

THE BRAINCASE OF *GIGANOTOSAURUS CAROLINII* (DINOSAURIA: THEROPODA) FROM THE UPPER CRETACEOUS OF ARGENTINA

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ABSTRACT—*Giganotosaurus carolinii* is one of the largest known theropod dinosaurs. Its remains include a well-preserved braincase that displays a suite of derived characters unique to the animal, and others that help establish its relationships amongst the Theropoda. These include the development of a broad frontoparietal skull table that forms a shelf overhanging the supratemporal fenestra, the reorientation of the metotic fissure and fenestra ovalis onto the occiput, the ventral extension of the supraoccipital on either side of the foramen magnum, a broad but low occipital condyle, and pneumatization of the basioccipital. Some characters suggest affinities with South American abelisaurids, but many support a sister grouping of *Giganotosaurus* and *Carcharodontosaurus* within a larger group that includes the Asian sinraptorids. The close affinities of *Giganotosaurus* with the northern African *Carcharodontosaurus* support the hypothesis of intercontinental connections until mid-Cretaceous times.

INTRODUCTION

In 1993, a remarkable specimen was discovered in the province of Neuquén in Patagonia. The fossil represents one of the largest carnivorous dinosaurs ever reported. *Giganotosaurus carolinii* (Coria and Salgado, 1995) had an estimated maxillary tooth row length of 92 cm, a 44 cm long quadrate, an estimated skull length of 1.6 m, a 143 cm long femur, a 112 cm long tibia, and a minimum estimated total length of 12 meters. The postcranium was slightly disarticulated, and the skull was scattered over an area of approximately ten square meters. The braincase, found lying on its ventral surface, is well-preserved and includes all of the elements that surrounded the brain, although the distal extremities of the parasphenoid-basisphenoid, paroccipital processes, and basioccipital had been destroyed before the specimen was discovered.

Braincases are useful for understanding taxonomic relationships because they tend to be more conservative than those parts of the skeleton associated more directly with feeding, locomotion or other highly adaptive functions (Bakker et al., 1988). Furthermore, study of the anatomy of brains and braincases can provide information on the sensory adaptations and neurological complexity of animals. This, in turn, can provide indirect clues about lifestyles, ecological niches or behavioral evolution.

The original description of *Giganotosaurus* (Coria and Salgado, 1995) included a short list of diagnostic features, none of which were based on braincase characters. In this paper, we present a description of the braincase of *Giganotosaurus carolinii*, including a suite of autapomorphic characters for the taxon. The phylogenetic relationships of this South American theropod are assessed on the basis of comparisons with the main groups of theropods in which braincase anatomy is known.

Abbreviations—**IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; **MACN**, Museo Argentino de Ciencias Naturales, Buenos Aires; **MPCA**, Museo Provincial “Carlos Ameghino,” Cipolletti, Río Negro; **MUCPv-CH**, Museo de la Universidad Nacional del Comahue, El Chocón collection, Neuquén; **OMNH**, Oklahoma Museum of Natural History, Norman; **RSM**, Royal Saskatchewan Museum, Regina; **SGM**, The Ministère de l’Energie et des Mines, Rabat, Morocco; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842

THEROPODA Marsh, 1881

CARCHARODONTOSAURIDAE Stromer, 1931

Diagnostic Braincase Characters of Carcharodontosaurids: (1) supratemporal fossa restricted by overhanging frontoparietal shelf and does not extend onto posterodorsal surface of frontal; (2) opening for fifth cranial nerve is behind nuchal crest; (3) large open area ventromedial to paroccipital process that exposes middle ear region from behind; (4) interorbital septum between sphenethmoid and cultriform process ossified; (5) absence of median ridge between exits of sixth cranial nerves; (6) neck of occipital condyle invaded by ventrolateral pair of pneumatic cavities that join medially inside condylar neck.

GIGANOTOSAURUS CAROLINII Coria and Salgado, 1995

Diagnostic Braincase Characters of *Giganotosaurus carolinii*: (1) dorsal expansion of supraoccipital almost three times width of foramen magnum; (2) supraoccipital with superficial, ventral extensions on either side of foramen magnum contacting dorsal surface of occipital condyle; (3) occipital condyle much broader than high; (4) ventral articular surface of condyle extends anteriorly on both sides of ventral midline depression.

Type Specimen—MUCPv-CH-1

Distribution—Candeleros Formation, Río Limay Subgroup (Albian-Cenomanian), of the Neuquén Group. Fifteen km south of Villa El Chocón, Neuquén Province, Argentina.

Description—The braincase of *Giganotosaurus* is represented in the holotype by frontals, parietals, supraoccipital–epiotic, the bases of the exoccipital–opisthotics, most of the basioccipital, the more proximal parts of the basisphenoid–parasphenoid, the orbitosphenoids, and the sphenethmoid. Fusion has obliterated most of the sutures (Fig. 1), which suggests that the holotype represents a mature individual.

The frontal of *Giganotosaurus* is relatively short (about 200 mm as preserved, less than 15% of the estimated skull length), but broad (the fused frontals are 244 mm across between the back of the prefrontal sutures, and 211 mm between the supra-orbital notches that pass between frontals, prefrontals and post-orbitals). The paired, diverging nasal processes represent, as restored, almost a third of the frontal length. The preserved

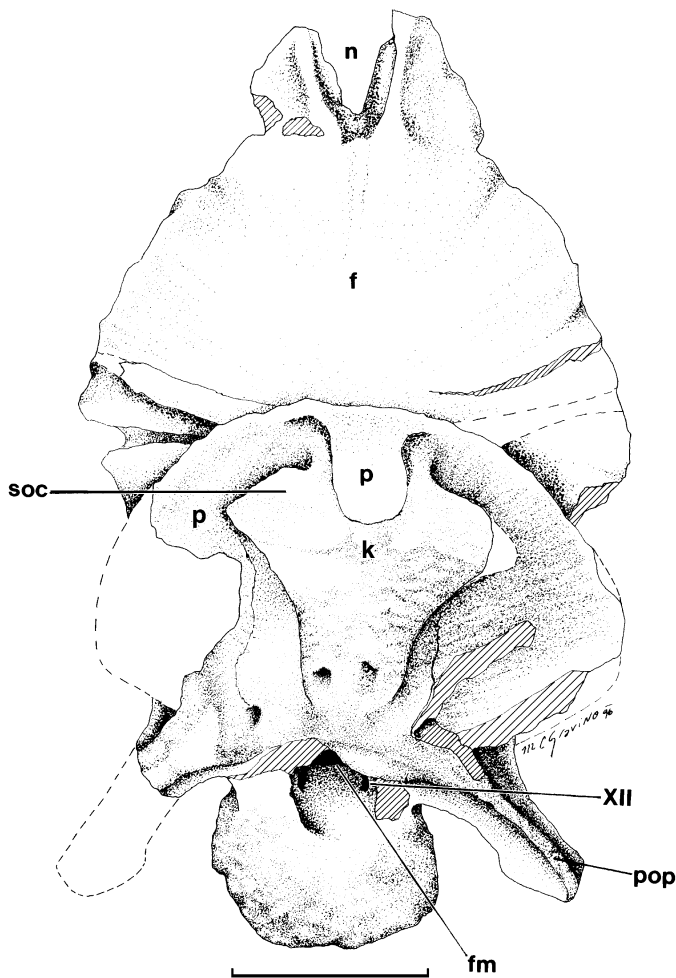


FIGURE 1. *Giganotosaurus carolinii* (MUCPv-CH-1) in dorsal view. Scale equals 10 cm. **Abbreviations:** f, frontal; fm, foramen magnum; k, supraoccipital knob; n, nasal suture of frontal; p, parietal; pop, paroccipital process; soc, supraoccipital; XII, foramen for cranial nerve XII.

