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CRANIAL ENDOCAST OF THE CRETACEOUS THEROPOD DINOSAUR ACROCANTHOSAURUS ATOKENSIS

JONATHAN FRANZOSA[1] and TIMOTHY ROWE[1,2]
[1]Jackson School of Geosciences, jfranzosa@yahoo.com
[2]Texas Memorial Museum, The University of Texas at Austin, Austin, Texas 78712 U.S.A.

ABSTRACT—*Acrocanthosaurus atokensis*, a large carcharodontosaurid theropod, is known from several specimens collected in the 1990s, as well as the two original specimens collected in the 1940s. The holotype, OMNH 10146, contains a well-preserved and complete braincase that was scanned at the High Resolution X-ray Computed Tomography (CT) Facility at The University of Texas at Austin. The resulting images were manipulated using graphics and volume rendering programs to produce a complete digital endocast of the endocranial cavity. The images reveal all of the cranial nerves except for the vestibulocochlear nerve. Also visible are: (1) the pituitary fossa; (2) the fenestra ovalis; (3) the entrance of the internal carotid arteries; (4) all three semicircular canals; and (5) several smaller arteries and veins. This complete endocast allows for: (1) the description of the previously undescribed endocranial cavity of *Acrocanthosaurus*; (2) determination of skull orientation using the semicircular canals; and (3) comparisons with closely related taxa such as *Carcharodontosaurus*, *Giganotosaurus*, *Allosaurus*, and *Sinraptor*. The comparisons can consist not only of characters that can be seen in the braincase and endocast, but also of quantitative, volumetric measurements that are available through the volume rendering program used to create the endocast. These comparisons uphold the proposed relationships of *Acrocanthosaurus* being within the clade Carcharodontosauridae and the sister taxon to *Carcharodontosaurus*, and allow for new characters to be applied to the data matrices used to determine the relationships.

INTRODUCTION

Understanding the evolution of the brain and intelligence has attracted the interest of paleontologists for more than three centuries, in large part through the examination of natural casts of the endocranial cavities in fossilized skulls (Marsh, 1880; Edinger, 1948; Jerison 1973). However, natural endocasts are rare, and although the endocranial cavity itself may be preserved more or less intact in many fossils, its geometry is hidden from view by the bones of the braincase. The endocranial cavity is generally inaccessible for study without destructive preparation, and, consequently, endocasts are at present known in only a fraction of those taxa in which skulls are preserved.

In recent years, X-ray computed tomographic (CT) scanning has become increasingly feasible and refined as a tool for examining internal cranial anatomy in fossil vertebrates, (Conroy and Vannier, 1984; Rowe et al., 1997, 1999; Maisey, 2000, 2001a, b; Tykoski et al., 2002; Carlson et al., 2003) and for extracting digital endocasts from well-preserved fossil skulls (Rowe et al., 1995; Brochu, 2000; Larsson, 2001; Witmer et al., 2003). We report here on the structure of an endocast of the Early Cretaceous theropod *Acrocanthosaurus atokensis* Stovall and Langston, 1950, and compare it to endocasts described for some of its closest relatives among basal theropods. A phylogenetic analysis by Sereno et al. (1996) found *Acrocanthosaurus* to be the sister taxon to *Carcharodontosaurus saharicus*, forming the monophyletic clade Carcharodontosauridae, with *Giganotosaurus*. This clade has been maintained by more recent analyses (Holtz, 1998; Rauhut, 2003), although exact relationships have been questioned (Holtz, 1998).

The endocast of *Acrocanthosaurus* was digitally constructed from a high-resolution X-ray CT scan of the complete, uncrushed braincase of the type specimen. *Acrocanthosaurus* adds to a growing list of digital theropod endocasts that includes *Tyrannosaurus* (Brochu, 2000) and *Carcharodontosaurus* (Larsson et al., 2000; Larsson, 2001). With the accumulation of a more-dense taxonomic sample of basal theropod endocasts, the systematic utility of endocast characters can be explored at a finer level of detail than previously possible, and a clearer picture may begin to emerge of the history of the brain and skull in early theropods.

