Journal of Vertebrate Paleontology 27(4):902–916, December 2007

ARTICLE

A NEW SPECIES OF *CARCHARODONTOSAURUS* (DINOSAURIA: THEROPODA) FROM THE CENOMANIAN OF NIGER AND A REVISION OF THE GENUS

STEPHEN L. BRUSATTE[*,1] and PAUL C. SERENO[2]
[1]Department of the Geophysical Sciences, University of Chicago, 5734 South Ellis Avenue, Chicago, Illinois 60637, USA,
brusatte@uchicago.edu;
[2]Department of Organismal Biology and Anatomy, University of Chicago, 1027 East 57th Street, Chicago, Illinois 60637, USA,
dinosaur@uchicago.edu

ABSTRACT—The systematics and taxonomy of the large allosauroid *Carcharodontosaurus* are reviewed and a new species of this theropod is described from the Late Cretaceous (Cenomanian) Echkar Formation of Niger, which is roughly coeval with Cenomanian beds elsewhere in northern Africa. The type species, *C. saharicus*, was based originally on a pair of isolated teeth from Algeria, to which was referred a partial skull and skeleton from Egypt. All of this material was either lost or destroyed more than 50 years ago. Thus, a neotype is designated for *C. saharicus*, a well-preserved cranium from the Kem Kem beds in Morocco. Newly discovered material from Niger is distinct from that of *C. saharicus*, justifying the erection of a distinct southern species. *C. iguidensis*, n. sp. is represented by cranial (maxilla, braincase, dentary, lacrimal, teeth) and postcranial (vertebrae) remains and grew to the same large body size as *C. saharicus*. The skull displays several autapomorphies, including a laterally reduced external antorbital fossa, a maxillary anteromedial process that is broadly arched toward the midline, a prominent horizontal crest on the medial aspect of the maxilla, and a deeply invaginated fossa on the laterosphenoid. Unlike *C. saharicus* the ventral rim of the external antorbital fossa does not protrude laterally, the anteromedial process does not demarcate a deep ventral fossa, and the frontal-lacrimal suture is not elevated. The new material provides evidence of differentiation among Cenomanian-age faunas from the Sahara and supports a close relationship between *Carcharodontosaurus*, *Giganotosaurus*, and *Acrocanthosaurus*.

INTRODUCTION

The past decade has witnessed a renewed interest in the Cretaceous vertebrate record of Africa. Many new taxa have been discovered by expeditions to Morocco (Sereno et al., 1996; Russell, 1996; Monbaron et al., 1999), Tunisia (Benton et al., 2000), Egypt (Smith et al., 2001), Niger (Sereno et al., 1998, 1999, 2004), and South Africa (de Klerk et al., 2000). Many of these expeditions have also recovered material, especially isolated teeth, referred to *Carcharodontosaurus saharicus*, a large theropod dinosaur originally based on a pair of isolated teeth from Upper Cretaceous (Cenomanian) rocks in western Algeria (Depéret and Savornin, 1925, 1927). Despite recovery of a partial skull and skeleton in rocks of similar age in Egypt (Stromer, 1931), the taxon has remained enigmatic (Rauhut, 1995) because the Egyptian material was destroyed in World War II (Nothdurft et al., 2002). The recent discovery of a partial skull in eastern Morocco pertaining to *C. saharicus* (Sereno et al., 1996) and several new closely related taxa from Argentina, that together with *Carcharodontosaurus* comprise the Carcharodontosauridae (Coria and Salgado, 1995; Novas et al., 2005; Coria and Currie, 2006), have begun to document a large-bodied allosauroid radiation of major significance during the Cretaceous.

We describe new material of the genus *Carcharodontosaurus* from the Cenomanian-age Echkar Formation of Niger (Fig.1). Isolated teeth from this and other formations in Niger have long been attributed to *Carcharodontosaurus saharicus* (Lapparent, 1960). The new material comes from a region called Iguidi in central Niger (Lapparent, 1953). Important portions of the skull are preserved that show differences with both Moroccan and Egyptian specimens of *Carcharodontosaurus saharicus*. We therefore establish a new southern species of *Carcharodontosaurus* for this material and discuss anatomical features relevant to *Carcharodontosaurus*, carcharodontosaurids, and allosauroid phylogeny in general. This description also presents for the first time a detailed analysis of *Carcharodontosaurus* cranial osteology.

Institutional Abbreviations—**BMNH**, British Museum of Natural History, London; **MNN**, Musée National du Niger, Niamey; **MUCPv-CH**, Museo de la Universidad Nacional del Comahue, El Chocón collection, Neuquén; **NCSM**, North Carolina Museum of Natural Sciences, Raleigh; **OMNH**, Sam Noble Oklahoma Museum of Natural History, Norman; **SGM**, Ministére de l'Energie et des Mines, Rabat; **UCRC**, University of Chicago Research Collection, Chicago.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1888
THEROPODA Marsh, 1881
ALLOSAUROIDEA Marsh, 1878
CARCHARODONTOSAURIDAE Stromer, 1931

Definition—The most inclusive clade containing *Carcharodontosaurus saharicus* Depéret and Savornin 1927, but not *Sinraptor dongi* Currie and Zhao 1993a, *Allosaurus fragilis* Marsh 1877, or *Passer domesticus* Linnaeus 1758 (Sereno, 2005; Sereno et al., 2005).

---

[*]Corresponding author and present address: Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol, BS8 1RJ, U.K.

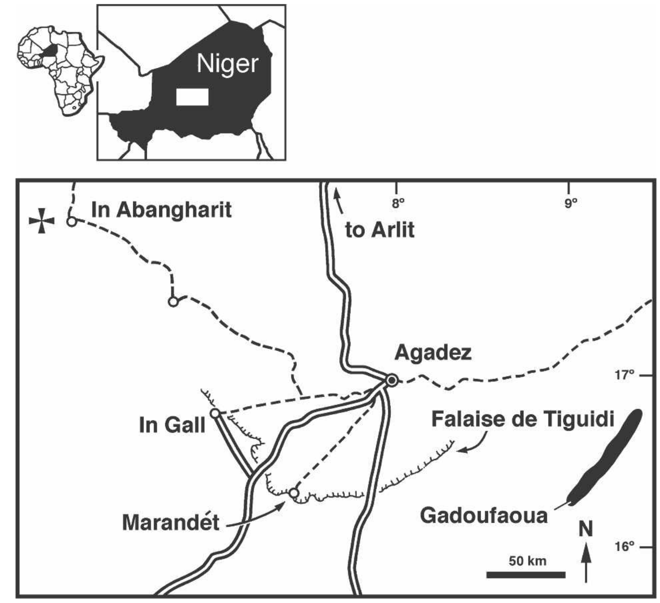

FIGURE 1. Map of the Republic of Niger showing the locality (cross) to the west of the oasis In Abangharit, where the type and referred material of *Carcharodontosaurus iguidensis* were discovered (after Sereno et al., 1999). Other fossiliferous areas include Gadoufaoua (Aptian-Albian) and the foot of the Falaise de Tiguidi (Neocomian).

CARCHARODONTOSAURUS Stromer, 1931
(Figs. 2–9)

Sigilmassasaurus Russell, 1996

Diagnosis—Allosauroid theropods characterized by pronounced grooved sculpturing of nearly the entire lateral surface of the maxilla; large internal carotid and paracondylar pneumatocoels (pneumatic recesses); deep funnel-shaped basisphenoid fossa; postaxial cervical centra with low and very broad proportions (nearly twice centrum height), a reniform posterior articular face, and a very well developed ventral keel that is as deep as the centrum in some vertebrae (Fig. 9; Stromer, 1931:pl. 1, fig. 2; Sereno et al., 1996:fig. 2D).

Holotype—*Carcharodontosaurus saharicus* was first described by Depéret and Savornin (1927: 265) as a new species of *Megalosaurus*, specifically as "*Megalosaurus* (*Dryptosaurus*) *saharicus*." The species was erected on the basis of two teeth found near a manmade subterranean water canal (in Arabic, a "foggara") in the vicinity of Timimoun, a small oasis in easternmost Algeria (Depéret and Savornin, 1927:figs. 1, 2). Although from roughly the same sandstone horizon and of comparable size, the teeth were found 3 km from each other and almost certainly pertain to different individuals. Both teeth are blade-shaped, have a nearly straight posterior margin, and have pronounced arcuate marginal enamel wrinkles. Based on their approximate symmetry about a sagittal plane, these teeth are probably from either the maxillary or mid dentary series (Sereno et al., 1996). At the time they were originally described, such pronounced marginal enamel wrinkles were unknown elsewhere among

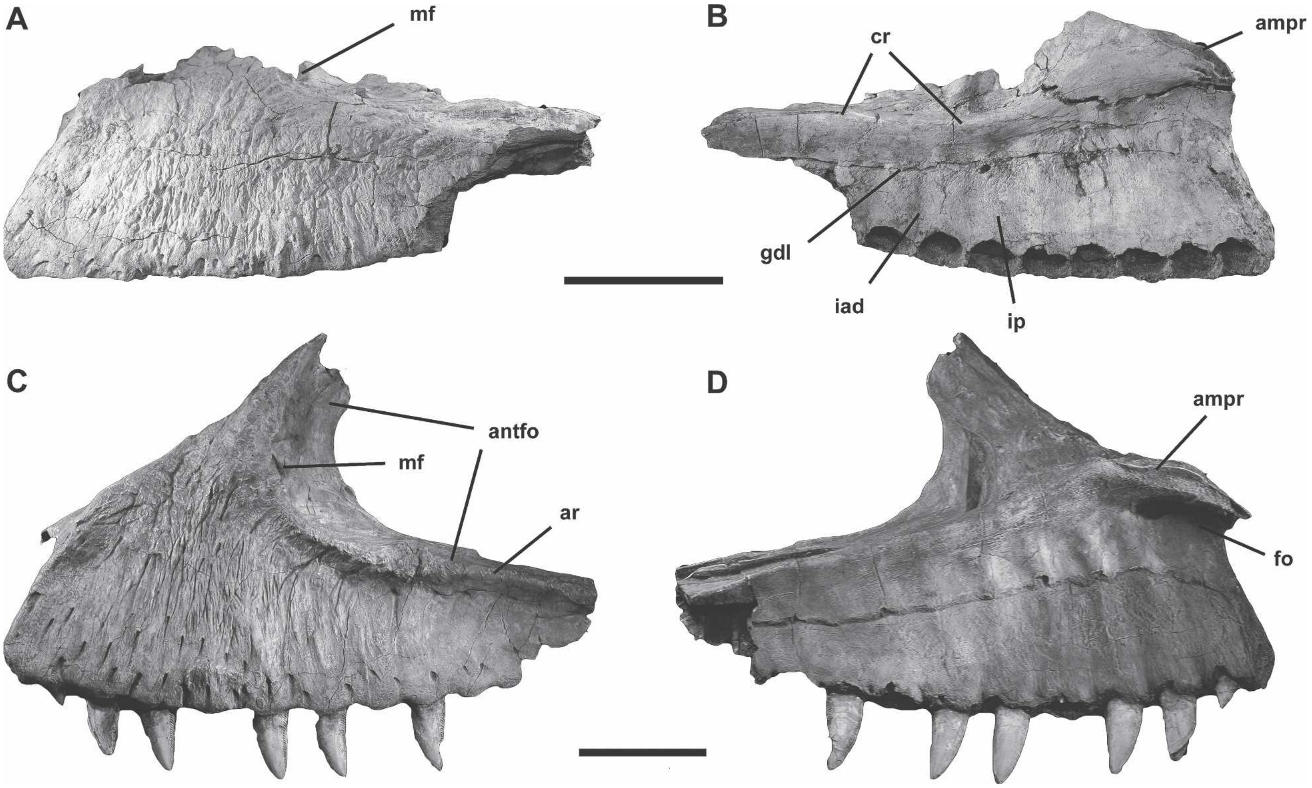

FIGURE 2. Maxillae of *Carcharodontosaurus*. **A**, *C. iguidensis* n. sp. (MNN IGU2), lateral view; **B**, *C. iguidensis*, medial view; **C**, *C. saharicus* (cast of SGM-Din 1), lateral view (reversed); **D**, *C. saharicus* (cast), medial view (reversed). **Abbreviations**: **ampr**, anteromedial process; **antfo**, antorbital fossa; **ar**, antorbital fossa ridge; **cr**, crest; **fo**, fossa; **gdl**, groove for the dental lamina; **iad**, interalveolar depression; **ip**, interdental plates; **mf**, maxillary fenestra. Scale bars equal 15 cm.

