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Brief report

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The endocranial morphology and inner ear of the abelisaurid theropod *Aucasaurus garridoi*

ARIANA PAULINA-CARABAJAL and CECILIA SUCCAR

A partial cranial endocast and right inner ear of the Cretaceous abelisaurid dinosaur *Aucasaurus garridoi* were digitally reconstructed from CT scans. The forebrain, midbrain, and hindbrain resemble the morphology described for the abelisaurids *Majungasaurus* and *Indosaurus*. However, *Aucasaurus* exhibits a floccular process that is relatively larger than that of *Majungasaurus*. In *Aucasaurus* the flocculus is enclosed in an 8-shaped floccular recess, similar in shape and size to that observed in *Abelisaurus*, suggesting that the two Patagonian taxa were capable of a slightly wider range of movements of the head. Here we describe the second inner ear known for the Abelisauridae. The labyrinth of the inner ear is similar in shape and size to the semicircular canals of *Majungasaurus*, although the lateral semicircular canal is shorter in *Aucasaurus*.

Introduction

Abelisaurid theropods with preserved skulls are known from the Late Cretaceous of South America: *Abelisaurus comahuensis* (Bonaparte and Novas 1985), *Carnotaurus sastrei* (Bonaparte 1985), *Aucasaurus garridoi* (Coria et al. 2002), *Ekrixinatosaurus novasi* (Calvo et al. 2004), *Skorpiovenator bustingorryi* (Canale et al. 2008); India: *Indosuchus raptorius* (Huene and Matley 1933), *Indosaurus matleyi* (Huene and Matley 1933), *Rajasaurus narmadensis* (Wilson et al. 2003); and Madagascar: *Majungasaurus crenatissimus* (Déperet 1896; Sampson et al. 1998). However, the braincase anatomy was described in few taxa and the evolution of their apomorphic features is poorly understood (Sampson and Witmer 2007; Paulina Carabajal 2011a, b). Among non-abelisaur ceratosaurians, the endocast and inner ear were described only for *Ceratosaurus* (Sanders and Smith 2005). Among Abelisauridae, a natural cranial endocast was preserved and described for *Indosuchus* (Huene and Matley 1933) and a CT-derived endocast and inner ear for *Majungasaurus* (Sampson and Witmer 2007). We present a description of the fourth ceratosaur endocast and inner ear and discuss the evolution of some abelisaur-specific morphologies.

The braincase of the type species of *Aucasaurus garridoi* (MCF-PVPH 236) is incomplete, lacking the basicranium and most of the occipital and lateral walls (Paulina Carabajal 2011a). The endocranial cavity is exposed ventrally allowing direct observation of some endocranial features and the production of a latex endocast (Succar and Paulina Carabajal 2011). The ossified otic capsule is complete, allowing study of the inner ear morphology using digital reconstructions based on CT scans.

Institutional abbreviations.—MCF, Carmen Funes Museum, Plaza Huincul, Neuquén Province, Argentina.

Other abbreviations.—asc, anterior semicircular canal; lsc, lateral semicircular canal; psc, posterior semicircular canal.

Material and methods

The braincase of *Aucasaurus* (MCF-PVPH 236) was scanned using a medical CT machine (SIEMENS Sensation 64), with slices at 0.63 mm intervals. Virtual three-dimensional inner ear and cranial endocasts were obtained and visualized using the software Mimics (14.0) and Geomagic (10.0) at the University of Alberta, Vertebrate Paleontology Laboratory. A latex cranial endocast was also made.

As mentioned by other authors (e.g., Hopson 1980) the basal theropod cranial endocast does not reflect the shape of the brain and associated soft tissues, but the endocranial space shape, which also reflects structures such as meninges and venous sinuses. As proposed by Sereno et al. (2007), to facilitate discussion we will refer to the digital cast structures as if they were the structures themselves (e.g., "olfactory bulb" instead of "olfactory bulb cavity endocast").

Description

Cranial endocast.—Only the dorsal portion of the endocranial cavity of *Aucasaurus* was 3D reconstructed. However, the main sections of the brain (forebrain, midbrain, and hindbrain) can be identified (Fig. 1). Small vascular impressions can be observed on the latex endocast, indicating the presence of an engrossed dura (Evans 2005), as in most basal theropods. These vascular impressions are located over the cerebral hemispheres, suggesting that this region of the endocast was more tightly filled by the brain than the posterior regions. The length of the cranial endocast, measured from the foramen magnum to the base of the olfactory tract is 100 mm, but reaches 160 mm when the olfactory tract and olfactory bulbs are included. These proportions are similar to the length of the endocasts of the abelisaurid *Majungasaurus crenatissimus* (Sampson and Witmer 2007) and the ceratosaur *Ceratosaurus nasicornis* (Sanders and Smith 2005).

