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Digital endocranial cast of *Pampatherium humboldtii* (Xenarthra, Cingulata) from the Late Pleistocene of Uruguay

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Abstract The diversity of the order Cingulata is much higher in the fossil record than that represented by the extant species. While pampatheres, one of its extinct groups, are superficially similar to armadillos, recent phylogenetic analysis grouped them with glyptodonts in the clade Glyptodonta. We describe here the first digital endocranial cast of a pampathere, *Pampatherium humboldtii*, from the Late Pleistocene of Uruguay and compare its morphology with that of glyptodonts and extant and fossil armadillos. Some of the characteristics observed are more similar to those of glyptodonts than to those seen in armadillos. The endocranial cast of *Pampatherium* has large pedunculate olfactory bulbs, a relative small cerebrum with only one cortical sulcus and a large cerebellum. Although all groups of cingulates, both extant and extinct, have a similar relative brain size, the relative brain size of pampatheres is larger than in glyptodonts and close to that of extant armadillos, The endocast morphology and the analysis of relative brain size of *Pampatherium* are congruent with their close affinity to glyptodonts and their inclusion in the clade Glyptodonta, although in a family of its own.

Keywords Pleistocene · Pampathere · 3D reconstruction · Endocast · Encephalization quotient

Institutional Abbreviation

MHD-P   Museo Histórico Departamental de Artigas, Uruguay

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Introduction

Xenarthrans form a group that originated in South America, although some of them reached North and Central America during the bidirectional dispersion phenomenon known as Great American Biotic Interchange (Webb 1976, 2006; Campbell et al. 2010; Woodburne 2010). They are one of the four major clades of placental mammals along with Afrotheria, Laurasiatheria and Euarchontoglires (Murphy et al. 2001; Delsuc et al. 2002; Hallström et al. 2007; Delsuc and Douzery 2008; O'Leary et al. 2013) and, according to the most recent phylogenetic reconstructions, is the most basal of these clades (O'Leary et al. 2013). Presently, this clade is not very diverse and is represented by only 31 species. However, the diversity of this group in the fossil record is much higher. There are more than 150 genera of extinct xenarthrans (McKenna and Bell 1997), and they are one of the most characteristic mammalian groups in South American Cenozoic faunas. During the Late Pleistocene, xenarthrans accounted for more than half of the megammamals in South American faunas (Fariña 1996). The uniqueness of this group may be reflected in the words of Patterson and Pascual (1968: 422): "No elements of the South American mammalian fauna are more characteristic than the members of the Xenarthra. Armadillos and glyptodonts, anteaters, ground sloths, and tree sloths together make up an assemblage unlike anything that evolved elsewhere in the world."

The Cingulata comprises two main clades, Dasypodoidea, consisting of living and extinct armadillos, and Glyptodontoidea, a group that includes glyptodonts and pampatheres, both extinct (McKenna and Bell 1997). Pampatheres (family Pampatheriidae) are superficially similar to armadillos, particularly because of the presence of the three areas of the carapace (movable bands, scapular

Birkhäuser

and pelvic shields) and the morphology of the skull, with a long snout, so it is more similar in appearance to armadillos than to glyptodonts. This led some authors to classify the pampatheres among Dasypodoidea (Simpson 1930; Hoffstetter 1958; Paula Couto 1979). However, Patterson and Pascual (1968) suggested that, according to dental and basicranial morphology, pampatheres are more closely related to glyptodonts. This relationship was strongly supported by the analyses of Gaudin and Wible (2006) and Fernicola (2008), who placed pampatheres within the clade Glyptodonta.

A few palaeoneurological studies, that is the analyses of a natural or artificial cast of the cranial cavity, have been made in cingulates. They include some Pleistocene glyptodonts (Serres 1865; Gervais 1869; Dechaseaux 1958; Tambusso and Fariña 2009; Vílchez Barral et al. 2013) and an Eocene armadillo (Dozo 1998). Recently, Tambusso and Fariña (2015) described the endocast of a Miocene glyptodont and compared it with those of several Pleistocene glyptodonts and extant armadillos. Their results show that the cerebrum of glyptodonts has a simple pattern of cortical sulci both in the Miocene and Pleistocene forms and that extant and extinct cingulates have the smallest brain size relative to body mass within xenarthrans. Furthermore, glyptodonts show smaller relative brain size than extant armadillos.

