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Novel information on the endocranial morphology of the abelisaurid theropod *Carnotaurus sastrei*

Nouvelles informations sur la morphologie endocrânienne de l'abélisauridé théropode Carnotaurus sastrei

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ABSTRACT

The endocranial morphology of the abelisaurid *Carnotaurus sastrei*, from the Upper Cretaceous of Patagonia, is studied using X-ray Computed Tomography (CT). The CT scans provided information that allowed the first reconstruction of the brain, inner ear and braincase pneumaticity for this South American taxon. The endocranial morphology confirms that abelisaurids share an overall conformation of the brain and inner ear. However, some traits, such as the height of the dorsal sinuses and the length of the flocculus in the cranial endocast, and a large subsellar recess in the basicranium, appear to characterize the South-American abelisaurids only. Moreover, the olfactory acuity of *Carnotaurus* resembles that reported for other abelisaurids (e.g., *Majungasaurus*, *Viavenator*), suggesting that the sense of smell had an important role. However, some attributes of the endocranial features of *Carnotaurus* (i.e. development and orientation of the olfactory bulbs and tracts) may imply particular olfactory capacities when compared with other abelisaurids.

Mots clés :
Abelisauridae
Paléoneurologie
Quotient d'encéphalisation de reptile
Pneumaticité
Crétacé

RÉSUMÉ

La morphologie endocrânienne de l'abélisauridé *Carnotaurus sastrei* du Crétacé supérieur de Patagonie est étudiée par tomodensitométrie X (CT). Les scans de CT délivrent une information qui permet la première reconstitution de la pneumaticité du cerveau, de l'oreille interne et du crâne de ce taxon sud-américain. La morphologie endocrânienne confirme que les abelisauridés partagent une conformation d'ensemble du cerveau et de l'oreille interne. Cependant, certains traits, comme la hauteur des sinus dorsaux et la longueur du flocculus dans l'endocaste crânien, et un grand évidement de sous-fosse dans le basicrâne semblent caractériser seulement les abélisauridés sud-américains. En outre, l'acuité olfactive de *Carnotaurus* ressemble à celle d'autres abélisauridés (e.g., *Majungasaurus Viavenator*), suggérant que le sens de l'odorat a joué un rôle important. Cependant, certains

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attributs des traits de l'endocrâne de *Carnotaurus* (i.e. le développement et l'orientation des bulbes et tractus olfactifs) peuvent impliquer des capacités olfactives particulières, en comparaison de ce qui est observé chez d'autres abélisauridés.

1. Introduction

In recent years, the knowledge on endocranial morphology of theropod dinosaurs has increased considerably through studies based on X-ray Computed Tomography (CT). So far, several analyses led to complete reconstructions of the cranial endocast and inner ear in different groups of non-avian theropods, including basal neotheropods (Paulina-Carabajal et al., 2015; Xing et al., 2014), coelophysoids (Raath, 1977, fig. 21), ceratosaurs (e.g., Paulina-Carabajal and Filippi, 2018; Paulina-Carabajal and Succar, 2015, Sanders and Smith, 2005; Sampson and Witmer, 2007), allosauroids (e.g., Franzosa and Rowe, 2005; Larsson, 2001; Paulina-Carabajal and Canale, 2010; Paulina-Carabajal and Currie, 2012; Rogers, 1998), megaraptorids (Paulina-Carabajal and Currie, 2017; Paulina-Carabajal and Porfiri, 2018), tyrannosaurids (e.g., Bever et al., 2011, and references therein; Saveliev and Alifanov, 2005; Witmer and Ridgely, 2009) and more derived coelurosaurs (e.g., Balanoff et al., 2018; Lautenschlager et al., 2012).

Abelisauridae is one of the most prominent families of mid-sized theropod dinosaurs that inhabited Gondwana and southern Europe in the Late Cretaceous (see Novas et al., 2013 and references therein). Remains including complete braincases are known for several taxa, such as *Abelisaurus comahuensis*, *Carnotaurus sastrei*, *Skorpiovenator bustingorryi, Viavenator exxoni* and *Aucasaurus garridoi* from Argentina (Bonaparte and Novas, 1985; Bonaparte et al., 1990; Canale et al., 2008; Coria et al., 2002; Filippi et al., 2016), *Majungasaurus crenatissimus* from Madagascar (Sampson and Witmer, 2007; Sues, 1980), *Arcovenator escotae* from France (Tortosa et al., 2013), and *Indosaurus matleyi, Indosuchus raptorius* and *Rajasaurus narmadensis* from India (Huene et Matley, 1933; Novas et al., 2004; Wilson et al., 2003). However, detailed descriptions of the abelisaurid braincase are available only for a few taxa (i.e. *Abelisaurus*, *Aucasaurus*, *Carnotaurus*, *Majungasaurus*, *Viavenator*; Paulina-Carabajal, 2011a, 2011b; Paulina-Carabajal and Filippi, 2018; Sampson and Witmer, 2007); and the endocranial morphology is known in very few taxa, such as *Aucasaurus* (Paulina-Carabajal and Succar, 2015), *Majungasaurus* (Sampson and Witmer, 2007), *Viavenator* (Paulina-Carabajal and Filippi, 2018) and *Indosaurus*, which is known from a natural partial endocast described by Huene et Matley (1933). Some endocranial features were described for *Abelisaurus* (Paulina-Carabajal, 2011b), and the neurovascular pattern has been described for *Carnotaurus* (Paulina-Carabajal, 2011a) and *Arcovenator* (Tortosa et al., 2013). Jurassic ceratosaurs such as *Ceratosaurus* and *Eoabelisaurus* have complete braincases (Gilmore, 1920; Pol and Rauhut, 2012), but only the endocranial morphology of *Ceratosaurus* has been studied (Franzosa, 2004; Sanders and Smith, 2005).

Carnotaurus sastrei (Bonaparte, 1985) is a derived brachyrostran abelisaurid from the Maastrichtian La Colonia Formation, Chubut province, Argentina (Novas, 2009). The type specimen preserves a complete skull, including a complete braincase that is articulated to the rest of the skull bones. Here, we describe for the first time the cranial endocast of this taxon (Figs. 1–3). Comparisons with other known abelisaurid cranial endocasts indicate that the overall conformation of the brain and inner ear are similar within the family, although some attributes appear to be characteristic of the South American forms (Fig. 4). The pneumaticity of the braincase is also compared with that for other abelisaurids.

2. Material and methods

The skull of the holotype of *Carnotaurus sastrei* (MACN CH-894) was CT-scanned in 2010, at the TCba Salguero Diagnostic Center (Buenos Aires, Argentina) using a CT 64 Ingenuity Core medical tomographer. The slice thickness was of 0.62 mm and the scan energy parameters were of 119 mA and 120 kV. The virtual three-dimensional cranial endocast was obtained and visualized using software 3D Slicer version 4.8 (Fedorov et al., 2012). Final illustrations were made using Adobe Photoshop (CS6).

The CT scans allowed the reconstruction of the main encephalic structures but few neurovascular passages. The large size of the field of view (FVO) (which included the complete skull of *Carnotaurus*, plus the space occupied by the frontal horns) prevented the observation of the smaller structures of the braincase, such as the complete semicircular canals of the inner ear and most canals for cranial nerves (CN) and blood vessel. The lack of contrast between bone and sediment probably caused by the ferric concretion from which the skull was extracted (F.E. Novas pers. comm.) affected the quality of the resulting images.

Measurements. The total volume of the cranial endocast of *Carnotaurus* was calculated using the tools of software Slicer version 4.8 (Table 1). The reptilian cranial endocast does not necessary reflect the original brain surfaces, but reflects the overall shape of the brain (e.g., Hopson, 1979). Following Sampson and Witmer (2007), we will refer to the cast structures as if they were the structures themselves (e.g., "olfactory bulb" instead of "olfactory bulb cavity endocast").

