

董氏中华盗龙(兽脚类:异特龙超科)脑颅新知: 筛区、颅腔解剖和具气腔

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摘要:董氏中华盗龙(*Sinraptor dongi*)是产自中国西北部新疆侏罗纪石树沟组上部的一种大型兽脚类。其正型标本包括了保存完好的脑颅,这是在最近的化石修理中额外发现的。脑颅中骨化筛骨的横切面为 U 形。在脑颅的解剖方位,蝶筛骨和眶蝶骨之间有一未骨化空间,表明该恐龙存活时具有软骨质的分隔蝶骨。利用乳胶颅腔模型和 CT 扫描技术对颅腔和含气隐窝的形态进行了研究,发现了一些此前未描述过的特点。其中尤为引人注目的是,发育良好的尾鼓室隐窝[一般认为是虚骨龙类(coelurosaurs)的典型特征]以及基蝶骨隐窝和相关气腔的内部形态。侧鼓室隐窝和基蝶骨隐窝有纵向通道连接,很可能同时具有气腔和血管功能。模型也表明,颅腔没有髓质隆起,小脑绒球隐窝的开孔为沙漏状。若不包含嗅束和嗅球,颅腔容积为 95 ml,脑容商在其他基干坚尾龙类(tetanurans)的范围内。虽然这些类群的第 II-IV 对脑神经相对位置各有差异,但前脑、中脑和后脑之间的角度与鲨齿龙类(carcharodontosaurids)[鲨齿龙(*Carcharodontosaurus*)及南方巨兽龙(*Giganotosaurus*)]相似。第 IX, X 和 XI 对脑神经穿过一个半月形的孔。在异特龙超科(Allosauroidea)中,中华盗龙(*Sinraptor*)在颅腔形态上与鲨齿龙、南方巨兽龙和异特龙(*Allosaurus*)的相似程度比它与高棘龙(*Acrocanthosaurus*)的相似程度更高。

关键词:中国,侏罗系,异特龙类,脑颅,古神经学

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NEW INFORMATION ON THE BRAINCASE OF *SINRAPTOR DONGI* (THEROPODA: ALLOSAUROIDEA): ETHMOIDAL REGION, ENDOCRANIAL ANATOMY, AND PNEUMATICITY

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Abstract *Sinraptor dongi* is a large theropod from the upper Shishugou Formation (Jurassic) of Xinjiang in northwestern China. The holotype includes a well-preserved braincase that recently benefited from additional preparation. The ossified ethmoidal elements are U-shaped in cross-section. When placed in anatomical position in the braincase, an unossified space remains between the sphenethmoid and the orbitosphenoid, suggesting there was a cartilaginous septosphenoid when the animal was alive.

The morphology of the endocranial cavity and pneumatic recesses was studied using a latex endocast and CT scans. This led to the recognition of some traits that have not been previously described. The presence of a well developed caudal tympanic recess (generally considered as characteristic of coelurosaurs) is particularly interesting, as is the internal morphology of the basisphenoidal recess and its associated pneumatic cavities. There is a longitudinal passage connecting the lateral tympanic recess with the basisphenoidal recess that probably had both pneumatic and vascular functions. Endocranially, there is no medullar eminence, and the opening for the floccular recess is hourglass-shaped. The volume of the endocranial cavity, excluding the olfactory tract and bulbs, is 95 ml, and the encephalization quotient falls within the range calculated for other basal tetanurans. The angles formed between forebrain, midbrain and hindbrain are similar to those in carcharodontosaurids (*Carcharodontosaurus* and *Giganotosaurus*), although the relative positions of cranial nerves II-IV varies amongst these taxa. Cranial nerves IX, X and XI pass through a single half-moon-shaped opening. Within Allosauroidea, the cranial endocast of *Sinraptor* is morphologically more similar to those of *Allosaurus*, *Carcharodontosaurus* and *Giganotosaurus* than to that of *Acrocanthosaurus*.

Key words China, Jurassic, allosauroids, braincase, paleoneurology

1 Introduction

Basal theropod braincases are rare, and even rarer are natural or artificial endocasts. These have been studied in detail in taxa such as *Acrocanthosaurus atokensis* (Franzosa and Rowe, 2005), *Allosaurus fragilis* (Rogers, 1998), *Carcharodontosaurus iguidensis* (Brusatte and Sereno, 2007), *C. saharicus* (Larsson, 2001), *Ceratosaurus nasicornis* (Sanders and Smith, 2005), *Giganotosaurus carolinii* (Paulina Carabajal and Canale, 2010), *Majungasaurus crenatissimus* (Sampson and Witmer, 2007), and *Syntarsus rhodesiensis* (Raath, 1977).

The braincase of *Sinraptor dongi* (Fig. 1) was described in detail by Currie and Zhao (1993a), at the time when the name of the taxon was first established. Recently, further mechanical preparation and new CT scans have revealed more detailed information about the endocranial structure and braincase pneumaticity of this taxon, and we present the resulting morphological data in this paper. For example, the presence of the caudal (posterior) tympanic recess (Witmer, 1997) was not noticed when the first CT scans were done in 1993. Additional information is presented on the ossified ethmoidal elements, the sphenethmoid and mesethmoid, of the specimen. The ethmoidal region is a poorly known part of the braincase because it remains cartilaginous in most subadult and adult theropods (Currie, 1997), although it ossifies in abelisaurids (Paulina Carabajal, 2011a,b; Sampson and Witmer, 2007), carcharodontosaurids (Brusatte and Sereno, 2007; Brusatte et al., 2010) and tyrannosaurids (Ali et al., 2008).

The endocranium corresponds to the space inside the braincase occupied by the brain and other soft tissues. An endocast represents the morphology of the outer surfaces of those soft tissues that are not preserved but left impressions on the internal walls of the braincase. The sediment filling the endocranial cavity of *Sinraptor dongi* (IVPP V 10600) was removed, allowing the preparation of a latex endocast as well as a high resolution, three dimensional reconstruction based on CT scan images. The endocranial anatomy of the type specimen is described here, and compared with all other known allosauroid endocasts (*Acrocanthosaurus atokensis*, *Allosaurus fragilis*, *Carcharodontosaurus iguidensis*, *C. saharicus* and *Giganotosaurus carolinii*).