Known from the late nineteenth century (Gervais and Ameghino 1880), pampatheres are among the less studied members of the impressive South American megafauna (Fariña et al. 2013). They are rather large mammals, whose masses are estimated in the order of hundred kgs (Abrantes et al. 2005; Vizcaíno et al. 2006). Among the features that distinguish them from armadillos are that posterior teeth of pampatheres are not peg-like but bilobate. The diversity of the group is not high. Currently, six genera are recognized (Góis et al. 2013), although it should be noticed that the systematics of the clade requires revision, because historically there has been a predominant reliance on osteoderms for classification (see, for example, Edmund 1996; De Iuliis and Edmund 2002). This reflects the scarcity of good skull, and mandible remains that would allow the recognition of intraspecific variation. While glyptodonts first record appear in the Late Eocene, the earliest known pampathere, *Scirrotherium*, first appears in the Middle Miocene (Carlini and Zurita 2010). Scillato-Yané et al. (2005), based on a combination of osteoderm and craniodental features, as well as size, recognized two genera and five species of Pleistocene pampatheres: *Pampatherium humboldti*, *P. typum*, *Holmesina majus*, *H. occidentalis*, and *H. paulacoutoi*. In South America, *H. occidentalis* occurs in the northwestern part of the continent, including Colombia, Ecuador, Peru and Venezuela. *H. majus* is known with certainty only from Brazil, *H. paulacoutoi* is

reported from Brazil and Argentina, *P. typum* had a wide distribution in Bolivia, Brazil Paraguay and Argentina, and *P. humboldti* is known from Brazil and Uruguay (Scillato-Yané et al. 2005). Góis et al. (2012) recognized *H. rondoniensis* in the southeastern part of the Amazonia, Brazil. *Holmesina septentrionalis* and *Pampatherium mexicanum* are also known in North America (Edmund 1996). Taxa that inhabited the arid southeastern regions of South America are inferred to have had a diet based on coarse vegetation, while that of *H. occidentalis*, known from deposits of humid lowlands during the last glacial maxima, must have fed on softer items (Vizcaíno et al. 2006).

In this work, we describe the first digital endocranial cast of a pampatheres from the Late Pleistocene of Uruguay, with the aim of contributing to the knowledge of gross brain morphology in extinct xenarthrans, as well as to assess through it the previously proposed phylogenetic relationships between pampatheres and glyptodonts.

Materials and methods

Specimen

Complete and undistorted skull of *Pampatherium humboldtii* (MHD-P-28), with partial damage in the right frontal and fragmentary zygomatic arches (Fig. 1). The skull comes from Cuareim River deposits of the Sopas Formation (Late Pleistocene; Ubilla et al. 2004), at Rincón de Pintado locality (30°26′ S, 56°24′ W), Artigas department, northern Uruguay.
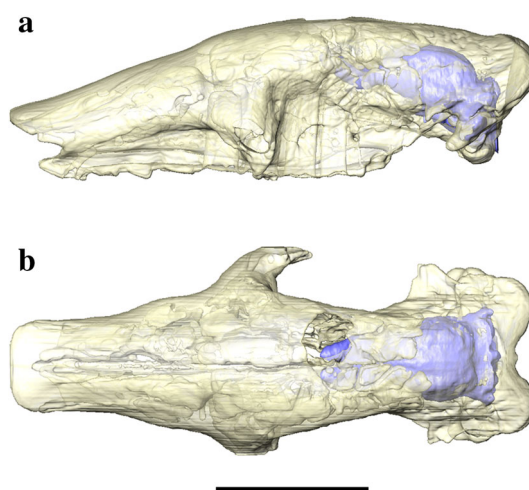

Fig. 1 Semitransparent digital rendering of the skull of *Pampatherium humboldtii* (MHD-P-28) showing the endocast in situ in **a** left lateral view and **b** dorsal view. *Scale bar* 10 cm

CT scanning and endocast extraction

The skull was CT scanned at Hospital Mautone (Maldonado department, Uruguay), in a General Electric (GE) 16 Slice Bright Speed CT scanner in the coronal plane at 120 kV and 200 mA, and the resulting slices have a thickness of 0.7 mm. The digital endocast was extracted from the CT slices using the software BioVis3D 3.0 and Amira 5.2 (2008, Visage Imaging), which allows three-dimensional reconstruction of structures from a series of two-dimensional images.