Body mass calculation. Body mass is a useful parameter to calculate the Reptile Encephalization Quotient (REQ; Hurlburt, 1996; Hurlburt et al., 2013). We used two sources of information to estimate the body mass for *Carnotaurus*: one was the femoral circumference method (FCM)

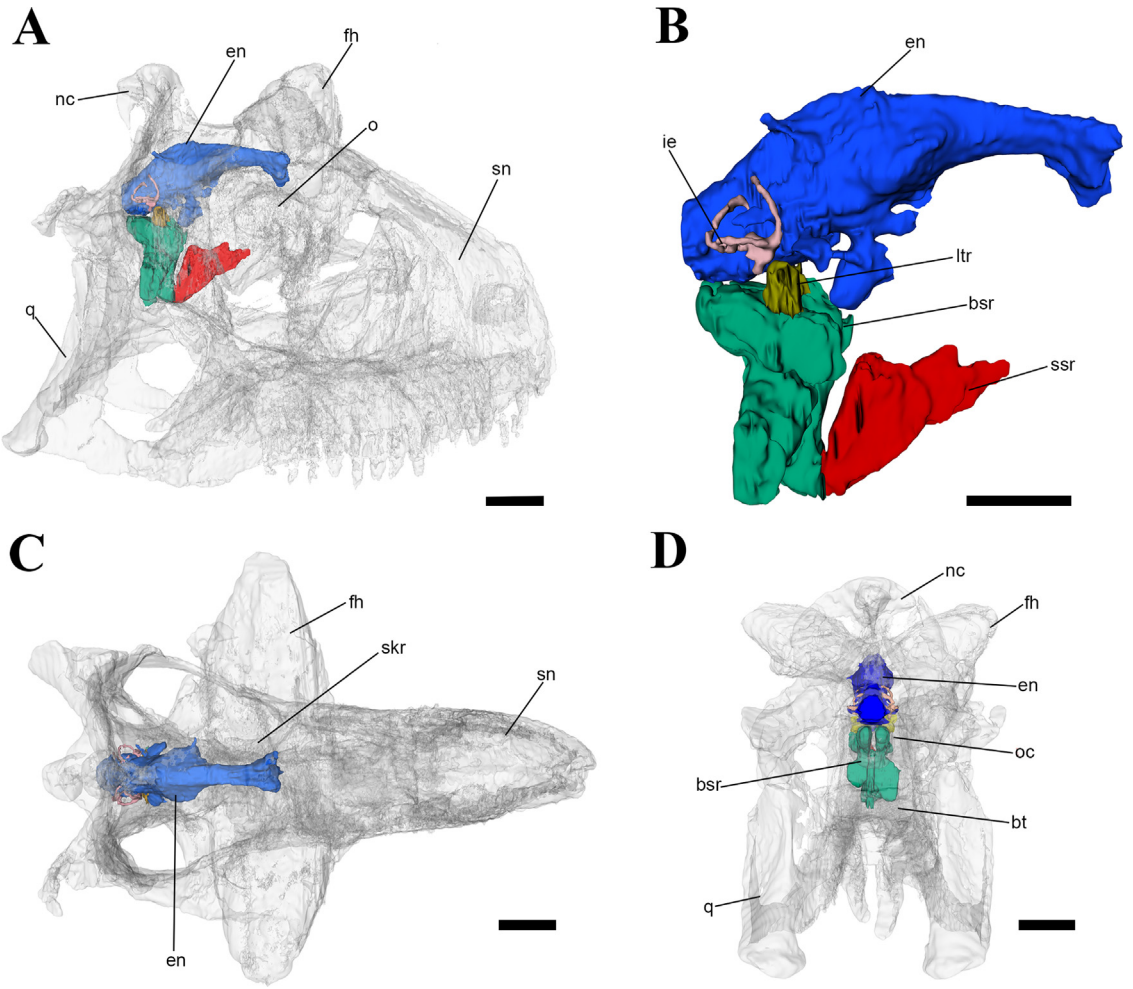

Fig. 1. Digital reconstruction of the skull, cranial endocast and braincase pneumaticity of *Carnotaurus sastrei* (MACN-CH 894) in lateral (A and B), dorsal (C), and posterior views (D). Bone is rendered semi-transparent (A, C and D) to allow observation of internal structures. bsr: basisphenoidal recess; bt: basal tuber; en: endocast; ie: inner ear; fh: frontal horns; ltr: lateral tympanic recess; nc: nuchal crest; o: orbit; oc: occipital condyle; q: quadrate; sn: snout; skr: skull roof; ssr: subsellar recess. Scale bars equal 20 cm (A, C and D) and 5 cm (B).

Fig. 1. Reconstitution numérique de la pneumaticité du crane, de l'endocaste crânien et du cerveau chez *Carnotaurus sastrei* (MACN-CH 894) en vues latérale (A et B), dorsale (C) et postérieure (D). l'os a été rendu semi-transparent (A, C et D) pour l'observation des structures internes. bsr : évidement basisphénoïdal ; bt *tuber*(?) basal ; en : endocaste ; ie : oreille interne ; fh : cornes frontales ; ltr : évidement latéral du tympan ; nc : crête nucale ; o : orbite ; oc : condyle occipital ; q : carré ; sn : museau ; skr : toit du cerveau ; ssr : évidement de sous-fosse. Les barres d'échelle représentent 20 cm (A, C et D) et 5 cm (B).

of Anderson et al. (1985), used here, and the other was the body mass calculated recently by Campione and colleagues (2014) using a modification of the quadrupedal equation (Campione and Evans, 2012) applied to bipedal non-avian theropods. The result of the latter analysis is approximately 1743 kg, with a 25% prediction error range of 1306–2179 kg. The FCM, calculated by $W = 0.16\,C_f\ 2.73$, where W is mass (g), and C_f is minimum femur circumference (which in *Carnotaurus* is 325 mm), resulted in a total weight of 1419 kg. Both values, the minimum (1419) and the maximum (1743) body weights, were used to calculate the REQ (Table 1).

Encephalization quotient calculation. This is a measure of the relative brain size among theropods (Jerison, 1973), modified by Hurlburt (1996) as the Reptile Encephalization Quotient (REQ) based on extant reptiles. Following Hurlburt et al. (2013), we used the equation $REQ = MBr/(0.0155 \times MBd^{0.553})$, where MBr is the brain mass and MBd is the body mass, to calculate the REQ of *Carnotaurus*. We use two body mass values, one calculated here using the method of Anderson et al. (1985) and the other estimated by Campione et al. (2014) to calculate the REQs at 100%, 70% and 50% of the endocranial volume (Table 1).

Olfactory ratios. Olfactory ratios can be used to interpret the olfactory acuity in extinct animals (see Zelenitsky et al., 2009 and references therein). It is calculated as the ratio between the greatest diameter of the olfactory bulb and the longest diameter of the cerebral hemisphere, and then multiplied by 100 (Zelenitsky et al., 2009, 2011).

Institutional abbreviations. MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires,