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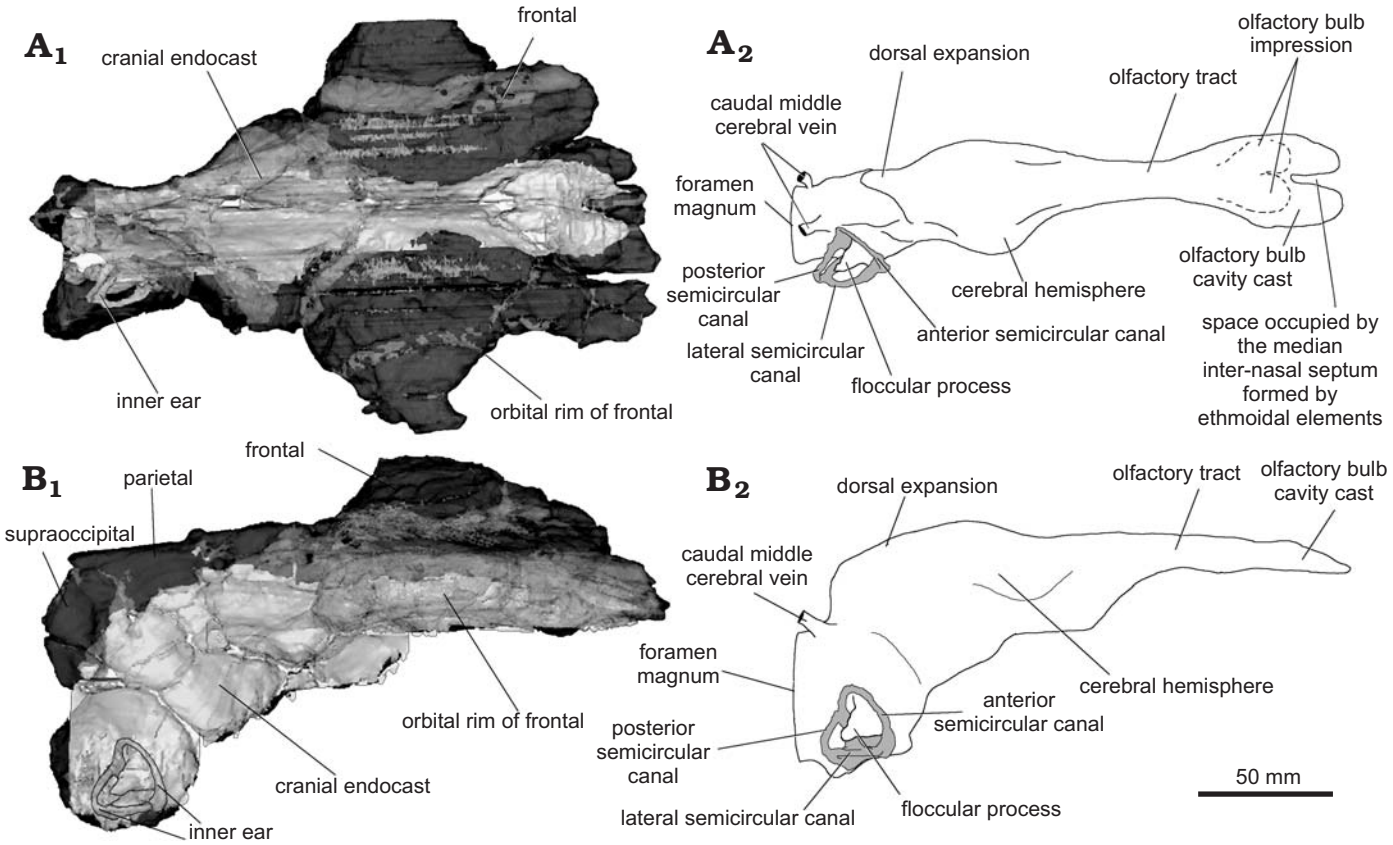


Fig. 1. Abelisaurid theropod *Aucasaurus garridoi* Coria, Chiappe, and Dingus, 2002 (MCF-PVPH 236), from the Upper Cretaceous of North Patagonia, in dorsal (**A**) and right lateral (**B**) views. Volume rendering of the braincase (semi-transparent) and cranial endocast (A_1, B_1), and line drawings of brain and inner ear (A_2, B_2).

The volume of the preserved endocranial cast of *Aucasaurus* is approximately 25 ml, excluding the olfactory tract and bulbs, which constitute approximately another 10 ml. Based on the morphology of *Majungasaurus* (Sampson and Witmer 2007), the reconstructed cranial endocast of *Aucasaurus* would have been approximately 45–50 ml. This estimate was made by multiplying the volume of the endocast of *Majungasaurus* by the ratio of the length of the endocast of both taxa.

