forming the ventral anchor of the membranous tentorium as in most other mammals (Gaudin et al., 2019).

One aspect of the biology of both Pholidota and Palaeaeodonta that has been rarely studied relates to the evolution of their neurosensory system, but here are some exceptions. A latex endocast of the Pholidota *Patriomanis americana* was produced by Emry (1970). A restoration of an endocranial cast based on the cranium of the Palaeaeodonta *Palaeaeodon ignavus* (AMNH 15086) was published by Matthew (1918) and reproduced by Simpson (1931). Additionally, two natural endocasts of the epoicotheriid palaeaeodont *Epoicotherium* sp. (FMNH UM483; AMNH 9245) were published by Patterson et al. (1992). Finally, a brain virtual endocast of *M. marshi* (USNM 452349) was generated for a study by Bertrand et al. (2022), but only quantitative data were produced and no anatomical description of the virtual endocast was published.

We here describe the brain virtual endocasts of *M. marshi* USNM 452349 and AMNH 131777. We also provide quantifications on the size of the brain and of its components for AMNH 131777 and compare these values to those obtained for USNM 452349 by Bertrand et al. (2022). We acknowledge that the relationships of palaeaeodonts to extant placentals are not fully settled. Because the few appropriate phylogenetic analyses (e.g., Gaudin et al., 2009; O'Leary et al., 2013) recovered palaeaeodont relationships with Pholidota,

we also report on the brain virtual endocasts of two extant pangolins, *Smutsia gigantea* and *Phataginus tricuspis*. Because of the scarcity of information on the endocasts of the extinct pangolins *Pat. americana* and the palaeaeodont *Pal. ignavus* and *Epoicotherium* sp., we only make references to these taxa when relevant information is available. We also propose potential morphological characters based on endocranial anatomy that could improve our understanding of the phylogenetic relationships of Palaeaeodonta, Pholidota, and Xenarthra. Finally, we provide some hypotheses related to the impact of myrmecophagy and slow locomotion on the brain evolution of Pholidotamorpha and other mammals with similar adaptations.

1.1 | 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; FMNH, Field Museum of Natural History, Chicago, IL, USA; UCMP, University of California Museum of Palaeontology, Berkeley, CA, USA; PSU, The Pennsylvania State University, State College, PA, USA; USGS, U.S. Geological Survey, Washington, D.C., USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

2 | MATERIALS AND METHODS

2.1 | Specimens studied

The two relatively complete crania of *M. marshi* (AMNH 131777; USNM 452349) used in the current study were recovered from the Bridger Formation of Wyoming (middle Eocene; Bridgerian NALMA). *Metacheiromys marshi* is considered one of the most dentally derived palaeaeodonts (Rose, 2008) as this taxon includes the most extreme tooth reduction among palaeaeodonts, with an almost completely edentulous jaw (Schoch, 1984). Regarding the dental formula, the upper teeth include a canine and one post-canine, while the lower teeth correspond to one incisor, one canine, and two post-canine teeth (Rose, 2008). Two extant pangolins were also included for comparison. *Smutsia gigantea* (giant pangolin) is a large nocturnal terrestrial pangolin (30–40 kg; 112.5–180 cm long) that can be found in African savannas and rainforests and in areas with large termite populations (Hoffmann et al., 2020). *Phataginus tricuspis* (white-bellied pangolin) is one of the smallest pangolins (up to 3 kg; 100 cm long), with a tail longer than its head and body combined. This semi-arboreal and nocturnal species is found in lowland tropical moist forests (both primary and secondary), as well as in savanna/forest mosaics of Africa (Jansen et al., 2020). Other comparisons were made with a latex endocast of *Pat. americana* (AMNH F:AM 78999; Emry, 1970), a reconstruction of a natural endocast of *Pal. ignavus* (AMNH 15086; Matthew, 1918; Simpson, 1931), and natural endocasts of *Epoicotherium* sp. (FMNH UM483; AMNH 9245; Patterson et al., 1992).

2.2 | Virtual endocast acquisition

To generate the virtual endocasts of the different specimens, CT scans of the crania were processed using Avizo Lite 2019.4 (Visualization Sciences Group, 1995–2019). *Metacheiromys marshi* (AMNH 131777) was CT-scanned with a 2010 GE phoenix nano-focus v|tome|x s240 at the American Museum of Natural History's Microscopy and Imaging Facility (MIF). The other specimen of *M. marshi* (USNM 452349) was scanned at the High-Resolution X-ray Computed Tomography Facility at UChicago PaleoCT (University of Chicago, Department of Organismal Biology and Anatomy, Chicago, IL, USA) by T. Gaudin. Both specimens were provided by JRW. In terms of the scanning settings: *M. marshi* (AMNH 131777) has a voxel size of 0.04240788 mm and was scanned with a voltage of 225 kV, and an amperage of 160 μ A. Regarding *M. marshi* (USNM 452349), the voxel size is 0.026012 and the specimen was scanned with a voltage of 190 kV and an amperage of 136 μ A. The two modern specimens: *S. gigantea* (AMNH 53855; Media ID: 000106417) and *P. tricuspsis* (AMNH 53874; Media ID: 000084693) were downloaded from Morphosource. Both specimens were uploaded by A. Harrington. The specimens are curated at the AMNH Mammalogy Department and were CT-scanned with a Nikon Metrology XT H 225 ST at the Duke Shared Materials Instrumentation Facility (SMiF, Duke University, NC, USA). *Smutsia gigantea* has a voxel size of 0.079287 mm and was scanned with a voltage of 193 kV and an amperage of 82 μ A, while *P. tricuspsis* has a voxel size of 0.046592 mm and was scanned with a voltage of 178 kV and an amperage of 82 μ A.

For this work, AMNH 131777 was segmented by ECB following the segmentation procedure for USNM 452349, segmented by OCB (Bertrand et al., 2022). The pen tool was used to isolate the endocranial cavity of the cranium because the inside was filled with sediment, and in some areas, the matrix was of similar density to the bone. Then interpolation was performed every three slices. In the extant *S. gigantea* and *P. tricuspsis*, the absence of sediment made the segmentation simpler. Interpolation was performed every five slices for the modern dataset instead of three for the fossils. Then, Biomedisa (Lösel et al., 2020) was used for semi-automatic interpolation using the CT data and the label field file of the segmentation that had been generated by hand for the extant specimens. This resulted in a completely segmented version of the virtual endocast that was cleaned in Avizo to generate the final versions of the endocasts. In the fossils, when the bone was not preserved or was detached from the matrix due to a fracture, a straight line was used to link the two nearest pieces of bone and to be conservative with the reconstruction of the endocast. In the three virtual endocasts made for this work, the post-processing protocol for USNM 452349 (Bertrand et al., 2022) was followed. The endocranial volume and the size of different brain components were quantified. To determine the endocranial volume, we generated a 'surface rendering' of the endocast in Avizo. The olfactory bulbs were isolated from the rest of the endocast using the 'volume edit' module and subsequently their volume was measured with the 'Surface Area Volume' option in Avizo (Figure S1). The petrosal lobules (= paraflocculi) were first resegmented in Avizo and their volume was calculated using the 'Surface Area Volume' for USNM 452349 in Bertrand et al. (2022). Because of

the poorer preservation of AMNH 131777 in this area and the great reduction of the subarcuate fossa (Jollie, 1968; where the petrosal lobules are located) on the endocast of *S. gigantea* and *P. tricuspsis*, the volume of the petrosal lobules was not calculated in these specimens. Finally, to calculate the neocortical surface area, the 'generate surface' function was used, and then this structure was isolated from the rest of the endocast through the 'extract surface' tool. The boundaries of the neocortical surface are defined by the rhinal fissure on the lateral aspect of the endocast, but this structure was challenging to identify with certainty on the lateral aspect along the entire length of the cerebrum in the two modern specimens of pangolins. Imam et al. (2018) illustrated the brain and specifically the boundaries of the paleocortex of *P. tricuspsis* (= *Manis tricuspsis*), which helped us in our segmentation of the neocortex in the extant taxa (Figure S1). However, the value for neocortical surface area of *S. gigantea* should be taken with caution as the brain of this species has not been published to guide our extraction and only *P. tricuspsis* was used. Linear measurements were taken following the procedure from Bertrand and Silcox (2016) for rodents that were also applied to other mammals (e.g., Bertrand, Jiménez Lao, et al., 2024). Rendering of the virtual endocasts inside the translucent crania were also produced in Avizo (Figure 1). The colours used for the endocasts correspond to what is calculated for the brain endocast (blue) and the petrosal lobule (green) volumes in Avizo. The remaining part in yellow corresponds to vessels in bony canals that are not counted as part of the endocranial volume because they would lead to an overestimation of the endocranial volume.

2.3 | Body mass and encephalization quotient estimations

The most common proxy used to estimate the body mass of a fossil mammal is the area of the first lower molar (Hopkins, 2018), but the taxa studied here either have reduced or no teeth, which means we had to use another proxy. We could have used limb-based mass estimations, with either the lengths of long bones or the midshaft cross-sectional dimensions of the humerus, femur, or both. However, there are no postcrania elements at our disposal to estimate the body mass of AMNH 131777. Another option is to estimate body mass using the occipital condyle width (OCW). This dimension has been found to be a strong predictor of body mass in therian mammals (Engelman, 2022). Therefore, we used the following equation: $\ln(\text{body mass}) = 7.70727 \times \ln(\text{OCW})^{2/3} - 8.21527$ (only therians equation). We used the same equation to estimate the body mass of USNM 452349, *S. gigantea*, and *P. tricuspsis* for consistency.

A standard practice in palaeoneurobiology is to calculate the Encephalization Quotient (EQ; Jerison, 1973). The EQ corresponds to the ratio between the actual brain size (E_i) of a species 'i' and the brain size that is expected for a hypothetical mammal of the same body mass (E_c ; Martin, 1990). The EQ was calculated following the equation from Jerison (1973) ($\text{EQ} = \text{brain size} / (0.12 \times (\text{body mass})^{0.67})$) and the equation from Eisenberg (1981) ($\text{EQ} = \text{brain size} / (0.0553 \times (\text{body mass})^{0.74})$). We used both because Jerison (1973)'s

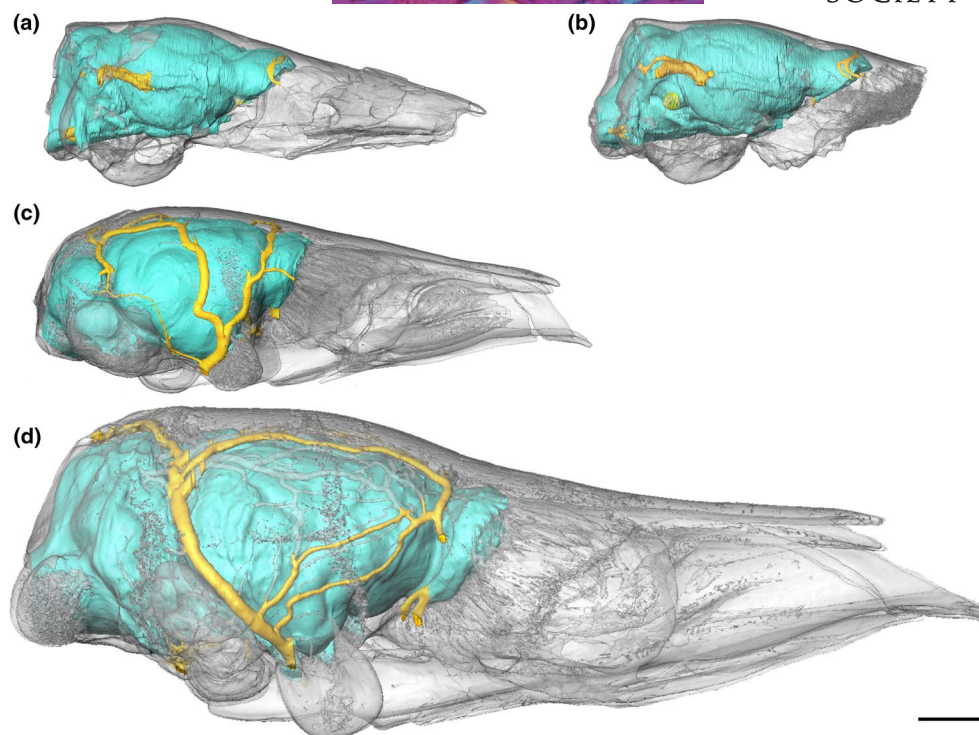


FIGURE 1 Right lateral views of the translucent crania with their virtual endocasts inside of *Metacheiromys marshi* (a) AMNH 131777; (b) USNM 452349; (c) *Phataginus tricuspis* (AMNH 53874); and (d) *Smutsia gigantea* (AMNH 53855). Only the major bony canals have been traced in yellow in extant pangolins. Scale bars represent 10mm.

equation may underestimate and Eisenberg (1981)'s equation may overestimate the EQ of a particular specimen because of differences between the samples that were used to produce these equations (see Bertrand et al., 2017).

2.4 | Cranial vascular system

Little has been published on the cranial vascular system of extant pangolins. Cranial arteries have been described for *P. tetradactyla* (= *Manis macrura*) by Hyrtl (1854) and *Manis javanica* by Bugge (1979). Radiographs of injected cranial arteries are illustrated for *P. tricuspis* (= *Manis tricuspis*) and *Manis pentadactyla* in Du Boulay and Verity (1973). Aspects of the intracranial venous system have been reported recently for extant pangolins as well as for *Pat. americana* (AMNH 78999) and *M. marshi* (USNM 452349) by Billet et al. (2026).

3 | DESCRIPTIONS AND COMPARISONS

3.1 | Overall brain endocast and encephalization quotient

The cranium of the two specimens of *M. marshi* does not show any deformation and only presents a few fractures that minimally alter the final endocast models with the exception of the poor preservation of

the subarcuate fossa in AMNH 131777. *Metacheiromys marshi* USNM 452349 has a larger brain endocast based on endocranial length and width (TL: total endocast length; CRMW: Cerebrum maximal width; Table 1) compared with AMNH 131777. Regarding *P. tricuspis*, it has similar dimensions to USNM 452349, while the endocast of *S. gigantea* displays the largest dimensions of the sample (Table 1). Based on body mass and endocranial volume, AMNH 131777 has an EQ of 0.49 and 0.66 based on Jerison's equation (1973) and Eisenberg's equation (1981), respectively (Table 1), while USNM 452349 has an EQ of 0.57 (Jerison equation) and 0.76 (Eisenberg equation; Table 1). For both *S. gigantea* and *P. tricuspis*, the EQ is 0.48 using Jerison's equation, which is very similar to the values for *M. marshi* using the same equation. With Eisenberg's equation, the values are again higher, at 0.52 and 0.60 for *P. tricuspis* and *S. gigantea*, respectively, but still lower than the values obtained for *M. marshi* (Table 1).

3.2 | Olfactory bulbs

In dorsal view, the mid-region of the olfactory bulbs in both specimens of *M. marshi* is wide (although wider in AMNH 131777) and then narrows anteriorly towards the tip and posteriorly at the level of the circular fissure (Figure 2a,b). In lateral view, the olfactory bulbs have a triangular form, with the narrowest point located anterodorsally (Figure 3a–d). In both *S. gigantea* and *P. tricuspis*, the olfactory bulbs are rounded in dorsal view and separated by an anteroposterior gap (Figure 2c,d), which is absent

TABLE 1 Linear measurements, surface areas, volumes, EQ, body mass measurements and their ratios for the endocasts of Palaeonodonta and extant pangolins.