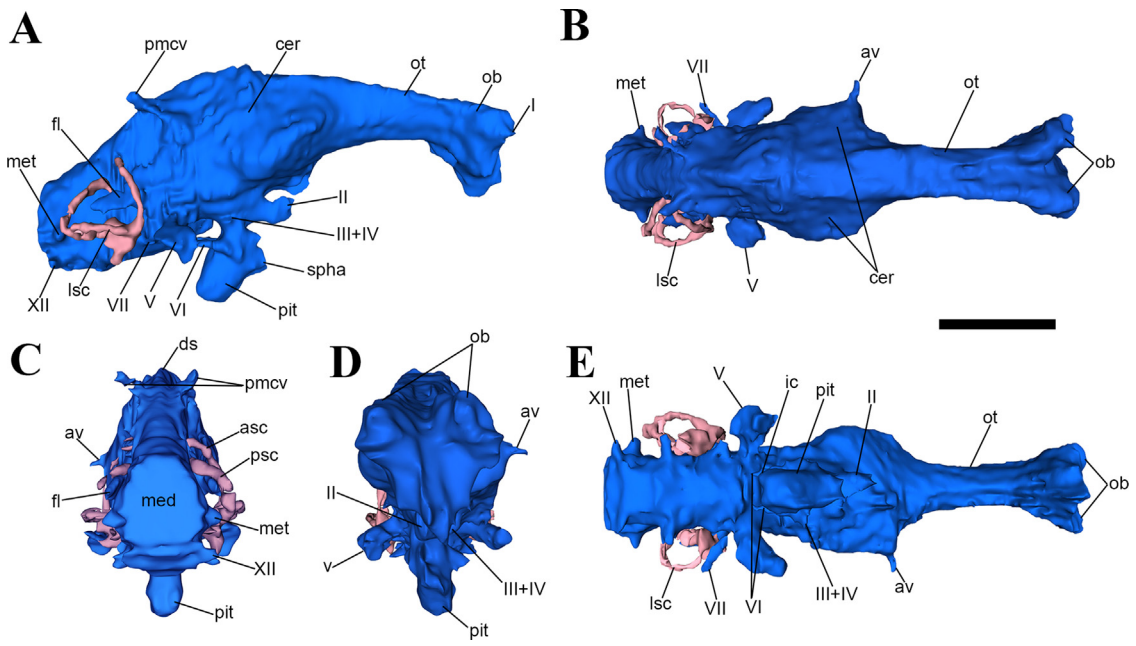

Fig. 2. Digital reconstruction of the cranial endocast and inner ear of *Carnotaurus sastrei* (MACN-CH 894) in right lateral (A), dorsal (B), posterior (C), anterior (D), and ventral (E) views. asc: anterior semicircular canal; av: anterior vein; cer: cerebral hemisphere; ds: dorsal sinus; fl: flocculus; ie: internal carotids; lsc: lateral semicircular canal; med: medulla oblongata; met: metotic passage (for CNs IX–XI); ob: olfactory bulbs; ot: olfactory tract; pit: pituitary; pmcv: posterior middle cerebral veins; psc: posterior semicircular canal; spha: sphenoidal artery; I-XII: cranial nerves. The scale bar equals 5 cm.
Fig. 2. Reconstitution numérique de l'endocaste crânien et de l'oreille interne de *Carnotaurus sastrei* (MACN-CH 894) en vues latérale droite (A), dorsale (B), postérieure (C), antérieure (D) et ventrale (E). asc : canal semi-circulaire antérieur ; av : veine antérieure ; cer : hémisphère cérébral ; ds : sinus dorsal ; fl : floculus ; ie : carotides internes ; lsc : canal semi-circulaire latéral ; med : medulla oblongue ; met : passage métotique (pour Ns IX-XI) ; ob : bulbes olfactifs ; ot : tractus olfactifs ; pit : pituitaire ; pmcv : veines médiocérébrales postérieures ; sn : museau ; psc : canal semi-circulaire postérieur ; spha : artère sphénoïdale ; I-XII : nerfs crâniens. Barre d'échelle = 5 cm.

Table 1
Selected measurements of endocranial values, Reptile encephalization quotient and olfactory ratios of *Carnotaurus* compared with those of other theropods.
Tableau 1
Mesures sélectionnées de valeurs endocrâniennes. Quotient d'encéphalisation de reptile et rapports olfactifs de *Carnosaurus* comparés à ceux d'autres théropodes.

Taxon	EV (cm^3)	EV (cm^3) 50%	EV (cm^3) 37%	BdM (kg)	REQ 37%	REQ 50%	REQ 100%	OR (%)
Carnotaurus	169.8	84.9	62.8	1419–1743	1.4–1.6	1.9–2.2	3.9–4.3	50
Viavenator[a]	141.6	70.8	52.4	–	–	–	–	57
Majungasaurus	106.4[b]	53.2	39.4	1130[b]	1.14	1.54	3.08	48.3[c]
Ceratosaurus	–	–	–		1.22[d]	1.66[d]	3.31[d]	48[c]
Allosaurus	169–188[e]	84.5–93.9	62.5–69.5	1400–2300[e]	1.3–1.8	1.8–2.4	3.28	50[c]
Giganotosaurus	275[e]	101.7	137.5	7000[f]	1.07	1.4	2.9	67[c]
Sinraptor	95[g]	47.5	35.1	1700[h]	0.81	1.1	2.19	55[g]
Murusraptor[i]	148.2	74.1	54.8	1551	1.33	1.8	3.6	45–50
Tyrannosaurus	414.2[e]	207.1	153.2	5654–7000	1.8–1.6	2.5–2.2	4.4–4.9	66–71[c]

EV: endocranial volumen; BdM: body mass; REQ: reptile encephalization quotient; OR: olfactory ratios.
[a] Paulina-Carabajal and Filippi, 2018.
[b] Sampson and Witmer, 2007.
[c] Zelenitsky et al., 2009.
[d] Franzosa, 2004.
[e] Paulina-Carabajal and Canale, 2010.
[f] Mazzetta et al., 2004.
[g] Paulina-Carabajal and Currie, 2012.
[h] Christiansen and Fariña, 2004.
[i] Paulina-Carabajal and Currie, 2017.

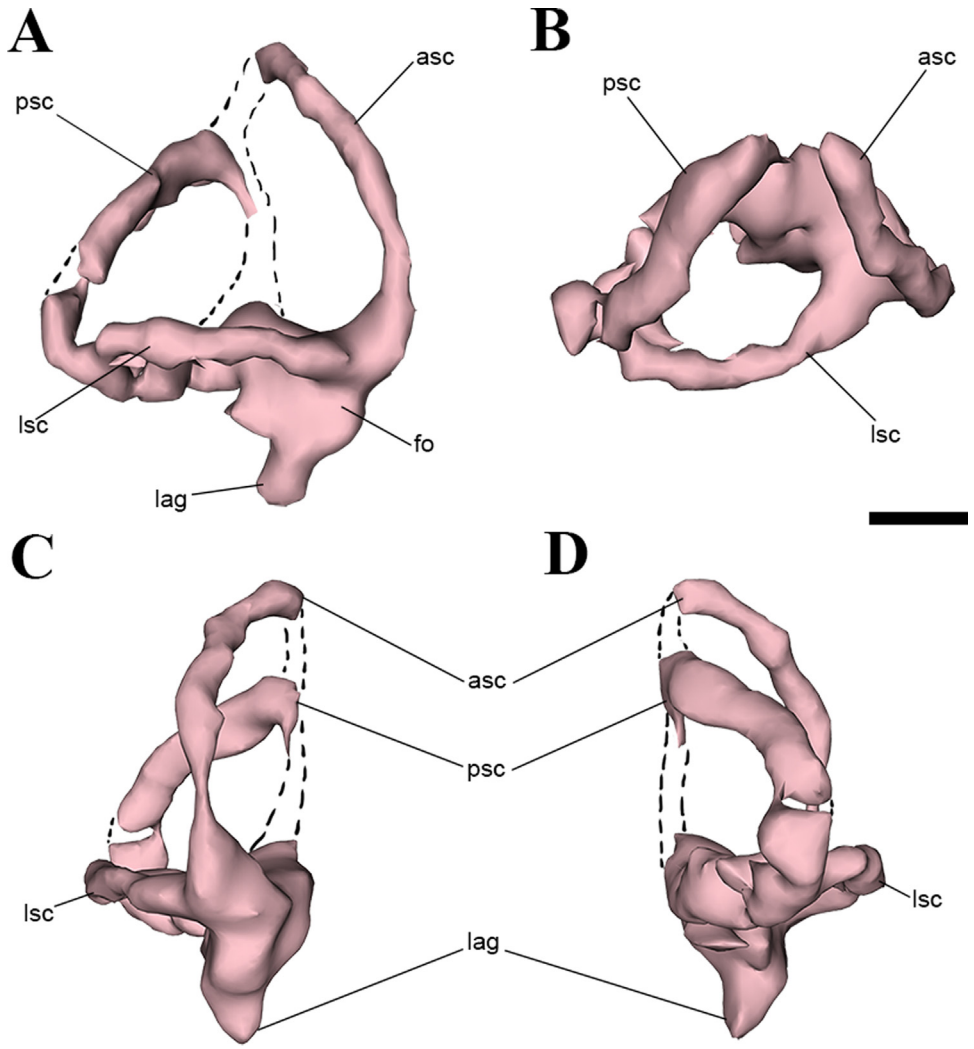

Fig. 3. Rendering of the right inner ear of *Carnotaurus sastrei* (MACN-CH 894) in lateral (A), dorsal (B), anterior (C) and posterior (D) views. The dashed lines indicate portions of the inner ear that are not reconstructed. asc: anterior semicircular canal; fo: fenestra ovalis; lag: lagena; lsc: lateral semicircular canal; psc: posterior semicircular canal. The scale bars equal 10 mm.

Fig. 3. Rendu de l'oreille interne droite de *Carnotaurus sastrei* (MAC-CH 894) en vues latérale (A), dorsale (B), antérieure (C) et postérieure (D). Les lignes en tireté indiquent les portions de l'oreille interne qui n'ont pas été reconstituées. asc : Canal semi-circulaire antérieur ; fo : fenestra ovalis ; lag : lagena ; lsc : canal semi-circulaire latéral ; psc : canal semi-circulaire postérieur. Les barres d'échelle représentent 10 mm.

Argentina; MAU, Museo "Argentino Urquiza", Rincón de los Sauces, Argentina; MPCA, Museo Provincial 'Carlos Ameghino', Cipolletti, Río Negro; MUCPv: Museo de la Universidad Nacional del Comahue, Neuquén, Neuquén, Argentina.