As in other basal theropods, the maximum width of the endocranial cast of *Aucasaurus* is anterodorsal to the floccular process, and corresponds to the lateral expansions of the cerebral hemispheres. The cerebral hemispheres are discernible in dorsal view of the endocast, as rounded lateral projections (Fig. $1A_2$). As mentioned, the latex endocast shows small vascular impressions on the dorsal and lateral aspects of the cerebral hemispheres.

The olfactory tract is long and relatively wide, and horizontally projected in front of the cerebral hemispheres, as in *Majungasarus*, but unlike the anterodorsally projected olfactory tract in *Ceratosaurus* (Sanders and Smith 2005: figs. 3A, 13B), nor the apparently anteroventrally projected tract in *Indosaurus* (Huene and Matley 1933: pl. 9: 3d). In *Aucasaurus*, the maximum width of the olfactory tract is 22 mm just posterior to the olfactory bulbs, whereas the minimal width is 14.5 mm (Fig. 1A). The cavities occupied by the olfactory bulbs are larger than the bulbs themselves, and they are separated by an osseous septum formed by the mesethmoid, as in other theropods such as abelisaurids, tyrannosaurids, and allosauroids (Ali et al. 2008; Paulina Carabajal 2011a, b; Paulina Carabajal and Currie 2012). In *Aucasaurus*, the septum itself is not preserved except for its dorsal section, a bony bar 5 mm wide, which is dorsally fused to the frontals at the midline. The shallow impressions of the olfactory bulbs, left on the ventral aspect of the frontal, are oval-shaped and slightly divergent anteriorly (Paulina Carabajal 2011a: fig. 3B; Fig. $1A_2$). These olfactory bulb impressions are smaller than the olfactory cavity enclosing them, as in other theropods (Ali et al. 2003).

The two passages for the caudal middle cerebral veins, enclosed by the supraoccipital, converge on the dorsal section of the dorsal sagittal venous cavity, dorsal to the labyrinth of the inner ear (Fig. $1B_2$). These vein passages are relatively short and are unknown in the braincases of *Carnotaurus* and *Abelisaurus* (Paulina Carabajal 2011a, b) due to poor preservation in this region. In *Aucasaurus* the dorsal expansion (pyramidal peak), the dorsal-most projection of the endocranial cavity, is short and slightly expanded over the level of the forebrain. Unlike in *Majungasaurus*, there is a marked dorsal expansion (see Sampson and Witmer 2007 and the discussion herein).

In *Aucasaurus*, the floccular process is located posterodorsal to cranial nerve V, and it projects posterolaterally into the space bounded by the anterior semicircular canal (Fig. $1B_2$). The floccular process is mediolaterally compressed with a longitudinal depression along its length separating it into a large dorsal lobe

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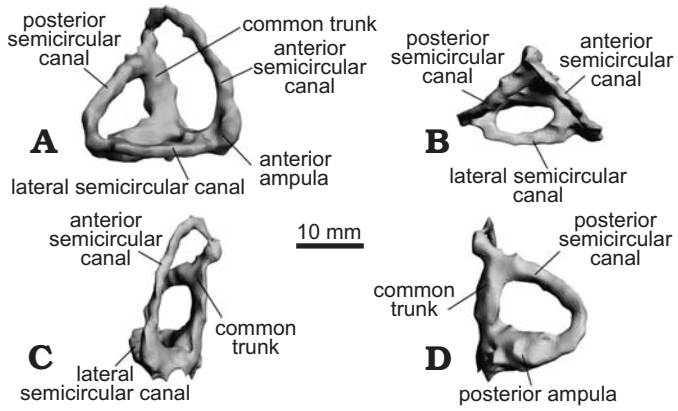


Fig. 2. Abelisaurid theropod *Aucasaurus garridoi* Coria, Chiappe, and Dingus, 2002, from the Upper Cretaceous of North Patagonia (MCF-PVPH 236). Digital reconstruction of the right inner ear in lateral (**A**), dorsal (**B**), anterior (**C**), and posterior (**D**) views.

and smaller ventral lobe. This morphology corresponds to the 8-shaped floccular recess on the anterior wall of the vestibular eminence of the braincase, and is also observed in *Abelisaurus comahuensis* (Paulina Carabajal 2011a) and possibly in *Indosaurus*, as deduced from the divided flocculus illustrated by Huene and Matley (1933: pl. 9: 3a).