	<i>Metacheiromys marshi</i> (AMNH 131777)	<i>Metacheiromys marshi</i> (USNM 452349)	<i>Smutsia gigantea</i> (AMNH 53855)	<i>Phataginus tricuspis</i> (AMNH 53874)
Measurements (mm)				
Total endocast length (TL)	35.12	40.05	69.33	40.22
Olfactory bulb length (OL)	7.83	9.09	15.00	7.60
Olfactory bulb width (OW)	15.59	16.21	30.10	18.74
Olfactory bulb height (OH)	8.31	8.09	18.49	11.40
Cerebrum maximal length (CRML)	18.09	19.26	38.85	20.30
Cerebrum maximal width (CRMW)	21.51	23.22	46.06	29.95
Cerebrum maximal height (CRMH)	15.39	16.02	34.33	20.70
Cerebellum maximal length (CLML)	9.50	10.26	19.45	11.81
Cerebellum maximal width (CLMW)	18.00	19.68	36.25	25.14
Occipital condylar width (OCW)	15.31	15.32	37.65	20.44
Ratios linear measurements (%)				
OL/TL	22.29	22.70	21.64	18.90
OL/OW	50.22	56.08	49.83	40.55
OL/OH	94.22	112.36	81.12	66.67
CRML/TL	51.51	48.09	56.04	50.47
CLMW/CRMW	83.68	84.75	78.70	83.94
OW/CRMW	72.48	69.81	65.35	62.57
OW/CLMW	86.61	82.37	83.03	74.54
OL/CRMH	50.88	56.74	43.69	36.71
CLMW/CRMH	83.68	84.75	78.70	83.94
Surface areas (mm ²) and volumes (mm ³)				
Total endocast surface area (TS)	2270.02	2678.25	9578.00	3555.60
Neocortical surface area (NS)	237.79	307.18	2647.17	1131.91
Total endocast volume (TV)	5725.65	6641.68	46404.20	11289.50
Olfactory bulb volume (OV)	407.28	425.83	2590.81	611.43
Petrosal lobule volume (PV)	—	10.23	—	—
Ratios surface areas and volumes (%)				
OV/TV	7.11	6.42	5.58	5.42
OV/BM	0.04	0.05	0.01	0.02
PV/TV	—	0.15	—	—
PV/BM	—	0.001	—	—
NS/TS	10.48	11.65	27.64	31.83
NS/BM	0.03	0.03	0.01	0.04
Encephalization quotient (EQ)				
EQ Jerison (1973)	0.49	0.57	0.48	0.48
EQ Eisenberg (1981)	0.66	0.76	0.52	0.60
Body mass (BM)	928.96	931.19	21662.95	2640.60

Note: The values in bold are published in Bertrand et al. (2022).

in *M. marshi* where instead we can observe the cast of the superior olfactory sinus (Figure 2a,b). The superior olfactory sinus is also visible in *Epoicotherium* sp. (Patterson et al., 1992: figure 19). In lateral view, the olfactory bulbs are shorter anteroposteriorly in both *S. gigantea* and *P. tricuspis* (Figure 3e–h) compared with *M.*

marshi (Figure 3a,b); however, the narrowest point of the olfactory bulbs is also the anterodorsal region as in *M. marshi* (Figure 2a,b). Emry (1970) described *Pat. americana* as having short olfactory bulbs anteroposteriorly, which is more similar to extant pangolins than to *M. marshi*. In contrast, the olfactory bulbs in *Pal. ignavus*

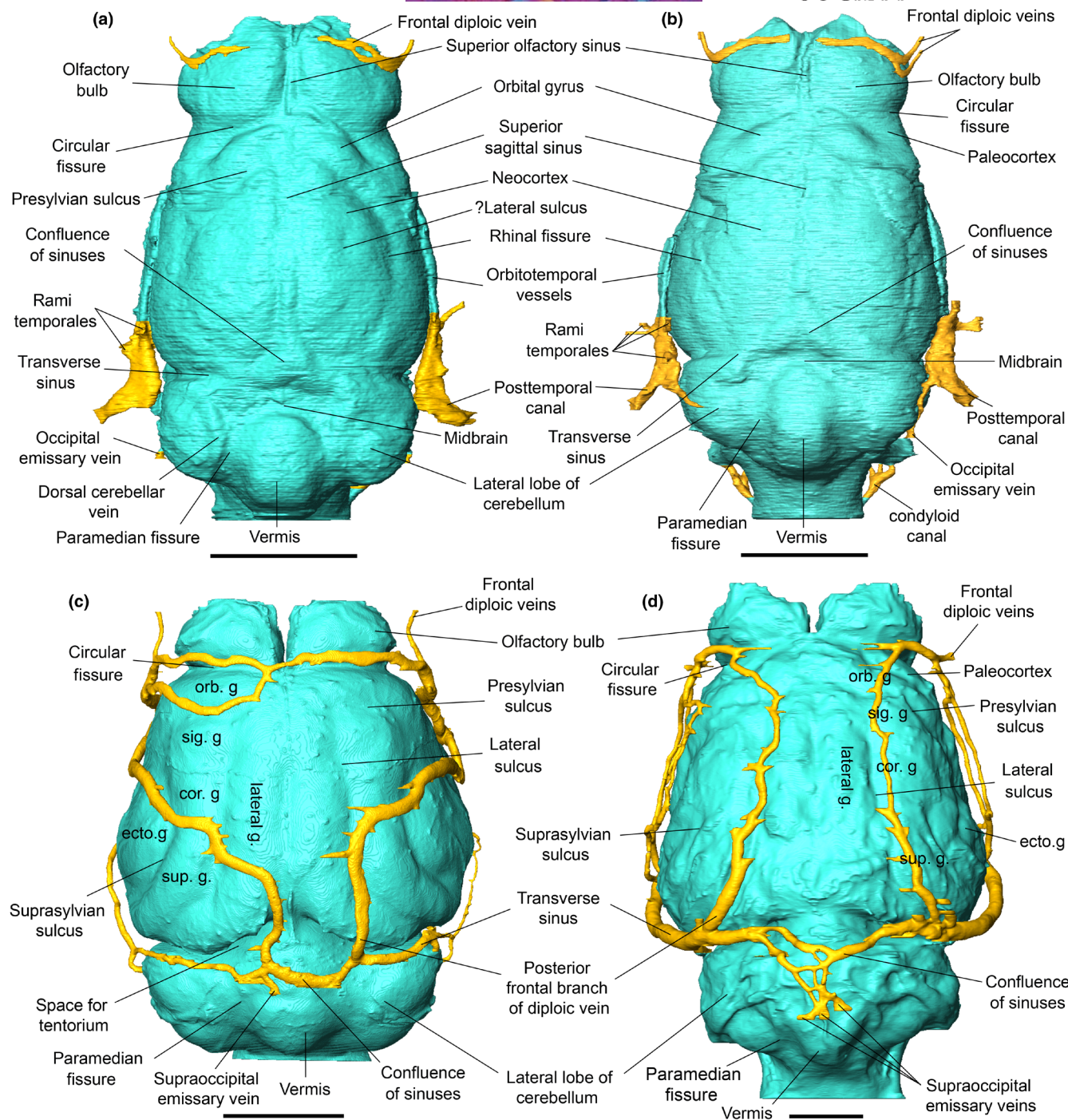


FIGURE 2 Virtual reconstructions in dorsal view of the brain endocasts of *Metacheiromys marshi* (a) AMNH 131777; (b) USNM 452349; (c) *Phataginus tricuspidis* (AMNH 53874); and (d) *Smutsia gigantea* (AMNH 53855). Cor. g, coronal gyrus; ecto. g, ectosylvian gyrus; lateral g, lateral gyrus; orb. g, orbital gyrus; sig. g, sigmoid gyrus; sup. g, suprasylvian gyrus. Bony canals are in yellow. Scale bars represent 10 mm.

have similar proportions to those of *M. marshi*, its close relative (Simpson, 1931). The olfactory bulbs of *Epoicotherium* sp. are anteroposteriorly shorter and mediolaterally wider (Patterson et al., 1992: figure 19) compared with *M. marshi* and the two extant pangolins. The circular fissure, which separates the olfactory bulbs from the rest of the endocast, appears expanded in *M. marshi* (Figure 2a,b) compared with the two modern species. It is narrower in *S. gigantea* (Figure 2d) and even more compressed

anteroposteriorly in *P. tricuspidis* (Figure 2c). The anterior aspect of the olfactory bulbs is oriented more ventrally in *M. marshi* compared with *S. gigantea* and *P. tricuspidis* in which it is oriented more anteriorly (Figure 1). One of the reasons might be due to the fact that the olfactory bulbs are more expanded anterodorsally in *M. marshi* than in both extant pangolins (Figure 1).

The olfactory bulbs of AMNH 131777 represent a total of 7.10% of the total volume of the endocast and 0.04% compared

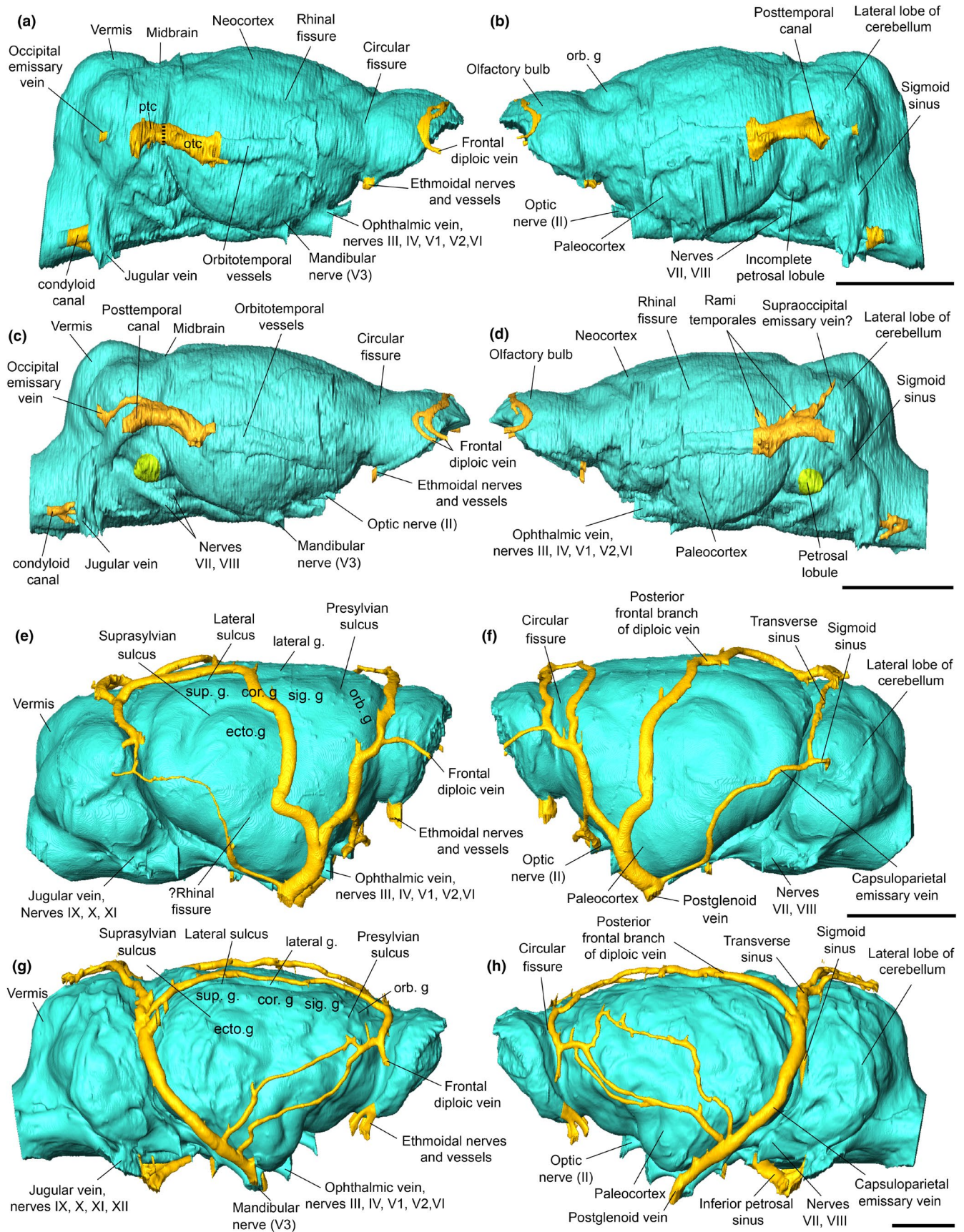


FIGURE 3 Virtual reconstructions in lateral view of the brain endocasts of *Metacheiromys marshi* (a, b) AMNH 131777; (c, d) USNM 452349; (e, f) *Phataginus tricuspidis* (AMNH 53874); and (g, h) *Smutsia gigantea* (AMNH 53855). Cor. g, coronal gyrus; ecto. g, ectosylvian gyrus; lateral g, lateral gyrus; orb. g, orbital gyrus; otc, orbitotemporal canal; ptc, post-temporal canal; sig. g, sigmoid gyrus; sup. g, suprasylvian gyrus. Bony canals are in yellow. The black dashed lines represent the border between the otc and ptc, which corresponds to the position of the transverse sinus. Scale bars represent 10 mm.

with body mass (Table 1). They account for a higher volume in USNM 452349 (Table 1), but represent a lower percentage in comparison to endocranial volume (6.42%), but higher compared with body mass (0.05%). In terms of the linear measurements of the olfactory bulbs, they are slightly higher in USNM 452349 than in AMNH 131777 (Table 1). In *S. gigantea*, the olfactory bulbs represent a lower percentage in relation to both endocranial volume (5.58%) and body mass (0.01%; Table 1) compared with *M. marshi*. In *P. tricuspidis*, the volume of the olfactory bulbs represents a similar ratio to *S. gigantea* in comparison to both endocranial volume (5.42%) and body mass (0.02%; Table 1). Using the ratios OL/OH, OL/OW, OL/TL (OL: olfactory bulb length, OH: olfactory bulb height, OW: olfactory bulb width), we observe that *M. marshi* has more elongated olfactory bulbs than the extant species, in which the bulbs appear to be compressed anteroposteriorly (Table 1, Figure 3).

3.3 | Cerebrum and midbrain

The cerebrum, as in all other mammals, is composed of two different parts, the neocortex and the paleocortex (= piriform lobe; Martin, 1990). In dorsal view, the cerebrum of *M. marshi* displays an elongated ovoid shape with a maximum width in the mid-region to posterior third that slightly narrows towards the olfactory bulbs, which means that the cerebrum is mediolaterally narrower anteriorly (Figure 2a,b). In the extant pangolins, the cerebrum is more rectangular in dorsal view, with the posterior region being wider than the anterior part (Figure 2c,d). *Patriomanis americana* has a smaller cerebrum compared with the extant pangolins (Emry, 1970). Both *Palaeonodon ignavus* and *Epoicotherium* sp., have a cerebrum that is mediolaterally narrower anteriorly compared with its posterior region than *M. marshi* and extant pangolins (Simpson, 1931; Patterson et al., 1992: figure 19). The cerebrum is separated from the olfactory bulbs by the circular fissure in all taxa including *Epoicotherium* sp. and it was likely the case as well in *Pal. ignavus* and *Pat. americana*, although it was not noted in the original descriptions of Simpson (1931) and Emry (1970). In dorsal view, the medial region of the cerebrum is more anteriorly positioned than the lateral edges in *M. marshi* and *S. gigantea* (Figure 2a,b,d), while in *P. tricuspidis* (Figure 2c) and *Epoicotherium* sp. (Patterson et al., 1992: figure 19), it is mediolaterally straight. In both specimens of *M. marshi*, the neocortical surface is delimited by the rhinal fissure laterally (Figures 2a,b and 3a,b), the transverse sinus posteriorly, and the circular fissure anteriorly (Figure 2a,b). In dorsal view, the neocortex does not expand laterally (Figure 2a,b) and in lateral view, the neocortex does not expand ventrally either, and is overall mainly

confined to the dorsal aspect of the endocast (Figure 3a,b). In dorsal and lateral views, the neocortex expands laterally, ventrally, and posteriorly more in both *S. gigantea* and *P. tricuspidis* compared with *M. marshi* (Figures 2c,d and 3e–h). In lateral view, the neocortex of the extant taxa is also delimited by the rhinal fissure from the paleocortex (Figure 3e–h). The neocortex of *M. marshi* (AMNH 131777) accounts for 10.54% of the total surface of the endocast (Table 1). In *M. marshi* (USNM 452349), it represents 11.65% of the endocast (Table 1). Compared with the fossils, the neocortex represents a much larger proportion of the brain in both *S. gigantea* (25.96%) and *P. tricuspidis* (32.25%). In relation to body mass, the neocortex is smaller in *S. gigantea* (0.01%) and higher in *P. tricuspidis* (0.04%) in comparison to *M. marshi* (0.03%). The rhinal fissure would have had a more dorsal position in *Pat. americana* compared with *Manis* (Emry, 1970). The same structure was also annotated with a question mark in *Pal. ignavus* but its position was not discussed in Simpson (1931: figure 9). The rhinal fissure in *Pal. ignavus* appears to be in a similar position as in *M. marshi*, also suggesting a neocortical expansion limited to the dorsal aspect of the endocast. Similarly in *Epoicotherium* sp. (Patterson et al., 1992: figure 19), the neocortex appeared to have been limited to the dorsal surface of the cerebrum delimited by the rhinal fissure laterally, although not labelled.