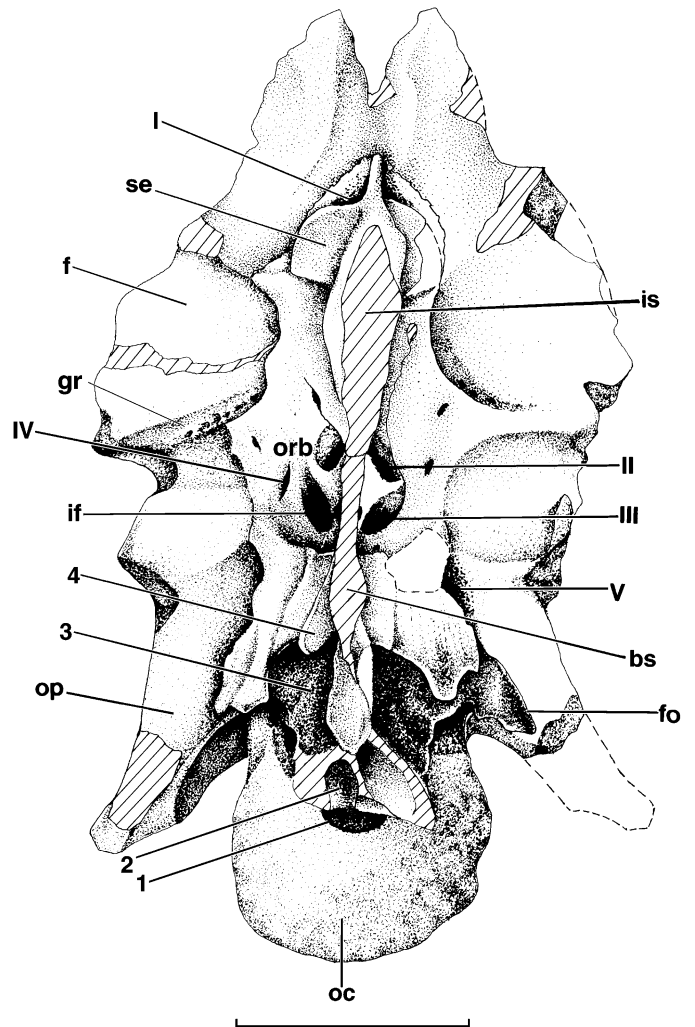


FIGURE 2. *Giganotosaurus carolinii* (MUCPv-CH-1) in ventral view. Scale equals 10 cm. **Abbreviations:** bs, basisphenoid–parasphenoid complex; f, frontal; fo, fenestra ovalis; gr, groove; if, infundibular foramen; is, interorbital septum; oc, occipital condyle; op, opisthotic; orb, region of the orbitosphenoid; se, sphenethmoid; 1, pneumatic recess; 2, basicranial fontanelle; 3, pneumatic recess plus openings for internal carotid; 4, preotic pendant; I, II, III, IV, V, exits for cranial nerves.

portion of each process has a well developed, raised ridge medially to strengthen the contact with the nasal. A similarly deepened surface is present in tyrannosaurids (TMP 81.10.1). The frontal of *Giganotosaurus* is thick, 31.5 mm anterior to the sphenethmoid (Fig. 2), but to a less degree than in tyrannosaurids. For example, the frontals of one specimen of *Tyrannosaurus rex* (RSM P283.2/5941), an individual that is somewhat smaller, are 65 mm thick in the same region. The fused interfrontal suture of *Giganotosaurus* is barely discernible anteriorly, which is comparable with the condition in *Carcharodontosaurus* (Stromer, 1931; Larsson, pers. comm., 1997, SGM-Din 1). Furthermore, the frontoparietal suture has been mostly obliterated by fusion, as in *Abelisaurus* (Bonaparte and Novas, 1985, MPCA 11098), possibly *Acrocanthosaurus* (OMNH 10146), *Carcharodontosaurus* (Stromer, 1931, Larsson, pers. comm., 1997, SGM-Din 1), *Carnotaurus* (Bonaparte, 1991, MACN-CH 894), and *Sinraptor hepingensis* (Gao, 1992; Currie and Zhao, 1993a). A remnant of the suture within the supratemporal fenestra is marked by an undulating, nearly ver-

tical ridge as in *Sinraptor* (Currie and Zhao, 1993a). Although the suture cannot be made out clearly on the skull roof, superficially broken bone may represent the anterior extent of the parietal, suggesting that the frontoparietal suture has the same position as in allosaurids and sinraptorids.

The dorsal surface of the paired frontals is broad and flattened. The lateral margins of the dorsal surface are somewhat raised laterally, especially at the margin of the dorsoventrally deep (67.5 mm) prefrontal suture. Similar ridges can be seen in allosaurids and tyrannosaurids, but they are never so prominent. In contrast, abelisaurids are highly variable in this region of the skull. The frontal of *Abelisaurus* is not appreciably thickened along this suture, whereas in *Carnotaurus* (MACN-CH 894), it slopes upward to the orbital 'horn'. Unlike the highly sculptured surfaces of the frontals of *Abelisaurus* (MPCA 11098) and *Majungatholus* (Sampson et al., 1998), those of *Giganotosaurus* are smooth as in *Carcharodontosaurus* (Stromer, 1931; Sereno et al., 1996), allosaurids and sinraptorids. Like all large theropods, there is a smooth-walled supraorbital notch that

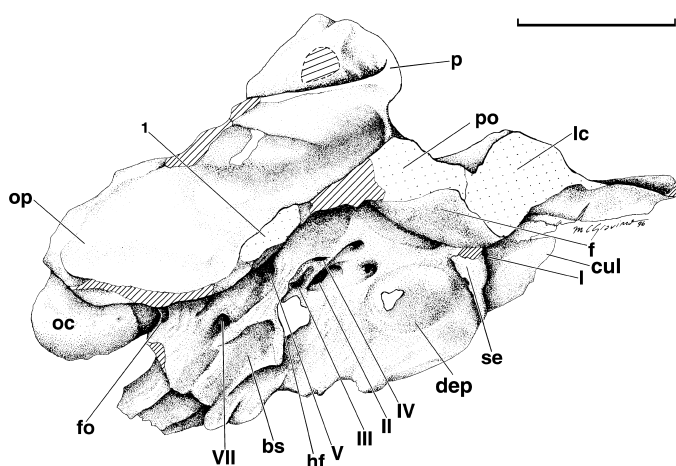


FIGURE 3. *Giganotosaurus carolinii* (MUCPv-CH-1) braincase in right lateral aspect. Scale equals 10 cm. **Abbreviations:** bs, basisphenoid–parasphenoid complex; cul, cultriform process; dep, depression; f, frontal; fo, fenestra ovalis; hf, hypophyseal fossa; lc, lacrima and prefrontal sutures of frontal; oc, occipital condyle; op, opisthotic; p, parietal; po, postorbital suture of frontal; se, sphenethmoid; I, posteroventrally directed ridge of laterosphenoid forming lower margin of channel for adductor musculature; II, III, IV, V, VI, VII, exits for cranial nerves.

separates the postorbital suture from that of the prefrontal. In relation to the size of the skull, the notch is almost inconspicuous in *Giganotosaurus*. Lateral to the notch, the lacrimal and postorbital contacted each other to exclude the frontal from the orbital margin. There is a long, relatively low (40 mm) suture for the postorbital that curves posteroventrally (Fig. 3). In dorsal aspect, there is no sign of the depression that extends anteriorly from the supratemporal fenestra for the jaw musculature of most theropods. Therefore the muscle insertions were positioned more posteriorly in *Giganotosaurus*, and no longer attached to the superficial skull roof. Intermediate conditions can be seen in *Acrocanthosaurus*, *Carnotaurus* and *Sinraptor*, where the supratemporal fossa is bounded anteromedially by an overlapping shelf of bone. In *Giganotosaurus*, the shelf has become more prominent, and has shifted anteriorly so that the frontal portion of the supratemporal fossa is almost vertical and not visible in dorsal view.