theropods. Teeth with similar, although often less pronounced, enamel wrinkles have long been found elsewhere in the Sahara (Lapparent, 1960; Benton et al., 2000).

We have observed marginal enamel wrinkles of identical form in the broadest crowns of *Giganotosaurus carolinii*, although they have yet to be figured (Coria and Salgado, 1995). Less pronounced wrinkles have been noted in other carcharodontosaurids, namely *Tyrannotitan chubutensis* (Novas et al., 2005) and *Mapusaurus roseae* (Coria and Currie, 2006). Although a few enamel wrinkles have been described in tyrannosaurids and certain basal tetanurans, these features are not developed to the degree observed in several carcharodontosaurids, in which they often extend along the entire distal margin of the crown. Enamel wrinkles, however, are problematic as a diagnostic character at the specific or generic level within Carcharodontosauridae, because they vary in strength and number along the tooth row and now are known in most carcharodontosaurids.

The holotypic teeth of *C. saharicus* may have been originally kept in a fossil collection in Algeria or in France (Paris, Lyon), where C. Depéret once taught. We were unable, however, to find any record of their existence in collections in either country. As with several other holotypic specimens described in the early twentieth century from the Sahara, the teeth are regarded as lost. Thus, there are several problems with the holotypic teeth of *Carcharodontosaurus* (*Megalosaurus*) *saharicus*: the two original specimens likely pertain to different individuals; the diagnostic characters originally cited are no longer diagnostic at the specific or generic level; and the specimens are lost.

Neotype—Stromer (1931) emphasized the similarity of the original teeth to teeth associated with better material from Egypt and transferred the species to the new genus *Carcharodontosaurus*. Unfortunately, these Egyptian fossils were never cast and were destroyed in 1944 during World War II in a British Royal Air Force bombing raid (Nothdurft et al., 2002). More recently, Sereno and colleagues (1996) described a well preserved skull with teeth from Morocco that is identical to both the original holotypic teeth and Stromer's Egyptian material. The Moroccan material, furthermore, was discovered near the Algerian border, a short distance from the Algerian oasis of Timimoun, the holotypic locality of *C. saharicus*. In the interest of preserving the now widely used generic and species names, *Carcharodontosaurus saharicus*, we designate this Moroccan skull below as the neotype of this taxon.

CARCHARODONTOSAURUS SAHARICUS
(Figs. 2C,D; 8A)

Neotype—SGM-Din 1, partial cranium lacking the premaxillae, squamosals, quadratojugals, quadrates, and most of the palate (Sereno et al., 1996:fig. 2).

Referred Material—SGM-Din 3, anterior cervical vertebra (Sereno et al., 1996:fig. 2D); SGM-Din 4, anterior cervical centrum; SGM-Din 5, mid cervical vertebra.

Locality and Horizon—The neotype was found east of the oasis of Er Remlia, eastern Morocco; the neotype and referred material are from the upper unit of the Kem Kem beds (Cenomanian), which have also yielded the theropods *Deltadromeus* and *Spinosaurus* and the diplodocoid sauropod *Rebbachisaurus* (Russell, 1996; Sereno et al., 1996).

Diagnosis—Carcharodontosaurid theropod with skull characterized by a laterally protruding ventral margin of the maxillary external antorbital fossa; a deep and ventrally-facing fossa between the inner wall of the maxilla and the anteromedial process; a deep and dorsoventrally protruding lacrimal-frontal suture; an invaginated anteromedial corner of the supratemporal fossa; and distinct enamel wrinkles on both mesial and distal margins of mesial (anterior) and mid maxillary crowns.

Comments—The material pertaining to *C. saharicus* from Morocco includes the neotype, the referred vertebral material cited above (SGN-Din 3 through 5), as well as additional fragmentary material that will not be reviewed here. Stromer (1934:pl. 1, fig. 2) described similarly stout cervical vertebrae from Egypt as "*Spinosaurus* B," that Sereno and colleagues (1996) later referred to *Carcharodontosaurus saharicus*. Similar very broad cervical vertebrae were also found near the cranial material of the new species from Niger (Fig. 9). Therefore, it is highly likely that *Carcharodontosaurus* was characterized by unusually broad cervical centra with a hypertrophied ventral keel.

Russell (1996), in contrast, coined a new genus and species, *Sigilmassasaurus brevicollis*, for several broad cervical vertebrae collected more recently in Morocco. The proportional differences cited by Russell (1996) to distinguish *S. brevicollis* from *C. saharicus*, however, are based on a misinterpretation of Stromer's measures for Egyptian "*Spinosaurus* B." As Stromer's material was later destroyed, all that remain are his text and figures. Stromer appears to have included the anteriorly projecting ball of the centrum in his measurement of centrum length (as determined by comparing his measurements and figures). Russell, in contrast, did not include this anterior projection, and as a result mistakenly concluded that the Moroccan centra were proportionally broader. There are now three disparate localities (Egypt, Morocco, Niger) with cranial remains of the large-skulled carnivore *Carcharodontosaurus* in association with very similar, unusually broad cervical vertebrae. We regard this as a noteworthy characteristic that currently distinguishes the genus.

CARCHARODONTOSAURUS IGUIDENSIS, sp. nov.
(Figs. 2A, B; 3–7; 8B; 9)

Holotype—MNN IGU2, left maxilla.

Referred Material—MNN IGU3, posterior skull roof and braincase including most of the frontal, parietal, supraoccipital, exoccipital-opisthotic, prootic, laterosphenoid, orbitosphenoid, basioccipital, basisphenoid-parasphenoid, and possibly sphenethmoid; MNN IGU4, right lacrimal, mid section; MNN IGU5, left dentary, anterior end; MNN IGU 6 through 10, teeth; MNN IGU11, mid cervical centrum.

Locality and Horizon—Echkar Formation (Cenomanian), west of the oasis In Abangharit in an area known as Iguidi, Republic of Niger (Fig. 1); in association with the abelisaurid *Rugops primus* (Sereno et al., 2004), spinosaurid teeth tentatively referred to *Spinosaurus* sp., unnamed rebbachisaurid and titanosaurian sauropods, and three unnamed crocodyliforms.

Lapparent (1953) first discovered the vertebrate fossils of Iguidi, most of which are preserved as deflation lag on outcrop exposed between migrating dunes. The maxilla was found in situ at the eastern edge of Iguidi, where Lapparent first encountered fossil bone and teeth. The referred cranial material (lacrimal fragment, braincase, anterior dentary), teeth, and cervical centrum were discovered at a single locality (C29) located approximately 3 km west of the maxilla. This locality has an area of approximately 50 m^2. The braincase and dentary were found in situ embedded in the red sandstone of the Echkar Formation. The lacrimal fragment, teeth, and cervical centrum, in contrast, were found in proximity but had eroded free of their original deposit. None of the material at this locality was preserved in articulation. The maturity of the braincase (obliterating fusion) contrasts with the immaturity of the cervical vertebra (centrum and neural arch disarticulated) and strongly suggests that multiple individuals are represented. Isolated teeth and vertebral fragments that may pertain to this species are present at more distant localities in Iguidi. The maxilla was chosen as the holotype because it is the most diagnostic bone preserved.

Etymology—*iguidi*, Iguidi; *ensis*, from (Latin).

Diagnosis—Carcharodontosaurid with maxilla characterized by a very reduced antorbital fossa limited to the proximity of the maxillary fenestra; an anteromedial process that is broadly arched toward the midline; and a prominent horizontal crest on the medial aspect of the main body; braincase excavated by a deep invaginated fossa on the anterior aspect of the laterosphenoid ala. *C. iguidensis* lacks the autapomorphies of *C. saharicus*, including the laterally protruding ventral margin of the maxillary external antorbital fossa; a well developed ventrally-facing fossa between the inner wall of the maxilla and the anteromedial process; a deepened and dorsoventrally protruding lacrimal-frontal suture; an invaginated anteromedial corner of the supratemporal fossa; a sigmoidal crest on the anterior wall of the supratemporal fossa, and marked enamel wrinkles along most of the mesial and distal margins of mesial (anterior) and mid maxillary crowns.

Comments—The description of the new species from Niger depends principally on two interpretations—namely, that the material belongs to a single species and that this species is distinct from *C. saharicus*. In the first case, isolated bones and teeth are referred here to *C. iguidensis* because they closely match the morphology of *C. saharicus* and because it is unlikely that there would more than three contemporaneous large-bodied carnivores in the same formation (*Rugops primus*, *Spinosaurus* sp., *Carcharodontosaurus iguidensis*). Until there is any evidence to the contrary, we assume that the carcharodontosaurid material from closely spaced localities in Iguidi from the Echkar Formation pertains to a single species. Second, none of the autapomorphies of *C. iguidensis* or other differences from comparable material of *C. saharicus* appear to be within the range of variation seen in *Mapusaurus roseae* (Coria and Currie, 2006), which is the only carcharodontosaurid presently known from abundant material from the same horizon. *C. iguidensis* differs from *C. saharicus* in aspects of the maxilla, braincase and dentition. Thus, a distinct southern species appears to be at hand.

The Echkar Formation in the Iguidi region of Niger underlies a resistant, fossiliferous shallow marine limestone that records a transgression across broad areas of north and western Africa (Reyment and Dingle, 1987). Regarded as late Cenomanian through Turonian in age on the basis of its invertebrate fauna (Ferrandini et al., 1985), this marine platform is visible from the localities yielding *Carcharodontosaurus* in Iguidi in Niger and the Kem Kem beds in Morocco (Sereno et al., 1996). As there is no evidence of a significant hiatus prior to this transgression, we regard the underlying Nigerienne and Moroccan terrestrial faunas as roughly coeval and probably early to mid Cenomanian in age (Sereno et al., 1996).