Institutional Abbreviations—OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma.

MATERIALS AND METHODS

The scanned specimen consists of a complete and undistorted braincase (OMNH 10146—formerly MOU or UOM 8-0-S9), which was separated from the rest of the skull (Fig. 1). The specimen was collected in 1940–1941 from the Lower Cretaceous (Aptian–Albian) Antlers Formation of Atoka County, Oklahoma, by Works Projects Administration (WPA) crews under the direction of Professor John Willis Stovall of the University of Oklahoma. The scanned braincase is part of an incomplete skeleton, designated as the holotype of *Acrocanthosaurus atokensis* Stovall and Langston, 1950 (see also Langston, 1947). The precise ontogenetic status of the specimen cannot be determined, although the fact that the exoccipital-basioccipital sutures are still unfused suggests that the specimen was not fully adult.

The specimen was scanned at the University of Texas High-Resolution X-ray CT Facility (Rowe et al., 1997; Ketcham and Carlson, 2001; Carlson et al., 2003; www.ctlab.geo.utexas.edu), by Drs. Richard Ketcham and Matt Colbert on January 12, 1999. Both the dataset and derivative visualizations are available on the Web (Table 1). The original dataset consisted of 342 1.0 mm-thick slices, taken at an inter-slice spacing of 0.8 mm in horizontal planes, from the top of the frontals to the bottom of the basicranial tubera.

Scanner energy was 420 kV and 4.7 mA, with 2 brass filters between the X-ray source and specimen. X-ray attenuation was measured using a P250D cadmium-tungstate solid-state linear array detector. The specimen was scanned in 190% offset mode, with 64 ms integration time. Slice thickness was collimated to 1.0 mm, inter-slice spacing was 0.8 mm, source-object-distance 660 mm, and image field of reconstruction was 255 mm. For each slice, 2000 views were taken, one ray averaged per view and one sample per view. Image reconstruction employed an offset of 330
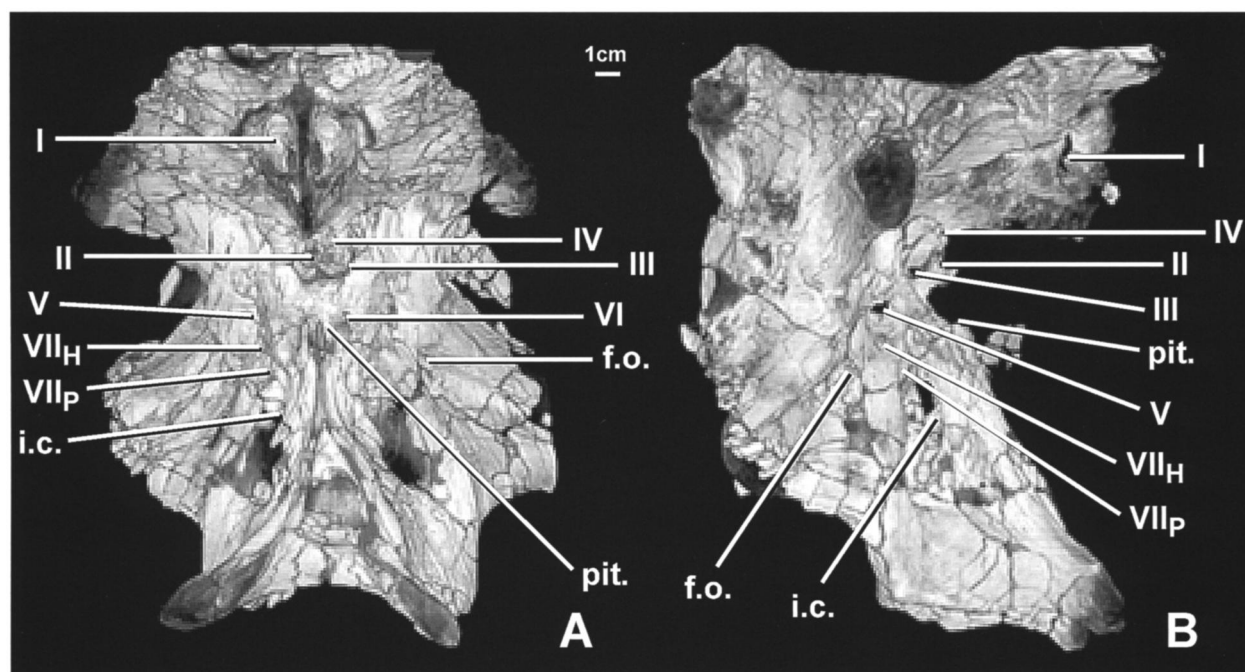
FIGURE 1.   **A**, Rostral and **B**, right lateral views of the braincase of the type of *Acrocanthosaurus atokensis*, OMNH 10146. This is the braincase from which the digital endocast was constructed. **Abbreviations: f.o.**, fenestra ovalis; **i.c.**, internal carotid canal; **pit.**, pituitary fossa; **I**, olfactory nerve foramen; **II**, optic nerve foramen; **III**, oculomotor nerve foramen, **IV**, trochlear nerve foramen; **V**, trigeminal nerve foramen; **VI**, abducens nerve foramen; **VII$_H$**, hyomandibular branch of the facial nerve foramen; **VII$_P$**, palatine branch of the facial nerve foramen.