Endocast volume and body mass relationship

Relative brain size analyses have been used to assess the encephalization grade and the evolution of the brain among different taxonomic groups and within them (Jerison 1973; Finarelli and Flynn 2007). Here, we analyse the relative brain size of *P. humboldtii* in order to compare its brain–body size relationship with that of other cingulates based on the ratio of actual brain size to expected brain size referred to as the encephalization quotient (EQ) (Jerison 1973). The actual brain size (E_i) is the measured volume of the brain (or endocast), and the expected brain size (E_e) is the expected volume of the brain (or endocast) in a mammal of the same body mass. For the expected brain size, we used the values obtained by Tambusso and Fariña (2015) from a linear regression on 796 extant mammals: $E_e = 0.050 \ m^{0.751}$, and that obtained only for xenarthrans: $E_e = 0.123 \ m^{0.606}$, were *m* is the body mass in grams. The body mass was estimated assuming geometric similarity with the pampathere *Holmesina occidentalis* (Vizcaíno et al. 2006) from total skull length and occipital height, respectively, TSL and OCH (Janis 1990; see also Fariña et al. 1998). The total volume of the digital endocast was calculated with Amira, and the volume of different regions of the endocast (i.e., olfactory bulbs, cerebrum and cerebellum) was also calculated and expressed as percentages of the total endocast volume. The endocast anatomical terms are based on Dozo (1987, 1998) and Butler and Hodos (1996).

Comparison with glyptodonts (*Glyptodon* sp., *Panochthus tuberculatus*, *Doedicurus clavicaudatus*, *Pseudoplohophorus absolutus*) and extant armadillos (*Dasypus novemcinctus*, *D. hybridus*, *Zaedyus pichiy*, *Chaetophractus villosus*, *Euphractus sexcinctus*) follow Tambusso and Fariña (2015).

Results

The olfactory bulbs of *Pampatherium humboldtii* are large, pedunculate and very elongated in the anteroposterior direction with the anteriormost ends dorsally displaced (Fig. 2a, b). They are not very divergent, forming an angle of 8.3° with each other, and remain close together along their entire length. Pedunculate olfactory bulbs are characteristic of glyptodonts, while in armadillos, the olfactory bulbs are sessile (Fig. 3). The olfactory peduncles are relatively short compared with the overall size of the bulbs, but allow a clear separation between them and the cerebrum. The volume of the olfactory bulbs is 8 % of the total endocast volume (Table 1); their maximum anteroposterior length is 32.3 mm and the maximum width is 12 mm.

The cerebrum has a maximum anteroposterior length of 61 mm and a maximum transverse width of 55.6 mm at mid-length, mainly due to the lateral extension of the palaeocortex. The maximum height is 51 mm. These measures give a length/width ratio of 1.1 and a length/height ratio of 1.2, which represent a rather anteroposteriorly elongated and dorsoventrally compressed cerebrum, which generally reflects the overall proportions of the skull. In the Late Miocene glyptodont *Pseudoplohophorus absolutus*, the length/width ratio is 0.9 and the length/height ratio is 1.1, while in the Pleistocene glyptodonts *Glyptodon* sp., *Panochthus tuberculatus* and *Doedicurus clavicaudatus*, the length/width ratio range is 0.9–1.1 and the length/height ratio range is 1.3–1.5 (Tambusso and Fariña 2015). In the extant armadillos, the length/width and length/height ratios have ranges of 0.7–0.9 and 0.9–1.1, respectively (Tambusso and Fariña 2015). The ratios of *P. humboldtii* are close to those of Pleistocene glyptodonts (Table 2). The rhinal fissure is continuous with a slightly sinuous and anterodorsally inclined path, with an posteroventrally inflection point at the mid-length (Fig. 2b) to form the origin of the suprasylvian sulcus, which is relatively short. No evidence of a presylvian sulcus is observed (Dozo 1998). In dorsal view, the superior longitudinal sulcus is observed (Fig. 2a). The pyriform lobe is smaller than in the extant armadillos and is comparable in size with that of glyptodonts (Fig. 3). The proportion of the cerebrum in the endocast is 68.6 % (Table 1). This is higher than in glyptodonts which have a range of 63.8–65.2 %, and close to that of extant armadillos with a range of 65.4–72.1 % (Table 1).