The ventral surface of the frontal is largely obscured by the laterosphenoid, orbitosphenoid and sphenethmoid (Fig. 2). There is no indication of a separate septosphenoidal ossification. A groove extends lateroposteriorly from a foramen (Fig. 2) that passed through the frontal-sphenethmoid suture into the olfactory tract, as in *Sinraptor* (IVPP 10600) and *Carcharodontosaurus* (Larsson, pers. comm., 1997, SGM-Din 1), but not tyrannosaurids. In both *Sinraptor* and *Carcharodontosaurus*, these grooves have well-marked edges that parallel the frontal-laterosphenoid suture. The groove is less conspicuous in *Giganotosaurus* where the two bones are completely fused.

Anteriorly, the parietal has a laterally projecting postorbital process as in all theropods. Although the suture is difficult to discern because of fusion, the distal end can be seen where it overlapped the frontal-laterosphenoid suture to contact the postorbital.

There is no sagittal crest such as those found in troodontids, tyrannosaurids and other coelurosaurians. Similar to *Carcharodontosaurus* (Stromer, 1931; Sereno et al., 1996), the midline of the parietal of *Giganotosaurus* is a broad, flat shelf of bone measuring 94.5 mm across (Fig. 4). The parietal extends laterally to overhang the medial part of the upper temporal open-

ing in a parietal shelf (Fig. 4) that is continuous with a ridge on the frontal. The supratemporal fenestra is anteroposteriorly remarkably short (about 40 mm) as in *Abelisaurus* (MPCA 11098), *Carcharodontosaurus* (Stromer, 1931; Sereno et al., 1996), and *Carnotaurus* (MACN-CH 894), but it clearly extended far laterally and somewhat posterolaterally. The medial margin of the supratemporal fossa is parallel with the dorsal longitudinal midline. Plesiomorphically, the parietals have a flattened, triangular surface in dorsal view between the supratemporal fenestrae, with the sharply defined edges converging posteriorly towards the midline. This condition is present in *Abelisaurus* (MPCA 11098), *Carnotaurus* (MACN-CH 894), *Ceratosaurs* (Gilmore, 1920), *Herrerasaurus* (Sereno and Novas, 1993) and *Monolophosaurus* (Zhao and Currie, 1993). In contrast, *Acrocanthosaurus* (Stovall and Langston, 1950), *Allosaurus* (Madsen, 1976) and *Sinraptor* (Currie and Zhao, 1993a) are more derived in this region in that the medial margins of the supratemporal fenestra are almost parallel, and are separated by more extensive, dorsally exposed parietal surfaces. The dorsal, intertemporal exposure of the parietal also seems to have been increased in *Piveteausaurus*, a poorly known theropod from the Jurassic of France (Taquet and Welles, 1977). This trend was carried to an extreme in *Giganotosaurus* and *Carcharodontosaurus* (Stromer, 1931: pl. I, fig. 4b; Sereno et al., 1996), both of which have widely separated supratemporal fenestrae. The parietals of troodontids and tyrannosaurids show yet another derived condition in which narrow, sharp-edged, raised sagittal crests extend anteriorly onto the frontals.

Behind the supratemporal fenestrae, broad, tall wings of the parietal are extensively exposed on the occiput above the paroccipital processes (Fig. 5). The nuchal crest, like those of *Acrocanthosaurus* (Stovall and Langston, 1950), *Allosaurus* (Madsen, 1976), *Carcharodontosaurus* (Stromer, 1931; Sereno et al., 1996), and *Sinraptor* (Currie and Zhao, 1993a), does not rise high and sharply from the dorsal surface of the intertemporal region, unlike *Carnotaurus* (MACN-CH 894), tyrannosaurids (Bakker et al., 1988) and troodontids (Currie, 1985). In

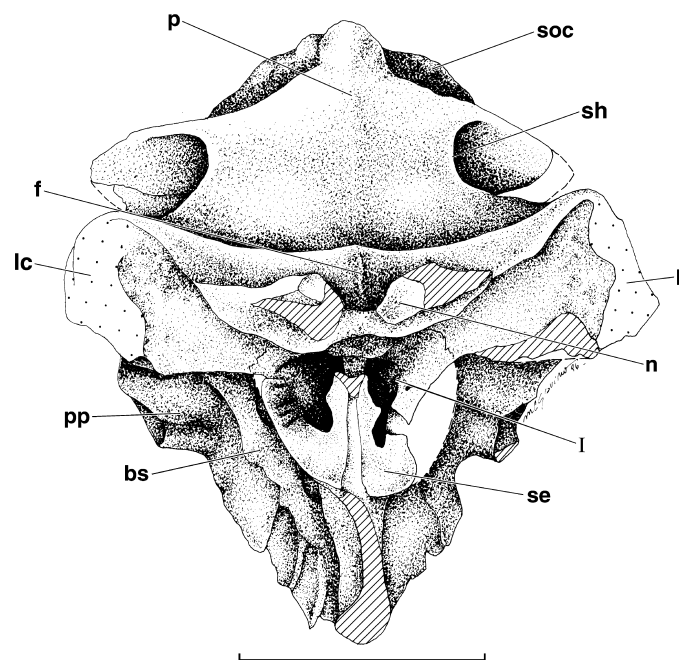


FIGURE 4. *Giganotosaurus carolinii* (MUCPv-CH-1) in anterior view. Scale equals 10 cm. **Abbreviations:** bs, basisphenoid; f, frontal; lc, lacrima and prefrontal sutures on frontal; n, nasal suture of frontal; p, parietal; pp, paroccipital process; se, sphenethmoid; sh, parietal shelf; soc, supraoccipital; I, foramen for cranial nerve I.

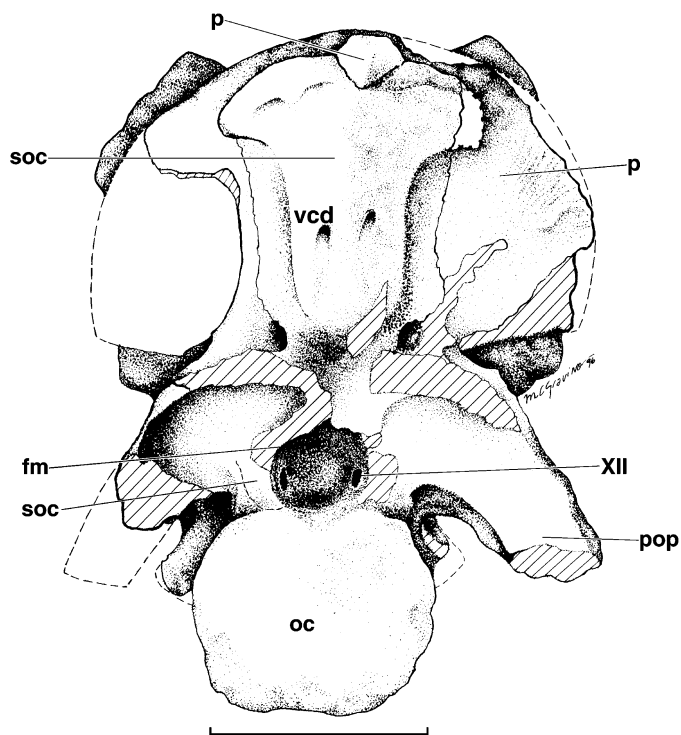


FIGURE 5. *Giganotosaurus carolinii* (MUCPv-CH-1) in posterior view. Scale equals 10 cm. **Abbreviations:** fm, foramen magnum; oc, occipital condyle; p, parietal; pop, paroccipital process; soc, supraoccipital; vcd, foramen vena capitis dorsalis; XII, foramen for cranial nerve XII.

most theropods, including *Acrocanthosaurus* (Stovall and Langston, 1950), *Allosaurus* (Madsen, 1976) and tyrannosaurids (Bakker et al., 1988), the dorsal surfaces of the frontal, the intertemporal region of the parietal and the supraoccipital are on a single plane. Troodontids (Currie, 1985) and tyrannosaurids have a nuchal crest formed by the parietal that rises high above this plane. In *Giganotosaurus*, *Carcharodontosaurus* and *Sinraptor*, however, there is an inflection at the frontoparietal suture, and the parietal angles upwards from the frontal plane. Although in lateral profile the nuchal crest appears to be high compared to the level of the frontal, this is only because the supraoccipital is also higher than the frontal plane. Overall, the skull roof is at an obtuse angle to the occiput (Fig. 6), whereas in most other theropods this angle is acute.