As in *M. marshi*, there is no contact of the neocortex with the olfactory bulbs in the extant taxa because of the presence of the circular fissure anteriorly (Figure 3e–h). In dorsal view, the circular fissure is in contact with the neocortex medially and the paleocortex laterally in *M. marshi* (Figure 2a,b). In the extant species, the posterior region of the neocortex is separated from the cerebellum by the ossified tentorium, which acts as a physical barrier between these structures (Figure 3e–h; S2m–p). The orbital gyrus can be differentiated in the most anterior region of the neocortex in *M. marshi*, *S. gigantea*, and *P. tricuspidis* (see fresh brain of a *P. tricuspidis* in Imam et al., 2017: Figure 1a,b). This gyrus is delimited anteriorly by the circular fissure and posteriorly by the presylvian sulcus (Figure 2; as observed in the carnivore *Canis* in Lyras et al., 2023: figure 17.4e), medially by the superior sagittal sinus (or by the medial border of the hemispheres in extant pangolins as their superior sagittal sinus if they have one does not leave a trace on the endocast) and laterally by the rhinal fissure (Figures 2 and 3). In dorsal view, it is difficult to identify the presence or absence of other sulci in both specimens of *M. marshi* (Figure 2a,b). We note the possible presence of a lateral sulcus on the right hemisphere of *M. marshi* AMNH 131777 (Figure 2a) and *Epoicotherium* sp. (Patterson et al., 1992: figure 19). Simpson (1931) also mentioned that one or more longitudinal sulci may have been present in *Pal. ignavus*, but Patterson et al. (1992) noted that a presylvian sulcus (=transverse cerebral fissure) was not present in *Palaeonodon*. In *Epoicotherium* sp., a presylvian sulcus

and an orbital gyrus are both present and well developed (Patterson et al., 1992: figure 19).

In dorsal view, the gyri and sulci on the surface of the endocranium of *P. tricuspidis* are relatively well demarcated and some of them are visible in *S. gigantea* (Figure 2c,d). The orbital gyrus, presylvian, and lateral sulci are all visible in *P. tricuspidis* and *S. gigantea*. The lateral sulcus holds a similar position in the extant taxa as in *M. marshi* (Figure 2). Additionally, both extant taxa have a clearly demarcated lateral gyrus extending anteroposteriorly bordered by the cerebral hemisphere midline medially and the lateral sulcus laterally (Figure 2c,d). Lateral to the latter sulcus, there are three gyri running in an anterior to posterior direction: sigmoid, coronal, and suprasylvian gyri (Figure 2c,d). They could not be distinguished with ease, so we used Imam et al. (2017) as a guide to identify them in both *P. tricuspidis* and *S. gigantea*. Lateral to these gyri, a suprasylvian sulcus is present and more clearly visible in *P. tricuspidis* than in *S. gigantea* (Figure 2c,d). The most lateral region next to this sulcus corresponds to the ectosylvian gyrus (Figure 2c,d). In dorsal view, anterior to the orbital gyrus in *S. gigantea*, a sulcus and likely the paleocortex are visible (Figures 2d and 3g,h), suggesting that the neocortex only contacts the circular fissure medially as in *M. marshi*, but contrasts with *P. tricuspidis* in which the neocortex is in contact with the circular fissure mediolaterally (Figure 2c). Those different gyri and sulci can also be seen in lateral view with the ectosylvian gyrus as the most ventrally located neocortical gyrus (Figure 3e-h). We were able to identify the anterior and posterior ectosylvian gyri, which are separated by the sylvian sulcus (see Imam et al., 2017). The sylvian sulcus is very faint, is not visible in lateral view, and only visible when observed at specific angles. In lateral view, the paleocortex is more ventrally expanded in *P. tricuspidis* and *S. gigantea* in comparison to *M. marshi* (Figure 3). In ventral view, the paleocortex appears more developed anteriorly in *M. marshi* and *S. gigantea*, forming bulbous lobes also known as olfactory peduncles (Igado et al., 2021), in comparison to *P. tricuspidis*, which exhibits less pronounced lobes (Figure 4c). Emry (1970) described *Pat. americana* as displaying a pattern of sulci very similar to that of *Manis* without providing further details.

In dorsal and lateral views, *M. marshi* has a groove located posterior to the cerebrum and anterior to the cerebellum corresponding to the exposure of the midbrain (Figures 2a,b and 3a,b). In *P. tricuspidis* and in *S. gigantea*, the midbrain is not visible. It is covered mainly by the neocortex and also slightly by the cerebellum (see Imam et al., 2017: Figure 6a). *Patriomanis americana* and *Pal. ignavus* were also described as not displaying an exposed midbrain by Simpson (1931) and Emry (1970) but it is challenging to verify this claim as this region is not well preserved on the latex endocranium of *Pat. americanus*. On the reconstruction of the brain endocranium of *Pal. ignavus*, the midbrain is not annotated, only the confluence of sinuses is labelled and there appears to be little space between the sinuses and the vermis (Simpson, 1931: figure 9). In *Epoicotherium* sp., the midbrain is not visible and likely ventral to the cerebrum and cerebellum as these two structures are in contact with each other (Patterson et al., 1992: figure 19). An extensive dorsolateral gap is present between the cerebrum and the cerebellum in *P. tricuspidis* in

contrast to *S. gigantea*, in which the gap is shallower (Figures 2c,d and 3e-h). This space for the ossified tentorium is hidden dorsally by the large canal containing the transverse sinus in *S. gigantea*, which is relatively thinner in *P. tricuspidis* (Figures 2c,d and 3e-h). There is a clear development of the ossified tentorium in *P. tricuspidis* in contrast to *M. marshi* in which this structure is absent (Figure 5). In *P. tricuspidis*, the tentorium includes processes from the parietal, squamosal, and alisphenoid, while in *S. gigantea*, it is made of the same bones minus the alisphenoid. An ossified tentorium was present in the early pangolin *Pat. americana* but was less developed than in *Manis*. It is comprised of parietal and squamosal (Gaudin et al., 2016). According to Emry (1970), an ossified tentorium was present in the palaeoanodont *Pal. ignavus*, although less prominent than in *Manis*; however, he did not specify the bones comprising the tentorium. Similarly, *Epoicotherium* sp. was described as having an ossified tentorium by Patterson et al. (1992).

3.4 | Cerebellum

The cerebellum is slightly narrower than the maximum mediolateral dimension of the endocranium in all specimens, although to a higher degree in *S. gigantea* and potentially in *Pal. ignavus* (Figure 2; Simpson, 1931: figure 9). Interestingly, the cerebellum appears to be the narrowest mediolaterally in *Epoicotherium* sp. (Patterson et al., 1992: figure 19). The ratio between the cerebellum maximal width (CLMW) and the cerebrum maximal width (CRMW) shows that in *M. marshi* and *P. tricuspidis*, the cerebellum accounts for 83–84% of the width of the cerebrum, while in *S. gigantea*, the cerebellum accounts for only 78% of the cerebrum (Table 1). In dorsal view, each lateral lobe of the cerebellum is medially separated from the vermis by the paramedian fissure. A dorsal cerebellar vein left a trace lateral to the paramedian fissure in *M. marshi* (AMNH 131777; Figure 2a). The vermis and lateral lobes are of similar proportions in all taxa described here as well as in *Pat. americana* (Emry, 1970). The cerebellar lobes are slightly broader than the vermis in *Epoicotherium* sp. (Patterson et al., 1992: figure 19). These cerebellar structures were not compared in terms of their proportions in *Pal. ignavus* but appear to be of similar proportions (Simpson, 1931: figure 9). The cast of the vermis does not have any trace of the transverse fissures in the described specimens including in *Pal. ignavus* (Simpson, 1931). However, this is likely due to the transverse fissures not leaving a mark on the endocranial cavity as they are present on the brain of *P. tricuspidis* (Imam et al., 2017: figure 1). No description of cerebellum anatomy for *Pat. americana* was provided in Emry (1970) and the natural endocranium does not provide sufficient details for formulating a fair description of the cerebellar anatomy. The paramedian fissure is well marked on the endocranial surface of *M. marshi* and *P. tricuspidis* in comparison to *S. gigantea* in which this structure is harder to distinguish, which could be due to the dura mater being thicker in that region (Figure 2). In lateral view, the vermis is more dorsally expanded in *M. marshi* compared with *P. tricuspidis*

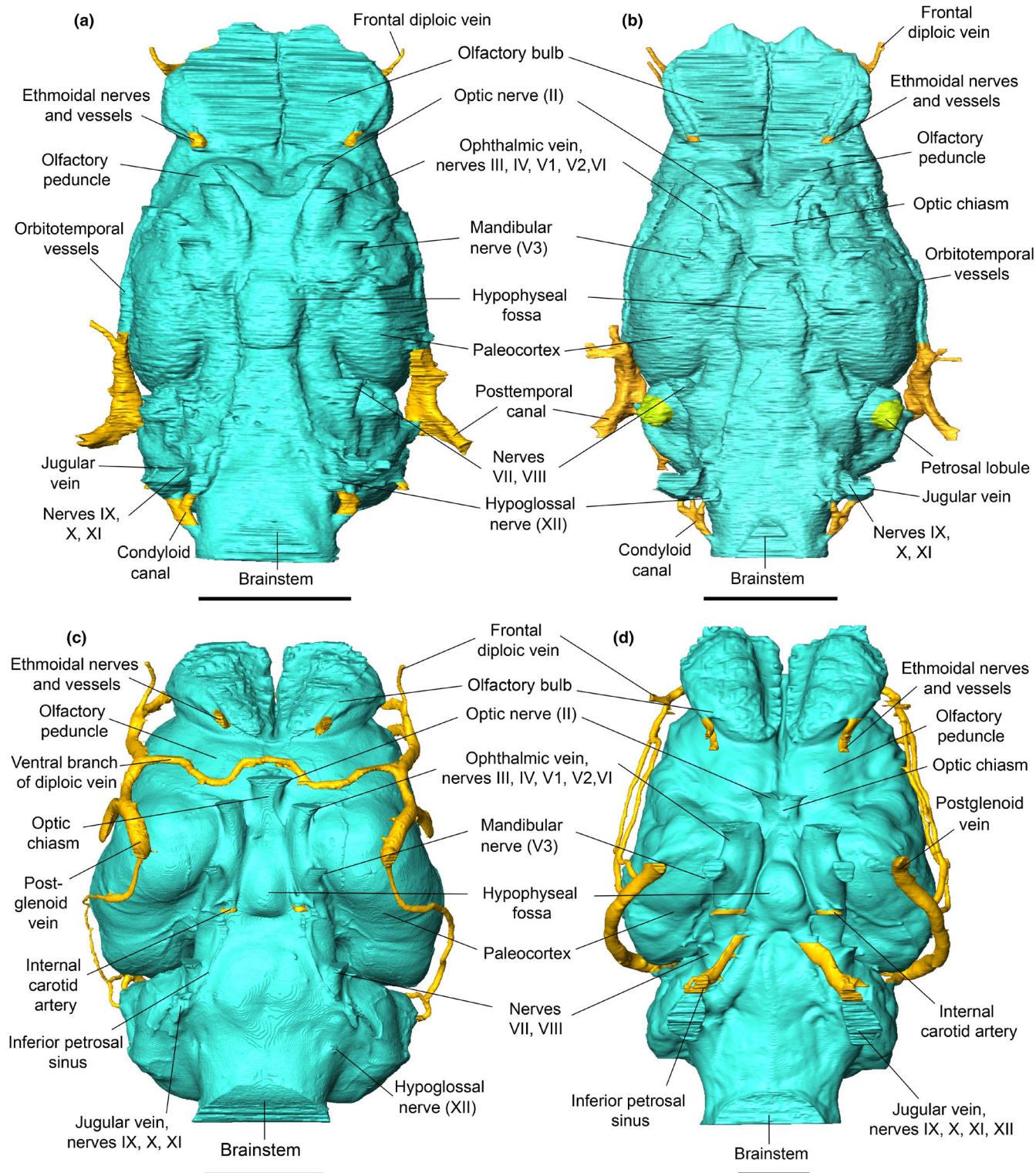


FIGURE 4 Virtual reconstructions in ventral view of the brain endocasts of *Metacheiromys marshi* (a) AMNH 131777; (b) USNM 452349; (c) *Phataginus tricuspidis* (AMNH 53874); and (d) *Smutsia gigantea* (AMNH 53855). Bony canals are in yellow. Scale bars represent 10 mm.

and *S. gigantea* (Figure 3). In lateral view, the petrosal lobules (only fully segmented in USNM 452349) are located anteroventral to the rest of the cerebellum (Figure 3c,d). Their combined volume is 10.23 mm³. The petrosal lobules represent 0.15% and 0.001% of the brain endocast and body mass, respectively. In *M. marshi*

(AMNH 131777), the volume of the petrosal lobules was not measured because only part of these structures could be reconstructed (Figure 3b). In *S. gigantea* and *P. tricuspidis*, the subarcuate fossae are very reduced and therefore the petrosal lobules could not be quantified in these two specimens (Figure 3e–h). Simpson (1931)

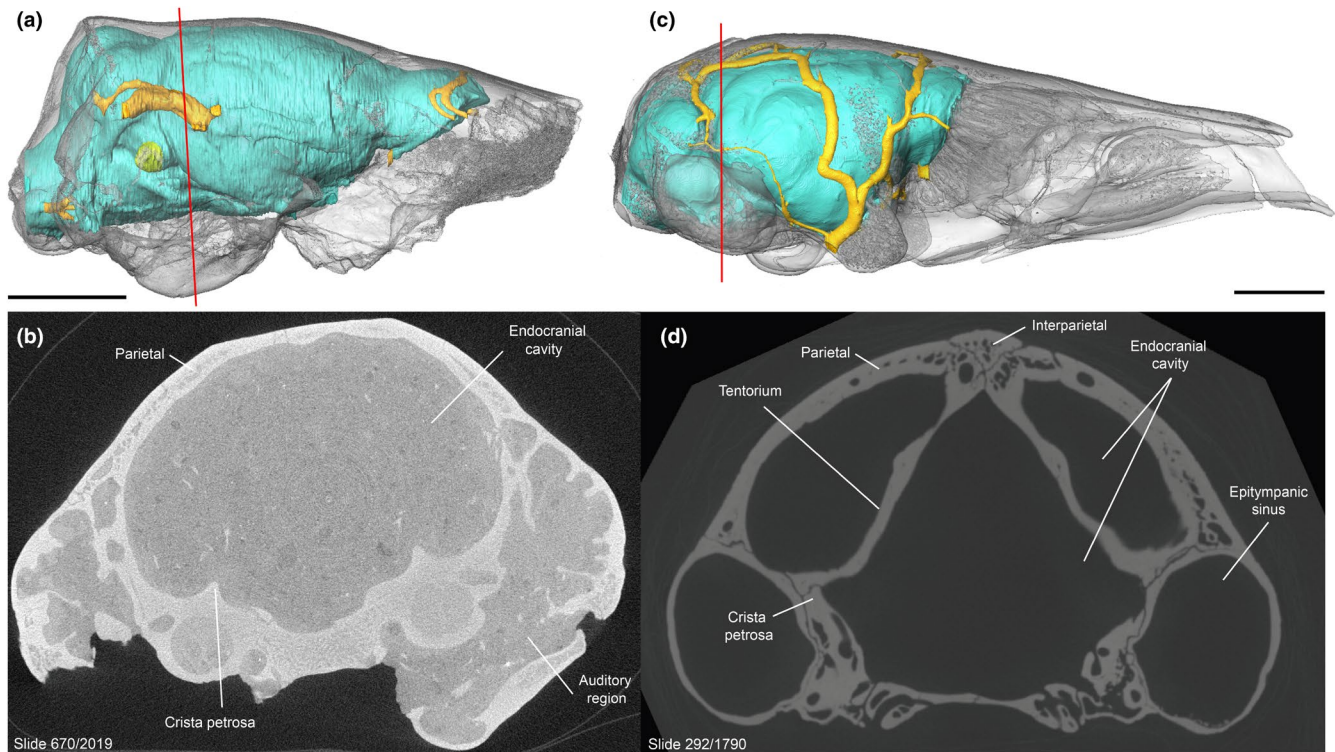


FIGURE 5 Translucent crania with the virtual endocast inside in lateral view and high-resolution X-ray computed tomography slices of (a, b) *M. marshi* (USNM 452349) and (c, d) *Phataginus tricuspis* (AMNH 53874). CT slices were taken at the levels indicated with the red lines of each specimen. Scale bars represent 10 mm.

mentioned that the floccular regions of the cerebellum (= petrosal lobules) are not visible in *Pal. ignavus*. CT scanning of a specimen of *Pal. ignavus* will be necessary to verify the presence or absence of these structures.