DESCRIPTION

Cranium

Maxilla—The main body of the left maxilla is well preserved but lacks most of the ascending ramus, posterior end of the main body, and all erupted teeth (Fig. 2A, B). The first eight alveoli in the main body of the maxilla are complete and span a combined length of 390 mm, as measured from the anterior extremity of the maxilla (Table 1). A comparable measurement of the neotype maxilla of *C. saharicus* is 470 mm. Thus, the maxilla of *C. iguidensis* is only about 83 percent of the length of *C. saharicus*. Other measurements between these specimens, such as the dorsoventral depth of the maxilla above the sixth alveolus and the depth below the groove for the dental lamina, are subequal, suggesting that the maxilla of *C. iguidensis* is substantially shorter anteroposteriorly than that of *C. saharicus* (Fig. 2).

TABLE 1. *Carcharodontosaurus iguidensis*, measurements (mm) of left maxilla (MNN IGU2).

Alveolus 1, maximum anteroposterior diameter	36
Alveolus 2, maximum anteroposterior diameter	42
Alveolus 3, maximum anteroposterior diameter	45
Alveolus 4, maximum anteroposterior diameter	45
Alveolus 5, maximum anteroposterior diameter	44
Alveolus 6, maximum anteroposterior diameter	47
Alveolus 7, maximum anteroposterior diameter	44
Alveolus 8, maximum anteroposterior diameter	45
Alveolus 1–8, maximum anteroposterior length	390
Floor of maxillary antrum to alveolar margin (alveolus 3), depth	190
Floor of maxillary fenestra to alveolar margin (alveolus 6), depth	188

Several other differences between these species are manifest in lateral and medial views. The alveolar margin of *C. iguidensis* is thicker transversely than that in *C. saharicus*, and the alveoli themselves are more broadly exposed in medial view (Fig. 2B, D). In lateral view, the ventral margin of the maxilla in *C. iguidensis* is almost straight rather than noticeably convex, has more subtle undulation of its ventral margin than *C. saharicus*, and the grooved texture on its lateral surface descends nearly to the ventral margin (Fig. 2A, C; 3C). The ventralmost foramina in *C. iguidensis* are located just above the alveolar margin (Fig. 3C), whereas in *C. saharicus* they are somewhat more elevated and separated by a smooth margin (Fig. 2C). Stromer's (1931:pl. 1, figs. 6a, b) figures of the Egyptian maxilla are somewhat ambiguous but appear most similar to the neotype maxilla of *C. saharicus*.

In lateral view, the maxilla is heavily sculptured by distinct subparallel ridges and grooves, the latter housing neurovascular tracts. The general form and orientation of these grooves are similar to that observed in *C. saharicus* (Sereno et al., 1996): near the anterior end of the antorbital fossa they are curved, while elsewhere they tend to be linear and angle somewhat anteroventrally (Fig. 2). *Giganotosaurus* (Coria and Salgado, 1995) and some specimens of *Mapusaurus* (Coria and Currie, 2006) also exhibit neurovascular grooves, but these tend to be shorter and shallower. In contrast, a basal carcharodontosaurid from the underlying Elrhaz Formation in Niger (Brusatte and Sereno, 2006) and *Acrocanthosaurus* (Currie and Carpenter, 2000) do not exhibit these external grooves and do not have external foramina beyond the number typically present in *Allosaurus*, *Sinraptor*, and most other theropods. A similar rugose surface is seen in abelisaurid theropods (Bonaparte et al., 1990; Sampson et al., 1998; Lamanna et al., 2002; Sereno et al., 2004), but this appears to have arisen independently.

In lateral view, the main body decreases in depth posteriorly as in *C. saharicus*, *Mapusaurus*, and most theropods. *Giganotosaurus* differs in this regard, maintaining a relatively constant depth under the antorbital opening (Coria and Salgado, 1995). The anterior ramus is proportionately short as in other carcharodontosaurids. The straight articular surface for the premaxilla is inclined posterodorsally at approximately 60 degrees and beveled anteromedially. In *C. saharicus* a tab-like flange extends anteriorly on the medial side of the premaxillary articular surface and would have medially overlapped the posterior margin of the premaxilla (Fig. 2D). In *C. iguidensis* the homologous structure is developed only as a rugose swelling (Fig. 2B). The articular surface for the posterolateral process of the premaxilla is marked by a pair of depressions and foramina (Fig. 3B), whereas in *C. saharicus* this surface is flat. The maxilla of *C. iguidensis* does not appear to have participated in the margin of the external naris.

The ventral portion of the external antorbital fossa is very reduced in *C. iguidensis*, an autapomorphy of the new species. It is limited to a small area posterior to the maxillary fenestra, the ventral margin of which is preserved (Fig. 3A, B, antfo). Posterior to this area, the antorbital fossa tapers rapidly and a vertical flange rises with a textured lateral surface that clearly lies outside the pneumatic space of the fossa (Fig. 3A, fl). Farther posteriorly the fossa is present again, but only as a narrow, smooth band that is broadly exposed only in dorsal view. In *C. saharicus* (Sereno et

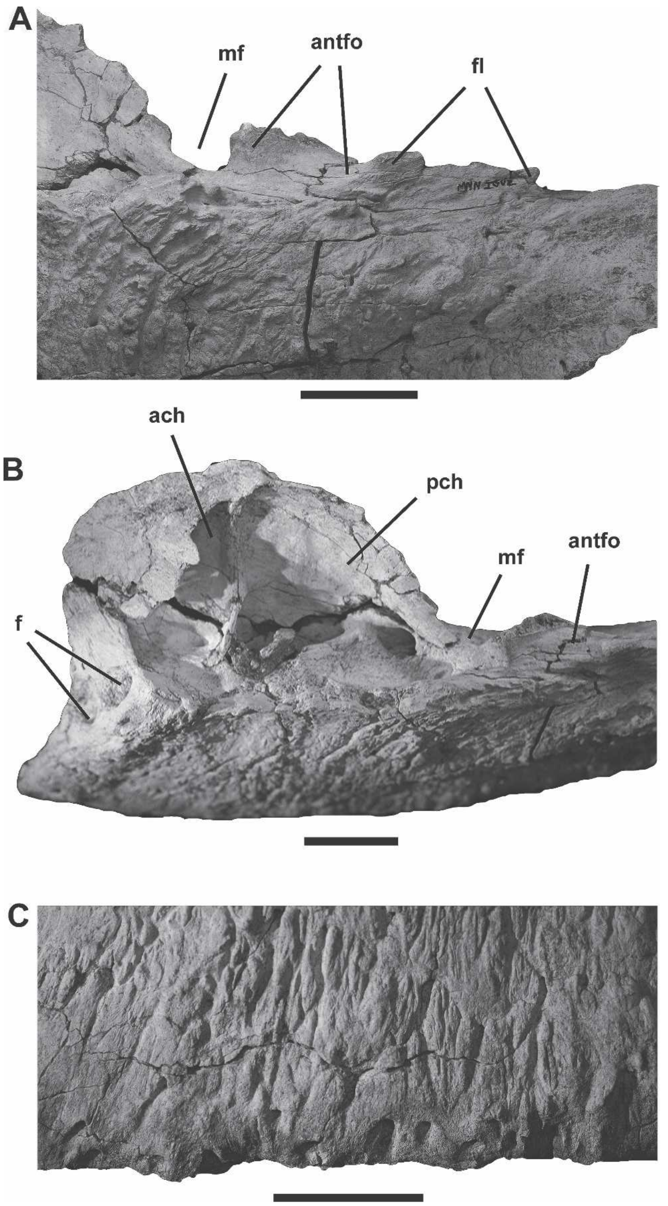

FIGURE 3. Close-up views of the maxilla of *Carcharodontosaurus iguidensis* n. sp. (MNN IGU2). **A**, ventral margin of the external antorbital fossa in lateral view; **B**, antorbital sinuses in dorsal view; **C**, ventral alveolar margin in lateral view. **Abbreviations**: **ach**, anterior chamber; **antfo**, antorbital fossa; **f**, foramen; **fl**, flange; **mf**, maxillary fenestra; **pch**, posterior chamber. Scale bars equal 5 cm.

al., 1996; Fig. 2C), *Giganotosaurus* (Coria and Salgado, 1995) and *Mapusaurus* (Coria and Currie, 2006), in contrast, the ventral margin of the fossa is maintained as a narrow band along the length of the fenestra. The protruding ventral rim of the antorbital fossa that characterizes *C. saharicus* (Fig. 2C) is not developed in *C. iguidensis* (Fig. 2A), in which the comparable region is gently depressed (Fig. 2A).

In dorsal view, the broken base of the anterodorsal process exposes the antorbital sinus region to view (Fig. 3B). The sinus is divided into two chambers (anterior and posterior) by a 10-mm thick, sinuous web of bone. Anatomical identification of these chambers is difficult and not without ambiguity. Likely they represent the promaxillary recess and maxillary antrum, respectively. The anterior chamber inflates the anteromedial process as does the promaxillary recess in other theropods (Witmer, 1997). The posterior chamber opens posterolaterally via an accessory antorbital fenestra, which is identified here as the maxillary fenestra based on comparison to *C. saharicus*. In *C. saharicus* (Fig. 2C), the promaxillary fenestra is autapomorphically absent, and the maxillary fenestra opens anteromedially into a large maxillary antrum whose morphology is nearly identical to the posterior chamber of *C. iguidensis*.

In *C. iguidensis*, the anterior chamber is 55 mm long anteroposteriorly, whereas the posterior chamber is 115 mm long. As in *C. saharicus* (Fig. 2D), the chambers are closed medially by a lamina of bone extending from the anteromedial process. Another lamina of bone encloses the chambers dorsally but is only partially preserved. At least one, or possibly several, foramina appear to communicate between the anterior chamber and the narial region, but their exact course is obscured by matrix. Two large foramina open in the floor of the posterior chamber, but their paths are uncertain.

In medial view, the maxilla of *C. iguidensis* has a strong, fluted anteromedial process for contact with the opposing maxilla and vomer. This process is particularly broad and inflated by the anterior chamber of the antorbital sinus (Fig. 2B, 3B). Unlike in *C. saharicus*, the process is arched and open in medial view and does not overhang a marked fossa (Fig. 2B, D). The interdental plates are deep and strongly fused as in most theropods. Although there is subtle vertical texture in places, the marked longitudinal striations that characterize abelisaurids are absent (Carrano et al., 2002; Rauhut, 2004b). The groove for the dental lamina is set high on the main body of the maxilla, above which is a strong crest (Fig. 2B). Anteriorly, this ridge curves dorsally, where it joins the anteromedial process. This contrasts with the condition in *C. saharicus* (Fig. 2D), in which a more subdued medial crest dissipates before reaching the anteromedial process. Vertical interalveolar depressions are present below and above the groove for the dental lamina in both species, indicating that the crypts for replacement teeth extend throughout the body of the maxilla (Fig. 2B, D).