3. Description

3.1. Endocranial morphology

The main encephalic structures of the forebrain, midbrain, and hindbrain are identifiable, as well as the bases of the largest cranial nerves and blood vessels (Figs. 1 and 2). The complete cranial endocast has a length of 179 mm from the foramen magnum to the anterior end of the olfactory bulbs, and its maximum transversal width across the cerebral hemispheres is 48.9 mm, resulting in a total volume of approximately 169.8 cm^3. The endocast is anteroposteriorly long and transversely narrow, as in other studied non-coelurosaur theropods. When compared to other abelisaurids, *Carnotaurus* is distinguished by having the olfactory tracts and anteroventrally oriented bulbs forming a curved loop (Fig. 2A), so that forebrain and hindbrain are not sub-horizontally positioned as in *Majungasaurus* (Sampson and Witmer, 2007), *Aucasaurus* (Paulina-Carabajal and Succar, 2015) and *Viavenator* (Paulina-Carabajal and Filippi, 2018) (Fig. 4). Although the endocast of *Indosaurus* is currently lost (M. Ezcurra, pers. comm.), the sketch made by Huene et Matley (1933) shows olfactory tracts (the olfactory bulbs are missing) that are seemingly ventrally curved, reminding the condition of *Carnotaurus*. The angle between midbrain and hindbrain is approximately 43–44°, a value

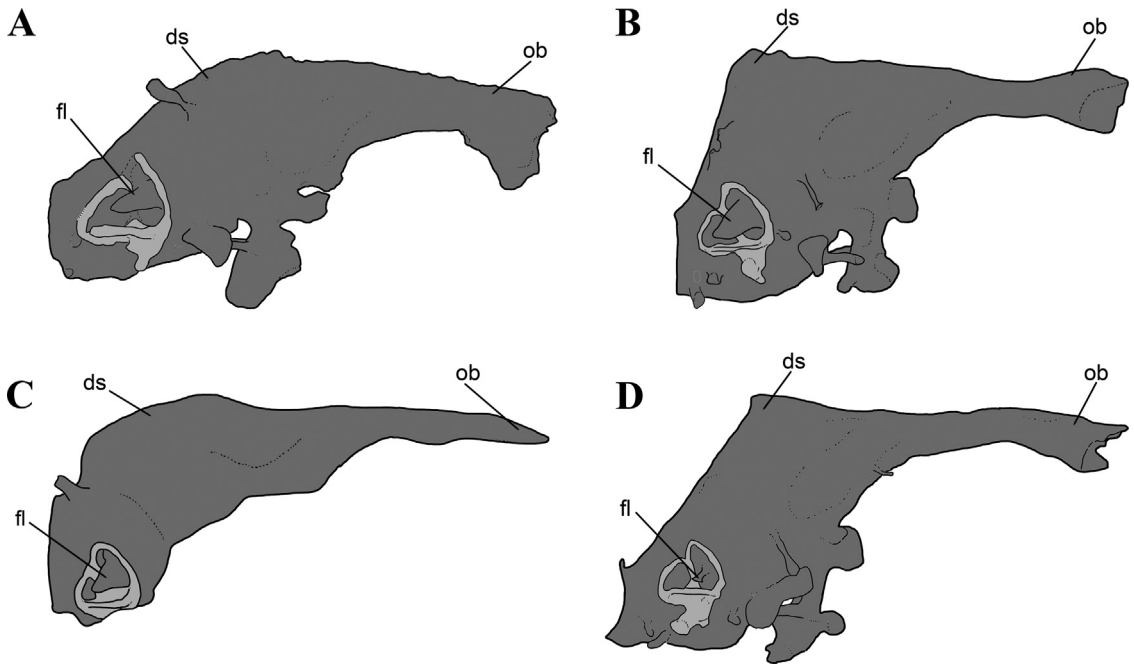

Fig. 4. Comparisons of the cranial endocasts in lateral view of (A) *Carnotaurus*, (B) *Viavenator* (modified from Paulina-Carabajal and Filippi, 2018), (C) *Aucasaurus* (modified from Paulina-Carabajal and Succar, 2015), and (D) *Majungasaurus* (modified from Sampson and Witmer, 2007). ds: dorsal longitudinal sinus; fl: flocculus; ob: olfactory bulbs. Not to scale.
Fig. 4. Comparaisons des endocastes crâniens en vue latérale de (A) *Carnotaurus*, (B) *Viavenator* (modifié d'après Paulina-Carabajal et Filippi, 2018), (C) *Aucasaurus* (modifié d'après Paulina-Carabajal et Succar, 2015) et (D) *Majungasaurus* (modifié d'après Sampson et Witmer, 2007). ds : sinus longitudinal dorsal ; fl : floculus ; ob : bulbes olfactifs. Non à l'échelle.

that resembles that for *Majungasaurus* (45°, Sampson and Witmer, 2007), but is greater than that of *Viavenator* (35°, Paulina-Carabajal and Filippi, 2018).

A low dural or dorsal expansion (= pyramidal peak) develops dorsally at the level of the root of CN V (Fig. 2A), as in *Majungasaurus* but unlike *Aucasaurus* and *Viavenator* where the dural expansion is developed at the level of the flocculus (Paulina-Carabajal and Filippi, 2018). This protuberance on the endocast indicates the presence of a dorsal longitudinal venous sinus that has been also related to the position of the pineal gland (Sampson and Witmer, 2007). However, the dural expansion in *Carnotaurus* is poorly projected dorsally compared to the well-developed dural expansions of the aforementioned abelisaurids (Fig. 4), and therefore the angle formed between the foramen magnum and the dural expansion in lateral view is also low, reaching a value of 40°.

The roots of almost all the cranial nerves are observed on the endocast, except for CN IV, probably CN VII (see below), and CN VIII, which is probably very small in diameter and difficult to observe, as in other studied theropods.

Forebrain–This region of the endocast includes the olfactory tracts and bulbs (CN I), cerebral hemispheres, CN II (optic nerve), the infundibular stalk and the pituitary body (= hypophysis). The olfactory tracts are elongated and curved anteroventrally, with a width of 21 mm. The olfactory bulbs are well developed, oval, and clearly separated medially (by the median septum of the mesethmoid), slightly diverging from the midline (Fig. 2B). Elongated and wide olfactory tracts and large olfactory bulbs are present in both ceratosaurs (Paulina-Carabajal and Filippi, 2018; Sampson and Witmer, 2007) and particularly carcharodontosaurids (Larsson, 2001; Paulina-Carabajal and Canale, 2010), in which the olfactory tracts and bulbs have nearly the same length as the rest of the endocast.

The cerebral hemispheres are well marked, aligned with the olfactory bulbs in lateral view (Fig. 2A); however, the inter-hemispherical fissure is not visible, obscured by the dorsal longitudinal sinus, as in most non-avian theropods (Hopson, 1979; Witmer et al., 2008). Anterolateral to the cerebral hemisphere, there is a blood vessel, visible on the left side, that would exit through a foramen located in the sphenetmoid (the "vascular foramen of the olfactory tract", see Paulina-Carabajal, 2011a, fig. 4) (Fig. 2B). Similarly positioned veins are present in *Majungasaurus*, named as the "venous canal" by Sampson and Witmer (2007). The roots of CNs II (optic tracts) are short, large in diameter and slightly divergent; the union of both nerves along the midline probably represents the position of the optic chiasm, although this region is not enlarged and bulbous, as in other dinosaurs (e.g., titanosaurids). The infundibular stalk is oval in section and projects ventrally contacting the pituitary body. The pituitary is posteroventrally projected and not particularly inflated, having a volume of approximately 3 cm^3 (it represents approximately 1.8 % of the total volume of the endocast). This relative size of the pituitary is also observed in other abelisaurids (Paulina-Carabajal and Filippi, 2018; Sampson and Witmer, 2007) and other non-avian theropods (Franzosa, 2004). Anterior to the pituitary is a large sphenoidal artery (Fig. 2),

which exits the pituitary fossa through an anterolateral fenestra in the basisphenoid ("fenestra rostral to the pituitary fossa", Paulina-Carabajal, 2011a, fig. 4; "foramen for or endocast of sphenoidal artery", Sampson and Witmer, 2007, fig. 14). The passages for the cerebral branches of the internal carotid arteries are barely visible in the posterior end of the pituitary.