3.5 | Cranial nerves and blood vessels

In lateral view, the ethmoidal nerve and vessels are located ventral to each olfactory bulb in all specimens (Figure 3). In *S. gigantea*, the canal containing these nerves and vessels divides into two branches that exit the cranium separately (Figure 3g,h). This contrasts with *M. marshi* and *P. tricuspis*, in which this canal is restricted to one foramen (Figure 3a–f). In ventral view, *M. marshi* has a canal for the optic nerve (II) located posterior to the circular fissure connected to the optic chiasm, which is located posteromedial to the cast of each optic nerve (Figure 4a,b). This configuration is different in the extant taxa, with *P. tricuspis* and *S. gigantea* having the optic canals more posteriorly located, the chiasm less prominent, and shorter canals for the optic nerves leading to the optic foramina (especially in *P. tricuspis*) compared with *M. marshi* (Figure 4c,d). These canals and the optic foramina are also much closer to the median sagittal plane in extant pangolins compared with *M. marshi*, in which they open far from each other mediolaterally (Figure 4). Using the CT data, we observe that in *P. tricuspis*, the optic nerves remain in the chiasma until they exit the cranium bilaterally through the optic foramen (Figure 4c). In ventral view, posterior to nerve II (optic), the sphenorbital fissure is present

and likely carried the ophthalmic vein and cranial nerves III (oculomotor), IV (trochlear), V_1 (ophthalmic), V_2 (maxillary), and VI (abducens) in all specimens (Figure 4). Indeed, this configuration is likely the ancestral condition for eutherians and is present in many placental mammals, including dermopterans, chiropterans, and carnivorans (Christensen & Evans, 1979; Novacek, 1986; O'Leary et al., 2013).

Posteromedial to the sphenorbital fissures, all specimens preserve the hypophyseal fossa that would have contained the hypophysis (pituitary gland) (Figure 4). This structure has a more rectangular shape and appears larger in *M. marshi* compared with *P. tricuspis* and *S. gigantea* in which it is smaller and more rounded (Figure 4). In ventral view, slightly anterolateral to the hypophyseal fossa, cranial nerve V_3 (i.e., mandibular branch of the trigeminal nerve) is present in all specimens (Figure 4). This branch exits the endocranial cavity through the foramen ovale. Cranial nerves VII (facial nerve) and VIII (vestibulocochlear nerve) can be identified and are located ventral to the boundary between the cerebrum and the cerebellum in *M. marshi* (Figure 3a,b) and anterior to this boundary (ventral to the cerebrum) in *P. tricuspis* and *S. gigantea* (Figure 3c,d). The separation between these two nerves is only visible in *M. marshi* (USNM 452349) because of the poor preservation in AMNH 131777 (Figure 4a,b). The two extant specimens, *P. tricuspis* and *S. gigantea*, have a longer common canal before splitting into separate canals (not traced beyond the common canal in Figure 4c,d) compared with the condition in *M. marshi*.

The exit of the internal jugular vein and cranial nerves IX (glossopharyngeal nerve), X (vagus nerve), and XI (accessory nerve) can

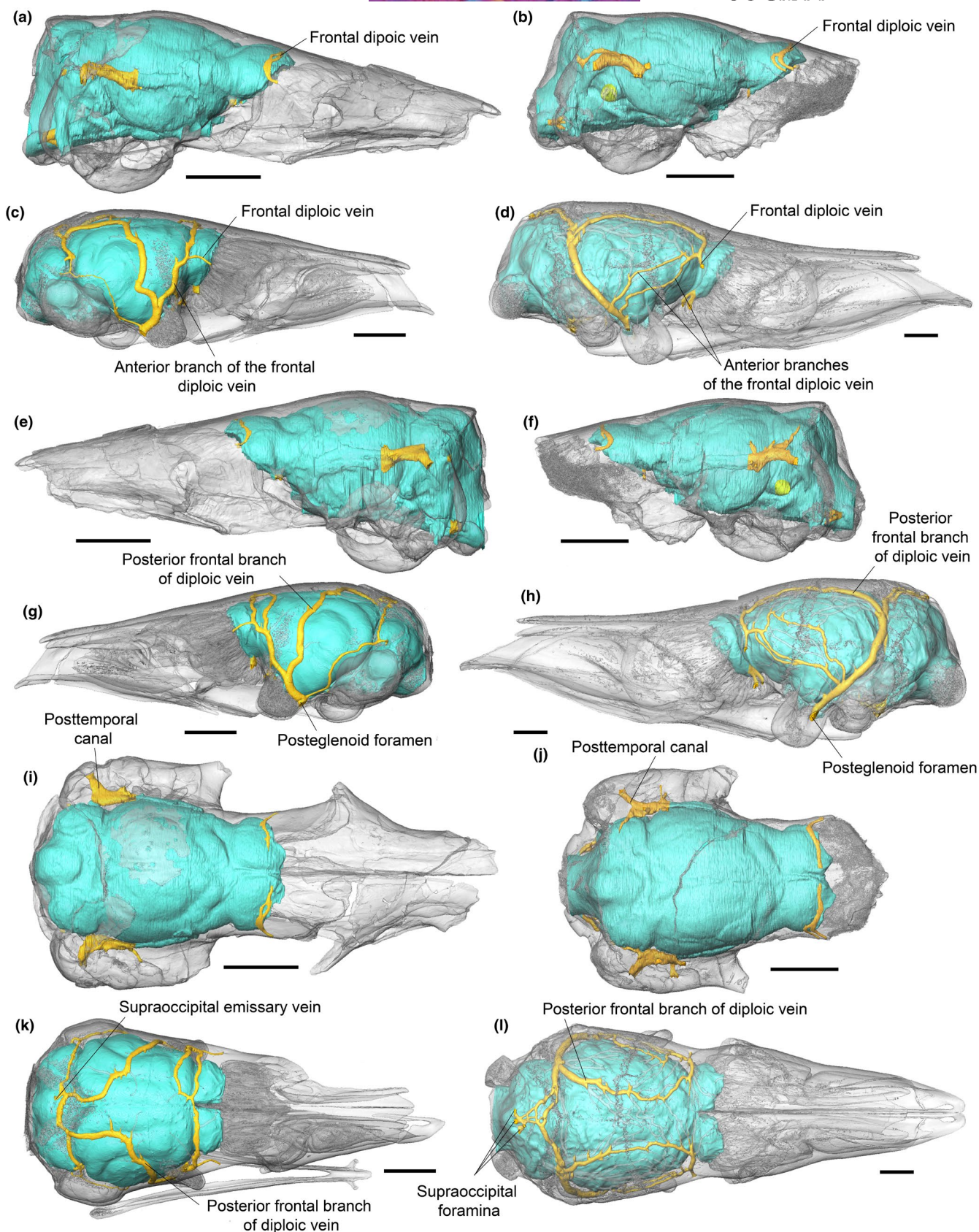


FIGURE 6 Translucent crania with their virtual endocasts inside of the (a–d) lateral right, (e–h) lateral left, (i–l) dorsal of (a, e, i) *Metacheiromys marshi* (AMNH 131777); (b, f, j) *M. marshi* (USNM 452349); (c, g, k) *Phataginus tricuspidis* (AMNH 53874); (d, h, l) *Smutsia gigantea* (AMNH 53855). Only the major bony canals have been traced in yellow in extant pangolins. Scale bars represent 10 mm.

be identified in *M. marshi*. In contrast to other mammals, such as rodents (e.g., Bertrand et al., 2019), there are two foramina instead of one jugular foramen in *M. marshi* (Figure 4a,b), as noted by Gaudin et al. (2019). The nerves would have exited more medially through the medial jugular foramen and the jugular vein through the lateral jugular foramen (see Gaudin et al., 2019). The cast for cranial nerve XII (hypoglossal) located posterior to the jugular foramina leaves the endocranial cavity through the hypoglossal foramen in *M. marshi* (Figure 4a,b). The extant *P. tricuspis* has a more typical arrangement with only one jugular foramen for the internal jugular vein and nerves IX, X, XI (Figure 4c), which is also the case in *Palaeonodon* (Matthew, 1918; Patterson et al., 1992) and *Pat. americana* (Gaudin et al., 2016). As in *M. marshi*, nerve XII exited through the hypoglossal foramen in *P. tricuspis* (Figure 4c). In contrast, in *S. gigantea*, only one large foramen is visible, suggesting that all nerves and vessels (i.e., IX, X, XI, XII and the internal jugular vein) would have exited through this opening (Figure 4d). A separate hypoglossal foramen is absent in *S. gigantea* (Gaudin & Wible, 1999).

In lateral view, a large longitudinal channel containing arteries and veins runs between the occiput and orbit in both specimens of *M. marshi* (Figure 3a–d). The posterior part of this channel is enclosed in a canal, whereas the anterior part is open on the virtual endocast. Although a continuous structure, the bone enclosed portion is actually two named canals: the posterior half opposite the cerebellum is the post-temporal canal and the anterior half opposite the cerebrum is the orbitotemporal canal (see Wible, 1987). The primary occupants of the orbitotemporal canal were the ramus supraorbitalis and accompanying vein and of the post-temporal canal are the arteria and vena diploëtica magna (Wible, 1987). The vessels on the virtual endocast anterior to the orbitotemporal canal are the continuation of the ramus supraorbitalis and accompanying vein, which we refer to as orbitotemporal vessels. The orbitotemporal vessels sent arteries and veins to the temporalis muscle (rami temporales) through foramina in the braincase wall. Gaudin et al. (2019) reported five foramina on the right and four on the left for AMNH 131777, two in the squamosal bilaterally and the remainder in the parietal. The orbitotemporal vessels do not leave a trace on the endocranial surface and the post-temporal canal is absent in *P. tricuspis* and in *S. gigantea* (Figure 3e–h), and in *Pat. americana* (Billet et al., 2026). The orbitotemporal vessels appear to leave a trace on the endocast of *Epoicotherium* sp. and the orbitotemporal canal might also be present (Patterson et al., 1992: figure 19). Bugge (1979) reported the arteria diploëtica magna as absent in *Manis javanica*, but a small ramus supraorbitalis runs open in the endocranium. It is uncertain whether or not the African pangolins had a similar ramus supraorbitalis. Foramina for rami temporales are absent in *Pat. americana* (Gaudin et al., 2019) and extant pangolins (Jollie, 1968).

In dorsal view of the endocast of *M. marshi*, the superior sagittal sinus running medially between the cerebral hemispheres connects to the transverse sinus, which in turn is connected to the confluence of sinuses, forming the posterior margin of the neocortex (Figure 2a,b). The same configuration was observed in *Pal. ignavus*

by Simpson (1931) and in *Epoicotherium* sp. (Patterson et al., 1992: figure 19). In extant pangolins and *Pat. americana*, the presence of the superior sagittal sinus cannot be determined with certainty as it does not leave a trace on the surface of the endocranial cavity (Figure 2c,d); instead, there is a vast network of diploic canals in the frontal and parietal (Billet et al., 2026). The transverse sinus, which connects to the confluence of sinuses in *P. tricuspis* and *S. gigantea*, has branches directed posteriorly, but these are not present on either specimen of *M. marshi* (Figure 2c,d). After inspecting the CT data carefully, we confirm that this branch leads to a multitude of small canals in the interparietal and supraoccipital in *P. tricuspis*, while these canals are relatively larger in *S. gigantea*. Their content likely corresponds to supraoccipital emissary veins exiting caudally through multiple supraoccipital foramina in both specimens, although they are more numerous and larger in diameter in *S. gigantea* (Figure 6a,b).

In placentals, the transverse sinus divides into three branches: the capsuloparietal emissary vein (CEV) or temporal sinus, the sigmoid sinus (SS), and the superior petrosal sinus (SPS; e.g., Wible, 1984; Novacek, 1986; Muizon et al., 2015). The CEV exits the cranium as the postglenoid vein via the postglenoid foramen, the SS as the internal jugular vein via the jugular foramen, and the SPS runs anteriorly on the endocranial surface of the petrosal. The postglenoid foramen is absent in *M. marshi* (Gaudin et al., 2019), and there is no indication of the CEV or of the SPS (Figure 2a,b). However, a postglenoid foramen is present in *Palaeonodon* sp. USGS 21876 (Patterson et al., 1992). In *P. tricuspis* and *S. gigantea*, the CEV is continuous with the transverse sinus, but they are both encased in canals (Figure 3e–h). In lateral view, the CEV starts posterior to the tentorium at the level of the lateral lobe of the cerebellum and runs anteroventrally, reaching the level of the ventral aspect of the paleocortex and leaving the cranium through the postglenoid foramen as the postglenoid vein (Figure 3e–h). The whole canal (i.e., transverse sinus, CEV, and postglenoid vein) is much larger in *S. gigantea* than in *P. tricuspis* (Figure 3e–h). Billet et al. (2026) found a similar canal for these veins in *Pat. americana* and extant pangolins. Neither *P. tricuspis* nor *S. gigantea* show evidence of the SPS.

A large SS is seen in *M. marshi* (Figure 3a,b). Its most dorsal segment is in a short canal that communicates with the post-temporal canal. It then lies against the cerebellum and its path has a slightly posteroventral orientation that becomes completely ventral on the brainstem, exiting at the jugular foramen. Additionally, the SS is connected to the condyloid vein, which is encased in a canal in *M. marshi* (Figure 3a,b). The content of the condyloid canal would have exited via the foramen magnum in this taxon (Figure 4a,b). The condyloid canal is also connected to the hypoglossal foramen. One difference between the two specimens of *M. marshi* is that in AMNH 131777 the anterior end of the condyloid canal splits into two canals, while in USNM 452349, there are three canals including two leading to the SS and one to the hypoglossal foramen (Figure 4a,b). The SS is tiny in the extant pangolins. In *S. gigantea*, the SS on the left side is first in a short canal oriented dorsoventrally and then connects to the endocranial cavity as in *M. marshi*; a similar canal is absent

on the right side (Figure 3g,h). In *P. tricuspis*, the SS is also within a short canal, but it is oriented anteroposteriorly before it too joins the endocranial cavity. This specimen also exhibits asymmetry, as one side presents two canals while the other only one (Figure 3e–f). The path of the SS is challenging to identify on the surface of the endocranial cavity, but it appears to exit via the jugular foramen as in *M. marshi* (Figure 3a–f). The condyloid canal is absent in both *P. tricuspis* and *S. gigantea* (Figure 4c,d). In lateral view in *M. marshi*, the tract for the occipital emissary vein (not preserved on the left side of USNM 452349) is connected to the SS and to the post-temporal canal – and exited the cranium posteriorly through the mastoid foramen (Figure 3a–d) as in the dog (Evans & de Lahunta, 2012; Wible, 2008). There is also a separate posterior exit out of the cranium for the content of the post-temporal canal through the post-temporal foramen in *M. marshi* (Gaudin et al., 2019). The occipital emissary vein canal is absent in *P. tricuspis* and *S. gigantea* (Figure 3e–h). The inferior petrosal sinus is hard to trace in *M. marshi* (Figure 4a,b), as noted by Gaudin et al. (2019). It is present in both *P. tricuspis* and *S. gigantea* (Figure 4c,d). This sinus runs open on the endocranial in *P. tricuspis* but is encased inside a canal in *S. gigantea*.