and reconstruction scale of 900. A ring-free correction filter was later applied to each slice, to reduce ring artifact.

To facilitate segmentation of the endocast as a subset of the total volume, the dataset was digitally re-sliced into 277 coronal slices extending from the tip of the frontals to the back end of the skull (with the same slice thickness and spacing as the original dataset) in Scion Image Beta 4.0.2 (Scion Corp., Frederick, Maryland). The slices were processed for viewing in Adobe Photoshop 6.0 (Adobe Systems, Inc., San Jose, California). Construction of the endocast was done manually, by outlining the endocranial cavity and nerve passageways in each slice, then assigning all contained pixels a unique color value (Franzosa, 2001). The endocranial volume thus labeled in the dataset was volume-rendered and isosurfaced using an in-house isosurfacing program to generate a digital endocast whose surfaces and volume could be measured.

DESCRIPTION

For the following description of the endocast, the terminology is predominately that of *Nomina Anatomica Avium* (Baumel et al., 1993). We acknowledge that the terms used to describe the

TABLE 1.   Ancillary web resources available at: www.DigiMorph.org/specimens/acrocanthosaurus_atokensis/

Web resources available
Transverse slice movie
Sagittal slice movie
Horizontal slice movie
Transverse volumetric rendering of braincase
Sagittal volumetric rendering of braincase
Horizontal volumetric rendering of braincase
3-D model of endocast
Inspector applet
Cutaway movies of braincase

endocast are terms meant for the actual brains, in keeping with tradition (e.g. Jerison, 1973; Hopson, 1979). Although we realize that an endocast does not completely and faithfully reproduce the brain, the use of brain terms to describe the endocast discourages the creation of new terms for endocast features that can be described more easily by the terms that were created for the feature on an actual brain.

The endocast of *Acrocanthosaurus atokensis* measures 14.88 cm from the front of the olfactory bulbs to the foramen magnum, and has a volume of 190.8 cm^3 (Fig. 2). The rostralmost portion of the endocast represents the olfactory bulbs and tracts (CN I). The olfactory bulbs are swollen and distinctive, evidently filling the rostral endocranial fossa (ethmoid fossa), which is enclosed dorsally by the frontals, and ventrally and laterally by the mesethmoid, which also supplies a median septum separating the two bulbs. This cavity lacks a rostral wall, and the endocast is therefore constrained rostrally by the rostral extent of the portion of the mesethmoid that forms the ventrolateral limit of the olfactory bulb and tract. As delimited, the olfactory bulb and tract measure 6.6 cm long.