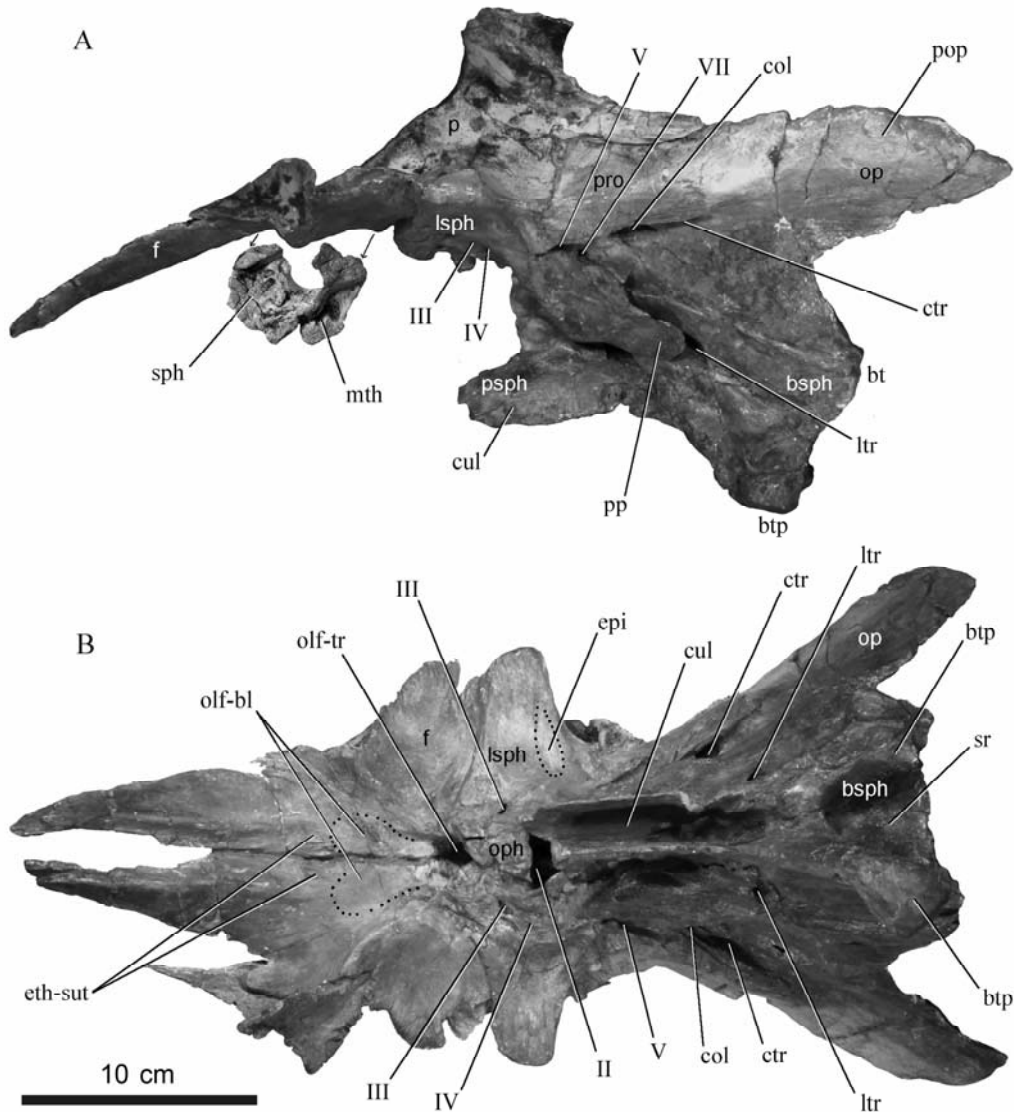


Fig. 1 *Sinraptor dongi* (IVPP V 10600), braincase in left lateral (A) and ventral (B) views

Ethmoidal elements in anatomical position in (A)

Abbreviations: bsph. basisphenoid; bt. basal tuber; btp. basiptyergoid process; col. columellar recess; ctr. caudal tympanic recess; cul. cultriform process; epi. impression of the epipterygoid on the laterosphenoid; eth-sut. contact marks for the sphenethmoid on the frontal; f. frontal; lsph. laterosphenoid; ltr. lateral tympanic recess; mth. mesethmoid; olf-bl. olfactory bulb impression on the frontal; olf-tr. olfactory tract impression on the frontal; op. opisthotic; oph. orbitosphenoid; p. parietal; pop. paroccipital process; pp. preotic pendant; pro. prootic; psph. parasphenoid; sph. sphenethmoid; sr. subsellar recess; II-VII. cranial nerve foramina

2 Material and methods

The ossified ethmoidal elements, which include the sphenethmoids and mesethmoids, were found separated from the rest of the braincase. These are poorly known elements within dinosaurs because they are often unossified (probably present as cartilaginous structures), explaining why they were not recognized when the specimen was originally described (Currie and

Zhao, 1993a).

The endocranial cavity of *Sinraptor dongi* (IVPP V 10600) was prepared mechanically by the first author and a latex endocast was made. An endocast was also digitally reconstructed from high resolution CT scans of the complete braincase, which were done in July 2009. The CT scanner is at the University of Alberta Cardiovascular and Stroke Research Centre (ABACUS) and is a Siemens Somatom Sensation 64 model. Eight hundred coronal slices of the braincase were obtained (in 1 mm increments), and 446 of them were used to reconstruct the brain. The latex endocast shows some traits (such as small vascular marks) that are not observed in the digital reconstruction. The three-dimensional reconstruction was made using the software Mimics (version 12) and the illustrations were generated with Adobe Photoshop (version SC3). The volume of the endocast was calculated by water displacement.

The encephalization quotient (EQ) was calculated using the formula $EQ = E_i/E_e$, where E_i is the brain size and E_e is the expected size. E_e is calculated with the equation $E = k \cdot p^{2/3}$, where p is the body mass and k is a constant that equals the value of E when $p = 1$ (Hopson, 1980). The body masses of *Sinraptor*, *Allosaurus* and *Tyrannosaurus* were estimated by Christiansen and Fariña (2004).

Comparative taxa The following theropod specimens were examined first-hand for the present study: *Abelisaurus comahuensis* (MPCA 11908), *Acrocanthosaurus atokensis* (NCSM 14345), *Albertosaurus sarcophagus* (TMP 81.10.01), *Allosaurus fragilis* (UUVP 5961); *Carcharodontosaurus iguidensis* (MNN IGU 2), *C. saharicus* (SGM-Din 1), *Carnotaurus sastrei* (MACN-CH 894), *Ceratosaurus nasicornis* (MWC 1.1), *Daspletosaurus* sp. (TMP 2001.36.01), *Giganotosaurus carolinii* (MUCPV-CH 1), *Gorgosaurus libratus* (TMP 94.12.602), *Majungasaurus crenatissimus* (FMNH PR2100), *Piveteausaurus divesensis* (MNHN 1920-7), and Coelurosauria indet. (MCF-PVPH 411). Information on the inner ear of *Acrocanthosaurus* was obtained from http://www.digimorph.org/specimens/acrocanthosaurus_atokensis/acro-y-axis.mov

Institutional abbreviations FMNH, Field Museum of Natural History, Chicago; MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires; MCF-PVPH, Museo “Carmen Funes”, Plaza Huincul, Neuquén; MNHN, Muséum National d’Histoire Naturelle, Paris; MNN IGU, Musée National du Niger, Niamey; MPCA, Museo Provincial “Carlos Ameghino”, Cipolletti, Río Negro; MUCPV-CH, Museo de la Universidad Nacional del Comahue, Villa el Chocón, Neuquén; MWC, Museum of Western Colorado, Grand Junction; NCSM, North Carolina State Museum of Natural Sciences, North Carolina; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing; OMNH, Oklahoma Museum of Natural History, Oklahoma; PVL, Instituto Miguel Lillo, Tucumán; PVSJ, Museo de la Universidad Nacional de San Juan; SGM, Ministère de L’Energie et des Mines, Rabat, Morocco; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; UUVP, University of Utah, Salt Lake City.

3 Description

Braincase Ethmoidal elements The sphenethmoids enclose the olfactory tract and olfactory bulbs. They are firmly fused to the mesethmoid, which itself forms the median septum separating the olfactory bulbs anteriorly (Ali et al., 2008). In those theropods with ossified ethmoidal elements, the sphenethmoid is usually fused dorsally to the frontal, although its relationships to more posterior elements vary among taxa. For example, the sphenethmoid contacts the orbitosphenoid posteriorly in *Piveteausaurus* (MNHN 1920-7) and tyrannosaurids (Ali et al., 2008). In the holotype of *Sinraptor*, the sphenethmoid is U-shaped and is not fused to the frontal, even though it is indistinguishably fused with the mesethmoid (Fig. 2).