Metacheiromys marshi, *Pat. americana* (Gaudin et al., 2016), *P. tricuspis*, and *S. gigantea* have a frontal diploic vein foramen (Figures 2–4 and 6). However, in *M. marshi* this opening is more ventrally positioned in the orbit, whereas it is near the dorsal orbital rim in the others (Figure 6; Billet et al., 2026). Additionally, we observe intraspecific variation in *M. marshi*, with USNM 452349 displaying two foramina (on the right side only), while AMNH131777 only has one as in extant pangolins (Figure 6a,b). The frontal diploic vein has an extensive area of drainage in the pangolins, but this is more limited in *M. marshi*. In the pangolins, it drains veins that occupy a canal running along the circular fissure (Figure 3e–h), but a similar canal and vein are not present in *M. marshi* (Figure 3a,d). Additionally, the extant pangolins have a large posterior frontal branch of the frontal diploic vein within a canal (Figure 3e–h), but these are absent in *M. marshi* (Figure 3a,d). We observe some variation between *P. tricuspis*, and *S. gigantea* in terms of the configuration of the frontal diploic vein. Indeed, in lateral view, the posterior frontal diploic vein of *P. tricuspis* turns ventrally at the level of the coronal gyrus and then connects to an anterior branch of the frontal diploic vein that drains through the postglenoid foramen (Figures 3e,f and 6c,g). Based on a large intraspecific sample (>10 specimens), Billet et al. (2026) found that *P. tricuspis* has a unique pattern of diploic veins within extant pangolins. The classical path that links the CEV and the transverse sinus is very reduced to absent and is replaced by a more extensive diploic network in the frontal area in *P. tricuspis* (also see Figure 3e–h). In *S. gigantea*, the posterior frontal diploic vein continues on the dorsal aspect of the cerebrum until reaching the level of the circular fissure where it turns ventrally and exits through the frontal diploic foramen (Figure 6d,h,i). We also note the presence of anterior branches of the frontal diploic vein in *S. gigantea*, which connect to the capsuloparietal emissary vein (Figures 3g,h and 6d,h). This connection is absent in *P. tricuspis* (Figure 3e,f). Finally, a ventral branch

of the frontal diploic vein is present only in *P. tricuspis* (Figure 4c); it occupies a canal in the frontal, orbitosphenoid, and presphenoid and the left and right vessels communicate on the midline.

Narrow grooves for the internal carotid artery and one of its branches, the stapedia artery, are present on the promontorium of the petrosal in *M. marshi* (Gaudin et al., 2019). However, these arteries appear to leave no trace on the endocranial cavity. It is uncertain if the small stapedia artery is connected via a ramus superior to the ramus supraorbitalis anteriorly and into multiple rami temporales posteriorly as in other fossil laurasiatherians (see Bertrand, Jiménez Lao, et al., 2024). In extant pangolins, the internal carotid is small and the stapedia artery is absent at least in adult pangolins (Bugge, 1979; Gaudin et al., 2019; Guth, 1961; Wible, 1984, 1987). A small canal for the internal carotid artery, posterior to the mandibular nerve (V_3), is visible in ventral view in *P. tricuspis* and *S. gigantea* (Figure 4c,d).

4 | DISCUSSION

4.1 | Endocranial anatomy and potential phylogenetic signals

Morphological features that might represent synapomorphies uniting Palaeonodonta and Pholidota have been challenging to establish because many morphological features are also adaptations to myrmecophagy and fossoriality, and thus potentially prone to convergence (Rose, 2006; Gaudin et al., 2019, 2020). As noted in the Introduction, *Metacheiromys* shares many features of the auditory region with xenarthrans, but also has a decent number of features in common with pangolins (Gaudin et al., 2019). In the Descriptions and comparisons section above, we only made comparisons with extant pangolins as we have followed the view that Palaeonodonta are likely stem pangolins (Gaudin et al., 2009; O'Leary et al., 2013). In the following, however, we include xenarthrans in our discussions.

Metacheiromys and extant pangolins have many endocranial dissimilarities including features associated with the olfactory bulbs and the cerebellum. Noticeable differences include the presence of the following features in *Metacheiromys* that are absent in pangolins: (1) superior olfactory sinus, (2) trace of the orbitotemporal vessels on the endocranial surface, (3) post-temporal canal (present in xenarthrans; Le Verger et al., 2021), (4) trace of the superior sagittal sinus on the endocranial surface, (5) trace of the transverse sinus on the endocranial surface, (6) well-developed SS, (7) condyloid canal, (8) occipital emissary vein, and (9) separate foramina for the exit of the internal jugular vein and for cranial nerves IX, X, and XI. We note that the subarcuate fossa is not absent in pangolins but is reduced, while it is more expanded in *Metacheiromys*. It is worth noting that the absence of venous grooves on the endocranial surface of extant pangolins was coded in the phylogenetic analyses of Gaudin and Wible (1999) and Gaudin et al. (2009). Other features present in the extant pangolins but absent in *Metacheiromys* include: (1) the network of diploic

veins in the frontal and parietal (Billet et al., 2026), (2) supraoccipital veins, (3) the ossified tentorium, and (4) the capsuloparietal emissary vein and postglenoid foramen (Table 2). Additionally, the inferior petrosal sinus in *Metacheiromys* is hard to distinguish in comparison to extant pangolins. Other notable differences include the presence of a small neocortex, low number of sulci and gyri, and an exposed midbrain in *Metacheiromys*. Those last anatomical characteristics are likely related to the expansion of the neocortex in extant pangolins (see below).

Nevertheless, *Metacheiromys* and pangolins also share endocranial features that might not be plesiomorphic for all mammals and could potentially be synapomorphies. Among these features, we note two morphological characters: the presence of an orbital gyrus and a presylvian sulcus (Table 2). The orbital gyrus and presylvian sulcus should be considered as co-occurring structures because the orbital gyrus is delimited from the rest of the neocortex by the presylvian sulcus (Imam et al., 2017). Therefore, if the presylvian sulcus is absent, the orbital gyrus will be also absent. We checked the literature for the presence of this sulcus in Pan-Carnivora and Xenarthra to deduce whether or not this sulcus could be a synapomorphy for Pholidotomorpha. The presylvian sulcus is not present in stem Carnivora, specifically in the Eocene Carnivoraformes 'Miacididae' *Vulpavus palustris* (Flink et al., 2021; Lyras et al., 2023; Radinsky, 1977). This sulcus is present in the Eocene stem Carnivoramorpha 'Creodonta' Hyaenodontoida *Cynohyaenodon cayluxi* and *Proviverra typica*; however, these taxa are nested well within 'Creodonta' and the more basal *Thinocyon velox* does not have a presylvian sulcus (Dubied et al., 2019; Flink et al., 2021; Radinsky, 1977). The presence of a presylvian sulcus and the orbital gyrus in 'Creodonta' and in extant Carnivora for which these structures are well developed (Lyras & Van der Geer, 2003) might be derived, although more early diverging members of these groups would be needed to evaluate which condition is more likely to be plesiomorphic. Similarly, it is possible that the common ancestor of Carnivora and Pholidota did not have this pattern (i.e., orbital gyrus and presylvian sulcus), and instead that it evolved independently in both groups, but more basal taxa are required to test this hypothesis.

The extant xenarthran Cingulata (armadillos) *Zaedyus pichiy*, *Chaetophractus villosus*, and *Dasypus novemcinctus* also have a presylvian sulcus, but the orbital gyrus is only well developed in *Z. pichiy* based on the figures published by Tambusso and Fariña (2015) and Troyelli et al. (2023). However, the brain natural endocast of the Eocene xenarthran Cingulata *Utaetus buccatus* presents lateral sulci, but does not have a presylvian sulcus (Dozo, 1998). Regarding Folivora (sloths), the extant *Choloepus* and *Bradypus* and the late Pleistocene *Glossotherium robustum* and *Catonyx tarijensis* also present an orbital gyrus and presylvian sulcus, although the orbital gyrus is not very developed (Boscaini, Iurino, Mamani Quispe, et al., 2020; Boscaini, Iurino, Sardella, et al., 2020). Because of the lack of data for Eocene Folivora, the ancestral condition for Xenarthra cannot be resolved. It is possible that the presence of an orbital gyrus and presylvian sulcus also appeared convergently in Xenarthra, but more

basal representatives will be required to determine the ancestral condition for the group.

As mentioned in the Results section, the Eocene pangolin *Pat. americana* was described as having a cerebral sulcus pattern similar to that of extant pangolins but no images or detailed comparisons were provided by Emry (1970) and the AMNH latex endocast of that specimen does not have sufficient details to make a conclusion. Based on this current understanding of the evolution of the presylvian sulcus, it is likely that early pangolins already had this sulcus and this would support the hypothesis that *Metacheiromys*, *Epoicotherium*, and Palaeonodonta more generally are the sister-clade to Pholidota. It is worth noting that the presence of the orbital gyrus and presylvian sulcus represents very labile structures, with a high level of homoplasy as described above for xenarthrans. However, this is not surprising because brain structures might increase in size when used for a specific behaviour (Bertrand & Krubitzer, 2025). Therefore, we acknowledge the challenge in teasing apart phylogenetic signal from convergence and that the presence of these structures might have also been acquired independently in palaeonodonts and pangolins. Ultimately, more basal members of each group will be crucial to determine the ancestral condition of the orbital gyrus and presylvian sulcus in these various clades.

In the scenario in which palaeonodonts and pangolins are sister-clades, it is possible that the tentorial process of the parietal either arose convergently in Carnivora and in Pholidota or that it was lost in *Metacheiromys*. The next step will be to CT scan the specimen of *Pal. ignavus* (AMNH 15086) to verify the presence and composition of a tentorial process. Another feature shared by both Carnivora and Pholidota is the presence of the dense network of diploic veins enclosed in canals, which is not present in *Metacheiromys* (Billet et al., 2026). This pattern could have also been acquired convergently in both clades as a course within a canal or within the endocranial cavity appears to also be fairly homoplastic as a course in a canal is present in humans (Rangel de Lázaro et al., 2016). Additionally, a large network of veins in canals is present in tillodonts (Bertrand, Jiménez Lao, et al., 2024). Alternatively, if these features (ossified tentorium and dense network of diploic veins within canals) are truly absent in palaeonodonts and can be considered synapomorphies of Carnivora and Pholidota, this would suggest that palaeonodonts might not be so closely related to pangolins.

4.2 | Neurosensory ecology of pholidotomorpha

The auditory region and the postcrania have shown that *Metacheiromys* was likely fossorial and a myrmecophagous mammal like extant pangolins (Gaudin et al., 2019). The size of three brain regions was measured (i.e., olfactory bulbs, neocortex, and petrosal lobules) to study the behavioural ecology of *Metacheiromys*. We used previous research showing that the size of a brain structure is generally correlated with its function (Jerison, 1973). To study that relationship, we looked at the size of a structure in relation to both

TABLE 2 Notable morphological features described in the text for the specimens belonging to Palaeaanodonta and Pholidota.

Morphological features	<i>Metacheiromys marshi</i> (AMNH 13177)	<i>Metacheiromys marshi</i> (USNM 452349)	<i>Palaeaanodon ignavus</i> (AMNH 15086)	<i>Epoicotherium</i> sp. (FMNH UM483; AMNH 9245)	<i>Phataginus tricuspsis</i> (AMNH 53874)	<i>Smutsia gigantea</i> (AMNH 53855)	<i>Patriomanis americanus</i> (AMNH F:AM 78999)
Dissimilarities between Palaeaanodonta and Pholidota							
Cast of the superior olfactory sinus	Present	Present	—	Present	Absent	Absent	—
Shape of each olfactory bulb (dorsal view)	Triangular	Triangular	Rounded	Mediolaterally elongated	Rounded	Rounded	—
Relative olfactory bulb dimension (lateral view)	Anteroposterior > dorsoventral	Anteroposterior > dorsoventral	Anteroposterior > dorsoventral	Anteroposterior < dorsoventral	Anteroposterior < dorsoventral	Anteroposterior < dorsoventral	Anteroposterior < dorsoventral
Shape of the cerebrum (dorsal view)	Ovoid shape	Ovoid shape	Anterior wider than posterior	Anterior wider than posterior	Rectangular (posterior wider)	Rectangular (posterior wider)	—
Rhinal fissure direction	Anteroposterior	Anteroposterior	—	—	Posteroventral	Posteroventral	—
Expansion of neocortex	Confined dorsally	Confined dorsally	—	Confined dorsally	Expands in all directions	Expands in all directions	—
Sigmoid gyrus	Absent	Absent	—	Absent	Present	Present	—
Coronal gyrus	Absent	Absent	—	Absent	Present	Present	—
Suprasylvian gyrus	Absent	Absent	—	Absent	Present	Present	—
Suprasylvian sulcus	Absent	Absent	—	Absent	Present	Present	—
Ectosylvian gyrus	Absent	Absent	—	Absent	Present	Present	—
Lateral gyrus	Absent	Absent	—	Absent	Present	Present	—
Vermis dorsal expansion in lateral view	Strong	Strong	—	—	Weak	Weak	—
Petrosal lobules	Not well preserved but well developed	Well developed	Absent (likely due to preservation)	—	Weakly developed	Weakly developed	—
Optic canal length	Long	Long	—	—	Short	Short	—
Optic chiasma	Well developed	Well developed	—	—	Weakly developed	Weakly developed	—
Optic canal position compared with the circular fissure	Posterior	Posterior	—	—	Greatly posterior	Greatly posterior	—
Shape of the hypophyseal fossa	Rectangular and larger	Rectangular and larger	—	—	Rounded and smaller	Rounded and smaller	—
Cranial nerves VII and VIII position to cerebrum/cerebellum limit	Ventral	Ventral	—	—	Anterior	Anterior	—

(Continues)

TABLE 2 (Continued)

Morphological features	<i>Metacheiromys marshi</i> (AMNH 131777)	<i>Metacheiromys marshi</i> (USNM 452349)	<i>Palaeonodon ignavus</i> (AMNH 15086)	<i>Epoicotherium</i> sp. (FMNH UM483; AMNH 9245)	<i>Phataginus tricusps</i> (AMNH 53874)	<i>Smutsia gigantea</i> (AMNH 53855)	<i>Patriomanis americanus</i> (AMNH F:AM 78999)
Exit of the jugular vein and nerves IX, X and XI	Two foramina	Two foramina	One foramen	—	One foramen	One foramen	One foramen
Hypoglossal foramen	Medial to the jugular vein	Medial to the jugular vein	Posterior to the jugular vein	—	Posterior to the jugular vein	Absent	Posterior to the jugular vein
Orbitotemporal vessels trace on endocranial surface	Present	Present	—	Present	Absent	Absent	Absent
Orbitotemporal canal	Present	Present	—	?Present	Absent	Absent	Absent
Superior sagittal sinus trace on endocranial surface	Present	Present	Present	Present	Absent	Absent	Absent
Transverse sinus	Trace on endocranial surface	Trace on endocranial surface	—	Present	Located in separate canal	Located in separate canal	—
Post-temporal canal	Present	Present	—	—	Absent	Absent	Absent
Rami temporales	Present	Present	—	—	Absent	Absent	—
Sigmoid sinus size	Large and long	Large and long	—	—	Small and short	Small and short	—
Condylloid canal	Present	Present	—	—	Absent	Absent	—
Supraoccipital emissary vein	Absent	Absent	—	—	Numerous and small canals	More numerous and larger canals	—
Occipital emissary vein	Present	Present	—	—	Absent	Absent	—
Capsuloparietal emissary vein	Absent	Absent	—	—	Present	Present	Present
Posterior frontal branch of the diploic vein	Absent	Absent	—	—	Present	Present	Present
Internal carotid artery trace on the endocranial cavity	Absent	Absent	—	—	Present	Present	—
Similar features present in Palaeonodonta and Pholidota							
Circular fissure	Present	Present	Likely present	Present	Present	Present	Likely present
Orbital gyrus	Present	Present	—	Present	Present	Present	—
Presylvian sulcus	Present	Present	—	Present	Present	Present	—
Cerebellum width	Narrower than the cerebrum	Narrower than the cerebrum	—	Narrower than the cerebrum	Narrower than the cerebrum	Narrower than the cerebrum	—
Paramedian fissure	Present	Present	—	Present	Present	Present	—

TABLE 2 (Continued)

Morphological features	<i>Metacheiromys marshi</i> (AMNH 131777)	<i>Metacheiromys marshi</i> (USNM 452349)	<i>Palaeonodon ignavus</i> (AMNH 15086)	<i>Epoicotherium</i> sp. (FMNH UM483; AMNH 9245)	<i>Phataginus tricuspsis</i> (AMNH 53874)	<i>Smutsia gigantea</i> (AMNH 53855)	<i>Patriomanis americanus</i> (AMNH F:AM 78999)
Sphenoidal fissure	Present	Present	—	—	Present	Present	—
Mandibular nerve (V3)	Present	Present	—	—	Present	Present	Present
Frontal diploic vein	Present	Present	—	—	Present	Present	Present
Lateral sulcus	Likely present	Likely present	Likely present	Likely present	Present	Present	Likely present
Other features with variable states in Palaeonodonta and Pholidota							
Inferior petrosal sinus	Hard to distinguish	Hard to distinguish	—	—	Within endocranial cavity	In a separate canal	—
Ossified tentorium	Absent	Absent	?Weakly developed	Present	Very developed	Very developed	Somewhat developed
Medial/lateral regions of the cerebrum anteriorly (dorsal view)	Medially more anterior	Medially more anterior	—	Mediolaterally straight	Mediolaterally straight	Medially more anterior	—
Anterior part of the paleocortex (ventral view)	Well-developed bulbous lobes	Well-developed bulbous lobes	—	—	Weakly developed bulbous lobes	Well-developed bulbous lobes	—
Midbrain exposure	Present	Present	Absent	Absent	Absent	Absent	Absent
Exits of the ethmoidal nerve and vessels	One foramen	One foramen	—	—	One foramen	Two foramina	—
Sigmoid sinus orientation	Dorsoventrally	Dorsoventrally	—	—	Anteroposteriorly	Dorsoventrally	—
Number of condyloid canals	2	3	—	—	Not applicable	Not applicable	—

endocranial volume and body mass (for a review see Bertrand & Krubitzer, 2025).