The olfactory tracts project toward the cerebral hemispheres as separate bilateral tracts that merge along the midline caudal to the median septum before joining the cerebral hemispheres. A comparable septum also occurs in *Carcharodontosaurus* and *Giganotosaurus* (Larsson, 2001; Coria and Currie, 2002). In *Allosaurus* and *Sinraptor*, there is no evidence that the olfactory tract was separated by the mesethmoid (Madsen, 1976; Currie and Zhao, 1993), but it is unclear whether this is an artifact of preservation. The tract meets the cerebral hemispheres in a transition involving the ventral and lateral expansion of the forebrain. The cerebral hemispheres reach their maximum width (4.35 cm) dorsal to the trigeminal (CN V) and facial (CN VII) nerves.

A longitudinal ridge on the endocast overlies the cerebral hemispheres and represents the sinus sagittalis dorsalis. The right and left optic nerves (CN II) project to the cerebral hemi-
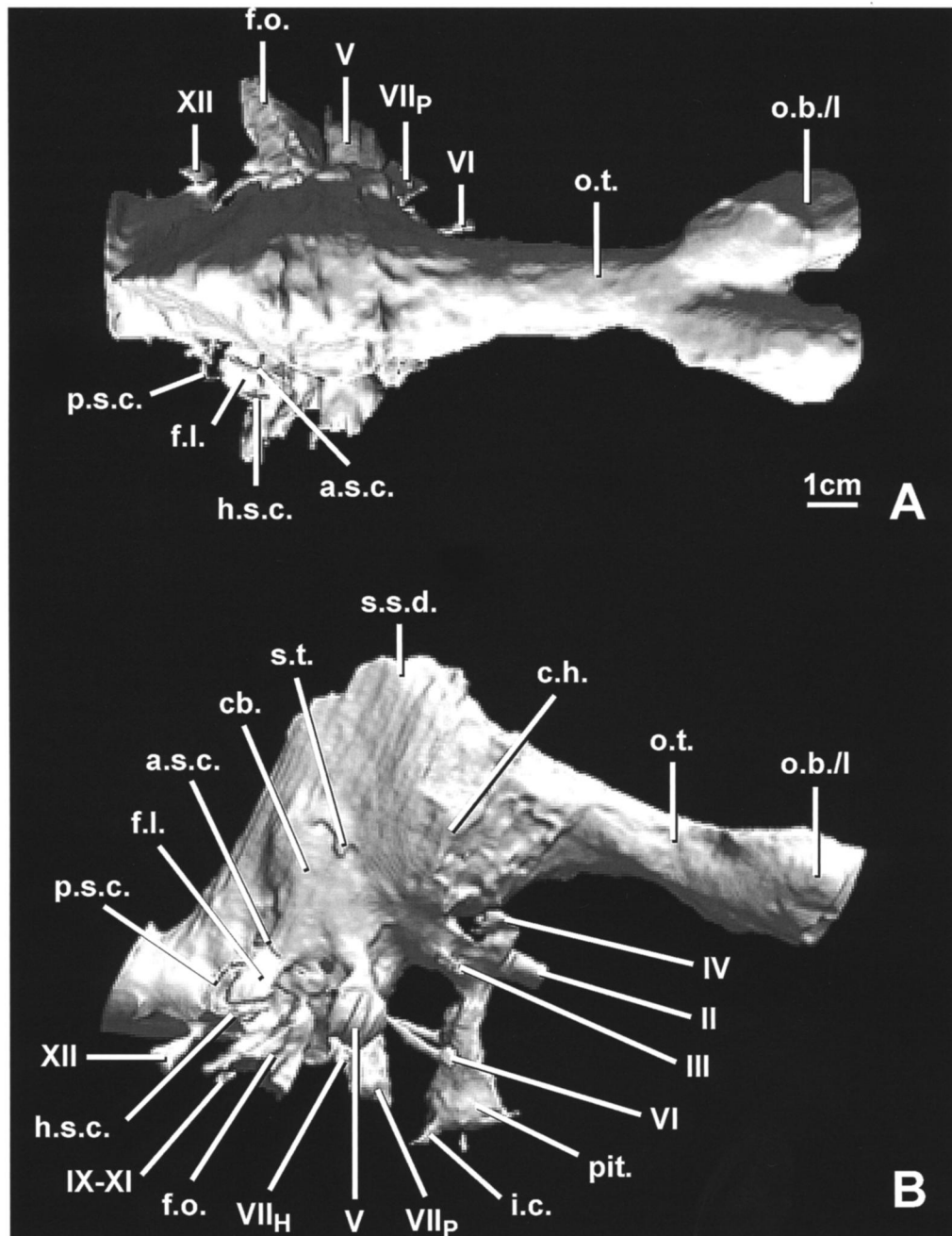
FIGURE 2. An isosurface rendering of the *Acrocanthosaurus atokensis* endocast in **A**, dorsal and, **B**, right lateral views. Discernible cranial nerves and other features are labeled. Rostral is to the right. **Abbreviations**: **a.s.c.**, anterior semicircular canal; **cb.**, cerebellum; **c.h.**, cerebral hemisphere; **f.l.**, floccular lobe; **f.o.**, cast of fenestra ovalis; **h.s.c.**, horizontal semicircular canal; **i.c.**, internal carotid artery; **o.b.**, olfactory bulb; **o.t.**, olfactory tract; **pit.**, pituitary; **p.s.c.**, posterior semicircular canal; **s.s.d.**, sinus sagittalis dorsalis; **s.t.**, sinus transversus; **I**, olfactory nerve; **II**, optic nerve; **III**, oculomotor nerve; **IV**, trochlear nerve; **V**, trigeminal nerve; **VI**, abducens nerve; **VII_H**, hyomandibular branch of the facial nerve; **VII_P**, palatine branch of the facial nerve; **IX**, glossopharyngeal nerve; **X**, vagus nerve; **XI**, accessory nerve; **XII**, hypoglossal nerve.