The ventral surface of the frontal, at the base of the nasal process, has a clear contact surface for the sphenethmoid (Fig. 1B). When articulated, an unossified section 19.3 mm long remains between the sphenethmoid and the orbitosphenoid (Fig. 1A), which corresponds to a short section of the olfactory tract that lacked ossified lateral and ventral walls at the time of death. Although it is possible that there was a separate ossified element filling this gap, the absence of distinct contact surfaces on the frontal suggests that this was unlikely. A similar condition is observed in the theropod MCF-PVPH 411 (Coria and Currie, 2002b; Paulina Carabajal, 2009) from the Upper Cretaceous of Patagonia. In *Sinraptor*, the midline septum separates two olfactory chambers (Fig. 2A). However, the olfactory bulbs proper would have been located behind the septum, as suggested by the impressions left in the frontal (Fig. 1B). The olfactory bulbs were enclosed by the sphenethmoids ventrolaterally and by the frontals dorsally. However, the sphenethmoid is not completely ossified anterolaterally, which leaves a large open space on each side. A small wing-like tab projects posterovertrally from the posterior portion of the mesethmoid on each side. It delimits the cavity for the olfactory bulb anteriorly and overhangs a large groove that communicates with the anteroventral portion of the olfactory bulb cavity. The wing-like projection separates this groove ventrally and the main part of the median septum dorsally. At the base, the projection is pierced by two small foramina dorsally, whereas the ventral portion is pierced by a single, larger foramen that is not completely closed on the left side (Fig. 2A). These three foramina are dorsal to the groove, and all of them correspond to passages for blood vessels into the anterior portion of the olfactory bulb cavity, probably for the ethmoidal veins and arteries as in extant birds (Sedlmayr, 2002).

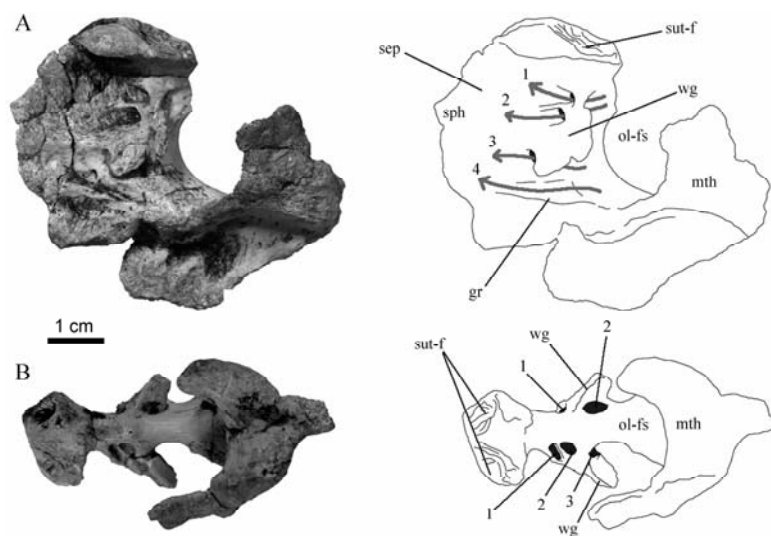


Fig. 2 *Sinraptor dongi* (IVPP V 10600), ethmoidal elements in left lateral (A) and dorsal (B) views. Abbreviations: gr. groove; mth. mesethmoid; ol-fs. fossa for olfactory bulbs; sep. median septum; sph. sphenethmoid; sut-f. sutural surface for frontal; wg. wing-like projection; 1-4. vascular foramina

Pneumatic cavities The sediment filling the basisphenoidal recess, subsellar recess, lateral (anterior) tympanic recess and caudal (posterior) tympanic recess was removed, thereby permitting a higher quality of CT scan imaging than was previously possible.

One of the most interesting revelations was the identification of the caudal tympanic recess in *Sinraptor*, found behind the columellar recess (Fig. 1). The borders of the opening are delimited by the prootic and the opisthotic, at the base of the paroccipital process (Witmer, 1997), as in other theropods (e. g. Brochu, 2003; Currie, 2003; Paulina Carabajal, 2009). The opening of the caudal tympanic recess is anteroposteriorly elongate and narrow, and is posi-

tioned just below the posterior portion of the prootic on the prootic-opisthotic contact in a depressed area. Because of this, the caudal tympanic recess is not totally visible in lateral view, and it was further obscured by sediment prior to mechanical preparation. CT scans showed that, although the external opening of the caudal tympanic recess is small, the recess deeply excavates the base of the paroccipital process, and extends anteriorly to the level of the posterior section of the lateral tympanic recess (Fig. 3E).

The columellar recess is also a deep cavity within the prootic-opisthotic suture (Fig. 1A). It is divided by a longitudinal ridge into two portions; a smaller dorsal section representing the columellar recess proper, and a more ventral region that was apparently exclusively pneumatic. The CT scans show that this recess is well developed internally, and invades the bones lateral to the inner ear (Fig. 3).

The lateral tympanic recess is a deep, narrow pneumatic cavity excavated into the basisphenoid, posteroventral to the preotic pendant (Fig. 1A). The preotic pendant, probably formed mainly by the prootic, is well developed and overhangs the anterodorsal portion of the recess. The recess is deep but is not divided into chambers as in some other theropods such as

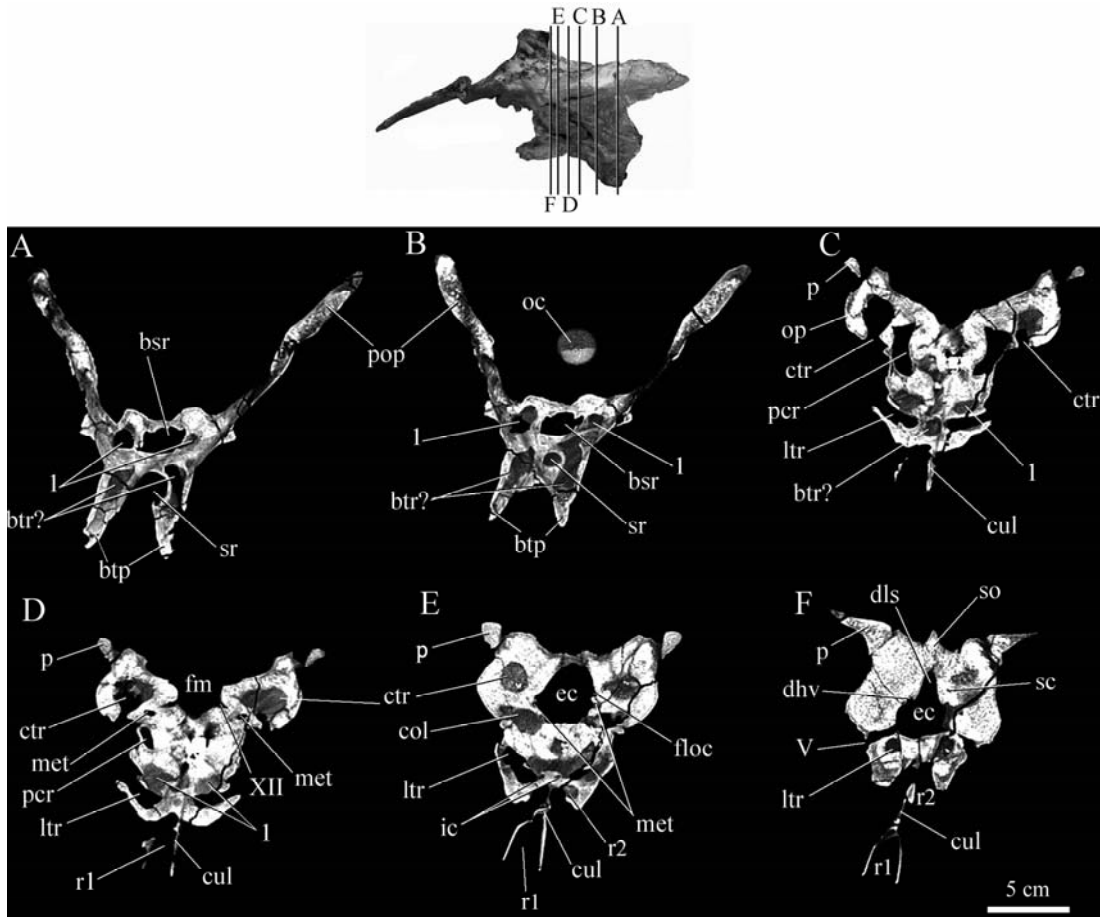


Fig. 3 *Sinraptor dongi* (IVPP V 10600), coronal tomographic slices

At the top, the braincase is seen in left lateral view with lines indicating the tomographic slices A-F. Abbreviations: bsr. basisphenoidal recess; btp. basiptyergoid process; btr?. basiptyergoid recess?; col. columellar recess; ctr. caudal tympanic recess; cul. cultriform process; dhv. dorsal head vein; dls. dorsal longitudinal sinus; ec. endocranial cavity; floc. floccular recess; fm. foramen magnum; ic. internal carotid artery passage; ltr. lateral tympanic recess; met. metotic foramen; oc. occipital condyle; op. opisthotic; p. parietal; pcr. paracondylar recess; pop. paroccipital process; r1. recess ventral to the cultriform process; r2. depression lateral to the cultriform process; sc. semicircular canal of the inner ear; so. supraoccipital; sr. subsellar recess; V, XII. cranial nerve foramina; l. passage connecting the basisphenoidal recess to the lateral tympanic recess