The anterior eight and portions of the ninth through the eleventh alveoli are preserved. None of the alveoli house functioning or replacement teeth that are about to erupt. The first alveolus is the smallest (Table 1), while the others are large, comparable in size, and aligned along a gentle curve in ventral view.

Lacrimal—What appears to be the mid-section of the right lacrimal is preserved (MNN IGU4). This bone is pneumatic and has a flat external surface marked by narrow vascular grooves reminiscent of those on the lacrimal of *C. saharicus* (Sereno et al., 1996:fig. 2A). Few other comparisons can be made given the small portion preserved.

Frontal—The subtriangular frontal (Fig. 4, 5) is completely fused along its posterior half to its counterpart and to the parietals posteriorly, as usually occurs in large theropods such as *C. saharicus*, *Giganotosaurus* (Coria and Currie, 2002), *Acrocanthosaurus* (Stovall and Langston, 1950; OMNH 10146), and *Tyrannosaurus* (Brochu, 2002). The anterior tip of each frontal is separated by a narrow median gap. In ventral view, the interfrontal suture is present anteriorly and disappears posteriorly as it reaches the depression for the olfactory bulbs at mid length. An apparently similar separation of the frontals in dorsal view (Fig. 5A) is in reality a fracture that has followed the open ventral portion of the suture. Other sutural contacts of the frontal are open, including those for the postorbital and lacrimal laterally and the laterosphenoid and orbitosphenoid ventrally. The bone is transversely widest where it would have contacted the postorbital. More anteriorly, the fused frontals measure 135 mm from one lacrimal contact to the other and 150 mm in length, measurements that are identical to those in *C. saharicus* (SGM-Din 1).

In dorsal view, the surface of the frontal is smooth and rela-

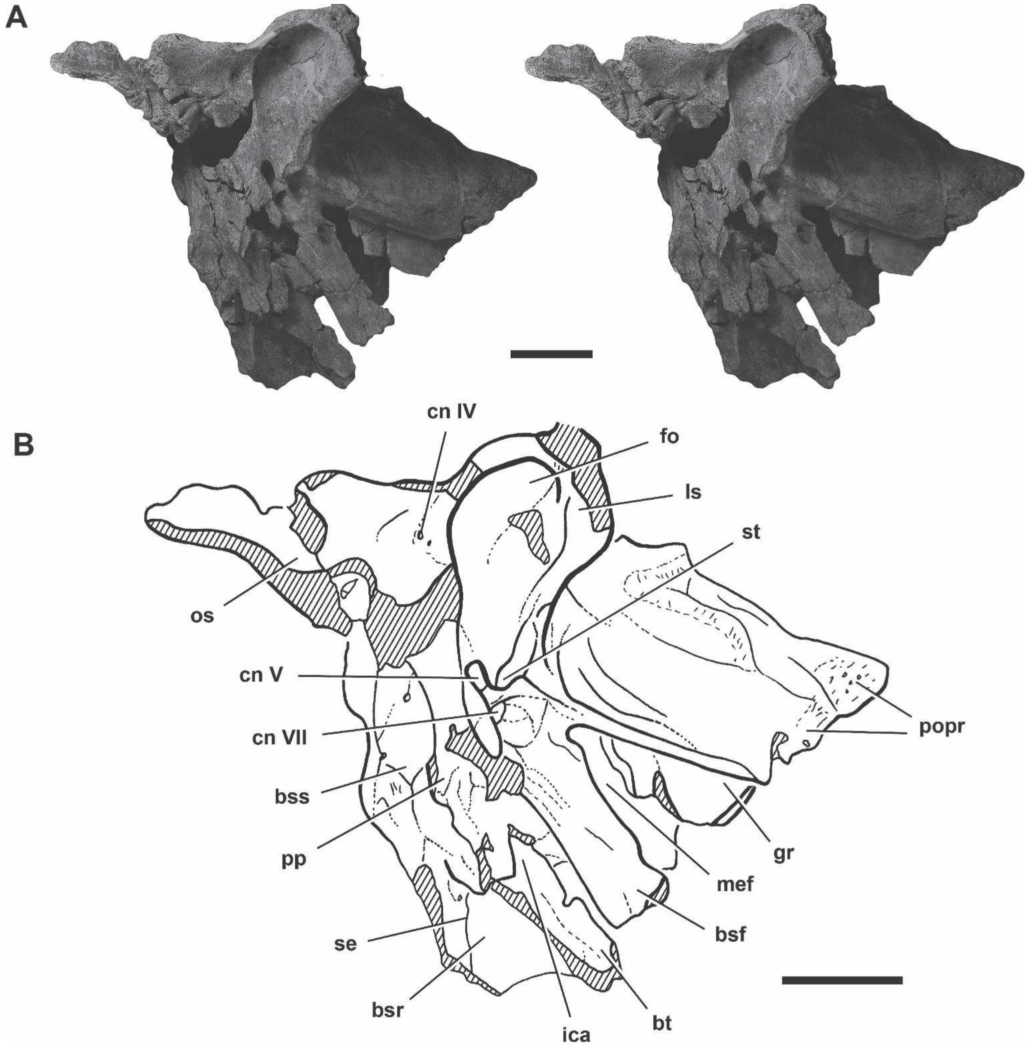

FIGURE 4. Stereopairs (**A**) and line drawing (**B**) of the braincase of *Carcharodontosaurus iguidensis* n. sp. (MNN IGU3), in left anterolateral view. **Abbreviations**: **bsf**, basisphenoid flange; **bsr**, basisphenoid recess; **bss**, basisphenoid sinus; **bt**, basal tubera; **cn IV**, **V**, **VII**, foramen for cranial nerves IV, V, VII; **fo**, fossa on the laterosphenoid ala; **gr**, groove for the stapes; **ica**, foramen for the internal carotid artery; **ls**, laterosphenoid; **mef**, metotic fissure; **os**, orbitosphenoid; **popr**, paroccipital process; **pp**, preotic pendant; **se**, septum; **st**, strut dividing separate openings for branches of the trigeminal nerve. Scale bars equal 5 cm. Cross-hatching indicates broken bone.

tively flat but forms a shallow, broadly rounded sagittal crest along its anterior half, as in *C. saharicus* (Fig. 5A, B). Posteriorly, the frontals participate in the supratemporal fossae, forming much of their anterior walls. The supratemporal fenestrae would have been anteroposteriorly short and widely separated on the midline; dorsal exposure of the supratemporal fossa is limited, because the anterior wall slopes at approximately 45 degrees posteroventrally, as in *C. saharicus* and *Giganotosaurus* (Coria and Currie, 2002). This differs from the condition in *Allosaurus* (Madsen, 1976), *Sinraptor* (Currie and Zhao, 1993a), and other basal theropods, in which the anterior portion of the fossa is developed as a broad depression on the dorsal surface of the frontal.

Anteriorly, the broken nasal processes begin to diverge from the midline in ventral view, indicating that they were separated by processes of the nasals. Laterally, rugose articular surfaces for the lacrimal and postorbital meet above the orbit, clearly excluding the frontal from the orbital margin, as in *C. saharicus*, *Giganotosaurus*, *Mapusaurus*, and *Acrocanthosaurus*. In contrast, at least a small frontal contribution to the rim is present in *Allosaurus*, *Sinraptor*, *Monolophosaurus* (Zhao and Currie, 1993), spinosaurids (Sues et al., 2002), and most other theropods. A deep subconical pit is present near the posterior end of the lacrimal suture (lateral view) and anterior margin of the orbital fossa (ventral view). In *Allosaurus*, a similar pit accommodates the posterior end of the prefrontal. In *C. saharicus*, in contrast, the lacrimal and prefrontal are completely coossified, and the prefrontal is manifest only as a conical process of the lacrimal, which inserts deep into the frontal pit. A small portion of the conical process preserved in articulation with the pit on the right frontal indicates that *C. iguidensis* likely had a condition similar to *C. saharicus*.

Ventrally, the frontal is marked by rugose attachment scars for the laterosphenoid and orbitosphenoid. Between opposing scars for these bones are two tear-drop-shaped depressions for the olfactory bulbs. Although a pair of shallow parasagittal grooves for the olfactory tracts are present, they are not as distinct as those seen in troodontids (Currie, 1985), therizinosauroids (Kirkland et al., 2005), and oviraptorosaurs (Osmólska, 2004).

Three principal differences are apparent between the frontals of *C. iguidensis* and *C. saharicus*, the latter probably exhibiting the derived condition. The articulation for the prefrontal process