The cerebellum is a large structure but proportionately smaller than in glyptodonts, representing 23.4 % of the endocast volume, close to the values of extant armadillos, while in glyptodonts, the values are between 26.5 and 30 % (Table 1). The maximum length is 13.8 mm, and the maximum transverse size is 46.7 mm resulting in a length/width ratio of 0.3 which is smaller than in glyptodonts (0.4–0.55) and close to some extant armadillos (0.3–0.6). It is possible to distinguish the vermis and laterally, separated by two prominent paramedian sulci, the cerebellar

Fig. 2 Digital endocast of
Pampatherium humboldtii
(MHD-P-28) in **a** dorsal view;
b left lateral view; and **c** ventral
view. *cblh* cerebellar
hemisphere, *cer* cerebrum, *hr*
hypophyseal region, *ic* internal
carotid, *jv* jugular vein, *ob*
olfactory bulb, *oct*? ossified
cerebellar tentorium, *op*
olfactory peduncle, *pl* pyriform
lobe, *pms* paramedian sulcus, *rf*
rhinal fissure, *sls* superior
longitudinal sulcus, *ss*
suprasylvian sulcus, *trs*
transverse sinus, *ts*? transverse
sulcus, *v* vermis, *II–XII* cranial
nerves. *Scale bar* 10 cm
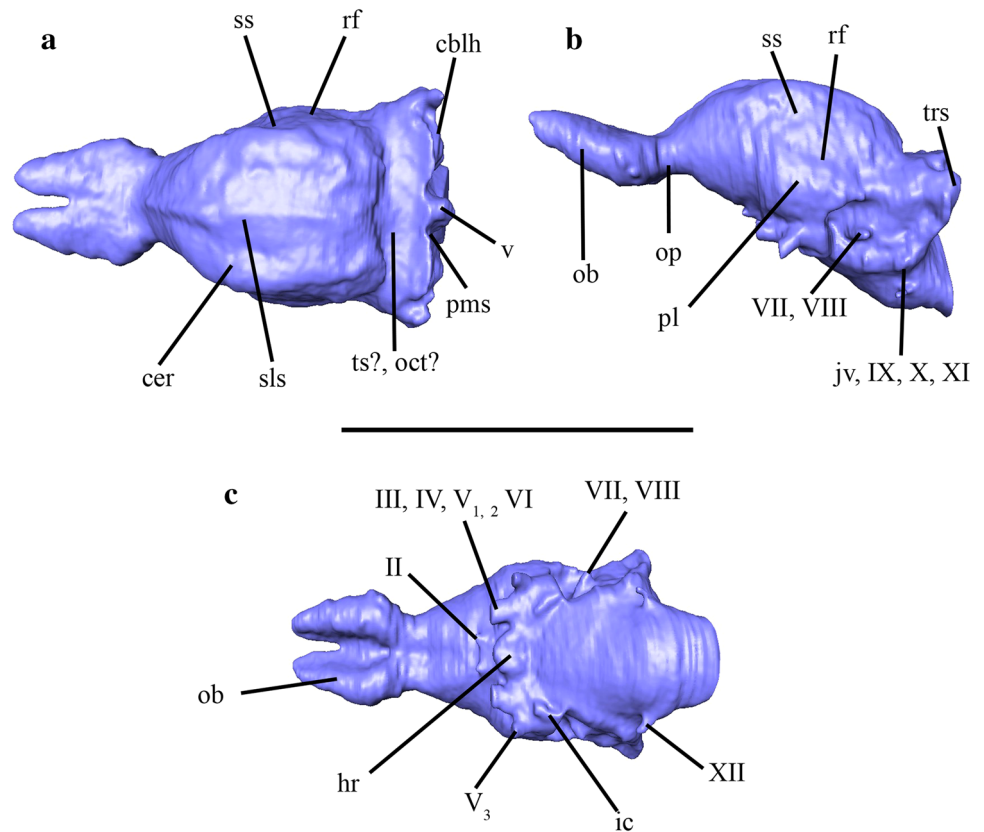
hemispheres (Fig. 2a). Unlike glyptodonts and more comparable with extant armadillos, the vermis is not larger than the cerebellar hemispheres (Fig. 3). The separation between the cerebrum and cerebellum appears to be mediated by an ossified cerebellar tentorium that spans across all the width of the cerebellum and obliterates the transverse sulcus (Fig. 2a). In extant armadillos, a posteromedial ossified cerebellar tentorium is observed but there is not any clear evidence of the presence of this structure in glyptodonts (Fig. 3; Tambusso and Fariña 2015). Part of the transverse sinus is seen lateral to the cerebellar hemispheres.