Abelisaurus (Paulina Carabajal, 2011a), *Piatnitzkysaurus* (PVL 4073), and *Troodon* (Currie, 1985). The presence of well developed recesses (regardless of whether or not they are divided into chambers) directly affects basicranial pneumaticity, and has been used in theropod phylogenetic analyses (Rauhut, 2003; Paulina Carabajal, 2009). The CT scans show how the lateral tympanic recess projects anteriorly to reach the level of the foramen for the trigeminal nerve, although the recess is slightly more ventral (Fig. 3F). This recess and the internal passageway for the trigeminal nerve do not merge internally.

The basiptyergoid processes and the basal tubera posteroventrally delimit a large quadrangular space, inside which can be identified three sets of pneumatic cavities (Fig. 4). The basisphenoidal recess is the most posterior cavity, and deeply excavates the bone between the basisphenoid (which forms its anterior wall) and the basioccipital (which forms its posterior wall). The anterior wall of the basisphenoidal recess is a transversely wide bony septum that posteriorly delimits a pair of oval recesses that deeply invade each of the basiptyergoid processes. These two cavities are delimited anteriorly by the basiptyergoid web, which is the lamina that transversely joins the basiptyergoid processes. These cavities excavate the medial walls of the processes rather than the lateral walls, which is the reason they are only visible in ventral view. The CT scans show that, as in the basiptyergoid recesses of other theropods (Currie, 2003; Rauhut, 2003; Witmer, 1997), these recesses pneumatize all but the distal ends of both basiptyergoid processes, and are separated at the midline by a thin longitudinal septum (Fig. 3A,B). Each recess extends anteriorly to reach the level of the lateral tympanic recess, but is somewhat more ventral.

The last pair of cavities is posterolateral to the basiptyergoid web (Fig. 4). Each recess is subcircular, approximately 8 mm in diameter, and opens medially on the lateral wall of the basicranial box. The CT scans show how these cavities (labeled “1” in Fig. 4) extend anteriorly to reach the lateral tympanic recess (Fig. 3C,D), which has a small canal for the internal carotid artery that communicates with the pituitary fossa.

The subsellar recess is posterior to the basiptyergoid processes (Fig. 1A). A deep longitudinal recess ventrally excavates the cultriform process, and is partially separated from the subsellar recess by a short septum. The cavity seems to be a continuation of the subsellar recess, and is similar to what has been observed in the basicranium of the basal theropod *Piveteausaurus*

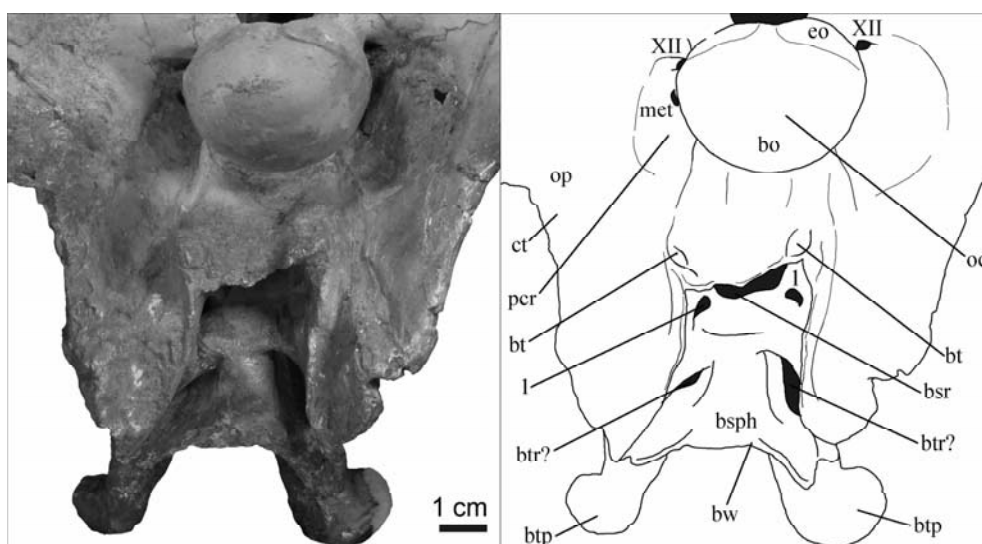


Fig. 4 *Sinraptor dongi* (IVPP V 10600), basicranium in posterior view

Abbreviations: bo. basioccipital; bsph. basisphenoid; bsr. basisphenoidal recess; bt. basal tuber; btp. basiptyergoid process; btr?. basiptyergoid recess?; bw. basiptyergoid web; ct. crista tuberalis; eo. exoccipital; met. metotic foramen; oc. occipital condyle; op. opisthotic; per. paracondylar recess; l. foramen for passage communicating the basisphenoidal recess with the lateral tympanic recess; XII. cranial nerve foramen

(MNHN 1920-7).

Endocast The complete endocast of *Sinraptor dongi* is 20 cm long from the olfactory bulbs to the foramen magnum, and has a maximum width of 5.5 cm across the cerebral hemispheres, dorsal to cranial nerves (CN) II and III (Figs. 5,6). Taking the endocast to be delimited anteriorly by the narrowest transverse constriction of the olfactory tract and posteriorly by the exit of CN XII (hypoglossal), its volume is 95 ml. There are no traces of sutures between