Midbrain–The midbrain is characterized by the low dural expansion (= pyramidal peak). As in other basal theropods, the optic lobes are not observed in the endocast; they possibly were positioned close to the midline, as in other abelisaurids such as *Majungasaurus* (Sampson and Witmer, 2007), *Viavenator* (Paulina-Carabajal and Filippi, 2018) and non-avian theropods (Franzosa, 2004; Franzosa and Rowe, 2005; Rogers, 1998). Near the base of the infundibular stalk, there is no distinction between the roots of CNs III and IV, which probably left the endocranial cavity through a single foramen. On the lateral surface of the braincase, however, there are separate foramina for these nerves defining the contact between the orbitosphenoid and the laterosphenoid (Paulina-Carabajal, 2011a, fig. 4).

Hindbrain–This region comprises the cerebellum, the medulla oblongata, and the roots of cranial nerves V–XII. As in other abelisaurids (Paulina-Carabajal and Filippi, 2018; Sampson and Witmer, 2007), the cerebellum is not markedly expanded laterally and is positioned just below the posterior middle cerebral veins (Figs. 2 and 4). The only discernible structure of the cerebellum in the endocast is the flocculus, which is well defined, although it is small when compared to the larger flocculi of coelurosaurian theropods and pterosaurs (e.g., Franzosa, 2004; Hopson, 1979; Witmer et al., 2003). The flocculus in *Carnotaurus* is a blade-like structure, which is posterolaterally projected into the space formed by the anterior semicircular canal (Fig. 2A). This situation is strongly reminiscent of that of the South-American abelisaurids *Aucasaurus* (Paulina-Carabajal and Succar, 2015) and *Viavenator* (Paulina-Carabajal and Filippi, 2018), and contrasts with the relatively smaller flocculus described for *Majungasaurus* (Sampson and Witmer, 2007). The posterior middle cerebral veins extend posterodorsally. Although the foramina for these veins are not clearly observed on the braincase due to poor preservation of this region, these veins likely pierced the supraoccipital, exiting through foramina bounded between the later and the parietal, as in other theropods (Paulina-Carabajal and Currie, 2017; Witmer and Ridgely, 2009) and extant birds (Franzosa, 2004).

The roots of CN V (trigeminal nerve) are visible on both sides of the endocast, being large in diameter and expanded laterally. Although all the branches leave the endocranial cavity through a single foramen, the ophthalmic branch (V_1) bifurcates from the maxillo-mandibular branch ($V_{2,3}$) and exits the braincase anteriorly through a foramen enclosed entirely by the laterosphenoid (Paulina-Carabajal, 2011a) (Fig. 2). This bifurcation indicates an almost intracranial location of the trigeminal ganglion (Sampson and Witmer, 2007). Dorsal to CN V, there is a blood vessel (poorly visible in the CT scans), which would correspond to the anterior middle cerebral vein, which possibly exits through a foramen enclosed by the laterosphenoid. The passages for CN VI (abducens nerve) are on the ventral side of the medulla and project anteroventrally, reaching the posterior portion of the pituitary body, entering the pituitary fossa and probably leaving the endocranial cavity through the fenestra for the sphenoidal artery (Paulina-Carabajal, 2011a: fig. 4). The passage for CN VII (facial nerve) is difficult to identify in the CT scans, although its root is clearly posterior to CN V (Fig. 2). This nerve is posterolaterally oriented and leaves the endocranial cavity through a foramen enclosed by the prootic. Cranial nerve VIII (vestibulocochlear nerve) is not observed in the CT scans, probably due the small diameter of these passages, as in other theropods (Paulina-Carabajal and Currie, 2017). The passages for cranial nerves IX–XI (glossopharyngeal, vagus, and accessory nerves, respectively) are united in a common canal, the metotic passage, and apparently leave the endocranial cavity through a single foramen (metotic foramen). Finally, the root of the CN XII (hypoglossal nerve) leaves posteroventrally the medulla oblongata through a single canal.

3.2. Inner ear

The complete osseous labyrinth is difficult to trace in the CT scans, but the right inner ear is partially reconstructed and illustrated in Fig. 3. All the semicircular canals and the lagena were digitally extracted, but not the common crus. The semicircular canals are slender, with a diameter of the tube that varies between 2.5 and 3.6 mm, with the lateral semicircular canal (LSC) slightly wider. The anterior semicircular canal (ASC) is larger, somewhat curved posteriorly, and taller than the posterior semicircular canal (PSC), as in most theropods (Sampson and Witmer, 2007); unusually, the LSC appears to be relatively larger than the PSC, but this may be accentuated by the lack of the common crus. The contour of the ASC and PSC is oval, whereas the LSC is more circular. In dorsal view (Fig. 3B), the angle between ASC and PSC is about of 85°; this angle resembles that present in the abelisaurids *Viavenator* (85°, Paulina-Carabajal and Filippi, 2018) *Majungasaurus* (∼85°, Sampson and Witmer, 2007, fig. 19) and *Aucasaurus* (92–95°, Paulina-Carabajal and Succar, 2015). The fenestra ovalis is partially reconstructed. The lagena is conical and short, as in other abelisaurids and most theropods (e.g., Witmer and Ridgely, 2009). It has a length of approximately 6 mm.

The size, shape, angle between ASC and PSC and the general morphology of the inner ear of *Carnotaurus* closely resemble those of other known abelisaurids so far (e.g., *Aucasaurus, Majungasaurus*, *Viavenator*; Paulina-Carabajal and Filippi, 2018; Paulina-Carabajal and Succar, 2015; Sampson and Witmer, 2007). This inner ear morphology is conservative and present in many mid-sized theropods, such *Ceratosaurus* (Sanders and Smith, 2005) and allosauroids (Franzosa and Rowe, 2005; Rogers, 1998).

3.3. Pneumaticity

The braincase pneumaticity is usually associated with the systems of air-filled diverticula originated from the cervical pulmonary air sacs and paratympanic systems leaving large excavations on the lateral and ventral sides

of the braincase (Sampson and Witmer, 2007; Witmer et al., 2008). *Carnotaurus* includes the lateral (=rostral) tympanic recess, the basisphenoidal recess and the subsellar recess (Fig. 1A), also present in other abelisaurids (Paulina-Carabajal, 2011b; Paulina-Carabajal and Filippi, 2018; Sampson and Witmer, 2007). The lateral tympanic recess probably originated from the paratympanic system, whereas the basisphenoidal and the subsellar recesses originated from the median pharyngeal system (Dufeau, 2011; Witmer, 1997).

In the braincase of *Carnotaurus*, the lateral tympanic recess is an irregular cavity on the lateral side of the basisphenoid and probably part of the prootic, just posteroventrally to the preotic pendant (Paulina-Carabajal, 2011a). The CT scans show that this recess is considerably smaller compared to the basisphenoidal and subsellar recesses (Fig. 1B). It is not clear if this space is divided into two main chambers as in *Abelisaurus* and *Viavenator* (Paulina-Carabajal, 2011b; Paulina-Carabajal and Filippi, 2018), or whether it has a connection with the basisphenoidal recess, although the evidence from the known abelisaurid braincases indicates the opposite. Sampson and Witmer (2007) reported a connection between the lateral tympanic recess and the posterior surface of the basioccipital in *Majungasaurus*, but this feature appears to be absent in *Carnotaurus*.

The basisphenoidal recess is a fairly large conical deep excavation in the ventral side of the basisphenoid, as in other abelisaurids (Paulina-Carabajal, 2011b; Paulina-Carabajal and Filippi, 2018; Sampson and Witmer, 2007) (Fig. 1C). The basisphenoidal recess further expands posteriorly and is divided into two large lateral cavities, which strongly affect the basioccipital internally, at the base of the occipital condyle (Fig. 1B and D). Each of these paired cavities is divided into a dorsal chamber anteroposteriorly and a ventral chamber dorsoventrally. The dorsal chamber posteriorly reaches the neck of the occipital condyle; each one is separated by a median septum that partially divided the basisphenoidal recess (Fig. 1D). This condition of the posterior expansion of the basisphenoidal recess invading the neck of the occipital condyle is present in some tetanurans (Paulina-Carabajal and Currie, 2017; Witmer, 1997), *Ceratosaurus* ("basioccipital sinuses", Sanders and Smith, 2005) and the abelisaurids *Aucasaurus, Ilokelesia*, *Viavenator* (Paulina-Carabajal, 2011b; Paulina-Carabajal and Filippi, 2018) and *Ekrixinatosaurus* (MUCPv-294, as shown by fractures). On the other hand, the ventral chamber extends posteroventrally, invading the basioccipital, but without pneumatizing entirely the basal tuber. A similar situation is reported in *Rajasaurus* (Wilson et al., 2003), where the basisphenoidal portion of the basal tuber is hollow. The basisphenoidal recess of *Carnotaurus* communicates anteroventrally with the subsellar recess.