Most cranial nerves (CN) and some vascular elements were reconstructed and observed on the ventral surface of the endocast (Fig. 2c). The optic nerve (CN II) is located in the middle region of the endocast. Posterior to the optic nerve is the hypophyseal fossa (a convexity on the endocast were the hypophysis is located) and lateral to it, the canal for the oculomotor (CN III), trochlear (CN IV), ophthalmic and maxillary branches of the trigeminal (CN V_{1-2}) and abducens nerves (CN VI) are found. The course of this canal is similar to that of most glyptodonts and armadillos (Tambusso and Fariña 2015). Posterolateral to the CN VI, the canal for the mandibular branch of the trigeminal nerve (CN V_3) begins and then follows a ventrolateral course.

The diameter of this canal, relative to the whole endocast is similar to that of extant armadillos and smaller than in glyptodonts. The canal of the internal carotid lies posterior and medial to CN V_3. At the base of the cerebellum, the cast of the facial (CN VII) and the vestibulocochlear nerves (CN VIII) is observed. Posteroventral to these nerves is the jugular foramen, which transmits the glossopharyngeal (CN IX), the vagus (CN X) and the spinal accessory (CN XI) nerves, as well as the jugular vein. Posterior and ventral to the jugular foramen is the cast of the hypoglossal nerve (CN XII).

The total volume of the endocast of *P. humboldtii* is 133 cm^3, and the body mass, estimated from skull measurements, is 209.5 kg. The values of EQ obtained are 0.27 from the equation based on all mammals and 0.64 from the equation based only on xenarthrans. These EQ are slightly larger than that of Pleistocene glyptodonts, which have ranges of 0.12–0.23 and 0.39–0.61, but smaller than the Late Miocene glyptodont *Pseudoplohophorus* with EQ values of 0.40 and 0.84 (Table 1); the value from the equation based on only xenarthrans is closer to those of extant armadillos, whose ranges are 0.59–0.82 (Table 1). The EQ values of *Pampatherium* are higher than those of another pampathere, *Vassallia* (0.17 and 0.44) calculated from the data in (Carlini and Zurita 2010: 334, Table 14.3).
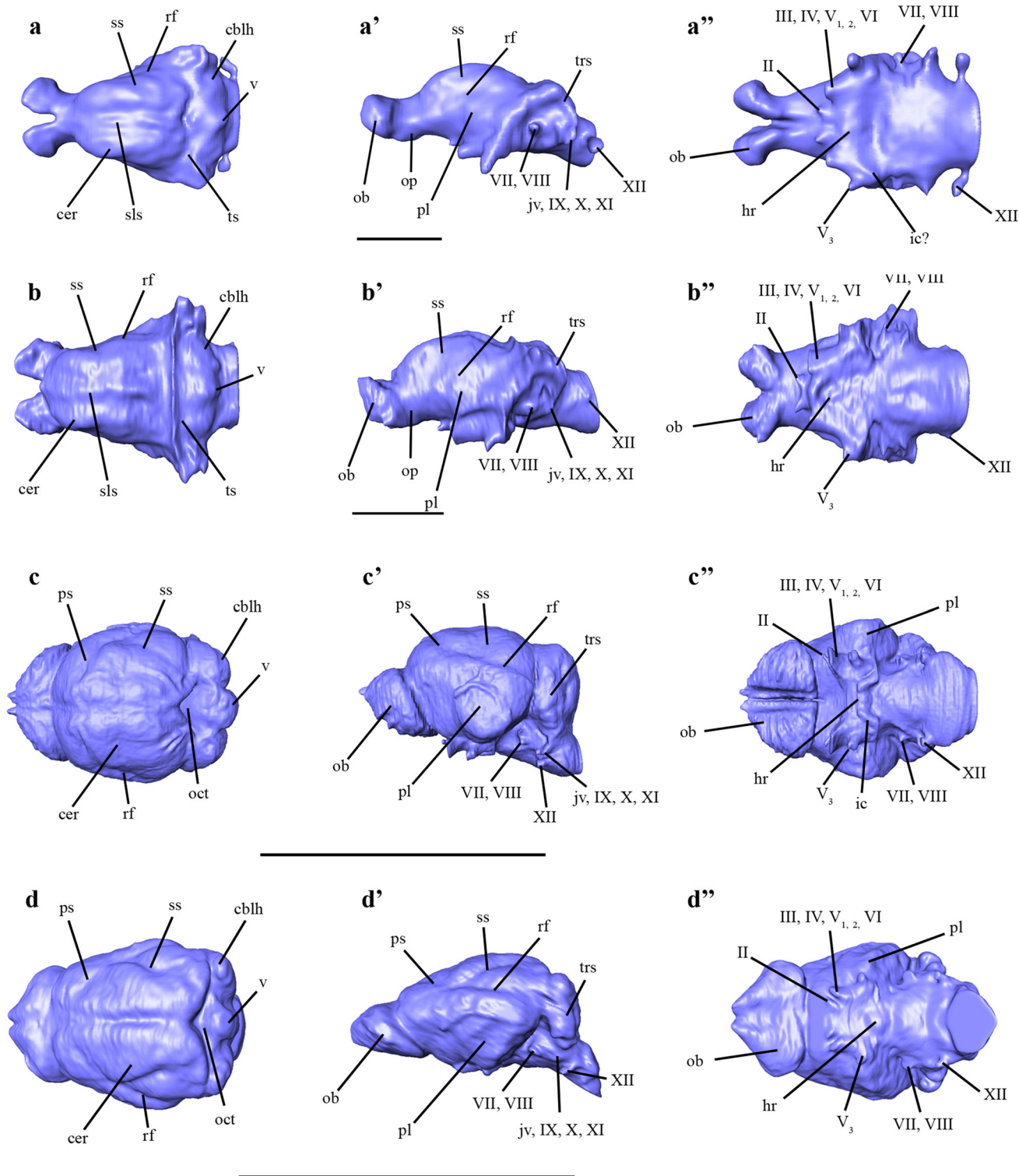
Fig. 3 Digital endocast of *Glyptodon* sp. in **a** dorsal view; **a′** left lateral view; **a″** ventral view; *Doedicurus clavicaudatus* in **b** dorsal view; **b′** left lateral view; **b″** ventral view; *Dasypus novemcinctus* in **c** dorsal view; **c′** left lateral view; **c″** ventral view; *Zaedyus pichiy* in **d** dorsal view; **d′** left lateral view; and **d″** ventral view. *cblh* cerebellar hemisphere, *cer* cerebrum, *hr* hypophyseal region, *ic* internal carotid, *jv* jugular vein, *ob* olfactory bulb, *oct* ossified cerebellar tentorium, *op* olfactory peduncle, *pl* pyriform lobe, *ps* presylvian sulcus, *rf* rhinal fissure, *sls* superior longitudinal sulcus, *ss* suprasylvian sulcus, *trs* transverse sinus, *ts* transverse sulcus, *v* vermis, *II–XII* cranial nerves. *Scale bar* 5 cm