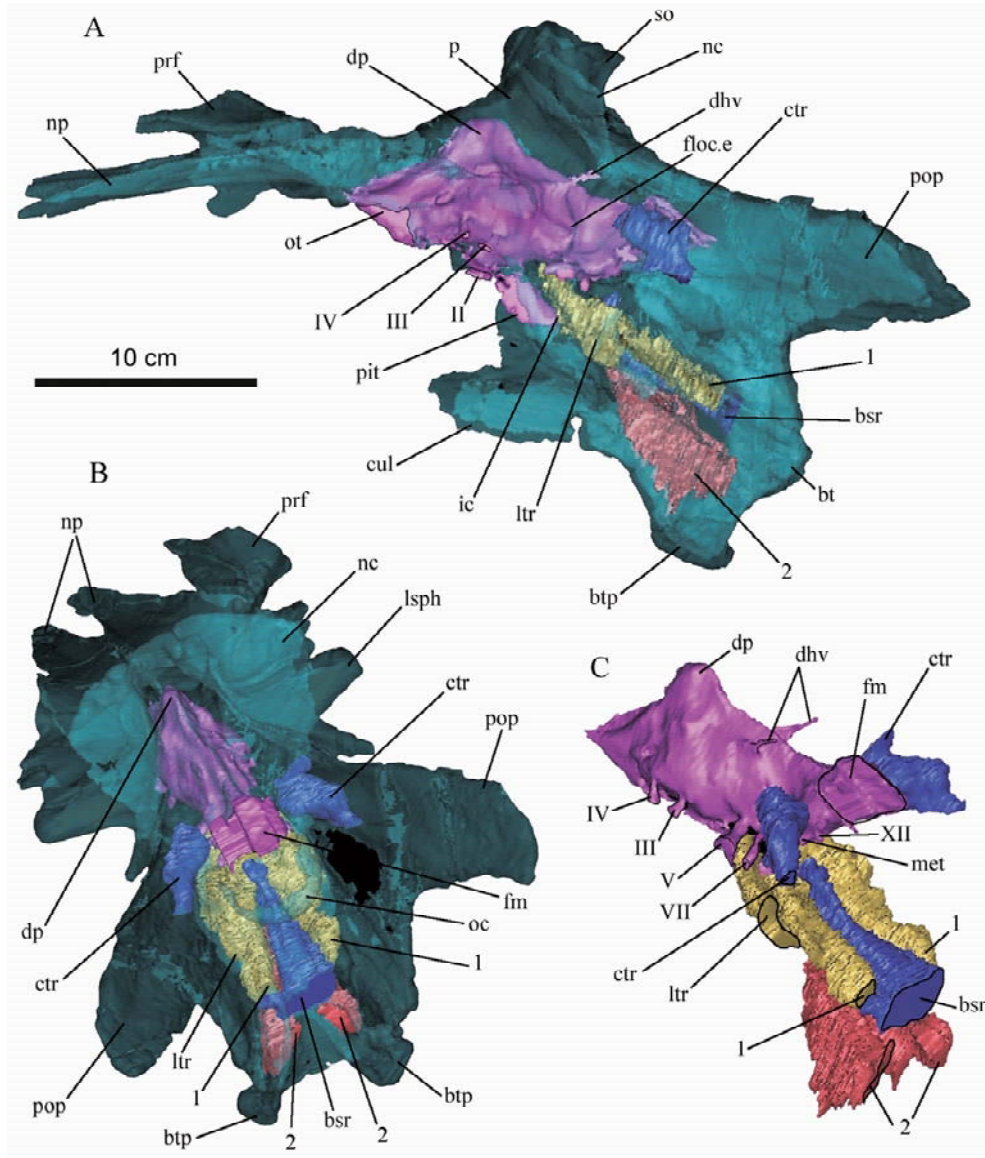


Fig. 5 *Sinraptor dongi* (IVPP V 10600), 3D reconstruction of the braincase, endocast and pneumatic cavities in left lateral (A) and posterdorsal (B) views; isolated endocast and pneumatic cavities in left posterolateral view (C). Color code: endocast is violet, caudal tympanic and basisphenoidal recesses are blue, basiptyergoid? recess is red and lateral tympanic recess is yellow

Abbreviations: bsr. basisphenoidal recess; bt. basal tuber; btp. basiptyergoid process; ctr. caudal tympanic recess; cul. cultriform process; dhv. dorsal head vein; dp. dural peak; flocc. e. floccular recess endocast; fm. foramen magnum; ic. internal carotid artery passage; lsph. laterosphenoid; ltr. lateral tympanic recess; met. metotic foramen; nc. nuchal crest; np. nasal process of frontal; oc. occipital condyle; ot. olfactory tract; p. parietal; pit. pituitary fossa endocast; pop. paroccipital process; prf. prefrontal; so. supraoccipital; 1. passage communicating between basisphenoidal recess and lateral tympanic recess; 2. basiptyergoid recess?; II, III, IV, V, VII, XII. cranial nerves

bones of the braincase on the surface of the endocast, which reaffirms that the braincase belongs to a subadult or adult specimen. Small and diffuse vascular marks are present, but only on the dorsal surface of the midbrain dural endocast.

The olfactory bulbs in *Sinraptor* are aligned with the forebrain. The midbrain is posteroventrally inclined, and is parallel to the hindbrain, even though it is ventral to the forebrain. In the endocast, the angles among the olfactory tract, midbrain and hindbrain are similar to those observed in the two species of *Carcharodontosaurus* (Larsson, 2001; Brusatte and Sereno, 2007) and in *Giganotosaurus* (Paulina Carabajal and Canale, 2010). The olfactory tract is relatively short, and the olfactory bulbs were enclosed by ossified ethmoidal elements (which are not fused with the braincase). The olfactory tracts are not medially separated by the mesethmoid, which is similar to the situation in *Allosaurus* (Franzosa and Rowe, 2005) and *Giganotosaurus* (Paulina Carabajal and Canale, 2010). Separation of the olfactory tract has been described in *Acrocanthosaurus* (Franzosa and Rowe, 2005) and *Giganotosaurus* (Coria and Currie, 2002a), although a reexamination of the latter taxon indicates that they are not separate (Paulina Carabajal and Canale, 2010). The most dorsal section of the endocast, the dural peak, is aligned with CN II in *Sinraptor*, but is anterior to that foramen in *Giganotosaurus* (Fig. 7).

In *Sinraptor*, the base of the floccular process is mediolaterally constricted, dividing the process into two sections. The dorsal portion of the process is smaller and probably corresponds to a vascular component (Fig. 5A). In a lateral view of the endocast, the dorsal head vein (posterior middle cerebral vein) is dorsal to CN V, and is positioned close to the midline along with its counterpart (Fig. 5A,B).

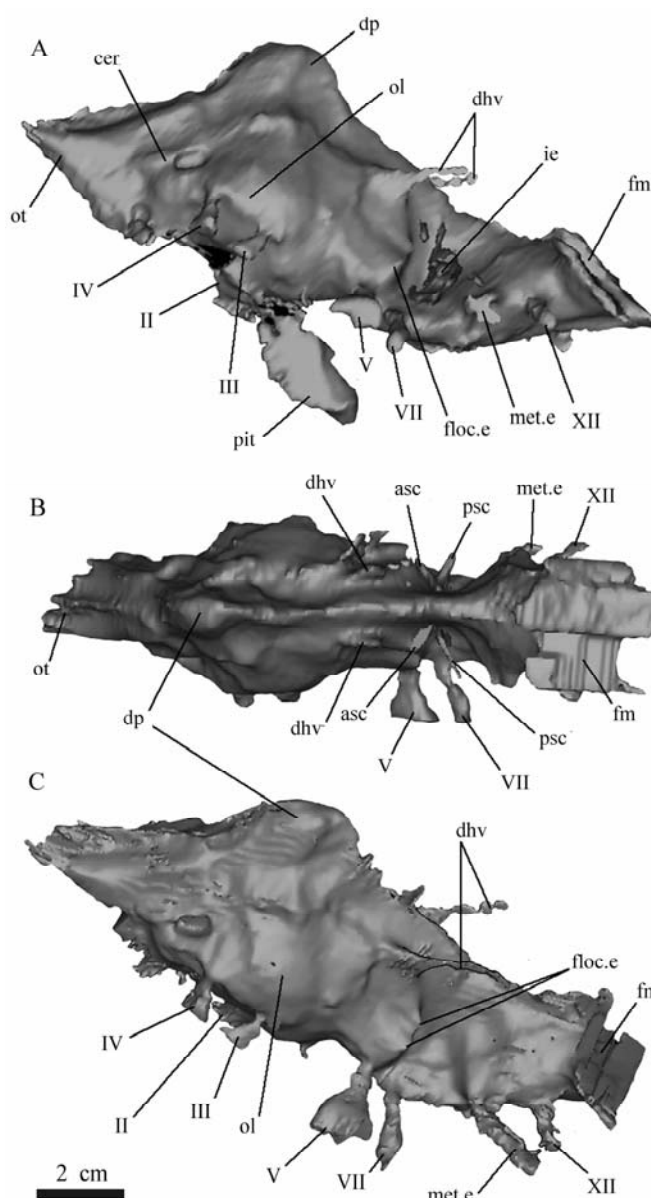


Fig. 6 *Sinraptor dongi* (IVPP V 10600), 3D digital reconstruction of endocasts in left lateral (A), dorsal (B) and left dorsolateral (C) views, inner ear reconstructed in A and B

Abbreviations: asc. anterior semicircular canal of inner ear; cer. cerebrum; dhv. dorsal head vein; dp. dural peak; flocc. e. floccular recess endocast; fm. foramen magnum; ic. inner ear; met. e. metotic foramen endocast; ol. optic lobe; ot. olfactory tract; pit. pituitary fossa; psc. posterior semicircular canal of inner ear; II-V, VII, XII. cranial nerves

Cranial nerve I is represented by the olfactory tract and olfactory bulbs in the endocast. The olfactory bulbs left shallow impressions in the ventral surface of the paired frontals, which roof the olfactory bulbs and olfactory tract (Fig. 1B). The foramina for CN II are confluent and form a single, slightly hourglass-shaped opening enclosed by the orbitosphenoids (Fig. 1B). The posterior margin of this opening reaches the plane of the posterior border of the postorbital process of the laterosphenoid. In *Giganotosaurus*, the posterior margin of CN II (which is separated from its counterpart by an ossified interorbital septum) extends more posteriorly than the postorbital process of the laterosphenoid (Paulina Carabajal, 2009). In *Sinraptor*, CN III and IV are dorsolateral to CN II, and pass through relatively small foramina.