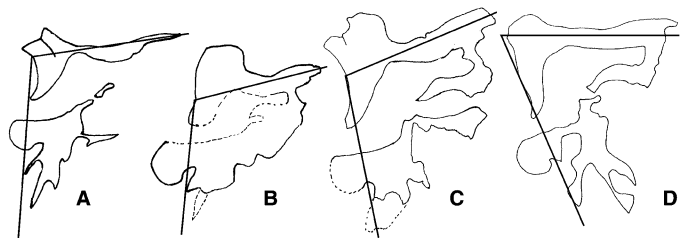


FIGURE 6. Longitudinal sagittal sections (taken from CT scans) of the braincases of *Sinraptor* (A, IVPP 10600), *Giganotosaurus* (B, MUCPv-CH-1), *Carcharodontosaurus* (C, SGM-Din 1), and *Acrocanthosaurus* (D, OMNH 10146). The one line is drawn through the frontal, whereas the other passes through the dorsal edge of the foramen magnum and the distal end of the basal tubera. Note that the angle between the skull roof and occiput is obtuse in each of the first three animals (A, B, C), whereas it is acute in most other theropods, including *Acrocanthosaurus* (D).

The parietal has a long, tongue-like process on the midline that overlaps the dorsal surface of the supraoccipital. Similar processes are known in *Abelisaurus* (MPCA 11098), *Carnotaurus* (MACN-CH 894), *Majungatholus* (Sampson et al., 1998) and *Sinraptor* (IVPP 10600). In *Giganotosaurus*, it extends 79 mm posteriorly from the front of the nuchal crest. The upper surface of this process is broadly convex. In contrast, the much shorter processes of *Allosaurus* (Madsen, 1976) and *Acrocanthosaurus* (OMNH 10146) are divided by tapering midline ridges. The parietal of *Giganotosaurus* would have had a long, posteroventrally oriented process along the dorsal margin of the paroccipital process.

Most of the occiput is preserved, and slopes strongly anterodorsally (Fig. 6B) above the foramen magnum, which is 38.5 mm wide and 41 mm high.

The lower margins of the paroccipital processes curve downwards as in *Sinraptor* (Currie and Zhao, 1993a), but not as sharply as in *Allosaurus* (Madsen, 1976). In dorsal view, the paroccipital processes are oriented posterolaterally (Fig. 1) at such a strong angle that the jaw articulations would have been far behind the occipital condyle if they had been preserved. This occurs to a more limited extent in *Carnotaurus*, possibly because of the abbreviated nature of the skull, and the jaw articulations are about 50 mm behind the condyle. The only theropods that compare in the posterolateral extension of the paroccipital processes are *Carcharodontosaurus* (Serenio et al., 1996) and *Sinraptor* (IVPP 10600).

The conspicuous midline ridge (Fig. 5) on the supraoccipital is constricted between the openings for the vena capitis dorsalis, but expands dorsally into a huge knob of bone 104 mm across and 62 mm long (anteroposteriorly). The width of the knob is 2.7 times that of the foramen magnum, and is 87% the width of the occipital condyle. This is similar in *Carcharodontosaurus*, in which the 73 mm wide dorsal expansion is not quite as well developed (Stromer, 1931). The parietal of *Giganotosaurus* protrudes only 25 mm above its suture with the top of the supraoccipital, which it caps with the tongue-like process (Fig. 5). Lateral to the midline ridge and above the exit for the vena capitis dorsalis, the supraoccipital is a thin plate of bone with a vertical lateral margin. Below the level of the foramen for the vena capitis dorsalis, there is a lateral process that extends along the dorsal border of each paroccipital process. The most remarkable feature of the supraoccipital is a ventral extension that covers the exoccipital lateral to the foramen magnum and contacts the dorsolateral surface of the occipital condyle. In most theropods, the supraoccipital only forms a small part of the dorsal margin of the foramen magnum in posterior view.

The oval, dorsoventrally low occipital condyle has a transverse diameter of 119 mm, and a vertical one of 82.5 mm. The condylar neck is 88 mm wide at its narrowest point. The condyle is oriented posteroventrally, parallel to the posterodorsal surface of the basioccipital region that extends into the basal tubera (Fig. 3). A faint suture shows that the dorsolateral region of the condyle was formed by the exoccipital, although its contribution seems to be relatively smaller than in most other theropods. This suture can be traced and confirmed in CT scan sections. The ventral surface of the condyle is excavated by a shallow, midline depression (Fig. 7), and in ventral aspect the articular surface of the condyle is C-shaped (Fig. 2).

The basioccipital would have formed the posterior regions of the basal tubera, although loss of this region obscures the precise relationship to the basisphenoid. The basal tubera were positioned below or posterior to the occipital condyle because there was a strongly acute angle between the occipital condyle and the lower part of the basioccipital as in *Sinraptor* (Currie and Zhao, 1993a) and *Carcharodontosaurus* (Fig. 6A–C). In contrast, these surfaces are almost perpendicular in abelisaurids (Bonaparte, 1991), *Acrocanthosaurus* (Fig. 6D), *Allosaurus*

(Madsen, 1976), *Dromaeosaurus* (Currie, 1995), *Herrerasaurus* (Sereno and Novas, 1993), *Piatnitzkysaurus* (Bonaparte, 1986) and *Troodon* (Currie, 1985), and the basal tubera are positioned below or anterior to the occipital condyle.

The neck of the occipital condyle is supported by two ridges that outline the ventral depression and converge at the base of the neck to form a median ridge on the posterior surface of the lower region of the basioccipital. The neck is also strengthened by a lateral ridge on either side of the lower surface, and by a dorsolateral ridge on the exoccipital. A concavity between these dorsolateral and ventrolateral ridges on each side of the condylar neck is pierced by two foramina for the XIIth cranial nerve (the more posterior one can be seen in Fig. 7). Furthermore, the concavity wraps around the posterior surface of the exoccipital and forms a deep pocket in the posteromedial surface of the paroccipital process. This whole region is adjacent to the posterior opening of the jugular foramen and fenestra ovalis, and probably held an air sac that was continuous with the middle ear air sac. The wide, well rounded medial ridge supporting the condyle from below is pierced on either side by a pneumatic opening (18 mm wide on the right side) that extends anteromedially (Fig. 7). CT scans suggest these passages met medially within the neck of the occipital condyle as in *Carcharodontosaurus* (Larsson, 1996). They are asymmetrical, and were almost certainly pneumatic in origin.