Concerning the olfactory bulbs, they have a relatively larger size in comparison to both brain and body mass in *Metacheiromys* compared with extant pangolins. Therefore, *Metacheiromys* relied more heavily on its sense of smell than extant pangolins. Molecular studies have found that pangolins have a large number of olfactory receptor genes compared with other mammals, indicating that pangolins have a very good sense of smell (Choo et al., 2016; Li et al., 2024). However, what is important is the ratio between the number of active (functional) vs. inactive (pseudogenes) receptor genes (Imam et al., 2018). The number of functional or intact chemoreceptor genes has been quantified for *Manis* (Martinez et al., 2025). From this study, *Manis* has an average number of intact chemoreceptor genes and therefore average olfaction within mammals. Behavioural and anatomical studies have shown contrasting results. In terms of cortical regions, no specialization of the olfactory system in the brain of pangolins was found in comparison to laboratory rats (Imam et al., 2018). Based on behavioural observations, olfaction might be used as sniffing behaviour when foraging for food as in other mammals (Mohapatra & Panda, 2014), but pangolins do not perform well at 'olfactory distance' and appear to only use olfaction when following scent trails (DiPaola et al., 2020). Additionally, nasal turbinates are not necessarily better developed in myrmecophagous mammals compared with their close relatives (Wright et al., 2024). This mismatch between molecular and morphological data is not uncommon and the link between molecular data and function such as olfaction is rarely tested (except in model organisms) and therefore the results of such studies should be interpreted with caution (Yohe & Krell, 2023). For example, in Yinpterochiroptera, some bats show very specialized olfactory systems, but most of the olfactory genes are lost (Yohe & Krell, 2023). This demonstrates the need to more systematically combine behavioural, anatomical, and genetic data to more fully understand the evolution of senses such as olfaction. It is possible that lower selective pressures in olfaction in the evolution of pangolins led to an expansion of the number of pseudogenes, as has occurred in primates (Niimura et al., 2018).

The orbital gyrus of the neocortex is relatively well developed in *Metacheiromys* and extant pangolins (Imam et al., 2017). This gyrus is part of the orbital cortex, which is located in the frontal lobe, also known as the orbitofrontal cortex in primates and rodents (Duvernoy, 2005; Hoover & Vertes, 2011; Price, 2007). The orbital cortex is also presumably present in pangolins (Imam et al., 2017) and lipotyphlans (Igado et al., 2021). Because different cortical areas are connected to achieve specific functions, the use of networks rather than cortex as a whole has been preferred to determine brain functions. Therefore, the orbital cortex is not the same as the orbital network and indeed the orbital network does not include the entire orbital cortex (Carmichael & Price, 1996; Hoover & Vertes, 2011; Price, 2007). Regarding the associated functions of the orbital network, it may be involved in assessing sensory objects such as food items and especially flavour, appearance, and texture (Price, 2007; Rolls, 2005). Based on behavioural studies and stomach content

analyses, pangolins are myrmecophagous mammals that are highly selective in terms of preferred prey (e.g., Karawita et al., 2020; Pietersen et al., 2016; Tamang et al., 2022). Based on the previous section, the senses used for this selection might not heavily favour olfaction. Myrmecophagous mammals have a specialized tongue and pangolins specifically have two relatively well innervated tactile organs on the tip of the tongue (Cheng, 1986; Doran & Allbrook, 1973; Kubota et al., 1962; Reiss, 2000). Pangolins also appear to have some taste buds but they are restricted to the lateral epithelium of each papilla (e.g., Casali et al., 2017; Doran & Allbrook, 1973; Kubota et al., 1962).

No stimulation studies appear to have been conducted on pangolins (Imam et al., 2018). Stimulations in the primary motor and somatosensory cortices located in the parietal lobe lead to tongue movements in bats, primates (Halley et al., 2022, 2025), and rodents (Pineda et al., 2025). This information is then sent to the orbitofrontal cortex to be processed, which then guides feeding behaviour through a reward system (Rolls, 2021). Therefore, a potential interpretation of the presence of a larger orbital gyrus could be that it is related to a specific food selection behaviour via the use of a specialized tongue that is needed for survival. This particular behaviour might have already been present in *Metacheiromys* more than 50 million years ago. This behaviour would coincide with the emergence of other morphological adaptations to myrmecophagy that are present in *Metacheiromys* as this species likely had a protrusile tongue also present in extant pangolins based on osteological correlates (Rose, 1978). The giant anteater (*Myrmecophaga tridactyla*) also has a protrusile tongue (Gaudin et al., 2018) and its brain shows a relatively well-developed orbital gyrus (see the Comparative Mammalian Brain Collections; Welker et al., 2001). Two other myrmecophagous mammals that also have a protrusile tongue (Reiss, 2000), the armadillos *Z. pichiy* and *D. novemcinctus*, have an orbital gyrus, but it is less developed (see Tambusso & Fariña, 2015; Troyelli et al., 2023).

The petrosal lobules have a role in controlling and maintaining eye movements during locomotion (Rambold et al., 2002) and they occupy the subarcuate fossa in mammals (e.g., Bertrand et al., 2020; Lang et al., 2022). These structures are relatively small in *Metacheiromys* and extremely reduced in pangolins, which might be related to their fossorial adaptations or more precisely to their slower mode of locomotion in comparison to more active mammals (Bertrand et al., 2021; Bertrand, Lang, et al., 2024; Goyens et al., 2022; Lang et al., 2022). The subarcuate fossa is also weakly developed in extant xenarthrans (Troyelli et al., 2023; Wible, 2010), which might be associated with this convergent lifestyle of fossoriality and myrmecophagy, suggesting a low reliance on this function to navigate their surroundings. However, there is an exception with the anteater *Tamandua tetradactyla* (UCMP 117518; Morphosource Media ID: 000766298), which shows relatively developed petrosal lobules. However, its close living relatives *Cyclopes didactylus* (PSU ANTH301.1; Morphosource Media ID: 000066622) and *Myrmecophaga tridactyla* (AMNH 133489; Morphosource Media ID: 000085043) have less developed subarcuate fossae. Additionally, the fossil anteater *Protamandua* was scored as having a deep and

large subarcuate fossa (Gaudin & Branham, 1998), but no CT data or images are available for this specimen. It is important to note that the reduction to absence of a subarcuate fossa could also be related to a packing-problem of fitting the brain into the cranium. Therefore, the function of the petrosal lobule might still be present in the non-lobule part of the cerebellum (see Bertrand et al., 2021; Troyelli et al., 2023). Additionally, the inner ear semicircular canals might influence the size of the subarcuate fossa (Billet et al., 2015). However, we note that in squirrels, the petrosal lobules (=paraflocculus in Bertrand & Silcox, 2016: figure 7) grow beyond the canals as the latter leave marks on the surface of the subarcuate fossa.

Finally, the neocortex in *Metacheiromys* is relatively smaller than in pangolins and is very close in size to another potential fossorial mammal from the late Eocene: *Anagale* (López-Torres et al., 2023). An increase in the neocortical surface and in the number of sulci has occurred through time in mammals (e.g., Bertrand et al., 2022; Jerison, 2012), which is also likely what occurred in the lineage leading to pangolins. However, the neocortex looks relatively smaller when compared with body mass in *S. gigantea* but larger in *P. tricuspis* in comparison to *Metacheiromys*. This result could suggest that increase in complexity of the neocortex occurred before the increase in body mass in *S. gigantea*. The EQ is slightly lower in extant pangolins than in *Metacheiromys*. In fossorial rodents, Aplodontiidae, there is a general decrease through time in all of the structures (i.e., petrosal lobules, olfactory bulbs, neocortex) and in the EQ in comparison to squirrels (Bertrand et al., 2018; Bertrand et al., 2021). In fossorial Euarchontoglires, the petrosal lobules are also significantly smaller compared with other locomotor categories of the same clade (Lang et al., 2022). Other arboreal rodents that move carefully through branches also appear to have relatively smaller petrosal lobules, olfactory bulbs, and neocortex (Bertrand, Lang, et al., 2024; Fernández Villoldo et al., 2023; Vincent et al., 2025). The fact that extant pangolins have a smaller relative brain size in comparison to their purported sister group, Palaeaeodonta, and more specifically *Metacheiromys* is especially interesting, because usually an increase in neocortical size leads to an increase in relative brain size, even if we consider that *Metacheiromys* has a derived condition in comparison to more basal palaeaeodonts. One possibility that will need to be tested with additional fossils is that a second increase in body mass might have occurred after the increase of the neocortex. Indeed, there is some evidence showing that Pleistocene fossils belonging to *S. gigantea* tend to be smaller than extant forms (Botha & Gaudin, 2007; Terhune et al., 2021). Therefore, possible interpretation of this result would be that specialization to fossoriality and/or slow arboreal locomotion (Gaubert et al., 2020; Gaudin et al., 2016) led to a decrease in several brain structures (olfaction and eye movement control). The reason for the increase in the neocortex in extant species (before the increase in body mass in *S. gigantea*) might be related to ecological circumstances during the Eocene when crown placental clades such as pangolins emerged. All crown clades taxa consistently show relatively larger neocortices than their respective stem relatives (Bertrand et al., 2022) and pangolins are no exception. The neocortex likely plays a major role in the survival of pangolins

today. In the future, it will be important to evaluate the brain endocasts of fossil pangolins to investigate when the increase of the neocortex and the potential decrease of both the olfactory bulb and the petrosal lobule size started in Pholidota, and how this related to body mass.

5 | CONCLUSION

We described the first brain virtual endocasts of palaeaeodonts, which have been considered the sister group to Pholidota (Gaudin et al., 2009). Because of shared morphological similarities related to myrmecophagy and fossoriality with both Pholidota and Xenarthra, it has been challenging to tease apart synapomorphies from convergent traits when evaluating palaeaeodont relationships (Gaudin et al., 2019, 2020; Rose, 2006). *Metacheiromys* and pangolins exhibit many differences in their endocranial morphology including features related to the olfactory bulbs, the cerebellum, the venous and arterial systems, which suggest some phylogenetic distance between *Metacheiromys* and pholidotans, as palaeaeodonts lack features that are present in extinct and extant pangolins. However, they display a similarity that could be viewed as a synapomorphy of Pholidotomorpha, with the presence of an orbital gyrus and a presylvian sulcus. Based on the fossil record, the evolution of these features in derived xenarthrans may be convergent.

We find that the size of the olfactory bulbs (olfaction) and the petrosal lobules (eye movement control) is smaller in pangolins compared with *Metacheiromys*, which aligns with trends recognized in aplodontiid rodents (Bertrand et al., 2018, 2021). The lack of petrosal lobules in most xenarthrans and pangolins is likely convergent as *Metacheiromys* had petrosal lobules. Overall, this suggests a lower need to maintain head and eye movement control during locomotion in animals engaging with a relatively slow-moving lifestyle such as fossoriality or carefully navigating from one tree branch to another. Regarding olfaction, despite some genetic data claiming that pangolins have an exceptional sense of smell (Choo et al., 2016; Li et al., 2024), our results support behavioural, anatomical, and quantitative and new genetic data that pangolins might not be relying on olfaction as much as previously thought (DiPaola et al., 2020; Imam et al., 2018; Martinez et al., 2025; Wright et al., 2024). The possible mismatch between these types of data could be the result of an expansion of the number of pseudogenes related to olfaction, as found for primates (Niimura et al., 2018). Probably the most interesting finding is the presence of the orbital gyrus in *Metacheiromys*, which is also well developed in pangolins and in the giant anteater. We hypothesize that the orbital gyrus might have played a major role in specialization for myrmecophagy and might be linked to the use of a protrusile tongue, as all of these taxa have this specialized tongue (Gaudin et al., 2018; Rose, 1978).

The relatively smaller brain of pangolins compared with *Metacheiromys* might be related to the smaller size of the olfactory bulbs and of the petrosal lobules. However, the neocortex takes up a larger proportion of the brain in pangolins compared with

Metacheiromys. Therefore, we hypothesize that after the increase in the neocortex in the evolution of pangolins, an increase in body mass occurred, which led to a decrease in relative brain size. Brain endocasts of fossil pangolins will be needed to verify whether this was the case. Overall, the study of the brain virtual endocast of *Metacheiromys* provides significant new information in relation to its phylogenetic position and to the evolution of behavioural adaptations of pangolins and other myrmecophagous mammals.

AUTHOR CONTRIBUTIONS

OCB and ECB conceived and designed the study, based on an earlier study of early placental mammal brains developed by OCB, JCW, and SLB. Supervision of ECB was performed by OCB and RMC. JRW acquired the CT data of the fossil specimens. ECB and OCB did the segmentations. ECB drafted the manuscript, tables, and figures. These files were first revised by OCB, RMC, and JRW. Analyses and interpretations were performed by ECB, OCB, and JRW, and critically reviewed by SLB. All authors revised the manuscript and provided final approval before submission.

ACKNOWLEDGEMENTS

This project started as the master's project of Eduard Cabasés Bru at the Institut Català de Paleontologia Miquel Crusafont. We thank T.J. Gaudin for organizing the scanning of the fossil specimens with JRW and sharing the data with us. We thank A. Harrington for uploading the CT data of the two extant pangolins and *Myrmecophaga tridactyla* funded by an NSF BCS 1825129 (to D.M. Boyer and A.R. Harrington), J. Wisor for *Cyclopes didactylus*, and N. Chatar for *Tamandua tetradactyla* in Morphosource. We thank the personnel of the American Museum of Natural History in the Department of Paleontology including R. O'Leary for access to the specimen of *M. marshi* (AMNH 131777) and M. Hill of the Microscopy and Imaging Facility (MIF) for scanning the specimen. We thank the personnel of the Smithsonian National Museum of Natural History for accessing the specimen of *M. marshi* (USNM 452349) and A. Neander of the UChicago PaleoCT in Chicago for scanning the specimen. This work was supported by Marie Skłodowska-Curie Actions: Individual Fellowship, H2020-MSCA-IF-2018-2020, no. 792611 (O.C.B.); Direcció General de Recerca de la Generalitat de Catalunya and managed by the Agència de Gestió d'Ajuts Universitaris i de Recerca, Beatriu de Pinós Programme, expedient number: 2021 BP 00042 (O.C.B.); Ministerio de Ciencia, Innovación y Universidades y Agencia Estatal de Investigación, Ayuda RYC2023-042630-I financiada por MICIU/AEI/<https://doi.org/10.13039/501100011033> y por el FSE+ (O.C.B.); Ministerio de Universidades y Union Europea-NextGenerationEU, Fundación Margarita Salas (R.M.C.); European Research Council (ERC) Starting Grant 756226 under the European Union's Horizon 2020 Research and Innovation Programme, <https://doi.org/10.13039/100010663>—H2020 European Research Council (S.L.B.); Leverhulme Trust, Philip Leverhulme Prize (S.L.B.); NSF DEB 1654952 (S.L.B.); Swedish Research Council Grant 2021-02973 (S.L.B.); NSF DEB 1654949 (J.R.W.); O.C.B. was also supported by the Generalitat de Catalunya/CERCA Programme, the

Agència de Gestió d'Ajuts Universitaris i de Recerca, Generalitat de Catalunya: 2021 SGR 00620 to David M. Alba (Institute Catala De Paleontologia), Agencia Estatal de Investigación of the Ministerio de Ciencia e Innovación: R + D + I project PID2020-117289GB-I00 (MCIN/AEI/<https://doi.org/10.13039/501100011033>) to David Alba and Isaac Casanovas-Vilar and R.M.C. by the Agencia Estatal de Investigación of the Ministerio de Ciencia e Innovación: R+D+I project PID2024-160207NB-I00 (MCIU/AEI/<https://doi.org/10.13039/501100011033>/FEDER EU). There is no conflict of interest. We thank G. Billet and an anonymous reviewer for their thorough reviews that improved the quality of this manuscript.