The foramen for CN V has an anterior constriction that is interpreted as an incipient separation of the ophthalmic branch from the maxillary and mandibular branches of the trigeminal nerve (Currie and Zhao, 1993a). However, as seen on the endocast (Fig. 6), all the branches leave the endocranial cavity through a single opening. A single foramen for the trigeminal nerve is observed in *Acrocanthosaurus*, *Carcharodontosaurus saharicus*, *Giganotosaurus* and *Shaochilong* (Brusatte et al., 2010), whereas in *Allosaurus* the ophthalmic branch is separate (Franzosa, 2004). In *C. iguidensis*, there is a “binocularshaped” opening that suggests that there was either an incipient division (Brusatte and Sereno, 2007) or perhaps even full division, in which case the “binocular shape” is due to the erosion of the septum between two separate cavities (Brusatte, pers. comm.). In the endocast of *Sinraptor*, CN V is in the same coronal plane as the flocculus of the cerebellum (Figs. 6, 7H).

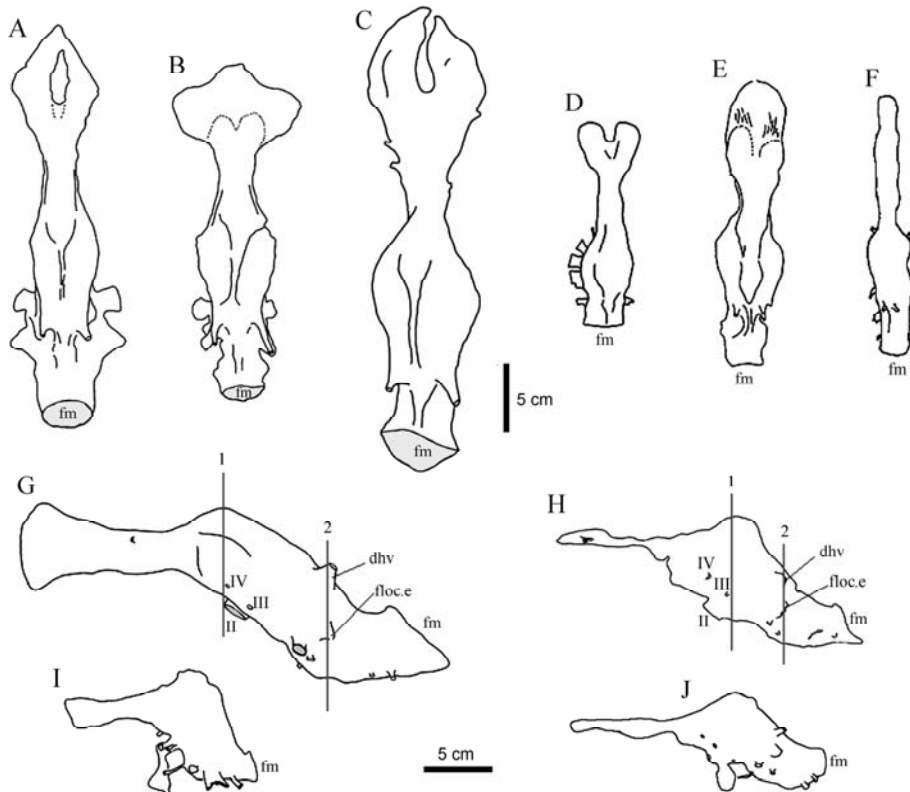


Fig. 7 Line drawings of the cranial endocasts of *Carcharodontosaurus saharicus* (A), *C. iguidensis* (B), *Giganotosaurus carolinii* (C, G), *Acrocanthosaurus* (D, I), *Sinraptor dongi* (E, H), and *Allosaurus* (F, J), in dorsal (A-F) and left lateral (G-J) views

A-D, G. after Paulina Carabajal and Canale, 2010; modified from A. Larsson, 2001; B. Brusatte and Sereno, 2007; D, I. after Franzosa and Rowe, 2005; F, J. after Franzosa, 2004

Abbreviations: dhv. dorsal head vein; floc. e. floccular recess endocast; fm. foramen magnum; 1. line aligned with cephalic flexure; 2. line aligned with pontine flexure; II-IV. cranial nerves

The sixth CN, which are visible in the CT scans, are separated transversely by 10 mm on the ventral surface of the medulla oblongata.

Cranial nerve VII is posterior to and smaller than CN V (Fig. 1A). In the endocast, the roots of the fifth and seventh cranial nerves are separated by 5 mm (Fig. 6A). In the braincases of *Acrocanthosaurus* (Franzosa and Rowe, 2005) and *Shaochilong* (Brusatte et al., 2010), there are two foramina for CN VII, corresponding to the hyomandibular and palatine branches.

In the braincase, there is a single opening for CN IX, X and XI, which is identified as the metotic foramen. In the endocast, these nerves form a single root that is half-moon-shaped at the base. This represents a cast of the fovea ganglii vagoglossopharyngealis (Baumel and Witmer, 1993) (Fig. 6A). This passage opens into the paracondylar pocket as the metotic foramen (Fig. 4).

The branches of CN XII leave the endocranial cavity through two foramina on each side, although only one is visible in the endocast. The passage for the second and smaller branch was identified only in the CT scans.

The dorsal head vein is in the same coronal plane as the floccular process in the endocast.

Inner ear Unfortunately, the entire osseous inner ear could not be reconstructed. However, the width and height of the endosseous labyrinth can be estimated (Fig. 6A,B). The labyrinth measures approximately 19 mm anteroposteriorly and 16 mm dorsoventrally. The anterior and posterior semicircular canals are both approximately 2 mm in diameter. The angle formed by the anterior and posterior semicircular canals is 65° (Fig. 6B). A similar angle is observed in *Acrocanthosaurus*, whereas the angle is approximately 72° in *Allosaurus* (Witmer and Ridgely, 2009).

4 Discussion

4.1 Ethmoidal region and pneumatic recesses

Sphenethmoid and mesethmoid: patterns of ossification The ethmoidal region of the braincase apparently remains cartilaginous in most adult theropods. When ossified, these elements enclose the olfactory tract and olfactory bulbs. The ethmoidal elements enclose the olfactory bulbs and tract ventrolaterally. Posteriorly, they contact the orbitosphenoid, which is often identified as the “mesethmoid” (Larsson, 2001; Brochu, 2003; Franzosa and Rowe, 2005; Sanders and Smith, 2005). In other cases, it is identified as the “sphenethmoid” (Taquet and Welles, 1977; Coria and Currie, 2002a), or even as the “presphenoid” in ornithischians (Evans et al., 2009). More recently, Ali et al. (2008) proposed the terms sphenethmoid for those ethmoidal elements enclosing the olfactory tract and olfactory bulbs, and mesethmoid for the median septum in tyrannosaurids, based on exhaustive comparisons (including those of embryos) of the ethmoidal elements in extant birds and crocodiles. We follow the conventions and terminology of Ali et al. (2008) here.