Less than half of each exoccipital-opisthotic complex is preserved, but they do not contact each other on the midline. Two branches of the XIIth nerve emerge from the lateral depression between the condyle and the paroccipital process. The ninth to eleventh cranial nerves and the jugular emerge from the metotic fissure behind the metotic strut (a plate of bone between the paroccipital process and the basal portion of the basioccipital sometimes referred to as the opisthotic buttress or crista tuberalis). Most of the metotic strut had been destroyed before the specimen was discovered, but the medial margin of a large opening is preserved posterior to the contact between the opisthotic and basisphenoid. This is where the metotic strut was either pierced by a fenestra or deeply invaded by an emargi-

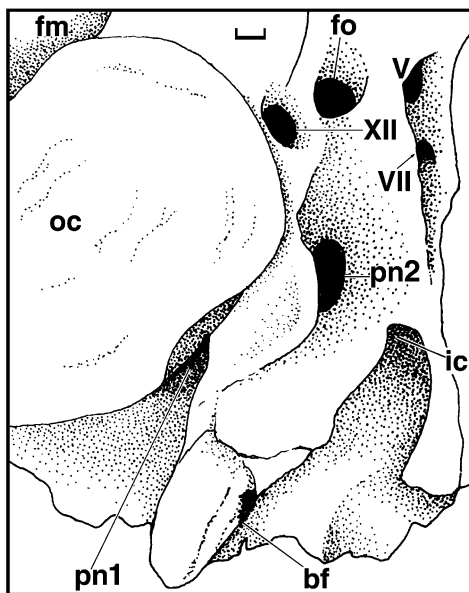


FIGURE 7. *Giganotosaurus carolinii* (MUCPv-CH-1), otic region, right side in posterior, lateral and ventral view. Scale equals 1 cm. **Abbreviations:** bf, basicranial fontanelle; fm, foramen magnum; fo, fenestra ovalis; ic, course of internal carotid; oc, occipital condyle; pn1, medial pneumatopore; pn2, common lateral pneumatopore; V, VII, XII, openings for cranial nerves.

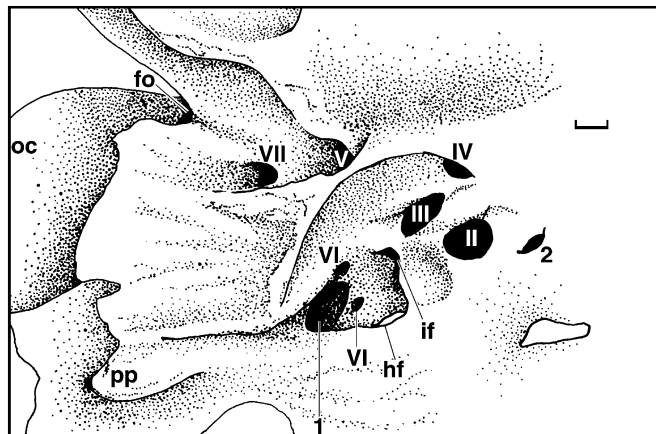


FIGURE 8. *Giganotosaurus carolinii* (MUCPv-CH-1), right hypophyseal fenestra and surrounding region viewed from lateral, ventral, and anterior perspective. Scale equals 1 cm. **Abbreviations:** oc, occipital condyle; fo, fenestra ovalis, hf, anteroventral corner of hypophyseal fenestra; if, infundibular foramen; pp, preotic pendant; 1, depression for pituitary; 2, foramen of unknown function; II, III, IV, V, VI, VII, openings for cranial nerves.

nation of the lower margin of the paroccipital process. The open area is positioned lateral and slightly dorsal to the metotic fissure, lateral to the occipital condyle beneath the paroccipital process. The stapes, which extended to the external auditory meatus posteroventral to the quadrate cotylus, would have been visible through this open area on its way posterolaterally as in *Carcharodontosaurus* (Larsson, pers. comm., 1997, SGM-Din 1). Some other theropods, such as *Acrocanthosaurus* (OMNH 10146) and *Chirostenotes* (Sues, 1997), are not as open but have a foramen or notch in this position.

The more ventral regions of the basisphenoid-parasphenoid complex were largely destroyed before the specimen was found. Still, it is clear that the anteroposteriorly short complex extended ventrally and posteriorly for a considerable distance. The preserved part of the cultriform process is thick (39.5 mm in transverse diameter) and solid.

The interorbital septum is ossified in *Giganotosaurus* between the cultriform process and the sphenethmoid, as in *Abelisaurus* (MPCA 11098) and *Carnotaurus* (MACN-CH 894). In the last genus, the fibrous bone texture of the surface is clearly distinguishable from the smoother surfaces of the sphenethmoid and cultriform process. There is a thin, plate-like interorbital septum below the sphenethmoid in *Ceratopsaurus* (Bakker, pers. comm., 1990), but it is separated from the cultriform process by a narrow cleft. In all other described theropods (including *Acrocanthosaurus*), there is a clear, usually wide, separation between the cultriform process and the sphenethmoid.

In *Giganotosaurus*, the dorsal part of the interorbital septum is transversely thick (39.5 mm). Anterior to the exit for the fourth cranial nerve on each side (Fig. 8), there is a deep depression (Fig. 3) that may mark the origin of ocular musculature.

The septum is pierced by a 35 mm high, 27.5 mm long hypophyseal fenestra (Figs. 3, 8). It can only be seen in theropods that ossify the interorbital septum, such as *Abelisaurus* (MPCA 11098) and *Carnotaurus* (MACN-CH 894).

The pituitary entered the hypophyseal fenestra through the midline infundibular foramen (diameter 10 mm) between the foramina for the third cranial nerves (Fig. 8). A 14 mm wide depression in the vertical, transverse plate at the back of the hypophyseal fenestra marks the position of the main part of the

pituitary (Fig. 8). Below that depression, there is a single opening for the common internal carotid.

The pair of exits for the sixth cranial nerves perforates the vertical, transverse plate dorsolateral to the pituitary depression near mid-height of the hypophyseal fenestra (Fig. 8). Each foramen has a diameter of 2.5 mm, and they are 17.5 mm apart. The flattened vertical, transverse plate of the basisphenoid at the back of the hypophyseal fenestra is unlike the equivalent regions in *Carnotaurus*, *Sinraptor*, troodontids and tyrannosaurids, all of which have prominent midline ridges. The structure of this region is very similar in *Carcharodontosaurus* (Larsson, pers. comm., 1997, SGM-Din 1).

Posteriorly, only the deepest regions of the basicranial fontanelle (=basisphenoidal sinus) have been preserved in MUCPv-CH-1 (Fig. 2). As in *Dromaeosaurus* (Currie, 1995), *Itemirus* (Kurzanov, 1976), *Piatmitzkysaurus* (PVL 4073) and most other theropods, the basicranial fontanelle divides into a pair of dorsolateral pits positioned immediately anterior to the basisphenoid-basioccipital suture. These blind pits are asymmetrical, and were undoubtedly pneumatic in origin.

Chure and Madsen (1998) have shown that the “crista prootica” is a lateral process of the basisphenoid in some, if not all, theropods. The term preotic pendant, proposed by Welles (pers. comm., 1996), is therefore used in this paper. The preotic pendant extended ventrally, medially and posteriorly below the main body of the prootic in *Giganotosaurus* (Fig. 8). This wing-like projection is not as prominent as the more vertical process of most theropods, including *Abelisaurus*, *Acrocanthosaurus*, *Allosaurus*, *Carnotaurus*, *Piatmitzkysaurus*, and tyrannosaurids. It is, however, as prominent as that of *Sinraptor*, and is more conspicuous than that of *Dromaeosaurus*.

Medial to each preotic pendant, a sinus extends anterodorsally (Fig. 2). The internal carotids passed through the sinuses to meet within the basisphenoid before exiting through the common, midline opening in the posteroventral region of the hypophyseal fenestra as in *Sinraptor* (IVPP 10600).