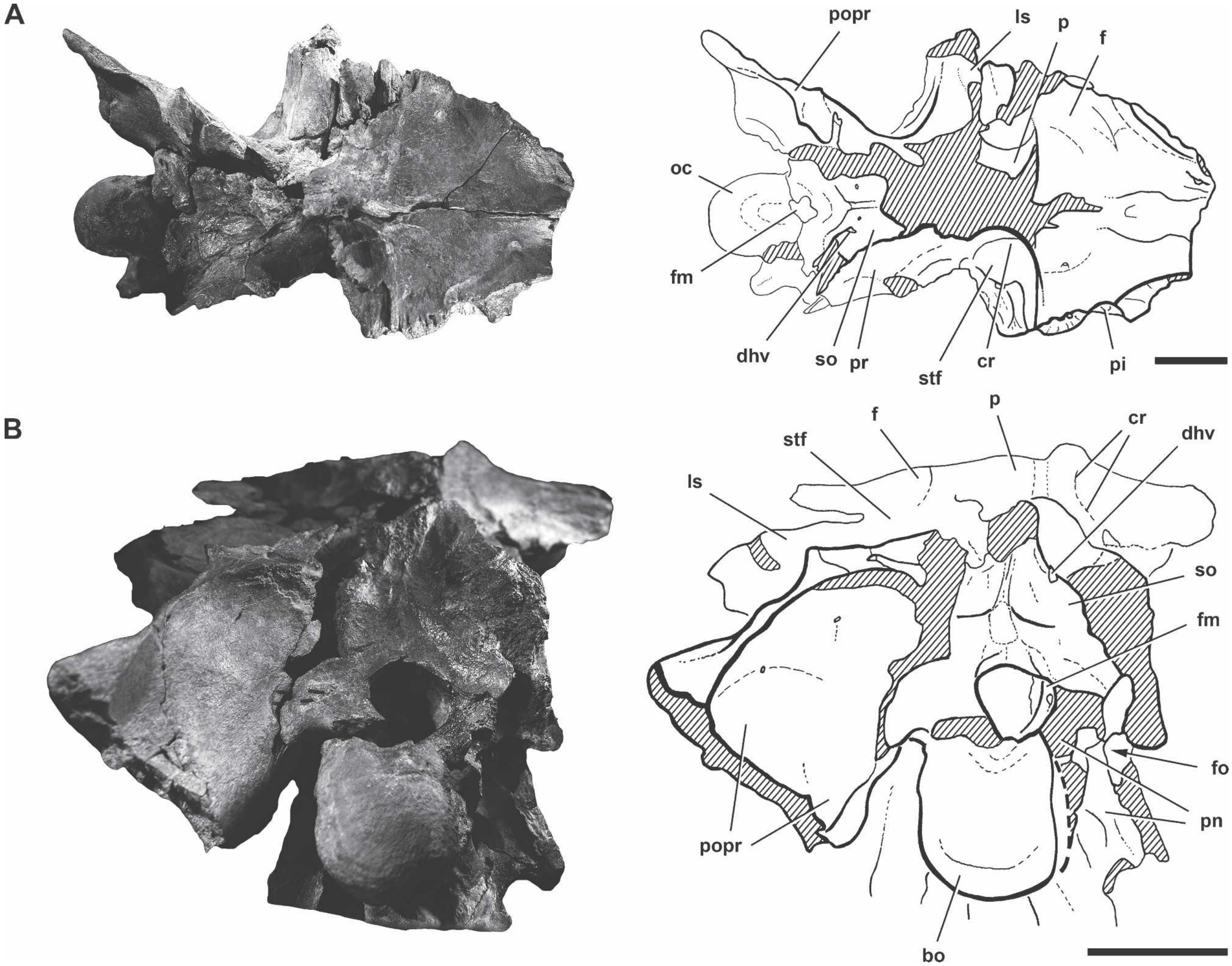

FIGURE 5. Photographs and line drawings of the braincase of *Carcharodontosaurus iguidensis* n. sp. (MNN IGU3) in dorsal (**A**) and posterior (**B**) views. **Abbreviations**: **bo**, basioccipital; **cr**, crest; **dhv**, foramen for the dorsal head vein (vena capitis dorsalis); **fo**, fenestra ovalis; **fm**, foramen magnum; **f**, frontal; **ls**, laterosphenoid; **oc**, occipital condyle; **p**, parietal; **pi**, pit for articulation of the prefrontal or prefrontal process; **pn**, pneumatic opening; **popr**, paroccipital process; **pr**, prootic; **so**, supraoccipital; **stf**, supratemporal fossa. Scale bars equal 5 cm. Cross-hatching indicates broken bone. Line with arrow denotes position of paracondylar pneumatocoel, which cannot be seen in this view.

of the lacrimal is extraordinarily deep in *C. saharicus* (65 mm), its dorsal margin arching well above the orbit in lateral view. The same contact in the comparably-sized skull of *C. iguidensis* measaures only 35 mm in depth. Second, the anteromedial corner of the supratemporal fossa is deeply invaginated in *C. saharicus*, but forms a near vertical, broadly arched wall in *C. iguidensis*. Third, a crest that extends across the anterior wall of the supratemporal fossa, possibly for muscle attachment, is S-shaped in *C. saharicus* but broadly C-shaped in *C. iguidensis* (Fig. 5A, B, cr).

Parietal—Only the ventral portion of the parietal is preserved (Fig. 5A, B). All of the sutural contacts of the parietal to adjacent bones are fused, and much of its dorsal surface and posterolateral processes are broken away. Ventrally, the parietal forms the central roof of the endocranial cavity.

Braincase—Most of the central portion and left side of the braincase are preserved, including an undistorted endocranial cavity (Figs. 4, 5). The ventral and lateralmost portions are broken away. Except for some of the frontal contacts, all braincase sutures are coossified, suggesting that this individual was an adult. Thus, bones are identified below by landmarks rather than sutures. In general, the braincase is very similar to the nearly complete braincases of *C. saharicus* (SGM-Din 1; Sereno et al., 1996), *Giganotosaurus* (Coria and Currie, 2002), and *Acrocanthosaurus* (OMNH 10146; Stovall and Langston, 1950). The foramen magnum is relatively small (30 mm wide, 25 mm deep) compared to the occipital condyle (approximately 60 mm in diameter). The braincase is highly pneumatic, with many passageways and fossae.

The posteroventrally-inclined supraoccipital is completely fused to the parietal dorsally and laterally and to the exoccipital-opisthotic ventrally. The supraoccipital is incomplete dorsally, preventing determination of the pronounced nuchal process that characterizes *C. saharicus* and *Giganotosaurus*. Two foramina for the dorsal head vein (vena capitis dorsalis) open posteriorly above the dorsal margin of the foramen magnum, presumably along a coossified suture (Fig. 5B). The foramina are separated by a low, midline ridge, the more pronounced dorsal extension of which is broken away. The dorsal rim of the foramen magnum has a sharp lip that projects posteroventrally. The contribution of the supraoccipital to the margin of the opening cannot be determined. Based on other tetanurans, it is unlikely that this element would have reached the occipital condyle, as shown in *Giganotosaurus* (Coria and Currie, 2002:fig. 5).

The basioccipital forms most of the subspherical occipital condyle, the central axis of which projects posteroventrally (with the frontals held horizontal). Traces of the suture with the pedicels of the exoccipital-opisthotic are present on each side and possibly across the condyle posteriorly. If this interpretation is correct, the pedicels of the exoccipitals join in the midline and exclude the basioccipital from the foramen magnum, unlike the condition in *Allosaurus* (Madsen, 1976). The condition in other carcharodontosaurids, including *Acrocanthosaurus*, is poorly established due to similar obliterating fusion.

Laterally, a large pneumatopore approximately 15 mm in diameter opens medially into the neck of the occipital condyle (Fig. 5B). This opening is tucked behind the pendant flange of the basisphenoid and is clearly visible only in posterolateral view. These paracondylar pneumatocoels lead to a parasagittal cavity below the endocranial cavity, that is divided posteriorly from its opposite by a thin sagittal septum. Similar basioccipital paracondylar pneumatopores are present in *C. saharicus* and *Giganotosaurus* (Coria and Currie, 2002). According to Rauhut (2004a), this pneumatopore may be an elaboration of the subcondylar recess, which is present in many non-allosauroid theropods.

The basal tubera descend abruptly from the neck of the occipital condyle. They project posteroventrally (with the frontals held horizontal) as a relatively flat sheet, with a shallow median pit and depression. The angle of descent is similar in *Giganotosaurus* (Coria and Currie, 2002). In *Acrocanthosaurus*, in contrast, the tubera descend vertically, have a narrower posterior surface, and are divided by a median trough (OMNH 10146). Distally, the tubera in *C. iguidensis* extend below the level of the occipital condyle, their knob-shaped distal ends separated by a web of bone with an arched ventral margin as in *C. saharicus*. Furthermore, the tubera are wider than the transverse diameter of the occipital condyle as in most theropods, not narrower as in *Allosaurus*, *Sinraptor*, and *Acrocanthosaurus*.

The central and posterior portions of the basisphenoid are preserved, whereas the basipterygoid processes and parasphenoid are broken away. This breakage exposes the posterior and lateral walls of a deep, inverted funnel-shaped basisphenoid recess (Fig. 4), a feature shared with *C. saharicus* and *Acrocanthosaurus*. Although the condition in *Giganotosaurus* and *Mapusaurus* remains uncertain due to incomplete preservation, the hypertrophied form of the basisphenoid recess may eventually prove to characterize all carcharodontosaurids (Sereno et al., 1996). The dorsal portion of the funnel-shaped recess is divided into anterior and posterior chambers by a thin transverse septum, the edges of which are preserved (Fig. 4, se). The anterior chamber appears to open anteriorly under the parasphenoid. The posterior chamber opens dorsally into the partially divided median space, into which also open the paracondylar pneumatopores that pierce the neck of the occipital condyle.

Lateral to the basipterygoid recess is another vertical inverted funnel-shaped pneumatic space that leads dorsally to the foramen for the internal carotid artery (Fig. 4, ica). Termed the lateral basisphenoid depression by Chure and Madsen (1996, 1998), this pneumatocoel is broadly exposed in lateral view. It surrounds the passage of the internal carotid artery, which enters the pituitary fossa dorsally via a small foramen. A rectangular flange of the basisphenoid forms the posterior edge of the carotid pneumatocoel (Fig. 4, bsf). Although hanging free in this specimen as a result of breakage, this flange is joined to the ventral margin of the paroccipital process and terminates above the basal tuber in *Acrocanthosaurus* and *C. saharicus*.

The middle portion of the floor of the endocranial cavity is divided by a low, sharp median ridge about 2 cm in length (eminentia medullaris of Huene 1907-1908), which is flanked by a groove on each side. This ridge and grooves are absent in *C. saharicus*, but similar structures have been reported in *Piatnitzkysaurus* (Rauhut, 2004a), a braincase possibly referable to *Stokesosaurus* (Chure and Madsen, 1998), and dromaeosaurids (Currie, 1995; Norell et al., 2004).

The fully coossified exoccipital-opisthotic forms the lateral and ventral margins of the foramen magnum (Fig. 5B). In posterior view, the exoccipitals are flat to each side of the foramen magnum and lack the shallow depressions seen in many coelurosaurs (Currie and Zhao, 1993b; Currie, 1995; Makovicky and Norell, 1998; Norell et al., 2004). A dorsolateral ridge on the exoccipital-opisthotic supports the occipital condyle neck. Ventral to this ridge, and lateral to the condyle, three foramina open into a groove, as best seen on the right side. These include two posterodorsal foramina for the exit of the hypoglossal (XII) nerve, which open laterally through the pedicle of the exoccipital-opisthotic, as in *Giganotosaurus* (Coria and Currie, 2002). More anteriorly, a larger foramen (jugular foramen) allows passage of the jugular vein and the vagus (X) and accessory (XI) nerves. The metotic strut that separates the jugular foramen from the adjacent fenestra ovalis is broken away. This partition, usually formed from both the exoccipital-opisthotic and prootic, is visible only on the roof of the combined openings.

The deep, platelike paroccipital process is preserved only on the left side and is broken distally and ventrally, but would have extended farther ventrally than the foramen magnum, as in *C. saharicus*, *Giganotosaurus*, *Acrocanthosaurus*, *Sinraptor*, and *Monolophosaurus*. It would have joined the basisphenoid flange below the ear region and continued as a web of bone to the lateral margin of the basal tuber (Fig. 4), as best preserved in *C. saharicus* (SGM-Din 1). This web of bone completely separates the otic region and its openings from the occiput. Coria and Currie (2002) have recently misinterpreted this region on the basis of an incomplete braincase of *Giganotosaurus*. Although they noted that the paroccipital processes and basisphenoid are broken ventrally, they claimed that in both *Carcharodontosaurus* and *Giganotosaurus* the fenestra ovalis opens onto the occiput, citing this configuration as a synapomorphy. They stated that the otic region is visible in posterior view of the braincase due to "enlargement of the jugular foramen" and "reorientation of the metotic fissure and fenestra ovalis onto the occiput" (Coria and Currie, 2002:fig. 7, p. 802, 808–809). In *C. saharicus* and *C. iguidensis*, this is clearly not the case. The structure and orientation of the otic region is typical of that in dinosaurs in general. On the left side of the braincase in *C. iguidensis*, the base of the paroccipital obscures the otic region in posterior view; even so it should be borne in mind that the ventral margin of the process is broken away (Fig. 5B). On the right side, the entire paroccipital process is broken away; even so the fenestra ovalis is not exposed but rather opens along the axis of the paroccipital process—posterolaterally and ventrally.