The subsellar recess is partially visible in left lateral and ventral views of the braincase, but is filled with sediment (Paulina-Carabajal, 2011a). The CT scans showed that the subsellar recess is well developed anterior to the basisphenoid recess and ventral to the base of the cultriform process (Fig. 1A). It is developed mainly anteroposteriorly, slightly smaller in volume than the basisphenoidal recess. Likewise, the size of the subsellar recess resembles the large recess present in *Abelisaurus* (Paulina-Carabajal, 2011b) and *Viavenator* (Paulina-Carabajal and Filippi, 2018), but differs with the smaller subsellar recess in *Majungasaurus* (Sampson and Witmer, 2007).

4. Discussion

4.1. Neurosensorial capabilities

The general shape and proportions of the cranial endocast of *Carnotaurus* resembles that in other abelisaurids (e.g., *Aucasaurus, Majungasaurus*, *Viavenator*), particularly in the development of the olfactory tracts and bulbs and the flocculi. However, it is worth mentioning the low dural expansion in *Carnotaurus*, which is the lowest compared with those of other abelisaurids such as *Aucasaurus*, *Majungasaurus*, and *Viavenator* (Paulina-Carabajal and Filippi, 2018; Paulina-Carabajal and Succar, 2015; Sampson and Witmer, 2007); hence, this trait is reflected in variable development within this clade of theropods (Fig. 4). *Majungasaurus* exhibits a tall and well-developed dural expansion with a marked peak, similar to that present in some large theropods (e.g., *Allosaurus*, *Tyrannosaurus*), Sampson and Witmer (2007) argued the possibility that the dural peak of *Majungasaurus* housed a pineal gland as in extant birds. If present in *Carnotaurus*, a pineal gland was not as well developed as that hypothesized for *Majungasaurus*.

Reptile encephalization quotient. The total volume of the cranial endocast of *Carnotaurus* is 169.8 cm^3. The values of 37% and 50% (following Hurlburt et al., 2013) as well as the resulting calculated REQs are shown in Table 1. The minimum calculated REQs of *Carnotaurus*, i.e. 1.4–1.9 (using body mass calculated by Campione et al., 2014) and 1.6–2.2 (using a measurement calculated here using Anderson et al., 1985 method) are much higher than those calculated for *Majungasaurus* (1.14–1.54) and the allosauroids *Sinraptor* (0.81–1.1) and *Giganotosaurus* (1.07–1.4), but are slightly greater than the REQs for *Ceratosaurus*, *Allosaurus* and the megaraptoran *Murusraptor* (Table 1). However, the REQ of *Carnotaurus* does not reach the higher values of tyrannosaurids (1.8–2.5).

Olfaction and olfactory acuity. The large size of the olfactory bulbs and the elongated olfactory tracts of *Carnotaurus* are similar in proportion to those in ceratosaurs (Franzosa, 2004; Sampson and Witmer, 2007) and allosauroids (Franzosa and Rowe, 2005; Larsson, 2001), indicating that olfaction was probably an important sense for this taxon, as well as most abelisaurids; and perhaps played a more important role than the sense of sight based on the reduced size of the optic lobes, a condition that markedly contrasts with that in maniraptoran theropods, including extant birds (Franzosa, 2004; Hopson, 1979).

The olfactory tracts and bulbs in *Carnotaurus* are anteroventrally curved (Fig. 4A), a condition shared apparently only with *Indosaurus* (Huene et Matley, 1933: pl. IX 3), although in the latter the tip of the forebrain is incomplete. Conversely, *Aucasaurus, Majungasaurus*, and *Viavenator* have horizontally disposed olfactory bulbs and tracts (Fig. 4B–D). The olfactory tracts and bulbs of *Ceratosaurus* are anterodorsally oriented (Sanders and Smith, 2005), a condition that not only contrasts with

Carnotaurus, but with all known abelisaurids. *Carnotaurus* has a dorsoventrally deep skull at the level of the snout, which is also reflected on the shape of the antorbital space. As was previously hypothesized (Sampson and Witmer, 2007), the nasal cavity was probably close to the opening for CN I (olfactory nerve), and thereby also the olfactory concha (Witmer, 1995). The ventrally oriented olfactory region and the deep antorbital space in *Carnotaurus* may reflect a difference in the location and development of the nasal concha inside the nasal cavity, which could be related with some particular olfactory capability in this taxon. However, further studies are necessary for a better understanding of the relation between these anatomical traits and their paleobiological significance.

Olfactory ratios are influenced by body size and should not be used to compare olfactory acuity directly among theropods (Zelenitsky et al., 2009). When the log-transformed olfactory ratio (1.7) and body mass (3.1–3.2; based on both estimated body masses, see § *Material and methods*) of *Carnotaurus* are plotted in the graphic published by Zelenitsky et al. (2009, fig. 2), the abelisaurid falls on predicted theropod olfactory ratio values (being just slightly higher than *Majungasaurus*). Allosauroids, ceratosaurians, and basal tyrannosauroids have or are close to having those predicted values for theropods of their respective body size, which suggests that their olfactory acuities represent the primitive condition for theropods (Zelenitsky et al., 2009). Unlikely, tyrannosaurids and dromaeosaurids have higher olfactory ratios than predicted for theropods of similar body size, which may indicate in this case a keener sense of smell (Zelenitsky et al., 2009). Although with a typical olfactory ratio, the particular orientation of the olfactory bulbs of *Carnotaurus* (and its possible relationship on the development of the nasal concha) is perhaps associated with a greater reliance on the sense of smell, than in other reported abelisaurids.

Hearing. The region of the osseous labyrinth corresponding to the lagena the sensory epithelium (= basilar papilla) of the sensory organ in life (Manley, 1973). The length of the lagena provides an estimate of the hearing sensitivity and auditory capabilities of extinct animals (Walsh et al., 2008; Witmer and Ridgely, 2009). The lagena of *Carnotaurus* is relatively short, being less than one quarter of the length of the inner ear, as in *Viavenator* (Paulina-Carabajal and Filippi, 2018), probably *Aucasaurus* and *Majungasaurus* (Paulina-Carabajal and Succar, 2015; Sampson and Witmer, 2007), and the present in some non-coelurosaurian theropods such allosauroids and megaraptorans (Paulina-Carabajal and Currie, 2017; Rogers, 1998). Studies by Gleich et al. (2005) estimated that large dinosaurs, for example, *Allosaurus*, with a body mass of approximately 1400 kg and a lagena of 8 mm long, have a best frequency of hearing range of 0.7–1.5 kHz and a high-frequency limit of hearing below 3 kHz. The estimated body mass of *Carnotaurus* (1419–1743 kg range) is slightly larger than that of *Allosaurus* (1400 kg) and the lagena reaches similar size (6 mm in length); thus, the hearing range in *Carnotaurus* is expected to be below 3 kHz. The shorter lagena in abelisaurids and many non-coelurosaurian theropods contrasts with the remarkably longer lagena of tyrannosaurids (Witmer and Ridgely, 2009) and therizinosaurs (Lautenschlager et al., 2012), among theropods.

Gaze stabilization. It is worth noting the difference in flocculus size among abelisaurids. The South American forms (Brachyrostra; Canale et al., 2008) share large flocculi that project posteriorly, reaching the posterior semicircular canal, whereas *Majungasaurus* has a markedly shorter flocculus (Fig. 4). Furthermore, Sampson and Witmer (2007) reported that the flocculi of *Rugops* and *Indosaurus*, have flocculi "only a little larger" compared to that of *Majungasaurus,* and regarded a small floccular process as a possible apomorphy of Abelisauridae. However, the recent evidence concerning Brachyrostra in which the flocculus is relatively larger (maybe not in volume but in length) than in the non-South American abelisaurids (Majungasaurinae; Tortosa et al., 2013) leads us to reconsider this trait. As the flocculus is important in gaze stabilization that coordinates the eye movement with the movements of the head, neck, and body (Walsh et al., 2013) and tends to be larger in animals that rely on quick movements of the head and body (Witmer et al., 2003, 2008), the difference within both clades of abelisaurids can be interpreted as different means of gaze stabilization. In this way, the South American abelisaurids (e.g., *Aucasaurus, Carnotaurus*, *Viavenator*) have relatively increased gaze-stabilization mechanisms compared with those of *Majungasaurus,* and perhaps *Rugops* and *Indosaurus*. However, caution is needed in using floccular size to infer ecological and behavioral traits in extinct animals, as shown by recent studies based on extant forms (Ferreira-Cardoso et al., 2017).