The prootic presumably forms most of the margin of the single opening for all branches of the fifth cranial nerve. The seventh cranial nerve is found posteroventral to the fifth (Fig. 8). The prootic also would have formed the anterior and dorsal margins of the fenestra ovalis (Figs. 7, 8).

The laterosphenoid probably forms the anterior margin of the opening for the trigeminal nerve. A depression in this margin marks the passage of the ophthalmic branch of the trigeminal, which did not have a separate opening from that of the main body of fifth cranial nerve the way it does in *Troodon*, tyrannosaurids and other Cretaceous theropods (Currie and Zhao, 1993b). As in other theropods, the laterosphenoid has an elongate suture with the parietal, and a long postorbital process. Posteroventral to this process, there is a pronounced ridge that formed the anteroventral wall of the chamber for the adductor musculature (Fig. 3). Although this ridge is present in *Sinraptor* and other theropods, the only other theropod that has developed such a pronounced, wall-like ridge is *Carcharodontosaurus* (Larsson, pers. comm., 1997, SGM-Din 1).

The orbitosphenoids of *Giganotosaurus* seem to have been well developed. Presumably the position of the fourth cranial nerve marks the contact between the orbitosphenoid and laterosphenoid. Based on topographic features, the orbitosphenoids extended 80 mm anteroposteriorly, and contacted laterosphenoids, frontals, sphenethmoids and the cultriform process.

The sphenethmoid of *Giganotosaurus* is well ossified, as it is in *Abelisaurus*, *Acrocanthosaurus* (Stovall and Langston, 1950), *Carcharodontosaurus* (Serenio et al., 1996), *Ceratosaurus* (Bakker, pers. comm., 1992) and *Tyrannosaurus* (Osborn, 1912). Although the ossification of this bone is largely related to maturity, it has never been reported in *Albertosaurus*, *Allosaurus*, *Sinraptor*, and many other large theropods. This sug-

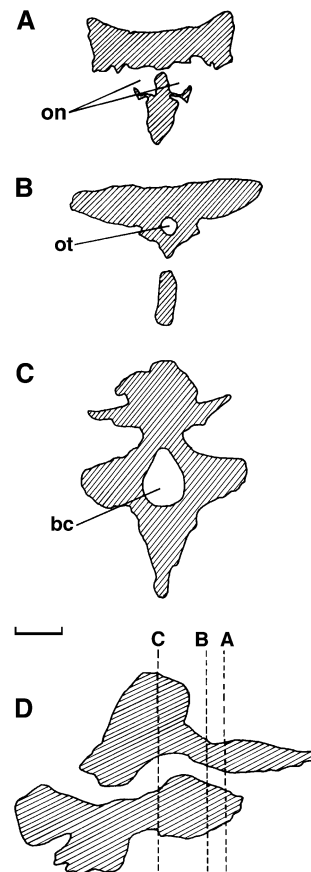


FIGURE 9. *Giganotosaurus carolinii* (MUCPv-CH-1), CT scans through braincase. **A**, Cross section at the front of the braincase showing the position of olfactory nerves. **B**, Cross section somewhat behind section A, indicating the location of the olfactory tract. **C**, Cross-section at the level of the maximum width of the brain. **D**, Longitudinal section of the braincase, showing the longitudinal profile of the endocranium and the levels where the cross-sections were made. Scale equals 5 cm. **Abbreviations:** bc, brain cavity; on, olfactory nerves; ot, olfactory tract.

gests that the ossification of this unit may have some taxonomic use. However, the pattern cannot be discerned until a much larger suite of identified braincases of known ontogeny have been studied.

The sphenethmoid forms a pair of tubes that encases the olfactory tracts. It is about 100 mm long, 70 mm deep and 90 mm wide. At its narrowest point, it is 65 mm across. The median septum that separated the right and left olfactory tracts extends 63.5 mm more anteriorly than the lateral walls. The right olfactory opening is 36.5 mm high, and has a mid-height width of 22 mm. In general appearance, the sphenethmoid is similar to those of the few other theropods that have this ossification.

The matrix inside the braincase has not been removed. However, CT scans reveal a number of characteristics. The brain cavity (Fig. 9) is relatively long (275 mm from the front of the sphenethmoid to the top of the foramen magnum) but narrow (greatest width is 77 mm), and has an estimated volume of 275 cc. Assuming that the brain had a specific gravity of 0.9, it would have weighed about 248 g. The body weight of *Giganotosaurus* is estimated to be 4.16 tonnes (using a femur shaft circumference of 520 mm in the method developed by Anderson et al., 1985), which gives an encephalization quotient of 1.9 (Hopson, 1980).

Cranial Nerves—The relatively long olfactory tracts in *Gi-*

giganotosaurus compare well with *Carcharodontosaurus* (Stromer, 1931; Larsson, 2001). The optic nerves exited the braincase through separate foramina anterior to the pituitary. The paired openings for the second and third cranial nerves have maximum diameters of 17.5 and 18.0 mm respectively. The third nerve emerges from the braincase level with the second (Fig. 8), and the two openings are very close together as in *Abelisaurus* (MPCA 11098), *Carcharodontosaurus* (Larsson, pers. comm., 1997, SGM-Din 1) and *Carnotaurus* (MACN-CH 894). The second and third cranial nerve foramina are separated by an 8 mm thick bar of bone. The third cranial nerves are more widely spaced than the optic nerves, and are separated by about 20 mm. The fourth cranial nerve passed through a much smaller foramen (diameter of about 2 mm) dorsal, anterior and lateral to the third. The openings for the fourth cranial nerves are 74 mm apart. All branches of the fifth nerve exited the braincase through a single opening, but the ophthalmic branch turned forward in a canal on the outer surface of the laterosphenoid. In contrast, this branch had a separate opening in allosaurids, troodontids and tyrannosaurids (Hopson, 1979; Currie, 1985). The abducens (sixth cranial) nerve passed down and forward from the floor of the braincase anteromedial to the trigeminal opening, and emerged lateral to the pituitary as in all theropods (Currie, 1985, 1995). The foramen for the seventh cranial nerve exits the braincase ventral to a straight line drawn through the openings for cranial nerves I, II, III, V and X (Fig. 3). The foramen for the tenth cranial nerve opens onto the occiput, where it is separated from the more lateral fenestra ovalis by a thin bar of bone. The ninth and eleventh cranial nerves probably left the braincase through the same foramen. Dorsal and slightly posterior to this opening is the exit for the one or more branches of the twelfth cranial nerve (Fig. 7).

Phylogenetic Implications

Currie and Carpenter (2000) recently undertook a phylogenetic analysis of *Acrocanthosaurus* to determine its relationships with other theropods. Adding braincase characters to their analysis produced the same results except that *Sinraptor* resolved as a sister taxon of carcharodontosaurids rather than being part of a polytomy with this family and allosaurids. In the revised analysis (Fig. 10A), 110 parsimony informative characters were used, which produced a single tree of length 221 (consistency index is 0.67, retention index is 0.64).

A data matrix of 15 braincase characters (Appendix I) was produced in order to see how it compares with the more extensive phylogenetic analysis. The braincase of *Giganotosaurus* displays specialized features that distinguish it from every other theropod, but these autapomorphic characters were not scored. As in the Currie and Carpenter (2000) analysis, *Herrerasaurus* was used as the outgroup. Two equally parsimonious trees were produced using PAUP (Swofford, 1998) and McClade (Maddison and Maddison, 1992) with a length of 17 steps, a consistency index of 0.88, and a retention index of 0.91. The strict consensus of braincase characters (Fig. 10B) linked *Giganotosaurus* with *Carcharodontosaurus* as in the more extensive analysis. *Sinraptor* became a sister taxon of this clade, which in turn grouped with *Abelisaurus*, *Acrocanthosaurus* and *Allosaurus* in an unresolved polytomy.