The axis of the paroccipital process angles about 45 degrees both ventrolaterally (in posterior view) and posterolaterally (in dorsal view) (Fig. 5). Consequently, the head and articular condyles of the quadrate may have articulated far posterior to the foramen magnum, as in *C. saharicus* and *Giganotosaurus*. The broken base of each paroccipital process reveals spongy bone with no development of the pneumatic spaces that are often present in coelurosaurs (Kurzanov, 1976; Clark et al., 1994; Sues, 1997; Makovicky and Norell, 1998; Brochu, 2002; Norell et al., 2004). The dorsal margin is rugose and pitted for articulation with the posterolateral wing of the parietal and the squamosal (Fig. 4). The preserved portion of the paroccipital process is relatively planar (about 10 mm thickness) as in *Acrocanthosaurus* (OMNH 10146) and shows no sign of distal twisting as occurs in some coelurosaurs (Currie, 1995; Norell et al., 2004).

A ridge on the anterior side of the exoccipital-opisthotic gains in strength as it passes anteromedially to join the ventral margin of the laterosphenoid. Ventral to this crest and inset lies the stapedial groove, which leads anteromedially to the fenestra ovalis (Fig. 4, gr). One fossa that may represent a pneumatic extension of the middle ear is located immediately above the jugular foramen, which is visible in posterolateral view of the braincase wall. Both *C. saharicus* and *Acrocanthosaurus* (OMNH 10146) have a similar fossa; the condition in *Giganotosaurus* was not described and remains unknown (Coria and Currie, 2002).

The prootic forms the anterior portion of the fenestra ovalis and borders foramina for the trigeminal (V) and facial (VII) nerves. The trigeminal foramen is about twice the size of the facial foramen and is located immediately anterodorsal to the latter, separated by a flattened septum. The two foramina are located within a single fossa, and the intervening septum is inset medially within the fossa (Fig. 4). In contrast, the fossa is shallower and the septum more superficial in *C. saharicus*, *Acrocanthosaurus*, and possibly *Giganotosaurus* (Coria and Currie 2002:fig 7). The inset septum is preserved on both sides of the braincase of *C. iguidensis*. Both trigeminal and facial foramina are located ventral to the nuchal process; a posterior position of these foramina has been regarded as a synapomorphy linking *Carcharodontosaurus* and *Giganotosaurus* (Coria and Currie 2002). The foramina are located anterior to the nuchal process in *Acrocanthosaurus*.

The trigeminal foramen is divided laterally by a strut of bone (Fig. 4, st), separating a dorsal portion for the ophthalmic branch (CN V1) from a larger ventral foramen for maxillary and mandibular branches (CN V2, 3). The strut has an anteroventral-posterodorsal orientation and is broken on both sides. The more complete left side preserves the broken bases of what may be a complete bridge of bone over the trigeminal opening. Neither *C. saharicus*, *Giganotosaurus*, nor *Acrocanthosaurus* (OMNH 10146) show similar separation of the trigeminal opening, although a second specimen of *Acrocanthosaurus* appears to have a completely divided foramen (NCSM 14345; P. Currie, pers. comm., February, 2006). The dorsal foramen in *C. iguidensis* exits anterolaterally not directly anteriorly as in some other dinosaurs with a divided trigeminal opening. Incipient bisection of the trigeminal foramen is present in *Sinraptor* (Currie and Zhao, 1993a) and *Dubreuillosaurus* (Allain, 2002). Separation by a complete septum is present in *Allosaurus*, *Piveteausaurus* (Taquet and Welles, 1977), and several coelurosaurs (Currie, 1985; Sues, 1997; Brochu, 2002).

The smaller facial foramen opens posterolaterally, and is separated from the trigeminal foramen by a narrow septum. In most theropods the facial nerve (CN VII) exits via a single foramen. However, two exits were described in *Acrocanthosaurus*: a dorsal foramen for the hyomandibular branch and a ventral foramen for the palatine branch (Franzosa and Rowe, 2005). In *C. iguidensis*, the internal side of the facial foramen on the wall of the endocranium is divided, with a smaller posterodorsal foramen passing into the middle ear cavity and a larger foramen exiting under the trigeminal opening. It is possible that the smaller foramen accommodated the chorda tympani, which passes through the middle ear cavity. It may exit laterally via a separate small foramen, which is preserved on both sides posterolateral to the trigeminal openings. This small foramen is obscured in lateral view by an overhanging ridge but is located near the upper end of the strut that divides the trigeminal opening (Fig. 4, st).

A preotic pendant (= crista prootica and ala basisphenoidalis of some authors) is preserved on the right side lateral to the pneumatized passage of the internal carotid artery; only the base of the process is present on the left side (Fig. 4). In medial view on the sidewall of the endocranium, the prootic contributes to the rounded rim of the floccular recess, which is bordered dorsally by a foramen for the dorsal head vein, which opens through the supraoccipital. Ventral to the floccular recess, the exits for the facial and vestibulocochlear (VIII) nerves lie within a shallow acoustic fossa, which is partially obscured by a fracture.

The laterosphenoid forms the anterolateral wall of the braincase. It is best preserved on the left side, which is lacking only the distal articular head (Fig. 4). The optic (II) and oculomotor (III) nerves exited anterolaterally via large foramina, the former anterior to the latter. Dorsally, the laterosphenoid arches laterally and expands into a transversely oriented ala (= capitate process), the anterior surface of which is more deeply pocketed in *C. iguidensis* than in *C. saharicus* (SGM-Din 1). The dorsal portion of the fossa is invaginated with a sharp anterior rim. The fossa extends approximately 10 mm dorsal to this rim.

The orbitosphenoid is fused to its opposite on the midline ventral to the olfactory bulbs and attaches to arcuate rugosities on the frontal (Fig. 4). The orbitosphenoid houses the cerebrum and is pierced by a foramen for the trochlear (IV) nerve. This foramen is larger on the right side than the left but still smaller than the other cranial nerve openings. The anterior portion of the orbitosphenoid is most complete on the right side, where there is preserved the dorsal portion of a fossa just below the flared openings for the olfactory tracts, as in *C. saharicus*. This portion of the bone may pertain to the sphenethmoid (Currie, 1997).

Lower Jaw

Dentary—A fragment of the anterior end of a very robust left dentary (Fig. 6) is referred to *C. iguidensis* based on its proximity to the holotypic locality and clear carcharodontosaurid affinity (Fig. 6). The first four and part of the fifth alveoli are preserved. The first two alveoli are small and nearly circular, whereas the third and fourth alveoli are larger and oval (Table 2). No teeth are preserved.

Several features of the dentary are uniquely shared with other carcharodontosaurids. The anterior end of the dentary has a squared profile as a result of anterodorsal and anteroventral processes (Fig. 6, adpr, avpr). A similar squared profile is also present in *Giganotosaurus* (Calvo and Coria, 2000), *Acrocanthosaurus* (NCSM 14345), and *Tyrannotitan* (Novas et al., 2005), and contrasts with the more rounded corners present in most theropods. Additionally, an anteroventral flange (Fig. 6, vpr) gives the dentary a 'chin,' which is present in *Giganotosaurus* and *Acrocanthosaurus* but apparently not in *Tyrannotitan*. Medially, the dentary symphysis in *C. iguidensis*, *Giganotosaurus*, and *Acrocanthosaurus* is reinforced by a discrete articular brace (Fig. 6C, abr), a raised, flattened process that articulates against its opposite in the midline. The high angle between the symphyseal surface and medial aspect of the dentary ramus clearly indicates that the symphyseal region was broad and rounded in dorsal view (Fig. 6D). A rounded symphyseal dentary arcade is characteristic of *Giganotosaurus*, *Acrocanthosaurus* and *Tyrannotitan* and differs from the narrow V-shaped arcades of many theropods, including some with broadened upper arcades such as tyrannosaurids.

In lateral view, the dentary is rugose, and is pierced by several neurovascular foramina (Fig. 6A). The largest foramina are located ventral to the alveolar margin and appear to form a linear series with exit grooves coursing dorsally. The posterior three are joined by a smooth external groove, which appears to have accommodated a large communicating branch. The posterior foramina in this series diverge from the alveolar margin, the most posterior possibly located just above mid-height of the dentary ramus. This ventrally deflected vascular groove is also present in *Giganotosaurus* (Calvo and Coria, 2000) and *Neovenator* (Naish et al., 2001), and differs from the more linear and elevated groove in *Allosaurus*, *Sinraptor*, and most theropods. A second series of foramina of smaller size are present posterodorsal to the anteroventral process. Like the other series, these foramina also