Ossified ethmoidal elements are known for abelisaurids (Paulina Carabajal, 2011a,b), *Acrocanthosaurus* (OMNH 10146, Stovall and Langston, 1950), *Carcharodontosaurus iguidensis* (Brusatte and Sereno, 2007), *C. saharicus*, *Ceratosaurus*, *Eustreptospondylus* (Sadleir et al., 2008), *Giganotosaurus* (Coria and Currie, 2002a), *Piveteausaurus* (Taquet and Welles, 1977), and tyrannosaurids (Ali et al., 2008), but represent four different patterns (Paulina Carabajal, 2009) (Fig. 8). Generally, the ethmoidal elements are firmly fused to each other, to the frontal dorsally, and to the orbitosphenoid posteriorly. In the basal tetanuran *Piveteausaurus* (MNHN 1920-7) and tyrannosaurids such as *Albertosaurus* (TMP 81.10.01), *Daspletosaurus* (TMP 2001.36.01), *Gorgosaurus* (TMP 94.12.602), and “*Nanotyrannus*” (Witmer and Ridgely, 2009), the sphenethmoid contacts the orbitosphenoid posteriorly in a visible suture (Fig. 8A). In *Acrocanthosaurus* (OMNH 10146, Stovall and Langston, 1950) and *Eustreptospondylus* (Sadleir et al., 2008), there is another ossified element between the sphenethmoid

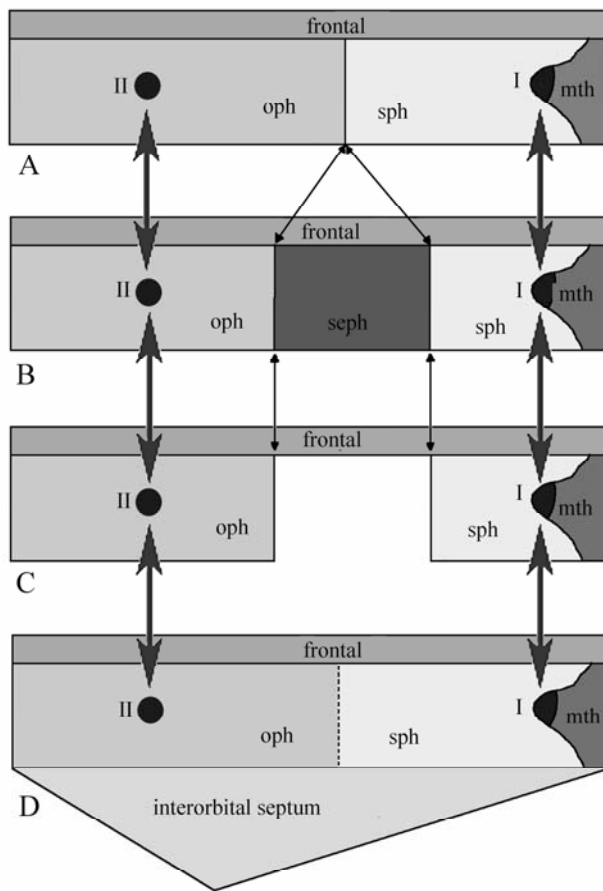


Fig. 8 Schematic of the ethmoidal region of the braincase in right lateral view showing the ossification patterns of the ethmoidal elements observed in; *Piveteausaurus* and tyrannosaurids (A), *Acrocanthosaurus* (B), *Sinraptor* and the specimen MCF-PVPH 411 (C), and neoceratosaurs and carcharodontosaurids (D)

Dashed lines indicate putative contacts that cannot be directly observed due to fusion; not to scale

Abbreviations; mth. mesethmoid; oph. orbitosphenoid; seph. septosphenoid; sph. sphenethmoid; I - II. cranial nerves

ethmoidal elements. However, this does not apply in reverse, because several taxa with ethmoidal elements lack ossified interorbital septa.

CT scans of the braincases of abelisaurids (Sampson and Witmer, 2007), *Acrocanthosaurus* (Franzosa and Rowe, 2005), *Giganotosaurus* (Coria and Currie, 2002a) and tyrannosaurids (Ali et al., 2008) show that the sphenethmoids form a ring around the olfactory bulbs and the anterior portion of the olfactory tract. This ring is fused dorsally to the frontal and is open dorsally in the region of the olfactory tract. As mentioned, in *Sinraptor* (IVPP V 10600) and MCF-PVPH 411, the sphenethmoids are U-shaped, and the frontal roofs the cavities for the olfactory tract and olfactory bulbs. However, the dorsal closure of the sphenethmoids could be related to ontogenetic stage, because these specimens seem to be subadult individuals.

In *Sinraptor*, the deep groove observed in the mesethmoid was probably left by a large vascular element. The three foramina dorsal to the groove represent the passages of blood vessels that enter the anterior region of the olfactory bulbs (Fig. 2). There are vascular foramina pierce-

and orbitosphenoid, identified as a septosphenoid (Welles and Langston, unpublished paper on *Acrocanthosaurus atokensis* braincase) (Fig. 8B). The discovery of a theropod braincase in Argentina (MCF-PVPH 411; Coria and Currie, 2002b) that shares with *Sinraptor* the presence of a gap between the sphenethmoid and the orbitosphenoid (Fig. 8C), suggests that the gap represents an unossified septosphenoid (Paulina Carabajal, 2009). In *Ceratosaurus* (MWC 1), the abelisaurids *Abelisaurus* (MPCA 11.098), *Carnotaurus* (MACN-CH 894) and *Majungasaurus* (Sampson and Witmer, 2007), and the carcharodontosaurids *Carcharodontosaurus iguidensis* (Brusatte and Sereno, 2007), *C. saharicus* (SGM-Din 1) and *Giganotosaurus* (MUCPV-CH 1), the ethmoidal elements are firmly fused to the frontal, the orbitosphenoid and the ossified interorbital septum (Fig. 8D). In the particular case of *Giganotosaurus*, the orbitosphenoids are medioventrally displaced, suggesting that the laterosphenoids are in contact with the ethmoidal elements (Paulina Carabajal, 2009). However, in those taxa the sutures are obscured by fusion, which prevents one from identifying whether or not there is a septosphenoid forming the walls of the olfactory tract. The presence of an ossified interorbital septum is always accompanied by the presence of ossified

ing the sphenethmoids in the abelisaurids *Abelisaurus* and *Carnotaurus* (Paulina Carabajal, 2011a,b), and in *Giganotosaurus* (Paulina Carabajal and Canale, 2010), although in each of these taxa, it is the olfactory tract that is vascularized, not the olfactory bulb. The olfactory bulbs in *Sinraptor* were probably posterior to the median septum (mesethmoid?), as indicated by the suture marks on the frontal for the sphenethmoids (Fig. 1B).

Pneumatic cavities Pneumatic cavities have been reported inside the paroccipital processes of several theropods, including the coelophysoids *Syntarsus kayentakatae* and *S. rhodesiensis* (Raath, 1977; Tykoski, 1998), ornithomimids (Makovicky and Norell, 1998), therizinosaurids (Clark et al., 1994), troodontids (Currie, 1985; Currie and Zhao, 1993b) and tyrannosaurids (Currie et al., 2003). However, the presence of a caudal tympanic recess as defined by Witmer (1997), forming “a large air space within the paroccipital process that opens into the tympanic cavity via an oval foramen on the front of the base of the paroccipital process”, is considered to be characteristic of coelurosaurs (Norell et al., 2006). The identification of this recess in the basal tetanuran *Sinraptor* (Paulina Carabajal, 2009), and apparently also in *Acrocanthosaurus* and *Allosaurus* (Dufeu, pers. comm., 2011), shows this trait appeared earlier in theropod evolution.