spheres, entering the braincase through a single median optic foramen formed by the orbitosphenoids. Although there is only a single opening, there is a portion of the orbitosphenoids that hangs down medially within the foramen. Whether or not this actually divided the two nerves and is broken cannot be determined. A single entrance is also present in *Allosaurus* and *Sinraptor*, whereas the optic nerves enter through separate foramina in *Carcharodontosaurus* and *Giganotosaurus* (Madsen, 1976; Currie and Zhao, 1993; Larsson, 2001; Coria and Currie, 2002). Madsen (1976) described *Allosaurus* as having a single optic fo-

ramen enclosed dorsally and ventrally by the orbitosphenoids. Hopson (1979), on the other hand, described a natural *Allosaurus* endocast as having stems of both optic nerves, suggesting that there were two optic foramina that presumably were separated by the orbitosphenoids.

Located caudal and dorsal to the optic nerve is a branch that is connected to the optic nerve. This may represent the trochlear nerve (CN IV), but this cannot be stated with certainty. Ventrolateral to this protrudes the stem of the oculomotor nerve (CN III). If the branch connected to the optic nerve actually trans-

mitted optic nerve fibers, then the trochlear nerve probably accompanied the oculomotor nerve in exiting the braincase. Comparable positioning and orientation of the oculomotor nerve occurs in *Carcharodontosaurus* and *Giganotosaurus* (Larsson, 2001; Coria and Currie, 2002). *Allosaurus* and *Sinraptor* both have separate exits for each of these nerves, but the trochlear nerve exits farther dorsally and rostrally, while the oculomotor nerve exit lies dorsolateral to the entrance for the optic nerves, rather than directly caudal to it.

Ventrally beneath the optic nerves, and between the oculomotor nerves, descends the pituitary. The pituitary fossa of the braincase is composed of the basisphenoid/parasphenoid complex. The rostral border of this fossa is not ossified, so the precise geometry of the pituitary cannot be accurately determined. Penetrating the ossified ventral portion of the fossa are the internal carotid arterial canals, which enter the pituitary from below and behind, most likely through the basisphenoid (the degree of fusion of the various bones makes the exact borders of each difficult to determine).