Braincase characters, therefore, support a monophyletic Carcharodontosauridae.

Synapomorphies of *Giganotosaurus* and *Carcharodontosaurus*—(1) The supratemporal fenestra of *Giganotosaurus* does not extend anteriorly onto the dorsal surface of the frontal, although this bone does form part of the anterior wall of the fenestra. In almost all other theropods, including *Sinraptor*, the fossa extends forward into a depression on the posterodorsal surface of the frontal. The Moroccan *Carcharodontosaurus*

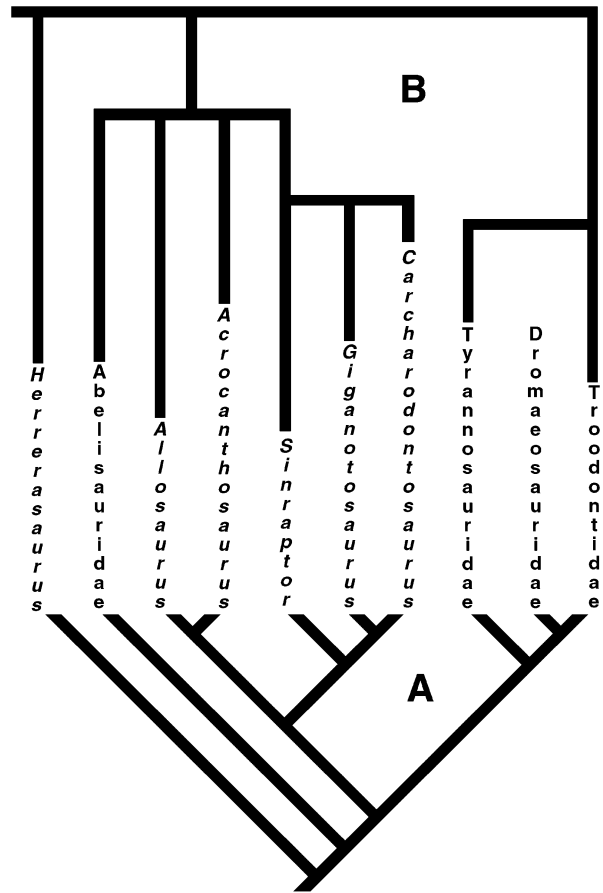


FIGURE 10. Cladogram based on phylogenetic analysis of 125 cranial and postcranial characters (A, after Currie and Carpenter, 2000) and 15 braincase characters (B, see Appendix 2).

(Serenio et al., 1996) exhibits a similar condition to that of *Giganotosaurus*. Furthermore, in *Giganotosaurus* and *Carcharodontosaurus* a shelf of bone formed by the frontal and parietal overlaps the anteromedial margin of the supratemporal fenestra. *Acrocanthosaurus*, *Carnotaurus* and *Sinraptor* have a shelf of bone that overhangs the anteromedial corner of the supratemporal fenestra, but this is relatively small and is restricted to the frontal.

(2) In lateral view, the fifth cranial nerve of most theropods, including abelisaurids, *Allosaurus*, coelurosaurs, *Herrerasaurus* and *Sinraptor*, is anterior to the level of the nuchal crest when the frontal is horizontal. Apomorphically, in *Giganotosaurus* and *Carcharodontosaurus*, the foramen is posterior to the nuchal crest.

(3) The fenestrae ovalis of *Giganotosaurus* and *Carcharodontosaurus* are unusual in that they are exposed from behind by the enlargement of the jugular foramen on the occiput. The evolution of such a character is easily understood because of the association of the fenestra ovalis with the metotic fissure. Primitively, the ninth to eleventh cranial nerves and the jugular vein passed laterally through the metotic fissure to open on the side of the skull (Raath, 1985). In primitive theropod skulls with relatively small paroccipital processes, the nerves and veins wrapped around the margins of the metotic struts. However, in more advanced theropods with larger, deeper paroccipital processes, a separate canal developed to connect the metotic fissure with the occiput. In *Sinraptor* (Currie and Zhao, 1993a), for example, the cranial nerves entered the metotic fissure from

the inside of the braincase, but turned posteriorly to exit the skull through a foramen on the occiput. The fenestra ovalis, however, can only be seen on the lateral surface of the braincase anterior to the ventral extension of the exoccipital. In *Troodon* (Currie and Zhao, 1993b), a bony wall almost completely separated the occipital and lateral openings. *Giganotosaurus* and *Carcharodontosaurus* maintained the integration of the jugular foramen and the fenestra ovalis, but both are visible in occipital view. This was accomplished in part by enlargement of the jugular foramen to expose the adjacent fenestra ovalis. A new strong ridge extends ventrally from the ventromedial surface of the paroccipital process (Fig. 8) to separate the fenestra ovalis from the foramen for cranial nerve VII. The stapes would have passed across the stapedia fenestra and extended from the middle ear along the anterior surface of the paroccipital process to the external auditory meatus posteroventral to the quadrate cotylus. In short, the fenestra ovalis maintains the orientation and functional relationships seen in other theropods, and the significant difference is that it can be seen in occipital view (Fig. 7). A similar situation developed in *Chirostenotes* (Sues, 1997), where the lower margin of the paroccipital process was emarginated to expose the fenestra ovalis from behind.

(4) In *Acrocanthosaurus*, *Allosaurus*, *Herrerasaurus*, *Sinraptor*, *Troodon* and *Tyrannosaurus*, the sphenethmoid did not have any bony contact with the cultriform process. In contrast, in *Carcharodontosaurus* and to an even greater degree in *Giganotosaurus*, the space between the cultriform process and the sphenethmoid is bridged by an ossified interorbital septum. Interestingly, a similar condition exists in *Abelisaurus* and *Carnotaurus*.

(5) Plesiomorphically *Allosaurus*, *Carnotaurus*, *Herrerasaurus*, *Sinraptor*, *Troodon*, and *Tyrannosaurus* each have a medial ridge dorsal to the hypophyseal fossa that separates the sixth cranial nerves. This region is flat and plate-like in *Giganotosaurus* and *Carcharodontosaurus*.

(6) In many theropods, including *Acrocanthosaurus* (OMNH 10146), troodontids (Currie, 1985) and tyrannosaurids (Russell, 1970), the basioccipitals are pneumatized. However, *Giganotosaurus* and *Carcharodontosaurus* are unique in having a pair of pneumatopores that invade the basioccipital beneath the neck of the occipital condyle to enter a common, medial pneumatic sinus.

Braincase synapomorphies of *Giganotosaurus*, *Carcharodontosaurus* and *Sinraptor* (Characters 7–10, 13, Appendix I)—(7) One of the most obvious characteristics shared by *Giganotosaurus*, *Carcharodontosaurus* and *Sinraptor* is the strong posteroventral orientation of the braincase in relation to the frontal region of the skull roof (Fig. 6). In theropods like *Herrerasaurus* and *Piatnitzkysaurus*, the basituberal processes are ventral to the occipital condyle, and the lower part of the basioccipital is almost perpendicular to the skull roof. This condition is retained by *Abelisaurus*, *Carnotaurus* and coelurosaurs (tyrannosaurids, troodontids). But in contrast, *Giganotosaurus*, *Carcharodontosaurus* and *Sinraptor* have basioccipitals that project strongly posteriorly below the occipital condyles, so that the basituberal processes are positioned more posteriorly than they are in most theropods.

(8) Plesiomorphically in *Herrerasaurus*, abelisaurids, and coelurosaurs, the temporal fossa has an almost vertical longitudinal axis, inclined at an angle of less than 120 degrees when the frontals are horizontal. In contrast, this angle is more than 120 degrees in *Giganotosaurus*, *Carcharodontosaurus* and *Sinraptor*.