DATA AVAILABILITY STATEMENT

The 3D models of the virtual endocasts are available upon request to the corresponding author.

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REFERENCES

- Alba, D.M., Hammond, A.S., Vinuesa, V. & Casanovas-Vilar, I. (2018) First record of a Miocene pangolin (Pholidota, Manoidea) from the Iberian Peninsula. *Journal of Vertebrate Paleontology*, 38, e1424716.
- Bertrand, O.C., Amador-Mughal, F., Lang, M.M. & Silcox, M.T. (2018) Virtual endocasts of fossil Sciuroidea: brain size reduction in the evolution of fossoriality. *Palaeontology*, 61, 919–948.
- Bertrand, O.C., Amador-Mughal, F., Lang, M.M. & Silcox, M.T. (2019) New virtual endocasts of Eocene Ischyromyidae and their relevance in evaluating neurological changes occurring through time in Rodentia. *Journal of Mammalian Evolution*, 26, 345–371.
- Bertrand, O.C., Amador-Mughal, F. & Silcox, M.T. (2017) Virtual endocast of the early Oligocene *Cedromus wilsoni* (Cedromurinae) and brain evolution in squirrels. *Journal of Anatomy*, 230, 128–151.
- Bertrand, O.C., Jiménez Lao, M., Shelley, S.L., Wible, J.R., Williamson, T.E., Meng, J. et al. (2024) The virtual brain endocast of *Trogosus* (Mammalia, Tillodontia) and its relevance in understanding the extinction of archaic placental mammals. *Journal of Anatomy*, 244, 1–21.
- Bertrand, O.C. & Krubitzer, L. (2025) The functional adaptations of mammalian brain structures through a behavioural ecology lens. *Nature Reviews Biodiversity*, 1, 703–716.
- Bertrand, O.C., Lang, M.M., Ferreira, J.D., Kerber, L., Kynigopoulou, Z. & Silcox, M.T. (2024) The virtual brain endocast of *Incamys bolivianus*: insight from the neurosensory system into the adaptive radiation of south American rodents. *Papers in Palaeontology*, 10, e1562.
- Bertrand, O.C., Michaud, M. & Kirk, E.C. (2025) How the neurosensory system provides clues for the adaptive radiation of mammals. In: Krubitzer, L. (Ed.) *Evolution of nervous Systems in Mammals. Evolution of nervous systems*. London: Elsevier Academic Press.
- Bertrand, O.C., Püschel, H.P., Schwab, J.A., Silcox, M.T. & Brusatte, S.L. (2021) The impact of locomotion on the brain evolution of squirrels and close relatives. *Communications Biology*, 4, 1–15.
- Bertrand, O.C., Shelley, S.L., Wible, J.R., Williamson, T.E., Holbrook, L.T., Chester, S.G.B. et al. (2020) Virtual endocranial and inner ear endocasts of the Paleocene 'condylarth' *Chriacus*: new insight into the neurosensory system and evolution of early placental mammals. *Journal of Anatomy*, 236, 21–49.
- Bertrand, O.C., Shelley, S.L., Williamson, T.E., Wible, J.R., Chester, S.G.B., Flynn, J.J. et al. (2022) Brawn before brains in placental mammals after the end-Cretaceous extinction. *Science*, 376, 80–85.

- Bertrand, O.C. & Silcox, M.T. (2016) First virtual endocasts of a fossil rodent: *Ischyromys typus* (Ischyromyidae, Oligocene) and brain evolution in rodents. *Journal of Vertebrate Paleontology*, 36, 1–19.
- Billet, G., Muizon, C. de, Schellhorn, R., Ruf, I., Ladevèze, S. & Bergqvist, L. (2015) Petrosal and inner ear anatomy and allometry amongst specimens referred to Litopterna (Placentalia). *Zoological Journal of the Linnean Society*, 173, 956–987.
- Billet, G., Hautier, L., Gaudin, T.J., Flynn, J.J., Ruf, I., Carrillo, J.D. et al. (2026) Brain drain: exceptional pattern of calvarial venation in pangolins and its phylogenetic significance for Ferae. *Zoological Journal of the Linnean Society*, 206, zlag020. Available from: <https://doi.org/10.1093/zoolinnean/zlag020>.
- Boscaini, A., Iurino, D.A., Mamani Quispe, B., Andrade Flores, R., Sardella, R., Pujos, F. et al. (2020) Cranial anatomy and paleoneurology of the extinct sloth *Catonyx tarijensis* (Xenarthra, Mylodontidae) from the late Pleistocene of Oruro, southwestern Bolivia. *Frontiers in Ecology and Evolution*, 8, 1–16.
- Boscaini, A., Iurino, D.A., Sardella, R., Tirao, G., Gaudin, T.J. & Pujos, F. (2020) Digital cranial endocasts of the extinct sloth *Glossotherium robustum* (Xenarthra, Mylodontidae) from the late Pleistocene of Argentina: description and comparison with the extant sloths. *Journal of Mammalian Evolution*, 27, 55–71.
- Botha, J. & Gaudin, T. (2007) An early pliocene pangolin (Mammalia; Pholidota) from Langebaanweg, South Africa. *Journal of Vertebrate Paleontology*, 27, 484–491.
- Bugge, J. (1979) Cephalic arterial pattern in New World edentates and Old World pangolins with special reference to their phylogenetic relationships and taxonomy. *Acta Anatomica*, 105, 37–46.
- Carmichael, S.T. & Price, J.L. (1996) Connectional networks within the orbital and medial prefrontal cortex of macaque monkeys. *Journal of Comparative Neurology*, 371, 179–207.
- Casali, D.M., Martins-Santos, E., Santos, A.L.Q., Miranda, F.R., Mahecha, G.A.B. & Perini, F.A. (2017) Morphology of the tongue of *Vermilingua* (Xenarthra: Pilosa) and evolutionary considerations. *Journal of Morphology*, 278, 1380–1399.
- Cheng, H. (1986) Anatomical studies of *Manis pentadactyla*'s tongue and structures relative to the tongue. *Memoirs of the Beijing Museum of Natural History*, 36, 1–9.
- Choo, S.W., Rayko, M., Tan, T.K., Hari, R., Komissarov, A., Wee, W.Y. et al. (2016) Pangolin genomes and the evolution of mammalian scales and immunity. *Genome Research*, 26, 1312–1322.
- Christensen, G.C. & Evans, H.E. (1979) *Miller's anatomy of the dog*. Philadelphia: Saunders.
- Cuvier, G. (1798) *Tableau élémentaire de l'Histoire Naturelle des animaux*. Paris: Baudouin.
- Delsuc, F., Scally, M., Madsen, O., Stanhope, M.J., de Jong, W.W., Catzeflis, F.M. et al. (2002) Molecular phylogeny of living xenarthrans and the impact of character and taxon sampling on the placental tree rooting. *Molecular Biology and Evolution*, 19, 1656–1671.
- DiPaola, J.D., Yindee, M. & Plotnik, J.M. (2020) Investigating the use of sensory information to detect and track prey by the Sunda pangolin (*Manis javanica*) with conservation in mind. *Scientific Reports*, 10, 9787.
- Doran, G.A. & Allbrook, D.B. (1973) The tongue and associated structures in two species of African pangolins, *Manis gigantea* and *Manis tricuspis*. *Journal of Mammalogy*, 54, 887–899.
- Dozo, M.T. (1998) Neuromorfología de *Utaetus buccatus* (Xenarthra, Dasypodidae): un armadillo del Eoceno temprano de la Provincia del Chubut, Argentina. *Ameghiniana*, 35, 285–289.
- Dozo, M.T., Paulina-Carabajal, A., Macrini, T.E. & Walsh, S. (2023) *Paleoneurology of amniotes: new directions in the study of fossil endocasts*. Cham: Springer.
- Du Boulay, G.H. & Verity, P. (1973) *The cranial arteries of mammals*. London and Tonbridge: William Heinemann Medical Books Limited.
- Dubied, M., Solé, F., Mennecart, B. & Hautier, L. (2019) The cranium of *Proviverra typica* (Mammalia, Hyaenodonta) and its impact on hyaenodont phylogeny and endocranial evolution. *Palaeontology*, 62, 983–1001.
- Duvernoy, H. (2005) Brain anatomy. In: Kuzniecky, R. & Jackson, G.D. (Eds.) *Magnetic resonance in epilepsy: neuroimaging techniques*. London: Elsevier Academic Press, pp. 29–97.
- Eisenberg, J.F. (1981) *The mammalian radiations: an analysis of trends in evolution, adaptation, and behavior*. Chicago: University of Chicago Press.
- Emry, R.J. (1970) A north American Oligocene pangolin and other additions to the Pholidota. *Bulletin of the American Museum of Natural History*, 142, 459–510.
- Engelman, R.K. (2022) Occipital condyle width (OCW) is a highly accurate predictor of body mass in therian mammals. *BMC Biology*, 20, 1–44.
- Evans, H.E. & de Lahunta, A. (2012) *Miller's anatomy of the dog*. St. Louis, USA: Elsevier Saunders.
- Fernández Villoldo, J.A., Verzi, D.H., Lopes, R.T., Dos Reis, S.F. & Perez, S.I. (2023) Brain size and shape diversification in a highly diverse south American clade of rodents (Echimyidae): a geometric morphometric and comparative phylogenetic approach. *Biological Journal of the Linnean Society*, 140, 277–295.
- Flink, T., Cote, S., Rossie, J.B., Kibii, J.M. & Werdelin, L. (2021) The neurocranium of *Ekweconfractus amorui* gen. Et sp. nov. (Hyaenodonta, Mammalia) and the evolution of the brain in some hyaenodontan carnivores. *Journal of Vertebrate Paleontology*, 41, e1927748.
- Foley, N.M., Mason, V.C., Harris, A.J., Bredemeyer, K.R., Damas, J., Lewin, H.A. et al. (2023) A genomic timescale for placental mammal evolution. *Science*, 380, eabl8189.
- Gaubert, P., Wible, J.R., Heighton, S.P. & Gaudin, T.J. (2020) Phylogeny and systematics. In: Challender, D.W.S., Nash, H.C. & Waterman, C. (Eds.) *Pangolins: science, society and conservation*. London: Academic Press, pp. 25–39.
- Gaubert, P., Wilson, D. & Mittermeier, R. (2011) Family Manidae. *Handbook of the Mammals of the World*, 2, 82–103.
- Gaudin, T.J. (2004) Phylogenetic relationships among sloths (Mammalia, Xenarthra, Tardigrada): the craniodental evidence. *Zoological Journal of the Linnean Society*, 140, 255–305.
- Gaudin, T.J. & Branham, D.G. (1998) The phylogeny of the Myrmecophagidae (Mammalia, Xenarthra, Vermilingua) and the relationship of Eurotamandua to the Vermilingua. *Journal of Mammalian Evolution*, 5, 237–265.
- Gaudin, T.J., Emry, R.J. & Morris, J. (2016) Skeletal anatomy of the north American pangolin *Patriomanis americana* (Mammalia, Pholidota) from the latest Eocene of Wyoming (USA). *Smithsonian Contributions to Paleobiology*, 98, 1–102.
- Gaudin, T.J., Emry, R.J. & Wible, J.R. (2009) The phylogeny of living and extinct pangolins (Mammalia, Pholidota) and associated taxa: a morphology based analysis. *Journal of Mammalian Evolution*, 16, 235–305.
- Gaudin, T.J., Gaubert, P., Billet, G., Hautier, L., Ferreira-Cardoso, S. & Wible, J.R. (2020) Evolution and morphology. In: Challender, D.W.S., Nash, H.C. & Waterman, C. (Eds.) *Pangolins: science, society and conservation*. London: Academic Press, pp. 5–23.
- Gaudin, T.J., Hicks, P. & Di Blanco, Y. (2018) *Myrmecophaga tridactyla* (Pilosa: Myrmecophagidae). *Mammalian Species*, 50, 1–13.
- Gaudin, T.J. & Wible, J.R. (1999) The entotympanic of pangolins and the phylogeny of the Pholidota (Mammalia). *Journal of Mammalian Evolution*, 6, 39–65.
- Gaudin, T.J., Wible, J.R., Hopson, J.A. & Turnbull, W.D. (1996) Reexamination of the morphological evidence for the cohort Epitheria (Mammalia, Eutheria). *Journal of Mammalian Evolution*, 3, 31–79.
- Gaudin, T.J., Wible, J.R., Rose, K.D., Emry, R.J. & Spaulding, M. (2019) Skeletal anatomy of the basicranium and auditory region in the metacheiromiid palaeonodont *Metacheiromys* (Mammalia, Pholidotamorpha) based on high-resolution CT scans. *Fossil Imprint*, 75, 484.