The large recess delimited by the basicranial box is subdivided into a deep basisphenoidal recess and two pairs of smaller recesses. The oval recess at the base of each basiptyergoid process is characteristic of *Sinraptor*.

4.2 Brain endocast

The endocast of *Sinraptor* is similar to those of *Carcharodontosaurus* and *Giganotosaurus*, especially with respect to the angles formed by the forebrain, midbrain and hindbrain. However, it is different in the relative size of the midbrain, which is proportionally longer in carcharodontosaurines (Fig. 7G,H). The endocast of *Sinraptor* also differs markedly from that of *Acrocanthosaurus*, which is shorter and has a midbrain that is strongly inclined posteroventrally, forming an angle with the hindbrain of approximately 90° (Fig. 7I). The maximum width of the hemispheres is dorsal to CN II and III in *Sinraptor*, but is dorsal to CN V and VII in *Acrocanthosaurus* (Franzosa and Rowe, 2005) and *Giganotosaurus* (Paulina Carabajal and Canale, 2010).

In *Sinraptor*, several CN and blood vessels have similar positions to their equivalents in *Carcharodontosaurus* and *Giganotosaurus*, although important differences are observed in the mid-brain. In the three genera, the floccular process and the dorsal head vein are vertically aligned—a coronal plane intersects the floccular process and the dorsal head vein (Fig. 7G, H). Posterior to that plane are CN IX to XIII. However, if the coronal plane is traced through the dural peak (the most dorsal section of the endocast that coincides with the cephalic flexure), the CN anterior or posterior to that plane are not the same in the different taxa. In *Sinraptor*, CN II, III and IV are in front the plane (Fig. 7H), whereas in *Giganotosaurus* and *Carcharodontosaurus*, the same nerves are posterior to the line (Fig. 7G). Although the angles of the cephalic and pontine flexures are similar in *Sinraptor* and *Giganotosaurus*, the midbrain is longer in carcharodontosaurids. The endocasts of *Acrocanthosaurus* (Franzosa and Rowe, 2005) and *Allosaurus* (Rogers, 1998; Franzosa, 2004) are similar to those of *Sinraptor* with respect to the positions of CN II-IV, although the flocculus is at the same level as CN VII rather than CN V (or CN V_{2,3} in the case of *Allosaurus*, because the ophthalmic branch has a separate foramen) (Fig. 7). The positions of nerves IX to XIII in the hindbrain are more or less the same in *Sinraptor* as in other theropod endocasts, suggesting that the medullar portion of the brain is more conservative.

The floccular recess is well developed in all theropods and opens anteriorly on the vestibular eminence. This recess is also present (although is relatively less developed) in prosauro-

pods, including *Adeopapposaurus* (PVSJ 568; Martínez, 2008), *Massospondylus* (Gow, 1990) and *Plateosaurus* (Galton, 1985), and in a few sauropod taxa (Galton and Knoll, 2006; Sereno et al., 2007). In non-avian theropods, the floccular recess reaches its greatest development in maniraptorans, in which it is at least three times the size of the trigeminal foramen.

Brain size and morphology The ratio of the volume of the brain to that of the whole cavity varies between 50% and 95% depending on the taxon, and the endocast represents the cast of the dura mater of the brain rather than the brain itself (Hopson, 1979, 1980; Sampson and Witmer, 2007). The presence of vascular impressions on the surface of the endocranial cavity in some ornithischians (Evans, 2005), and in some dromaeosaurid, oviraptorid and troodontid theropods (Osmólska, 2004), suggests that the brain may have come close to completely filling the cavity in these taxa. The complete delineation of the cerebral hemispheres and cerebellum in theropod endocasts can also show that the brain filled most of the endocast (Franzosa, 2004). In extant birds, the endocranial volume does provide a reliable estimate of brain size (Iwaniuk and Nelson, 2002). The latex endocast of *Sinraptor* has shallow vascular marks on the dorsal surface of the cerebral part of the brain, probably related to the optic lobes.

Non-maniraptoran theropods had brains that were less derived than those of maniraptorans, being more “reptilian” and similar in complexity and morphology to those of extant crocodylians (Maleev, 1965; Hopson, 1979, 1980; Rogers, 1999; Larsson et al., 2000; Larsson, 2001; Franzosa and Rowe, 2005; Sanders and Smith, 2005). The encephalization quotients indicate that within dinosaurs, theropods and some ornithomimids possess relatively large brains, although the relative brain sizes of all dinosaurs (except for Maniraptora) are within the range of extant crocodiles (Hopson, 1980; Maryanska et al., 2002; Osmólska, 2004). The encephalization quotient (EQ) is calculated from the brain size (volume or mass) of an individual. This is divided by the expected brain size for the individual’s body size, which is calculated using an allometric regression derived from a large group of animals (e. g. birds, reptiles, etc.) (Evans, 2005). Hopson (1980) used the ratio in living reptiles ($E = 0.005P^{0.66}$) to show that the average of EQ of most dinosaurs is similar to that of extant crocodiles. Using this method, the calculated EQ of *Sinraptor* is 0.14, which is within the range for large-bodied theropods as calculated by Hopson (1977). The calculated EQs for other allosauroids are similar (Table 1).

5 Conclusions

The new information on the braincase and endocranial anatomy of *Sinraptor* sheds light on the distribution of some characters within Theropoda. For example, the presence of a caudal tympanic recess is not characteristic of coelurosaurs alone, but is more widely distributed. It represents a probable synapomorphy of tetanurans, although it might also have appeared convergently in *Sinraptor* and coelurosaurs. The pattern of ossification of the ethmoidal elements and the development of a medial basiptyergoid recess seem to be characteristic traits for *Sinraptor*.

Comparison with other theropods suggests there are four ossification patterns of the ethmoidal elements: 1) the sphenethmoid contacts the orbitosphenoid posteriorly with a visible suture, and there is no ossified interorbital septum; 2) the sphenethmoid is firmly fused to the orbitosphenoid and the interorbital septum, and there are no visible sutures; 3) there is a septosphenoid between the sphenethmoid and the orbitosphenoid with visible sutures; 4) the sphenethmoid is U-shaped and is not fused to the frontal, the septosphenoid is not ossified and there is a space between the sphenethmoid and the orbitosphenoid. The final pattern, however, could be characteristic of subadult, large-bodied theropods, and may develop in more mature animals into one of the other patterns.

Comparisons between the endocast of *Sinraptor* and those of other, related theropods reveal more similarities with the carcharodontosaurines (*Carcharodontosaurus* and *Giganotosaurus*) and *Allosaurus* than with *Acrocanthosaurus* (Table 1).

Table 1 Endocranial traits within Allosauroidea

	<i>Sinraptor</i>	<i>Giganotosaurus</i>	<i>Allosaurus</i>	<i>Acrocanthosaurus</i>
Max. width of endocast is dorsal to	CN II and CN III	CN V and CN VII	CN II and CN III	CN V and CN VII
“Pontine” flexure angle	more than 90°	more than 90°	more than 90°	approx. 90°
Ophthalmic branch of CN V	not separated	not separated	separated	not separated
Floccular recess/flocculus	8-shaped	oval	oval	oval
Ossified ethmoidal elements	yes	yes	no	yes
CN XII	2 foramina	single foramen	single foramen	single foramen
Flocculus, aligned with	hdv, CN VII	hdv	hdv, CN VII	CN VII
Medial cerebral vein	no	no	yes	sinus?
CN VI penetrates the pituitary fossa	yes?	yes	yes	no
Olfactory tract	not separated	not separated	not separated	separated
CN III and CN IV	separated	separated	separated	not separated
CN VII, branches	single foramen	single foramen	single foramen	2 foramina
Endocast, volume (ml)	95	250	189	190.8
EQ	0.14	0.14	0.24	—

Abbreviations: CN II–XII. cranial nerves; hdv. head dorsal vein; EQ. encephalization quotient.

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