The abducens nerve (CN VI) projects through a canal in the basisphenoid that passes just lateral to the pituitary. In this respect, *Acrocanthosaurus* resembles coelurosaurian dinosaurs rather than *Allosaurus* and *Carcharodontosaurus* (Larsson, 2001), in which the abducens passes into the pituitary fossa (Currie, 1997). The abducens projects from the rostroventral surface of the endocast just medial and ventral to the exit for the trigeminal nerve.

As mentioned above, only one trigeminal root is present on each side of the endocast, indicating that the ophthalmic, maxillary, and mandibular branches did not separate until they were outside of the braincase (Fig. 3). This single branch for the trigeminal nerve is also seen in *Carcharodontosaurus* and *Giganotosaurus*, while *Allosaurus* has a separate projection representing the ophthalmic branch. In *Sinraptor* there is only one branch, but the foramen on the braincase is pinched in, indicating the beginnings of the separation of the ophthalmic foramen from that for the maxillary and mandibular branches (Currie and Zhao, 1993). The foramen for the trigeminal nerve in *Acrocanthosaurus* is bounded by the prootic.

The facial nerve projects just caudal and ventral to the trigeminal nerve. Unlike the trigeminal nerve, the facial nerve branches before exiting the braincase, the palatine branch extending forward, while the hyomandibular branch extends ventral to the trigeminal nerve (Fig. 3). While extending rostrally, the palatine branch passes through the prootic and basisphenoid, whereas the hyomandibular branch exits the facial foramen laterally through the prootic. *Acrocanthosaurus* is the only taxon among those examined to exhibit this branching of the facial nerve inside the braincase.

Just caudal to the facial nerve is the fenestra ovalis, which is enclosed by the prootic, and possibly portions of the opisthotic and epiotic, but it is difficult to be certain. Owing to fracturing in this region, the exact path of the vestibular and cochlear branches of the vestibulocochlear nerve cannot be established on either side of the braincase, and the exact size, shape, and extent of the inner ear are indeterminate.

Caudal and dorsal to this area is the flocculus. It extends caudoventrolaterally from the endocast, filling a space bounded by the semicircular canals. The orientation is the same as that seen in both *Carcharodontosaurus* and *Allosaurus*. In all three of these taxa, the floccular lobes extend perpendicular to the anterior semicircular canal and end near the posterior corner of the horizontal semicircular canal and the ventral edge of the posterior semicircular canal. Although preserved on both sides of the endocast, the floccular lobe and semicircular canals are more complete on the right side.