- Goyens, J., Baeckens, S., Smith, E.S.J., Pozzi, J. & Mason, M.J. (2022) Parallel evolution of semicircular canal form and sensitivity in subterranean mammals. *Journal of Comparative Physiology*, 208, 627–640.
- Gu, T.-T., Wu, H., Yang, F., Gaubert, P., Heighton, S.P., Fu, Y. et al. (2023) Genomic analysis reveals a cryptic pangolin species. *Proceedings of the National Academy of Sciences*, 120, e2304096120.
- Guth, C. (1961) *La région temporale des Edentés*. Le Puy: Imprimerie Jeanne D'Arc.
- Halley, A.C., Baldwin, M.K.L., Cooke, D.F., Englund, M., Pineda, C.R., Schmid, T. et al. (2022) Coevolution of motor cortex and behavioral specializations associated with flight and echolocation in bats. *Current Biology*, 32, 2935–2941.e3.
- Halley, A.C., Stepniewska, I., Wang, Q., Reed, J.L., Qi, H.X., Kaas, J.H. et al. (2025) Movement representations in motor, somatosensory, and posterior parietal cortex of the greater galago. *Cerebral Cortex*, 35, bhaf195.
- Heighton, S.P., Allio, R., Muriene, J., Salmona, J., Meng, H., Scornavacca, C. et al. (2023) Pangolin genomes offer key insights and resources for the world's most trafficked wild mammals. *Molecular Biology and Evolution*, 40, msad190.
- Hoffmann, M., Nixon, S., Alempijevic, D., Ayebare, S., Bruce, T., Davenport, T.R. et al. (2020) Giant pangolin *Smutsia gigantea* (Illiger, 1815). In: Challender, D.W.S., Nash, H.C. & Waterman, C. (Eds.) *Pangolins*. London: Academic Press, pp. 157–173.
- Hoover, W.B. & Vertes, R.P. (2011) Projections of the medial orbital and ventral orbital cortex in the rat. *Journal of Comparative Neurology*, 519, 3766–3801.
- Hopkins, S.S.B. (2018) In: Croft, D.A., Su, D.F. & Simpson, S.W. (Eds.) *Methods in paleoecology: reconstructing cenozoic terrestrial environments and ecological communities*. Cham: Springer International Publishing, pp. 7–22.
- Hyrtil, J. (1854) Beiträge zur vergleichenden Angiologie. IV. Das arterielle Gefäß-system der Edentaten. *Denkschriften der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe*, 6, 21–64.
- Igado, O.O., Braimah, S.F. & Obasa, A.A. (2021) Gross morphology of the brain and spinal cord of the African pygmy hedgehog (*Atelerix albiventris*). *Folia Veterinaria*, 65, 15–21.
- Imam, A., Ajao, M.S., Bhagwandin, A., Ihunwo, A.O. & Manger, P.R. (2017) The brain of the tree pangolin (*Manis tricuspis*). I. General appearance of the central nervous system. *Journal of Comparative Neurology*, 525, 2571–2582.
- Imam, A., Bhagwandin, A., Ajao, M.S., Spocter, M.A., Ihunwo, A.O. & Manger, P.R. (2018) The brain of the tree pangolin (*Manis tricuspis*). II. The olfactory system. *Journal of Comparative Neurology*, 526, 2548–2569.
- Jansen, R., Sodeinde, O., Soewu, D., Pietersen, D.W., Alempijevic, D. & Ingram, D.J. (2020) White-bellied pangolin *Phataginus tricuspis* (Rafinesque, 1820). In: Challender, D.W.S., Nash, H.C. & Waterman, C. (Eds.) *Pangolins*. London: Academic Press, pp. 139–156.
- Jerison, H.J. (1973) *Evolution of the brain and intelligence*. New York: Academic Press.
- Jerison, H.J. (2012) Digitized fossil brains: neocorticalization. *Biolinguistics*, 6, 383–392.
- Jollie, M. (1968) The head skeleton of a new-born *Manis javanica* with comments on the ontogeny and phylogeny of the mammal head skeleton. *Acta Zoologica*, 49, 227–305.
- Karawita, H., Perera, P., Dayawansa, N. & Dias, S. (2020) Dietary composition and foraging habitats of the Indian pangolin (*Manis crassicaudata*) in a tropical lowland forest-associated landscape in southwest Sri Lanka. *Global Ecology and Conservation*, 21, e00880.
- Kondrashov, P. & Agadjanian, A.K. (2012) A nearly complete skeleton of *Ernanodon* (Mammalia, Palaeodonta) from Mongolia: morphofunctional analysis. *Journal of Vertebrate Paleontology*, 32, 983–1001.
- Kubota, K., Kubota, J., Nakamura, T., Fukuda, N., Asakura, S., Nakagawa, S. et al. (1962) Comparative anatomical and neurohistological observations on the tongue of the pangolin (*Manis pentadactyla*, Linneus). *The Anatomical Record*, 144, 43–55.
- Lang, M.M., Bertrand, O.C., San Martín-Flores, G., Law, C.J., Abdul-Sater, J., Spakowski, S. et al. (2022) Scaling patterns of cerebellar petrosal lobules in Euarchontoglires: impacts of ecology and phylogeny. *The Anatomical Record*, 305, 3472–3503.
- Le Verger, K., González Ruiz, L.R. & Billet, G. (2021) Comparative anatomy and phylogenetic contribution of intracranial osseous canals and cavities in armadillos and glyptodonts (Xenarthra, Cingulata). *Journal of Anatomy*, 239, 1473–1502.
- Li, J., Guo, C., Xie, M., Wang, K., Wang, X., Zou, B. et al. (2024) Genomic signatures of sensory adaptation and evolution in pangolins. *BMC Genomics*, 25, 1176.
- López-Torres, S., Bertrand, O.C., Lang, M.M., Silcox, M.T., Fostowicz-Frelik, Ł. & Meng, J. (2023) Cranial endocast of *Anagale gobiensis* (Anagalidae) and its implications for early brain evolution in Euarchontoglires. *Palaeontology*, 66, e12650.
- Lösel, P.D., van de Kamp, T., Jayme, A., Ershov, A., Faragó, T., Pichler, O. et al. (2020) Introducing Biomedisa as an open-source online platform for biomedical image segmentation. *Nature Communications*, 11, 5577.
- Lyras, G.A. & Van der Geer, A.A.E. (2003) External brain anatomy in relation to the phylogeny of Caninae (carnivora: Canidae). *Zoological Journal of the Linnean Society*, 138, 505–522.
- Lyras, G.A., van der Geer, A.A.E. & Werdelin, L. (2023) Paleoneurology of carnivora. In: Dozo, M.T., Paulina-Carabajal, A., Macrini, T.E. & Walsh, S. (Eds.) *Paleoneurology of amniotes: new directions in the study of fossil endocasts*. Cham: Springer, pp. 681–710.
- Martin, R.D. (1990) Evolution of the primate central nervous system. In: *Primate origins and evolution. A phylogenetic reconstruction*. Princeton: Princeton University Press, pp. 357–426.
- Martinez, Q., Molinier, C., Barraza-Soltero, I.K., Berger, E., le Verger, K., Fabre, A.C. et al. (2025) The olfactory bulb endocast as a proxy for mammalian olfaction. *Proceedings of the National Academy of Sciences*, 122, e2510575122.
- Matthew, W.D. (1918) A revision of the lower Eocene Wasatch and Wind River faunas. Part V—Insectivora (continued), Glires, Edentata. *Bulletin of the American Museum of Natural History*, 38, 565–657.
- McKenna, M.C. & Bell, S.K. (1997) *Classification of mammals: above the species level*. New York: Columbia University Press.
- Meredith, R.W., Janečka, J.E., Gatesy, J., Ryder, O.A., Fisher, C.A., Teeling, E.C. et al. (2011) Impacts of the cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science*, 334, 521–524.
- Mohapatra, R.K. & Panda, S. (2014) Behavioural descriptions of Indian pangolins (*Manis crassicaudata*) in captivity. *International Journal of Zoology*, 2014, 795062.
- Muizon, C. de, Billet, G., Argot, C., Ladevèze, S. & Goussard, F. (2015) *Alcidedorbignya inopinata*, a basal pantodont (Placentalia, Mammalia) from the early Palaeocene of Bolivia: anatomy, phylogeny and palaeobiology. *Geodiversitas*, 37, 397–634.
- Murphy, W.J., Eizirik, E., Johnson, W.E., Zhang, Y.P., Ryder, O.A. & O'Brien, S.J. (2001) Molecular phylogenetics and the origins of placental mammals. *Nature*, 409, 614–618.
- Murphy, W.J., Eizirik, E., O'Brien, S.J., Madsen, O., Scally, M., Douady, C.J. et al. (2001) Resolution of the early placental mammal radiation using bayesian phylogenetics. *Science*, 294, 2348–2351.
- Murphy, W.J., Foley, N.M., Bredemeyer, K.R., Gatesy, J. & Springer, M.S. (2021) Phylogenomics and the genetic architecture of the placental mammal radiation. *Annual Review of Animal Biosciences*, 9, 29–53.
- Niimura, Y., Matsui, A. & Touhara, K. (2018) Acceleration of olfactory receptor gene loss in primate evolution: possible link to anatomical change in sensory systems and dietary transition. *Molecular Biology and Evolution*, 35, 1437–1450.

- Nojima, T. (1990) A morphological consideration of the relationships of pinnipeds to other carnivorans based on the bony tentorium and bony falx. *Marine Mammal Science*, 6, 54–74.
- Novacek, M.J. (1986) The skull of leptictid insectivorans and the higher-level classification of eutherian mammals. *Bulletin of the American Museum of Natural History*, 183, 1–112.
- Novacek, M.J. (1992) Mammalian phylogeny: shaking the tree. *Nature*, 356, 121–125.
- Novacek, M.J. & Wyss, A.R. (1986) Higher-level relationships of the recent eutherian orders: morphological evidence. *Cladistics*, 2, 257–287.
- O'Leary, M.A., Bloch, J.I., Flynn, J.J., Gaudin, T.J., Giallombardo, A., Giannini, N.P. et al. (2013) The placental mammal ancestor and the post-K-Pg radiation of placentals. *Science*, 339, 662–667.
- Patterson, B., Segall, W., Turnbull, W.D. & Gaudin, T.J. (1992) The ear region in xenarthrans (= Edentata, Mammalia). Part II. Pilosa (sloths, anteaters), palaeodonta, and a miscellany. 24.
- Pietersen, D.W., Symes, C.T., Woodborne, S., McKechnie, A.E. & Jansen, R. (2016) Diet and prey selectivity of the specialist myrmecophage, Temminck's ground pangolin. *Journal of Zoology*, 298, 198–208.
- Pineda, C.R., Bresee, C., Baldwin, M.K.L., Seelke, A.M.H. & Krubitzer, L. (2025) Organization of the perioral representation of the primary somatosensory cortex in prairie voles (*Microtus ochrogaster*). *Brain, Behavior and Evolution*, 100, 139–155.
- Price, J.L. (2007) Definition of the orbital cortex in relation to specific connections with limbic and visceral structures and other cortical regions. *Annals of the New York Academy of Sciences*, 1121, 54–71.
- Radinsky, L. (1977) Brains of early carnivores. *Paleobiology*, 3, 333–349.
- Rambold, H., Churchland, A., Selig, Y., Jasmin, L. & Lisberger, S.G. (2002) Partial ablations 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.
- Rangel de Lázaro, G., de la Cuétara, J.M., Pišová, H., Lorenzo, C. & Bruner, E. (2016) Diploic vessels and computed tomography: segmentation and comparison in modern humans and fossil hominids. *American Journal of Physical Anthropology*, 159, 313–324.
- Reiss, K.Z. (2000) Feeding in myrmecophagous mammals. In: Schwenk, K. (Ed.) *Feeding: form, function and evolution in tetrapod vertebrates*. New York: Academic Press, pp. 459–485.
- Rolls, E.T. (2005) Taste, olfactory, and food texture processing in the brain, and the control of food intake. *Physiology & Behavior*, 85, 45–56.
- Rolls, E.T. (2021) The orbitofrontal cortex, food reward, body weight and obesity. *Social Cognitive and Affective Neuroscience*, 18, 1–19.
- Rose, K.D. (1978) A new Paleocene epoicotheriid (Mammalia), with comments on the Palaeodonta. *Journal of Paleontology*, 52, 658–674.
- Rose, K.D. (2006) *The beginning of the age of mammals*. Baltimore: Johns Hopkins University Press.
- Rose, K.D. (2008) Palaeodonta and Pholidota. In: Janis, C.M., Gunnell, G.F. & Uhen, M.D. (Eds.) *Evolution of tertiary mammals of North America: volume 2: small mammals, xenarthrans, and marine mammals*. Cambridge: Cambridge University Press, pp. 135–146.
- Rose, K.D. & Emry, R.J. (1993) Relationships of Xenarthra, Pholidota, and fossil "edentates": the morphological evidence. In: Szalay, F.S., Novacek, M.J. & McKenna, M.C. (Eds.) *Mammal phylogeny*. New York: Springer-Verlag, pp. 81–102.
- Rose, K.D. (1978) A new Paleocene epoicotheriid (Mammalia), with comments on the Palaeodonta. *Journal of Paleontology*, 52, 658–674.
- Rose, K.D. (2006) *The beginning of the age of mammals*. Baltimore: Johns Hopkins University Press.
- Rose, K.D. (2008) Palaeodonta and Pholidota. In: Janis, C.M., Gunnell, G.F. & Uhen, M.D. (Eds.) *Evolution of tertiary mammals of North America: volume 2: small mammals, xenarthrans, and marine mammals*. Cambridge: Cambridge University Press, pp. 135–146.
- Rose, K.D., Emry, R.J., Gaudin, T.J. & Storch, G. (2005) Xenarthra and Pholidota. In: Rose, K.D. & Archibald, J.D. (Eds.) *The rise of placental mammals: origins and relationships of the major extant clades*. Baltimore: Johns Hopkins University Press, pp. 106–126.
- Schoch, R.M. (1984) Revision of *Metacheiromys* Wortman, 1903 and a review of the Palaeodonta. *Postilla, Yale Peabody Museum*, 192, 1–28.
- Shoshani, J. & McKenna, M.C. (1998) Higher taxonomic relationships among extant mammals based on morphology, with selected comparisons of results from molecular data. *Molecular Phylogenetics and Evolution*, 9, 572–584.
- Simpson, G.G. (1931) *Metacheiromys* and the Edentata. *Bulletin of the American Museum of Natural History*, 59, 295–381.
- Simpson, G.G. (1945) The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*, 85, 1–350.
- Storch, G. (2003) Fossil Old World "edentates" (Mammalia). In: Fariña, R.A., Vizcaino, S.F. & Storch, G. (Eds.) *Morphological studies in fossil and extant Xenarthra (Mammalia)*. Stuttgart: Senckenbergiana Biologica, pp. 51–60.
- Szalay, F.S. (1977) Phylogenetic relationships and a classification of the eutherian Mammalia. In: Hecht, M.K., Goody, P.C. & Hecht, B.M. (Eds.) *Major patterns in vertebrate evolution*. Boston: Springer, pp. 315–374.
- Tamang, S., Sharma, H.P. & Belant, J.L. (2022) Foraging burrow site selection and diet of Chinese pangolins, Chandragiri municipality, Nepal. *Animals*, 12, 2518.
- Tambusso, P.S. & Fariña, R.A. (2015) Digital cranial endocast of *Pseudophloeophorus absolutus* (Xenarthra, Cingulata) and its systematic and evolutionary implications. *Journal of Vertebrate Paleontology*, 35, e967853.
- Terhune, C.E., Gaudin, T., Curran, S. & Petculescu, A. (2021) The youngest pangolin (Mammalia, Pholidota) from Europe. *Journal of Vertebrate Paleontology*, 41, e1990075.
- Troyelli, A., Cassini, G.H., Tirao, G., Boscaini, A. & Fericola, J.C. (2023) Endocranial cast anatomy of the early Miocene glyptodont *Propalaeophloeophorus australis* (Mammalia, Xenarthra, Cingulata) and its evolutionary implications. *Journal of Mammalian Evolution*, 30, 907–922.
- Vincent, F., Souron, A., Casanovas-Vilar, I., Gamarra, J. & Bertrand, O.C. (2025) The brain endocast of the Canary Islands giant rats (*Canariomys*, Muridae, Rodentia): Paleobiological and evolutionary implications. *Journal of Mammalian Evolution*, 32, 1–28.
- Visualization Sciences Group. (1995–2019) Avizo Lite 2019.4. Berlin (ZIB), Germany: Konrad-Zuse-Zentrum für Informationstechnik.
- Wangmo, L.K., Dolker, S., Ghosh, A., Joshi, B.D., Sharma, L.K. & Thakur, M. (2025) Reply to Zijlstra (2025) - status of Indo-Burmese pangolin (manis indoburmanica). *Mammalian Biology*, 105, 703–707.
- Weber, M. (1904) *Die Säugetiere. Einführung in die anatomie und systematik der recenten und fossilen Mammalia*. Jena: Verlag von Gustav Fischer.
- Welker, W., Johnson, J.I. & Noe, A. (2001) Comparative Mammalian Brain Collections: giant anteater. <https://brainmuseum.org/specimens/pilosa/giantanteater/index.html>
- Wible, J.R. (1984) The ontogeny and phylogeny of the mammalian cranial arterial pattern. Ph.D. Thesis. Durham: Duke University.
- 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. (2008) On the cranial osteology of the Hispaniolan solenodon, *Solenodon paradoxus* Brandt, 1833 (Mammalia, Lipotyphla, Solenodontidae). *Annals of Carnegie Museum*, 77, 321–402.
- Wible, J.R. (2010) Petrosal anatomy of the nine-banded armadillo, *Dasypus novemcinctus* Linnaeus, 1758 (Mammalia, Xenarthra, Dasypodidae). *Annals of Carnegie Museum*, 79, 1–28.
- Wright, M., Martinez, Q., Ferreira-Cardoso, S., Lebrun, R., Dubourguier, B., Delsuc, F. et al. (2024) Sniffing out morphological convergence

in the turbinal complex of myrmecophagous placentals. *The Anatomical Record*, 309, 1–27.

Yohe, L.R. & Krell, N.T. (2023) An updated synthesis of and outstanding questions in the olfactory and vomeronasal systems in bats: genetics asks questions only anatomy can answer. *The Anatomical Record*, 306, 2765–2780.

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How to cite this article: Cabasés Bru, E., Moya-Costa, R., Wible, J.R., Brusatte, S.L. & Bertrand, O.C. (2026) Virtual brain endocasts of the palaeonodont *Metacheiromys marshi* and the neurosensory evolution of early Pholidotamorpha. *Journal of Anatomy*, 249, 821–846. Available from: <https://doi.org/10.1111/joa.70142>