4.2. Braincase pneumaticity

The braincase pneumaticity in *Carnotaurus* is well developed, as in other abelisaurids (Fig. 1). The lateral (= rostral) tympanic recess of *Carnotaurus* has proportions similar to those of *Majungasaurus* and *Viavenator*. However, the basisphenoidal recess appears to be strongly developed dorsoventrally. The ventral portion of this recess that affects the basal tubera is apparently more developed in *Carnotaurus* than in *Majungasaurus* and *Viavenator*. *Indosaurus* has basal tubera described as hollow by Wilson et al. (2003), although the feature is not illustrated, preventing further comparisons. Furthermore, the paired chamber that extends to the neck of the occipital condyle of *Carnotaurus* is present in the basicrania of *Ceratosaurus* (Sanders and Smith, 2005) and *Aucasaurus*, *Ilokelesia*, *Majungasaurus*, *Viavenator* (Paulina-Carabajal, 2011b; Paulina-Carabajal and Filippi, 2018; Sampson and Witmer, 2007) and *Ekrixinatosaurus* (MUCPv-294). The pneumatization of the neck of the occipital condyle is not characteristic of ceratosaurs, but is present in a variety of tetanurans such as allosauroids (Sampson and Witmer, 2007) and megaraptorids (Paulina-Carabajal and Currie, 2017). The subsellar recess of *Carnotaurus* is a large cavity, which is similar in size to the South American *Viavenator* (MAU-Pv-LI-530; Paulina-Carabajal and Filippi, 2018), and differs from the relatively smaller subsellar recess of the Malagasy *Majungasaurus* (Sampson and Witmer, 2007). By contrast, the basisphenoidal and subsellar recesses in *Abelisaurus* (MPCA 11.098;

Paulina-Carabajal, 2011b) are much larger than in any of the aforementioned abelisaurids.

Finally, both basipterygoid and paraoccipital processes of *Carnotaurus* are massive, a condition present in all abelisaurids (Paulina-Carabajal and Filippi, 2018). *Ceratosaurus* has paraoccipital processes extensively excavated by sinuses ("paroccipital process sinus", Sanders and Smith, 2005), as in most coelurosaurian theropods (Rauhut, 2003), but not in abelisaurids.

5. Conclusions

Although few species of Abelisauridae have been studied in terms of paleoneurological information, the new data provided here help to understand the variability of endocranial morphology within the clade. Furthermore, some inferences are made regarding the potential sensorial capabilities developed in the studied taxa. The CT scans also showed that the braincase pneumaticity of *Carnotaurus* is extensive as in other abelisaurids, characterized by relatively large basisphenoidal and subsellar recesses.

The endocranial morphology of *Carnotaurus* is similar to that observed in other abelisaurids. Furthermore, it shows the presence of a larger flocculus of the cerebellum in the South American forms, which also exhibit smaller and less dorsally projected dorsal longitudinal sinuses. A particular trait of *Carnotaurus* is the anteroventral curvature of the olfactory tracts and bulbs. This trait perhaps suggests a distinct development of the nasal concha and increased reliance on the sense of smell, which possibly was more acute than in the other documented abelisaurids. However, further studies are needed to understand the paleobiological significance of these endocranial traits.

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References

Anderson, J.F., Hall-Martin, A., Russell, D.A., 1985. Long-bone circumference and weight in mammals, birds and dinosaurs. J. Zool. Soc. Lond. A 207, 53–61.

Balanoff, A.M., Norell, M.A., Hogan, A.V.C., Bever, G.S., 2018. The endocranial cavity of oviraptorosaur dinosaurs and the increasingly complex, deep history of the avian brain. Brain Behav. Evol. 91, 125–135, http://dx.doi.org/10.1159/000488890.

Bever, G.S., Brusatte, S.L., Balanoff, A.M., Norell, M.A., 2011. Variation, variability, and the origin of the avian endocranium: insights from the anatomy of *Alioramus altai* (Theropoda: Tyrannosauroidea). PLoS ONE 6 (8), e23393.

Bonaparte, J.F., 1985. A horned Cretaceous carnosaur from Patagonia. Natl. Geogr. Res. 1, 149–151.

Bonaparte, J.F., Novas, F., 1985. *Abelisaurus comahuensis*, n. gen., n. sp., Carnosauria del Cretacico tardio de Patagonia. Ameghiniana 21, 259–265.

Bonaparte, J.F., Novas, F.E., Coria, R.A., 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. Natural History Museum of Los Angeles County. Contrib. Sci. 416, 1–41.

Campione, N.E., Evans, D.C., 2012. A universal scaling relationship between body mass and proximal limb bone dimensions in quadrupedal terrestrial tetrapods. BMC Biol. 10, 60.

Campione, N.E., Evans, D., Brown, C.M., Carrano, M., 2014. Body mass estimation in non-avian bipeds using a theoretical conversion to quadruped stylopodial proportions. Methods Ecol. Evol. 5, 913–923.

Canale, J.I., Scanferla, C.A., Agnolín, F.L., Novas, F.E., 2008. New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. Naturwissenschaften 96, 409–414.

Christiansen, P., Fariña, R.A., 2004. Mass prediction in theropod dinosaurs. Hist. Biol. 16, 85–92.

Coria, R.A., Chiappe, L.M., Dingus, L., 2002. A new close relative of *Carnotaurus sastrei* Bonaparte, 1985 (Theropoda: Abelisauridae) from the Late Cretaceous of Patagonia. J. Vert. Paleontol. 22, 460–465.

Dufeau, D., 2011. The evolution of cranial pneumaticiy in Archosauria: patterns of paratympanic sinus development. Faculty of the College of Arts and Sciences of Ohio University, OH, USA (PhD thesis, 175 p.).

Fedorov, A., Beichel, R., Kalpathy-Cramer, J., Finet, J., Fillion-Robin, J.C., Pujol, S., Buatti, J., 2012. 3D Slicer as an image computing platform for the Quantitative Imaging Network. Magn. Reson. Imaging 30, 1323–1341.

Ferreira-Cardoso, S., Araújo, R., Martins, N.E., Martins, G.G., Walsh, S., Martins, R.M.S., Kardjilov, N., Manke, I., Hilger, A., Castanhinha, R., 2017. Floccular fossa size is not a reliable proxy of ecology and behaviour in vertebrates. Sci. Rep. 7, 1–11, http://dx.doi.org/10.1038/s41598-017-01981-0.

Filippi, L.S., Méndez, A.H., Juárez Valieri, R.D., Garrido, A.C., 2016. A new brachyrostran with hypertrophied axial structures reveals an unexpected radiation of latest Cretaceous abelisaurid. Cretaceous Res. 61, 209–216, http://dx.doi.org/10.1016/j.cretres.2015.12.018.

Franzosa, J.W., 2004. Evolution of the brain in Theropoda (Dinosauria). University of Texas, Austin (PhD thesis, 357 p.).

Franzosa, J., Rowe, T., 2005. Cranial endocast of the Cretaceous theropod dinosaur *Acrocanthosaurus atokensis*. J. Vert. Paleontol. 25, 859–864.

Gilmore, C.W., 1920. Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. Bull. U. S. Natl. Mus. 110, 1–159.

Gleich, O., Dooling, R.J., Manley, G.A., 2005. Audiogram, body mass, and basilar papilla length: correlations in birds and predictions for extinct archosaurs. Naturwissenchaftern 92, 595–598.

Hopson, J.A., 1979. Paleoneurology. In: Gans, C. (Ed.), Biology of the Reptilia, 9. Academic Press, New York, pp. 39–146.

von Huene, F., Matley, C.A., 1933. The Cretaceous Saurischia and Ornithischia of the Central Provinces of India. Geol. Surv. India Palaeontol. Indica 1, 1–74.

Hurlburt, G.R., 1996. Relative brain size in recent and fossil amniotes: Determination and interpretation. University of Toronto, Toronto (PhD thesis 250 p.).

Hurlburt, G.R., Ridgely, R.C., Witmer, L.M., 2013. Relative size of brain and cerebrum in tyrannosaurid dinosaurs: an analysis using brain-endocast quantitative relationships in extant alligators. In: Parrish, J.M., Molnar, E., Currie, P.J., Koppelhu, E.S. (Eds.), Tyrannosaurid Paleobiology. Indiana University Press, Bloomington, pp. 134–154.

Jerison, H.J., 1973. Evolution of the brain and intelligence. Academic Press, New York.