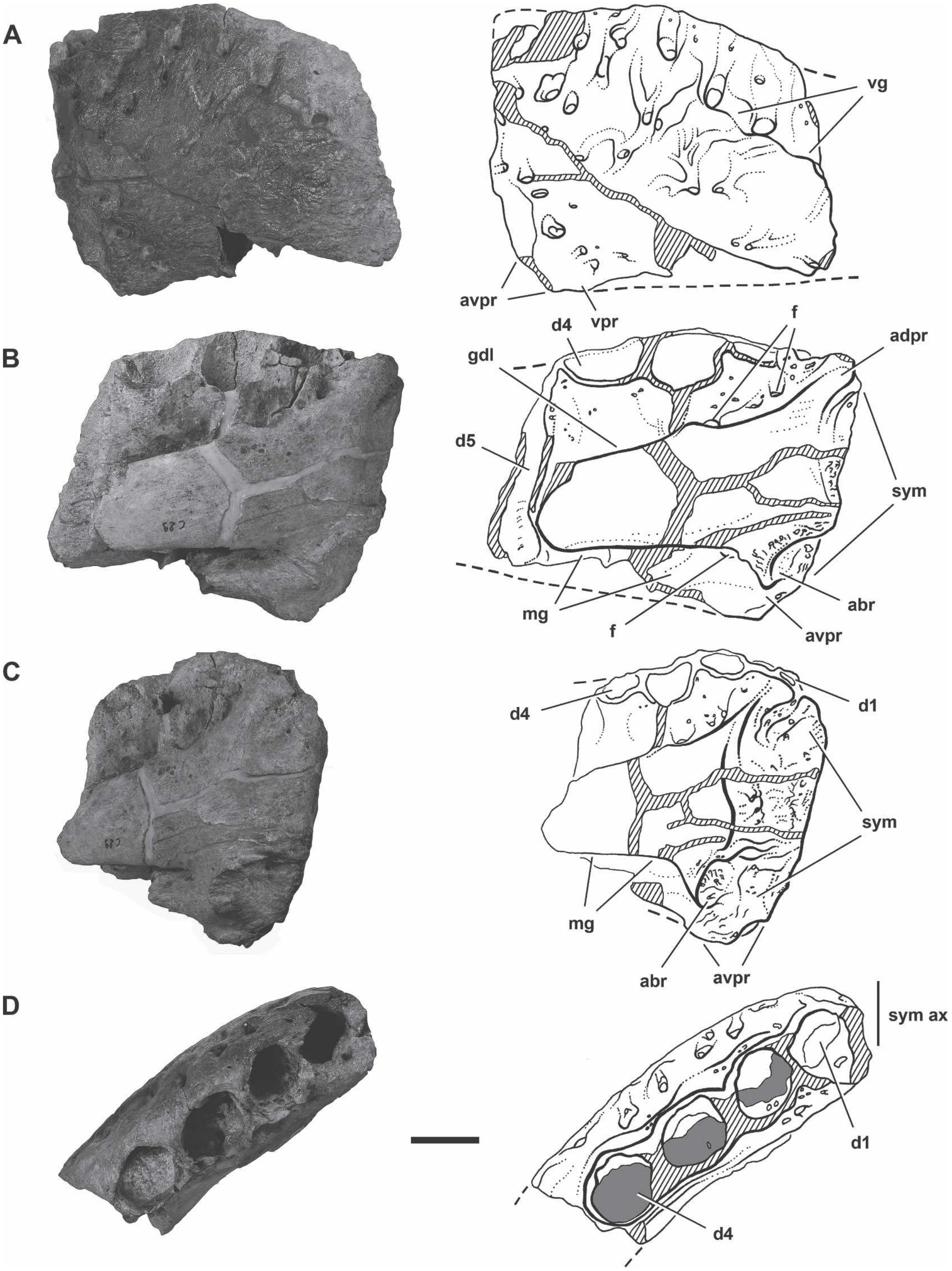

FIGURE 6. Photographs and line drawings of the anterior end of the left dentary of *Carcharodontosaurus iguidensis* n. sp. (MNN IGU5). **A**, lateral view; **B**, medial view; **C**, anteromedial view; **D**, dorsal view. **Abbreviations**: **abr**, articular brace; **adpr**, anterodorsal process; **avpr**, anteroventral process; **d1-5**, alveoli for dentary teeth 1-5; **f**, foramen; **gdl**, groove for the dental lamina; **mg**, Meckel's groove; **sym**, symphysis; **sym ax**, symphyseal axis (sagittal); **vg**, vascular groove; **vpr**, ventral process ("chin"). Scale bar equals 3 cm. Solid line in **D** indicates the plane of the dentary symphysis. Cross-hatching indicates broken bone, gray shade denotes matrix, and dashed lines show the projected continuation of broken bone.

have grooves that exit dorsally. In between these two rows are other foramina, some of which have divided, or V-shaped, exit grooves.

In medial view, a thickened band of the dentary lies between the fused interdental plates and Meckel's canal ventrally (Fig. 6B, C).The dental lamina lies deep within a groove along the top margin of the thickened band. This groove is enclosed by a roof of bone and pierced by several foramina from the third alveolus

TABLE 2. *Carcharodontosaurus iguidensis*, measurements (mm) of left dentary (MNN IGU5).

Alveolus 1, maximum anteroposterior diameter	26
Alveolus 2, maximum anteroposterior diameter	28
Alveolus 3, maximum anteroposterior diameter	34
Alveolus 4, maximum anteroposterior diameter	34
Alveoli 1–4, maximum anteroposterior length	390
Anterior end, depth	140
Symphysis, width	34

anteriorly (Fig. 6B). The roofed anterior portion curves dorsally, terminating along the posterior edge of the anterodorsal process. As a result, the interdental plates are dorsoventrally shallow anteriorly, but become progressively deeper posteriorly. Meckel's canal is present as a deep trough above the ventral margin of the dentary, and is deeply inset approximately 10 mm into the main body of the bone. It passes anteriorly into an oval foramen just posterior to the articular brace (Fig. 6B). A groove continues anteroventrally, passing between the articular brace and the anteroventral process.

Dentition

Crown—Several isolated teeth are referred to *C. iguidensis*, all of which were discovered in the vicinity of the holotypic locality (MNN IGU6-10). The crown, which is very similar to that in *C. saharicus* and *Giganotosaurus*, is blade-shaped with a distal margin that is only slightly recurved and often accompanied by arcuate enamel wrinkles. Although such wrinkles are also seen in some of the largest and most mature tyrannosaurids and certain basal tetanurans, they are more distinct and widespread along the tooth row in carcharodontosaurids, including *Giganotosaurus* and *Tyrannotitan*. However, in *C. iguidensis* the enamel wrinkles are never as numerous or well-developed as in the neotype of *C. saharicus* (Sereno et al., 1996), where they occur along most of the mesial and distal margins. In *C. iguidensis* the wrinkles are most visible toward the base of the distal carina (Fig. 7). On the distal carina, there are approximately 16 serrations every 5 mm at the crown base and 10 at the crown tip; on the mesial carina there are 13 and 9 every 5 mm, respectively. The denticles are unilobate, not bilobate as in *Tyrannotitan* (Novas et al., 2005).

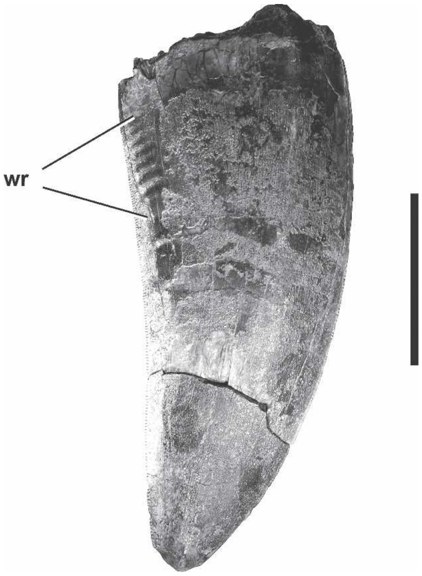

FIGURE 7. Isolated crown of *Carcharodontosaurus iguidensis* n. sp. (MNN IGU6) in lateral view. **Abbreviations**: **wr**, wrinkles in enamel. Scale bar equals 3 cm.

Endocast—The well-preserved interior of the braincase was split roughly in half when discovered, allowing for a direct observation of the endocranial cavity and molding for an endocast (Fig. 8B). The preserved portion of the endocast is 21 cm in length from the foramen magnum to the preserved end of the olfactory tract. With the skull roof held horizontal, the main axis of the endocast from cerebrum to cerebellum angles approximately 45 degrees posteroventrally. The olfactory tract and the brainstem at the foramen magnum are roughly horizontal, the former elevated above the latter as in *C. saharicus* (Larsson et al., 2000; Larsson, 2001) and *Allosaurus* (Hopson, 1979; Rogers, 1999). Compared to the endocast of *C. saharicus*, that of *C. iguidensis* has a distinctly broader cerebrum that is 15% greater in volume (Fig. 8), a feature that does not appear to be the result of crushing or distortion (Fig. 8A, B). Because the skulls of these species appear to be roughly similar in size, the larger cerebral volume in *C. iguidensis* is surprising. The difference, however, remains considerably less than the expanded cerebral volume measured in the comparably-sized coelurosaur *Tyrannosaurus* (Larsson et al., 2000).

Postcranium

Cervical Centrum—A single postaxial cervical centrum is preserved (Fig. 9). Its extremely low and broad proportions, hori-

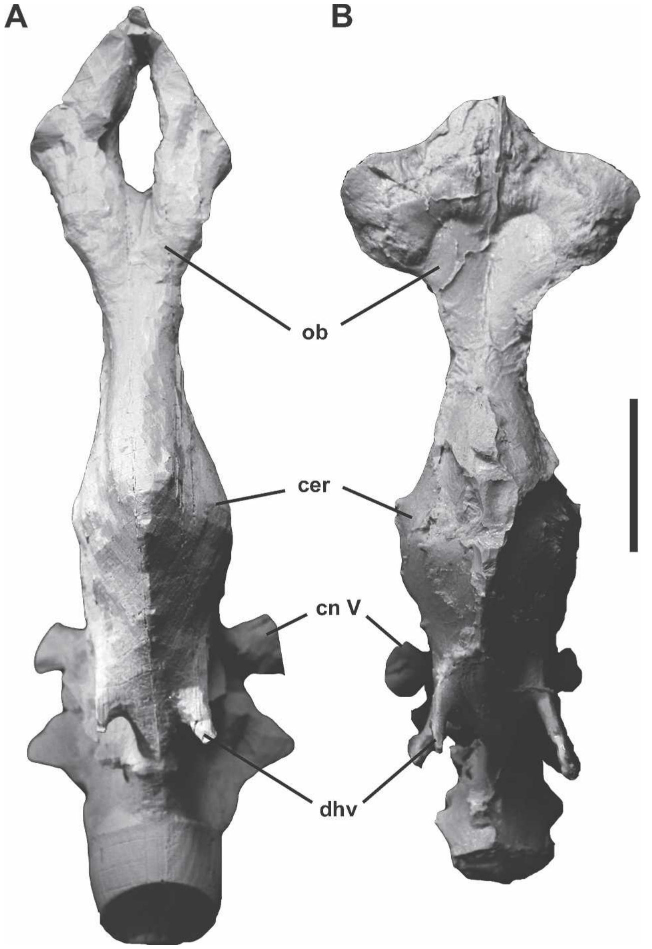

FIGURE 8. Endocasts of *Carcharodontosaurus* in dorsal view. **A**, *C. saharicus* (SGM-Din 1); **B**, *C. iguidensis* n. sp. (MNN IGU3). **Abbreviations**: **cer**, cerebrum; **cn V**, trigeminal nerve; **ob**, olfactory bulb; **dhv**, dorsal head vein (vena capitus dorsalis). Scale bar equals 5 cm.