On the ventrolateral surface of the endocast, directly behind the cast of the fenestra ovalis, are the roots for the vagus (CN X)
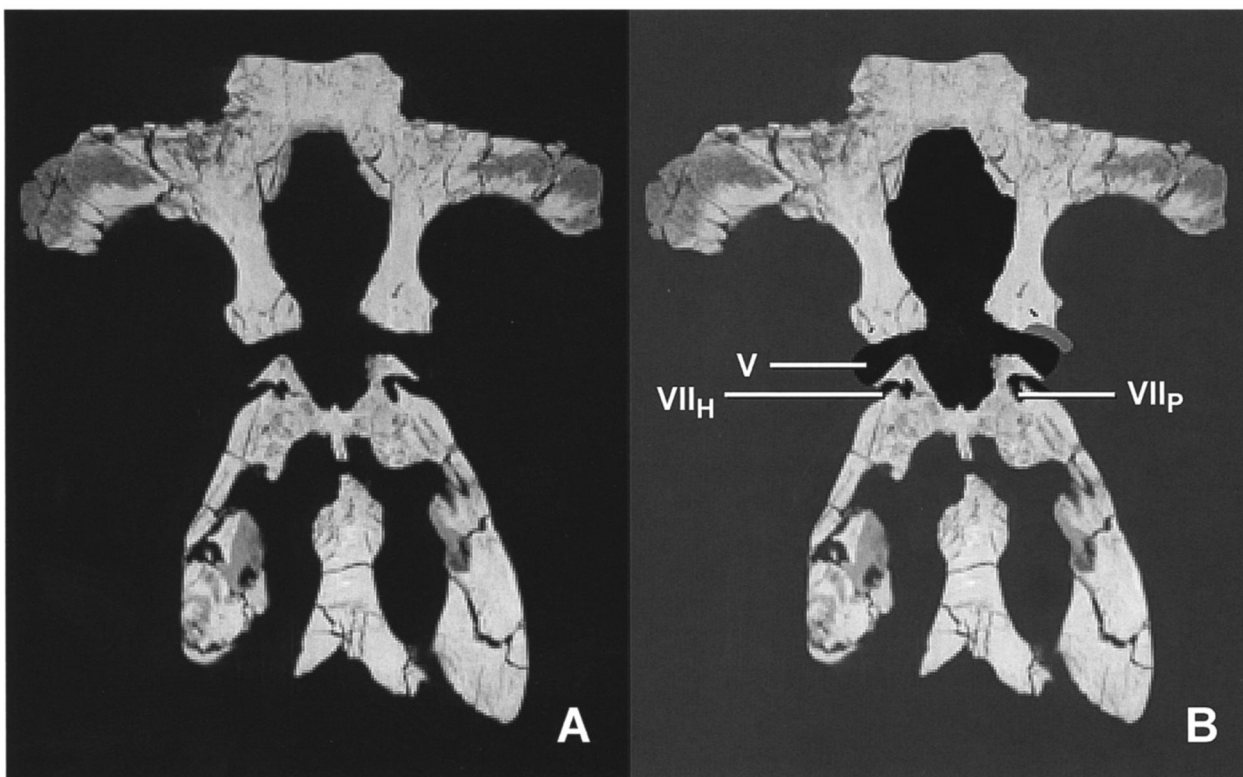

FIGURE 3. A transverse CT slice from the *Acrocanthosaurus atokensis* dataset. **A**, slice before any processing has been done; **B**, slice after endocranial space has been "filled-in" with black. **Abbreviations**: **V**, trigeminal nerve; **VII$_H$**, hyomandibular branch of the facial nerve; **VII$_P$**, palatine branch of the facial nerve.

and hypoglossal (CN XII) nerves. The foramina for each of these nerves are found in a deep pit in the exoccipitals of the braincase. On the left side of the braincase is a third foramen, not found on the right side, that is probably either a separate exit for the glossopharyngeal nerve (CN IX), or possibly for the external ophthalmic artery and vein. The accessory nerve (CN XI) is not distinct, and probably exited the braincase with the vagus nerve, as did the glossopharyngeal nerve, if not through the third foramen found on the left side of the braincase. Just caudal to these nerves is the foramen magnum, marking the end of the medulla oblongata, and of the endocast. The diameter of the foramen magnum is 35 mm transversely, and 27 mm vertically (Stovall and Langston, 1950).

There are several major features of the brain that cannot be discerned in the endocast, the most important of which are the optic lobes. Based on the shape of the endocast, the optic lobes in *Acrocanthosaurus* probably had not yet obtained the ventrolateral position seen in modern birds, and due to the venous sinuses in the braincase, the optic lobes did not leave any impressions on the inner walls. They were most likely positioned more dorsally and caudal to the cerebral hemispheres, more like what is seen in modern crocodilians. Also indiscernible in the endocast is the main body of the cerebellum. Some of the lateral margins can be seen, and the general position of the main body can be inferred based on the position of the floccular lobes, but, just as with the optic lobes, a large portion of it is covered with venous sinuses. While the venous sinuses and the internal carotid arteries are visible, the rest of the vasculature of the braincase is indiscernible.