Inner ear.—The complete right labyrinth of the inner ear of *Aucasaurus* was digitally extracted from the CT data, with the exception of the distal end of the lagena, which was enclosed by the missing basisphenoid (Fig. 2A–D). However, given the overall similarities of the labyrinths of *Majungasaurus* and *Ceratosaurus* (Sampson and Witmer 2007: fig. 19), we see no reason to believe that the lagena of *Aucasaurus* was significantly different.

The anterior semicircular canal (asc) is larger than the posterior semicircular canal (psc) and the lateral semicircular canal (lsc) is smaller than the other two, as in most theropods (see Sampson and Witmer 2007) and sauropods (Galton 1985). In *Aucasaurus*, the internal diameter (largest length across the canal from the inner edge) of each canal is approximately 16.5 mm (asc), 10.8 mm (psc), and 8.5 mm (lsc) respectively. The diameter of the tube of the three canals varies between 1.5–2.6 mm, with the psc the most robust canal. The angle formed between the anterior and posterior semicircular canals is approximately 92–95° in dorsal view (Fig. 2B). The common trunk is more robust than any of the three semicircular canals, differing from the slender common trunk in the inner ear of *Majungasaurus* and *Ceratosaurus* (Sampson and Witmer 2007).

The asc is taller than the psc and the common trunk (Fig. 2A, C). It is oval-shaped, with the longest axis dorsoventrally oriented, and 2.5 times the length of the minimum axis. The psc is also oval-shaped, but the main axis is mediolaterally oriented. The shape of this canal is more similar to that of *Majungasarus* than *Ceratosaurus*, which has a more rounded psc. In *Aucasaurus*, the psc is slightly curved (concave caudally) in dorsal view (Fig. 2B), as in *Ceratosaurs*, but unlike the straight psc in *Majungasaurus* (Sampson and Witmer 2007: fig. 19b, f). The lateral semicircular canal is oval-shaped, with the main axis anteroposteriorly oriented (Fig. 2B). It is slightly more robust than the other two canals, similar to the condition in *Ceratosaurus* (Sampson and Witmer 2007: fig. 19f). In *Aucasaurus*, the lsc is less laterally curved than in *Majungasaurus*.

Comparisons

Comparison of *Aucasaurus* with the abelisaurids *Majungasaurus* (Sampson and Witmer 2007) and *Indosaurus* (Huene and Matley 1933) and the ceratosaur *Ceratosaurus* (Sanders and Smith 2005) shows that the three taxa share a cranial endocast morphology with practically the same proportions for the forebrain, midbrain and hindbrain. In *Aucasaurus* the cerebral flexure is slightly more closed and the dorsal sagittal sinus (dorsal expansion) is less developed than in *Majungasaurus*.

In *Aucasaurus*, the floccular process is markedly larger than in *Majungasaurus*. As mentioned by Sampson and Witmer (2007), the flocculus of the cerebellum plays a role in coordinating eye movements (i.e., gaze) with movements of the head, neck, and body, and tends to be enlarged in taxa that rely on quick movements of the head and/or body (Butler and Hodos 1996; Winship and Wylie 2003; Witmer et al. 2003, 2008). Thus, apparent reduction of the flocculus in *Majungasaurus* may be associated with a decrease in reliance on quick movements and sophisticated gaze-stabilization mechanisms compared to *Aucasaurus*. However, the size of the semicircular canals of *Aucasaurus* suggests a relatively limited sensitivity to head acceleration. As described for the inner ear of *Majungasaurus* (Sampson and Witmer 2007), the osseous labyrinth of *Aucasaurus* is in general quite conservative in dinosaurs. As in other basal theropods, such as *Majungasaurus* (Sampson and Witmer 2007), *Ceratosaurus* (Sanders and Smith 2005), *Allosaurus* (Hopson 1979), *Acrocanthosaurus* (Franzosa and Rowe 2005), *Carcharodontosaurus* (Larsson 2001), and *Sinraptor* (Paulina Carabajal and Currie 2012), the asc is larger than the psc and the lsc is smaller than the other two. The lsc in *Majungasaurus* is longer than in *Aucasaurus* and *Ceratosaurus*. Canals with greater radii of curvature in general should have greater sensitivity, suggesting that *Aucasaurus* might have had less sensitivity to lateral turning movements of the head than *Majungasaurus* (Sampson and Witmer 2007). When the lsc is oriented horizontally, corresponding to the vertebrate "alert" posture, the main axis of the skull roof of *Aucasaurus* remains horizontal and parallel to the lsc (Fig. $1A_1$). The same occurs with the skull of *Majungasaurus* and *Ceratosaurus*. The horizontal head posture of non-coelurosaur theropods compared to the down-turned posture of many coelurosaurs suggests a fundamental behavioral shift in theropod head position. Further studies are needed, but the data presented here for *Aucasaurus* lend support to a conservative non-coelurosaurian theropod endocranium

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