(9) *Giganotosaurus*, *Carcharodontosaurus* and *Sinraptor* developed supratemporal fenestrae that open more anteriorly than dorsally as the back of the skull rotated up and forward around the frontoparietal suture. In lateral view the anterior margin of the supratemporal fenestra is below the level of the posterior

margin. Plesiomorphically, the anterior and posterior margins of the supratemporal fenestra are on the same plane.

(10) Plesiomorphically, a line drawn through the long axis of the frontal/parietal/laterosphenoid suture for the postorbital intersects the lateral margin of the nuchal plate of the parietal. This condition is retained in *Herrerasaurus*, abelisaurids and coelurosaurs. In contrast, *Giganotosaurus*, *Carcharodontosaurus* and *Sinraptor* have parallel postorbital articulations and parietal margins.

(13) *Giganotosaurus*, *Carcharodontosaurus* and *Sinraptor* each have a supraoccipital knob that is at least twice the width of the foramen magnum. In contrast, this feature is less than double the width of the foramen magnum in abelisaurids, *Acrocanthosaurus*, *Herrerasaurus*, *Troodon* and tyrannosaurids.

DISCUSSION

The braincase of *Giganotosaurus* shows many derived features in the temporal and occipital regions that link it with the African genus *Carcharodontosaurus*. These support the inclusion of these two theropods in the Carcharodontosauridae (Serenó et al., 1996; Harris, 1998). This phylogenetic hypothesis matches with paleobiogeographic ones proposed for African and South American dinosaur faunas (Calvo and Salgado, 1995; Jacobs et al., 1996; Sampson et al., 1996). Nevertheless, braincase characters suggest that *Acrocanthosaurus* is more distant in its relationship to *Giganotosaurus*.

The braincase anatomy of *Giganotosaurus* revealed in the present study supports the phylogenetic relationships proposed by Coria and Salgado (1995). In the present study, *Sinraptor*, *Carcharodontosaurus* and *Giganotosaurus* form a monophyletic group supported by five unequivocal braincase synapomorphies. *Giganotosaurus* and *Carcharodontosaurus* are linked by five unequivocal braincase synapomorphies and one that is equivocal (a single convergence with abelisaurids).

Serenó et al. (1996) included *Acrocanthosaurus* in the Carcharodontosauridae with *Giganotosaurus* and *Carcharodontosaurus*, and this view was supported by a more extensive analysis by Harris (1998). The braincase of *Acrocanthosaurus* (Stovall and Langston, 1950) lacks all of the carcharodontosaurid braincase synapomorphies revealed in this study, strongly suggesting that it is not related to this Gondwanan family. Of the eight characters Sereno et al. (1996) use to diagnose the Carcharodontosauridae, most are size related and are found in some large tyrannosaurids as well. A wide range of large theropods, including *Tyrannosaurus* and *Carcharodontosaurus*, share with *Giganotosaurus* a number of size-dependent characters, such as thickening of the skull roof, fusion of braincase sutures, anteroposterior shortness of the frontals and parietals, exclusion of the frontal from the orbital margin, ossification of the sphenethmoid, and high ratio of occipital condyle width to foramen magnum diameter. These cannot be used to establish the phylogenetic relationships of *Giganotosaurus*.

Furthermore, the coding of some characters by Sereno et al. (1996) is uncertain. For example, caudal pleurocoels are not found in *Giganotosaurus*, suggesting that their use in the diagnosis of the family needs to be reviewed. In addition, the supposed caudal pleurocoels of *Acrocanthosaurus* (Stovall and Langston, 1950; Currie and Carpenter, 2000) and *Carcharodontosaurus* (Rauhut, 1995) are only depressions in the sides of the centra and may not even be pneumatic in origin (Russell, 1996). True caudal pleurocoels are only known in some coelurosaurs (Currie et al., 1993; Britt, 1993).

The morphological differences in the dorsal part of the skull of different large theropods suggest there is a correlation between the width of the knob on top of the supraoccipital and the distance between the supratemporal fenestra. In those theropods with narrow intertemporal regions on the parietal, the

supraoccipital is narrow. Tyrannosaurids and troodontids have sharp sagittal crests, and the corresponding supraoccipitals are thin laminae overlapping the occipital wings of the parietals. In *Allosaurus* and *Sinraptor*, the widths between the supratemporal fenestrae are greater, and there are correspondingly wider supraoccipitals. This trend is carried to extremes in *Giganotosaurus* and *Carcharodontosaurus*, which have the widest separations between the supratemporal fenestrae and the most prominent supraoccipitals. These prominent supraoccipitals would have functioned like the high nuchal crests of tyrannosaurids as attachment points for the powerful musculature that elevated the head.

The jaw musculature of *Giganotosaurus* and *Carcharodontosaurus* did not extend up onto the skull roof as it does in most theropods, because the frontal and parietal shelf actually overhang the supratemporal fenestra. Instead, the musculature would have originated on the ventrolateral surface of this shelf.

The anterodorsal slope of the occiput, the strong downturn of the paroccipital process, the posterior position of the quadrates in relation to the occipital condyle, the posteroventral orientation of the basioccipital tuber and the basisphenoid, and the low but wide occipital condyle suggest greater capability for lateral movement of the skull in relation to the anterior cervical vertebrae. These features are probably also related to increases in the mass and length of the jaw musculature. Unlike Tyrannosauridae, which increased the mass of the jaw musculature laterally for increased bite power, sinraptorids and carcharodontosaurids shifted the jaw articulations posteriorly to increase the lengths of jaw muscles for faster jaw closure. To accommodate the changes in jaw musculature, there was a correlated restructuring of the braincase in the *Sinraptor/Giganotosaurus/Carcharodontosaurus* clade.

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APPENDIX 1

Character List.

1. Supratemporal fossa: extends onto posterodorsal surface of frontal (0); restricted by overhanging frontoparietal shelf (1).
2. Exit of fifth cranial nerve: in front or below the level of nuchal crest (0), behind (1).
3. Middle ear region, exposure in occipital view: not exposed (0), exposed (1).
4. Interorbital septum: not ossified (0), ossified (1).
5. Median ridge separates exits of sixth cranial nerves: present (0), absent (1).
6. Neck of occipital condyle invaded by ventrolateral pair of pneumatic cavities that join medially: absent (0), present (1).
7. Angle between occipital condyle and basitubera process: perpendicular or almost perpendicular (0), acute (1).
8. Temporal fossa: dorsoventral orientation (0), anterodorsal-posterodorsal orientation (1).
9. Supratemporal fenestra: face upward (0), face anterodorsally (1).
10. Nuchal plate of parietal with respect to postorbital attachments: not parallel (0), parallel (1).
11. Nuchal crest: low (0), high (1).
12. Sagittal crest: absent (0), present (1).
13. Width of dorsal expansion of supraoccipital: less than two times (0), at least two times (1) the width of the foramen magnum.
14. Parietal tongue-like process overlapping the supraoccipital: absent (0), present (1).
15. Occipital condyle: subspherical (0), dorsoventrally compressed (1).

APPENDIX 2

Character Matrix.

<i>Abelisaurus</i>	0001?	00000	00010
<i>Acrocanthosaurus</i>	00000	00000	00011
<i>Allosaurus</i>	00000	00000	00010
<i>Carcharodontosaurus</i>	11111	11111	00110
<i>Carnotaurus</i>	0001?	00000	10010
Dromaeosauridae	00000	00000	00000
<i>Giganotosaurus</i>	11111	11111	00111
<i>Herrerasaurus</i>	00000	00000	00000
<i>Sinraptor</i>	00000	01111	00110
Troodontidae	00000	00000	11000
Tyrannosauridae	00000	00000	11000