Larsson, H.C.E., 2001. Endocranial anatomy of *Carcharodontosaurus saharicus* (Theropoda: Allosauroidea) and its implications for theropod brain evolution. In: Tanke, D.H., Carpenter, K. (Eds.), Mesozoic Vertebrate Life. Indiana University Press, Bloomington, IN, USA, pp. 19–33.

Lautenschlager, S., Rayfield, E.J., Altangerel, P., Zanno, L.E., Witmer, L.M., 2012. The endocranial anatomy of Therizinosauria and its implications for sensory and cognitive function. PLoS ONE 7, e52289, http://dx.doi.org/10.1371/journal.pone.0052289.

Manley, G.A., 1973. Some aspects of the evolution of hearing in vertebrates. Nature 230, 506–509.

Mazzetta, G.V., Christiansen, P., Fariña, R.A., 2004. Giants and bizarres: body size of some southern South American Cretaceous dinosaurs. Hist. Biol. 16, 71–83.
Novas, F.E., 2009. The Age of Dinosaurs in South America. Indiana University Press, Bloomington, IN, USA.
Novas, F.E., Agnolín, F.L., Bandyopadhyay, S., 2004. Cretaceous theropods from India: A rewiew of specimens described by Huene and Matley (1933). Rev. Mus. Argentino Cienc. Nat., n.s. 6 (1), 67–103.
Novas, F.E., Agnolín, F.L., Ezcurra, M.D., Porfiri, J.D., Canale, J.I., 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: the evidence from the Patagonia. Cretaceous Res. 45, 174–215, http://dx.doi.org/10.1016/j.cretres.2013.04.001.
Paulina-Carabajal, A., 2011a. The braincase anatomy of *Carnotaurus sastrei* (Theropoda: Abelisauridae) from the Upper Cretaceous of Patagonia. J. Vert. Paleontol. 31, 378–386.
Paulina-Carabajal, A., 2011b. Braincases of abelisaurid theropods from the Upper Cretaceous of north Patagonia. Palaeontology 54, 793–806.
Paulina-Carabajal, A., Canale, J.I., 2010. Cranial endocast of the carcharodontosaurid theropod *Giganotosaurus carolinii*. Neues Jahrb. Geol. Pal. Abh. 258, 249–256, http://dx.doi.org/10.1127/0077-7749/2010/0104.
Paulina-Carabajal, A., Currie, P.J., 2012. New information on the braincase and endocast of *Sinraptor dongi* (Theropoda: Allosauroidea): Ethmoidal region, endocranial anatomy and pneumaticity. Vert. PalAs. 50, 85–101.
Paulina-Carabajal, A., Currie, P., 2017. The braincase of the theropod dinosaur *Murusraptor*: Osteology, neuroanatomy and comments on the paleobiological Implications of certain endocranial features. Ameghiniana 54 (5), 617–640, http://dx.doi.org/10.5710/AMGH.25.03.2017.3062.
Paulina-Carabajal, A., Filippi, L., 2018. Neuroanatomy of the abelisaurid theropod *Viavenator*: The- most complete reconstruction of brain and inner ear for a South American representative of the clade. Cretaceous Res. 83, 84–94, http://dx.doi.org/10.1016/j.cretres.2017.06.013.
Paulina-Carabajal, A., Porfiri, J.D., 2018. The neuroanatomy of *Megaraptor namunhuaiquii* (Theropoda: Megaraptoridae) from the Upper Cretaceous of Patagonia, a preliminary report. Reunión de Comunicaciones de la Asociación Paleontológica Argentina, Resúmenes, Puerto Madryn, Argentina.
Paulina-Carabajal, A., Succar, C., 2015. Endocranial morphology and inner ear of the theropod *Aucasaurus garridoi*. Acta Paleontol. Pol. 60, 141–144.
Paulina-Carabajal, A., Ezcurra, M., Novas, F.E., 2015. New information on the braincase and endocranial morphology of the Late Triassic theropod *Zupaysaurus rougieri* using CT scans. Ameghiniana 52 (4R), 32–33.
Pol, D., Rauhut, O.W.M., 2012. A Middle Jurassic abelisaurid from Patagonia and theearly diversification of theropod dinosaurs. Proc. R. Soc. Lond. B 279, 3170–3175.
Raath, M.A., 1977. The anatomy of the Triassic theropod Syntarsus rhodesiensis (Saurischia: Podokesauridae) and a consideration of its biology. Department of Zoology and Entomology, Rhodes University (PhD thesis, 123 p.).
Rauhut, O.W.M., 2003. The interrelationships and evolution of basal theropod dinosaurs. Spec. Pap. Palaeontol. 69, 1–213.
Rogers, S.W., 1998. Exploring dinosaur neuropaleobiology: Computed Tomography Scanning and analysis of an *Allosaurus fragilis* endocast. Neuron 21, 673–679.
Sampson, S.D., Witmer, L.M., 2007. Craniofacial anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. Soc. Vert. Paleontol. Mem. 8, 32–102.
Sanders, K.R., Smith, D.K., 2005. The endocranium of the theropod dinosaur *Ceratosaurus* studied with computed tomography. Acta Palaeontol. Pol. 50, 601–616.
Saveliev, S.V., Alifanov, V.R., 2005. A new study of the brain of the predatory dinosaur *Tarbosaurus bataar* (Theropoda, Tyrannosauridae). Paleontol. J. 41 (3), 281–289.
Sues, H.-D., 1980. A pachycephalosaurid dinosaur from the Upper Cretaceous of Madagascar and its paleobiogeographical implications. J. Paleontol. 54, 954–962.
Tortosa, T., Buffetaut, E., Vialle, N., Dutour, Y., Turini, E., Cheylan, G., 2013. A new abelisaurid dinosaur from the Late Cretaceous of southern France: Palaeobiogeographical implications. Ann. Paleontol. 100, 63–86.
Walsh, S.A., Iwaniuk, A.N., Knoll, M.A., Bourdon, E., Barrett, P.M., Milner, A.C., Nudds, R.L., Abel, R.L., Dello Sterpaio, P., 2013. Avian cerebellar floccular fossa size is not a proxy for flying ability in birds. PLoS One 8, e67176, http://dx.doi.org/10.1371/journal.pone.0067176.
Wilson, J.A., Sereno, P.C., Srivastava, S., Bhatt, D.K., Khosla, A., Sahni, A., 2003. A new abelisaurid (Dinosauria, Theropoda) from the Lameta Formation (Cretaceous, Maastrichtian) of India. Contrib. Mus. Paleont., Univ. Michigan 31, 1–42.
Witmer, L.M., 1995. Homology of facial structures in extant archosaurs (birds and crocodilians), with special reference to paranasal pneumaticity and nasal conchae. J. Morphol. 225, 269–327.
Witmer, L.M., 1997. Craniofacial air sinus systems. In: Currie, P.J., Padian, K. (Eds.), Encyclopedia of Dinosaurs. Academic Press, New York, pp. 151–159.
Witmer, L.M., Ridgely, R., 2009. New insights into the brain, braincase, and ear region of tyrannosaurs (Dinosauria, Theropoda), with implications for sensory organization and behavior. Anat. Rec. 292, 1266–1296.
Witmer, L.M., Chatterjee, S., Franzosa, J., Rowe, T., 2003. Neuroanatomy of flying reptiles and implications for flight, posture and behavior. Nature 425, 950–953.
Witmer, L.M., Ridgely, R.C., Dufeau, D.L., Semones, C., 2008. Using CT to peer into the past: 3D visualization of the brain and ear regions of birds, crocodiles, and non-avian dinosaurs. In: Endo, H., Frey, R. (Eds.), Anatomical Imaging: Towards a New Morphology. Springer, Tokyo, pp. 67–87.
Xing, L., Paulina-Carabajal, A., Currie, P.J., Xu, X., Dong, Z., Burns, M., 2014. Braincase anatomy of the basal theropod *Sinosaurus*, from the lower Jurassic of China, studied using CT scans. Acta Geol. Sin. 88, 1653–1664.
Zelenitsky, D.K., Therrien, F., Kobayashi, Y., 2009. Olfactory acuity in theropods: palaeobiological and evolutionary implications. Proc. R. Soc. Lond. B 276, 667–673.
Zelenitsky, D.K., Therrien, F., Ridgely, R.C., McGee, A.R., Witmer, L.M., 2011. Evolution of olfaction in non-avian theropod dinosaurs and birds. Proc. R. Soc. Lond. B 278, 3625–3634.