Table 1 Relative size of olfactory bulbs (ob), cerebrum (cer) and cerebellum (cbl) expressed as percentage of total endocast volumen in *Pampatherium humboldtii* and other extinct and extant cingulates, and encephalization quotients calculated from the equation of all mammals (EQt) and from the equation of xenarthrans only (EQx)

	ob (%)	cer (%)	cbl (%)	EQt	EQx
Pampatherium humboldtii	8	68.6	23.4	0.27	0.64
Glyptodon sp.[a]	7.4	64.8	27.8	0.16	0.47
Glyptodon sp.[a]	4.8	65.1	30.0	0.23	0.61
Panochthus tuberculatus[a]	9.7	63.8	26.5	0.22	0.60
Doedicurus clavicaudatus	8.4	63.8	27.8	0.12	0.39
Pseudohoplophorus absolutus[a]	5.7	65.2	29.2	0.40	0.84
Dasypus novemcinctus[a]	10.7	65.4	23.9	0.44	0.59
Dasypus hybridus[a]	7.3	67.8	24.9	0.44	0.62
Zaedyus pichiy[a]	10.6	70.7	18.7	0.55	0.64
Chaetophractus villosus[a]	9.5	72.1	18.4	0.61	0.82
Euphractus sexcinctus[a]	10.1	70.3	19.7	0.55	0.80

[a] Relative size and EQ values from Tambusso and Fariña (2015)

Table 2 Comparative characters on *Pampatherium humboldtii* (MHD-P-28), glyptodonts and armadillos endocast