ORIENTATION OF THE HEAD

The original scan of this specimen was such that the olfactory bulbs and tracts were in a horizontal position. While there is nothing wrong with this convention, it is not in keeping with the actual orientation of the head during the lifetime of the animal. With the anterior semicircular canals horizontal, rather than sloping dorsally, as they extend posteriorly, the other canals are similarly incorrectly oriented (Witmer et al., 2002, 2003). Rotating the rostral end of the endocast ventrally approximately 25 degrees (Fig. 2) places the semicircular canals in an orientation similar to that seen in *Carcharodontosaurus* and *Allosaurus*. The physical appearance of the canals is also similar in all three taxa. The anterior semicircular canal extends posterodorsally, lateral to the floccular lobe. The anterior edge of the posterior semicircular canal begins near the posterior edge of the anterior semicircular canal, and extends posteroventrally. The horizontal semicircular canal begins ventral to the anterior edge of the anterior semicircular canal, and extends posteriorly just ventral to the floccular lobe. After extending past the posterior edge of the floccular lobe, the horizontal semicircular canal meets the posterior semicircular canal, forming one continuous canal in the endocast, although the two canals were probably not continuous like this in life. This orientation gives the same subtriangular shape of the semicircular canals described for *Carcharodontosaurus* and *Allosaurus*.

DISCUSSION

Having an endocast of *Acrocanthosaurus* allows several questions to be addressed and answered. First, the braincase and endocast can give us characters that can be used to help corroborate or discredit ideas about the relationship of *Acrocanthosaurus* to other taxa. As was mentioned above, *Acrocanthosaurus* has been placed as the sister group to *Carcharodontosaurus saharicus* by Sereno et al. (1996), forming the monophyletic clade Carcharodontosauridae, with *Giganotosaurus*. Characters such as the division of the olfactory bulbs and tracts by a mesethmoid, which occurs in *Acrocanthosaurus*. *Carcharodontosaurs*, and *Gi-*

ganotosaurus, but not in *Allosaurus* or *Sinraptor*, help to strengthen the postulated relationships. Several other examples such as this can be found throughout the description above.

Second, the external shape of the endocast can tell us several things. The brain is only slightly sigmoidal, with very little expansion of the cerebral hemispheres, and the optic lobes are still in a dorsomedial position. This general shape more closely resembles what is seen in crocodiles than birds, and this same general appearance is seen in most early theropods (pers. obs.). This is important because even though *Acrocanthosaurus* was a theropod, its brain still retains a condition that is more similar to that of ancestral archosaurs than that of modern theropods (birds). The endocast, by preserving the semicircular canals, shows the proper orientation of the head. Most previous studies of theropods treat the orientation of the head as if the frontals were habitually held horizontally. Recent analyses of pterosaur endocasts (Witmer et al., 2002, 2003) have re-emphasized that the horizontal semicircular canal is a more accurate indicator of habitual head orientation, and that it doesn't always afford the same perspective as the frontals. In *Acrocanthosaurus*, the horizontal semicircular canal is in a horizontal position when the rostral portion of the skull is rotated ventrally approximately 25 degrees (Franzosa, 2004). This rotation suggests that rather than habitually looking straight ahead, the correct orientation of the skull would have the animal habitually looking somewhat down in front of itself.

Lastly, having endocasts allows quantitative comparisons to be made between different theropods. As was mentioned previously, along with *Acrocanthosaurus*, digital endocasts have been created for *Tyrannosaurus* (Brochu, 2000), *Carcharodontosaurus* (Larsson et al., 2000; Larsson, 2001), and also *Ceratosaurus* and *Allosaurus* for my dissertation (Franzosa, 2004). The datasets can be used as a source of characters, as was mentioned before, and these can be used not only for total-theropod-tree phylogenetic analyses, but can also be used in smaller analyses, such as that performed by Larsson et al. (2001). Such analyses are the basis of manuscripts currently in preparation. As more endocasts become available, these analyses will become more meaningful as the represented taxa increase in number. It will also allow some of the gaps that are currently seen in the evolution of the theropod brain to be filled.

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