	P. humboldtii	Glyptodonts	Armadillos
Olfactory bulbs type	Pedunculate	Pedunculate	Sessile
Olfactory bulbs size	Large	Large	Large
Cerebrum length/width ratio	1.1	0.9–1.1	0.7–0.9
Cerebrum length/height ratio	1.2	1.3–1.5	0.9–1.1
Rhinal fissure	Continuous	Continuous	Anterior and posterior
Suprasylvian sulcus	Present	Present	Present
Presylvian sulcus	Absent	Absent	Present
Cerebellum size	Large	Very large	Large
Cerebellum length/width ratio	0.3	0.4–0.55	0.3–0.6
Ossified cerebellar tentorium	Complete?	Absent?	Posteromedial

Data of glyptodonts and armadillos from Tambusso and Fariña (2015)

Discussion

The digital endocast of *Pampatherium humboldtii* presented in this work (Fig. 2) represents the first endocranial cast described for any pampathere. Jerison (1973: 334) mentions the volume of an endocast belonging to *Vassallia*, but makes no reference to its description in that work or any other.

The endocranial cast of *P. humboldtii* has some characteristics similar to those of glyptodonts and others similar to those of armadillos (Table 2). Although the cerebrum is slightly more developed than that of glyptodonts, particularly in the region of the temporo-occipital lobe, a continuous rhinal fissure and the absence of a presylvian sulcus are shared with glyptodonts (Figs. 2, 3a, b). This pattern of cortical sulci differs from that of extant armadillos, since they have a presylvian sulcus in the frontal lobe (Fig. 3c, d). Even though the early Eocene armadillo

Utaetus buccatus has a single neocortical sulcus, it could be the result of the fusion of the presylvian and suprasylvian sulci (Dozo 1998). Another important feature in *P. humboldtii* is the shape of the olfactory bulbs, which are very anteroposteriorly elongated; a feature not shared by any of the other two cingulate groups (Fig. 3).The clear separation between the olfactory bulbs and the cerebrum through the olfactory peduncles is only shared with glyptodonts, since both living and extinct armadillos have olfactory bulbs that are very close to the cerebrum (Dozo 1998), concealing the olfactory peduncles from sight in both dorsal or lateral view. Since only one pampatheriid species was considered, it cannot be stated that this distinctive feature is common to the whole family. However, it has been observed that both glyptodonts and armadillos are rather homogeneous in their neuroanatomical features, which suggests that other pampatheres may have had similar encephalic morphology as well.

Tambusso and Fariña (2015) observed that the relative brain size of armadillos and glyptodonts have the lowest values among xenarthrans. Vílchez Barral et al. (2013) shows values of EQ for glyptodonts and armadillos that are congruent with those of Tambusso and Fariña (2015) obtained from the equation that takes into consideration all mammals, but they make no mention of the equation used to calculate the expected volume of the endocast. The EQ of *Pampatherium* is congruent with these results, although its values are intermediate between those of glyptodonts and armadillos. These results show that all groups of cingulates have a similar relative brain size, both in extant and extinct forms.

Although a detailed phylogenetic analysis is beyond the scope of this work, we can make some mention regarding this aspect. The morphology of the endocast of extant and extinct sloths shows differences with that of cingulates, particularly regarding the pattern of cortical sulci. In sloths, the cerebrum is more developed and there is at least one cortical sulcus, the lateral sulcus (Dozo 1987, 1994), which is not present in cingulates. As mentioned above, the phylogenetic position of pampatheres has been debated given that they have many morphological characteristics similar to both glyptodonts and armadillos, and this pattern is also present in their endocranial morphology. However, the endocast tends to have a closer similarity with that of the Glyptodontoidea (particularly in the pattern of cortical sulci), corroborating other studies (De Iuliis and Edmund 2002; Gaudin and Wible 2006; Fernicola et al. 2008; Wolf et al. 2012).

Quintana (1992) and Vizcaíno et al. (2001) mention the possibility that at least some pampatheres might have been builders of some large burrows. However, according to the analysis of limb proportions of Abrantes et al. (2005), pampatheres do not seem to have been well equipped for digging. So far there is no analysis offering a correlation between the neuroanatomy and the digging habits in extant armadillos. Therefore, it is not yet possible to determine whether the brain morphology in *P. humboldtii* is congruent with the hypothesis that pampatheres were not particularly well suited for digging habits.

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