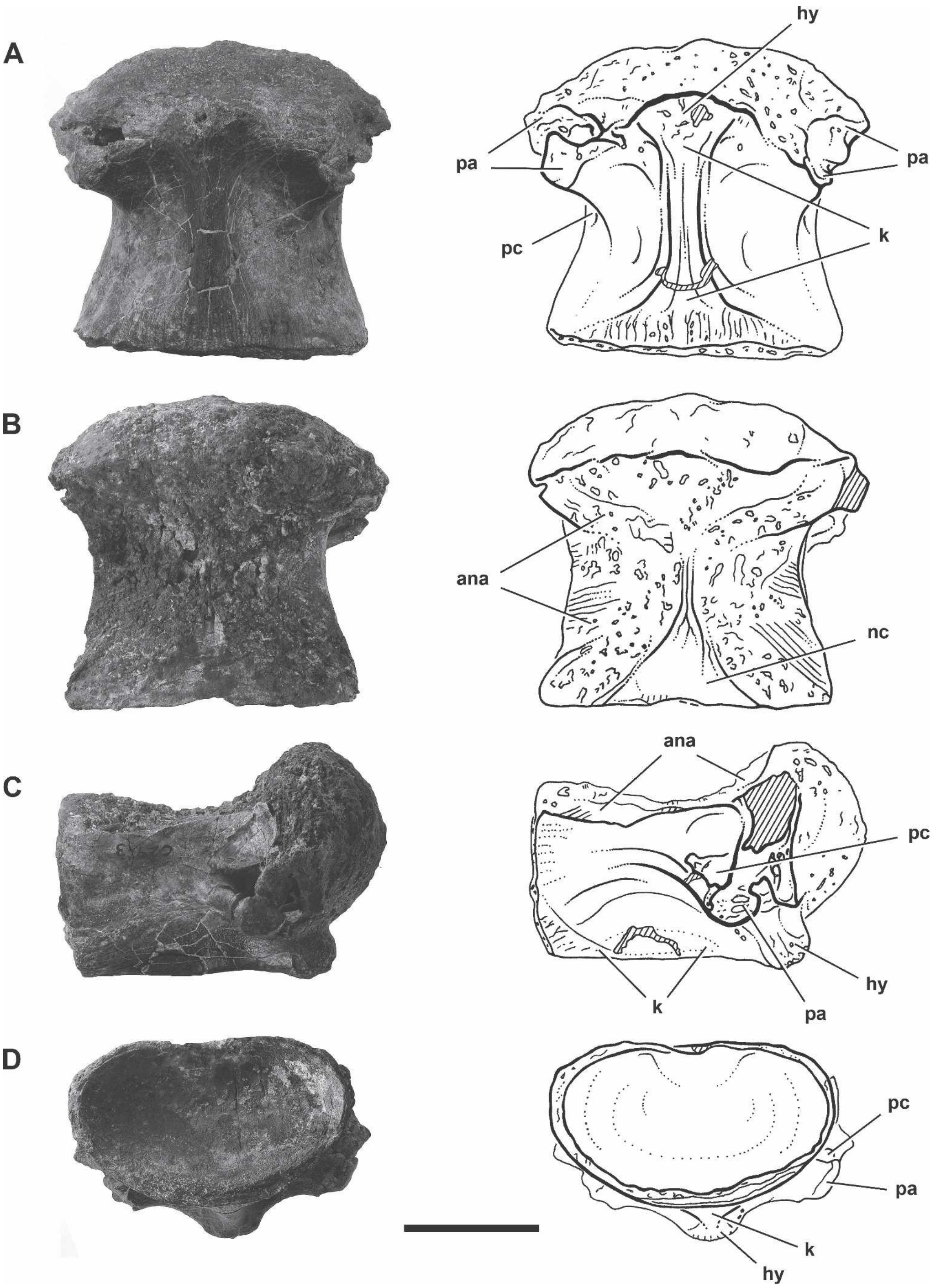

FIGURE 9. Photographs and line drawings of a cervical centrum of *Carcharodontosaurus iguidensis* n. sp. (MNN IGU11). **A**, ventral view; **B**, dorsal view; **C**, lateral view; **D**, posterior view. **Abbreviations**: **ana**, articular surface for the neural arch; **hy**, hypapophysis; **k**, ventral keel; **nc**, neural canal; **pa**, parapophysis; **pc**, pleurocoel. Scale bar equals 5 cm. Cross-hatching indicates broken bone.

zontal profile, kidney-shaped posterior articular surface (Fig. 9D), strong opisthocoely, and projecting ventral keel (Fig. 9A, C) closely resemble a vertebra from Morocco referred to *C. saharicus* (Sereno et al, 1996, fig. 2D) and another described by Stromer (1934:pl. 1, fig. 2) from Egypt. The extremely low and broad proportions are most easily measured on the rim of the posterior face, where centrum height is only slightly more than half (55) centrum width (Table 3).

In anterior view, the bulbous anterior end of the ventral keel forms a prominent hypapophysis that projects strongly below the

TABLE 3. *Carcharodontosaurus iguidensis*, measurements (mm) of cervical centrum (MNN IGU11).

Anteroposterior length (without anterior centrum face)	116
Anteroposterior length (with anterior centrum face)	90
Posterior centrum face, width	115
Posterior centrum face, height in midline	63
Depth of keel at mid length	20
Depth of centrum without keel at mid length	20
Maximum diameter of the parapophysis	35
Maximum diameter of the pleurocoel	21

dorsoventrally and transversely convex anterior articular face of the centrum (Fig. 9C). The keel is particularly well developed, equaling the depth of the remainder of the centrum. Anteriorly, the keel and centrum are separated by a shallow articular trough that received the ventral rim of the preceding vertebra (Fig. 9A). This trough is transversely convex, allowing the preceding vertebra to rotate from side to side and remain in articulation, but not to rotate farther ventrally.

In posterior view, the centrum is deeply concave and slightly reniform in shape, as the dorsal rim is slightly concave near the midline (Fig. 9B). In lateral view, the ventral margin of the centrum is nearly straight and formed by the strong ventral keel. The anterior face of the centrum is elevated somewhat above the posterior articular face. The oval parapophysis is located anteroventral to the smaller pleurocoel (Fig. 9C), and exposed equally in ventral and lateral views (Fig. 9A, C). In dorsal view, the scars for the neural arch are broad (Fig. 9B). They converge toward the midline and merge with one another along the anterior half of the centrum, as is also the case in *C. saharicus* (SGM-Din 3).

The very broad cervical proportions and strong development of the ventral keel characterize *Carcharodontosaurus* and appear to be absent in other allosauroids. The cervical series is only partially preserved in *Giganotosaurus*, *Mapusaurus*, and *Acrocanthosaurus*, but the centra appear to have subcircular posterior articular faces and much weaker ventral keels (Harris, 1998; Coria and Currie, 2006).

DISCUSSION

A new species, *Carcharodontosaurus iguidensis*, is established on the first well-preserved carcharodontosaurid specimens from Niger. Lapparent (1953, 1960) and Sereno and colleagues (1998) provisionally referred all carcharodontosaurid material from Albian and Cenomanian-age rocks in northern Africa to *Carcharodontosaurus* (*Megalosaurus*) *saharicus*. However, the recognition of *C. iguidensis* suggests that much isolated carcharodontosaurid material from the Sahara region may in fact pertain to this new species. Recognition of *C. iguidensis* reveals diversity at the specific level that was previously unknown, as has also proven to be the case with Nigerienne and Moroccan abelisaurid material from the same horizons (Mahler, 2005). Likewise, other undescribed vertebrates from the Cenomanian of Niger also show differences from their counterparts to the north in Morocco and Egypt (Sereno, unpubl. data). The presence of distinct species in the Cenomanian of Niger and Morocco suggests localized faunal differentiation, possibly the result of shallow continental seas that may have acted as temporary barriers (Reyment and Dingle, 1987). Alternatively, temporal discordance between these geographically widespread localities may explain this faunal differentiation, despite their similar geological disposition immediately under the Cenomanian-Turonian limestone platform. At present there is no way to distinguish between these alternative hypotheses in the absence of radiometric ages for any of the fossil-bearing deposits of Cretaceous age in the Sahara.

Remains of *C. iguidensis* were found in proximity to the basal abelisaurid *Rugops primus* (Sereno et al., 2004) and at least one spinosaurid taxon, tentatively referred to *Spinosaurus* sp. on the basis of teeth. The same triumvirate of large-bodied carnivores—a carcharodontosaurid, abelisaurid, and spinosaurid—is present in horizons of Early Cretaceous age in Niger (Brusatte and Sereno, 2006; unpubl. data) and may represent an ecological partitioning that existed for much of the Cretaceous on Africa, and possibly South America as well (Medeiros and Schultz, 2002). Each of these carnivores has very distinctive cranial and dental morphology, suggesting that their coexistence may have been enabled by dietary niche partitioning.

Furthermore, the identification of *C. iguidensis* also increases the known diversity within Carcharodontosauridae, a geographically widespread clade of Cretaceous allosauroid theropods that includes *Carcharodontosaurus* from northern Africa; *Giganotosaurus*, *Mapusaurus*, and *Tyrannotitan* from South America; *Acrocanthosaurus* from North America; and *Neovenator* from Europe (Hutt et al., 1996) (Brusatte and Sereno, unpublished data). Although recent studies have strongly supported an allosauroid affinity for carcharodontosaurids, much disagreement remains over the membership and relationships within this clade (e.g. Rauhut, 1995; Sereno et al., 1996; Harris, 1998; Currie and Carpenter, 2000; Holtz, 2000; Allain, 2002; Coria and Currie, 2002; Rauhut, 2003; Holtz et al., 2004; Novas et al., 2005). Whereas most studies agree that *Carcharodontosaurus* and *Giganotosaurus* (and the recently described *Mapusaurus*) form a clade of derived carcharodontosaurids, disagreements persist regarding the placement of *Acrocanthosaurus*, which some authors regard as more closely related to *Allosaurus* than to carcharodontosaurids (e.g., Currie and Carpenter, 2000; Allain, 2002; Novas et al., 2005). A reappraisal of allosauroid phylogeny is in progress by the authors (Brusatte and Sereno, unpubl. data). As this study will be published elsewhere, no numerical cladistic analysis is presented here. However, a brief discussion of several relevant characters is warranted, based on the new material described here.

Carcharodontosaurus (*C. saharicus* and *C. iguidensis*) and *Giganotosaurus* clearly comprise a clade of derived carcharodontosaurids, which also includes the recently-described *Mapusaurus* (Coria and Currie, 2006). These taxa share several characters, including a reduced extension of the supratemporal fossae onto the frontal, a pair of pneumatic openings piercing the occipital condyle neck, the posterior position of cranial nerves V and VII, and an ossified interorbital septum (unknown in *C. iguidensis*) (Coria and Currie, 2002). No clear synapomorphies link *C. iguidensis* and *Giganotosaurus* to the exclusion of *C. saharicus*.

Cranial and vertebral characters support the placement of *Acrocanthosaurus* within Carcharodontosauridae, a topology affirmed by the larger cladistic analysis undertaken by the authors (Brusatte and Sereno, unpubl. data). *Acrocanthosaurus* shares three unambiguous dentary synapomorphies with *Carcharodontosaurus* and *Giganotosaurus*: a squared-off anterior end, a ventral projection, and a broad, “U”-shaped snout. Additionally, these taxa are united by cervical vertebrae with anterior and posterior articular facets positioned at nearly the same level, while *Acrocanthosaurus* and *Carcharodontosaurus* are both characterized by cervical vertebrae with posterior articular surfaces at least 20% broader than tall. While *Acrocanthosaurus* shares no unambiguous maxillary or braincase synapomorphies with *Carcharodontosaurus* and *Giganotosaurus*, these three taxa are linked by several other cranial characters, including: fused frontals, a fused frontal-parietal suture, and a postorbital-lacrimal brow that excludes the frontal from the orbital rim. A more complete analysis of allosauroid phylogeny, including a detailed discussion of *Acrocanthosaurus*, will be presented by the authors elsewhere.

CONCLUSIONS

A new species of *Carcharodontosaurus*, *C. iguidensis* n. sp., is described from the Late Cretaceous Echkar Formation of Niger, which is roughly coeval with Cenomanian beds elsewhere in northern Africa (Egypt, Tunisia, Algeria, Morocco). The type species, *Carcharodontosaurus* (*Megalosaurus*) *saharicus*, was based originally on Algerian and, later, Egyptian specimens that were subsequently lost and destroyed, respectively. We designate a neotype for *C. saharicus* based on a well preserved cranium from Morocco that shares with *C. iguidensis* the marked groove texturing of the external surface of the maxilla. Several aspects of the skull of *C. iguidensis* and *C. saharicus* differ, justifying the erection of a distinct southern species. *C. iguidensis* and the abelisaurid *Rugops primus* are the first theropods to be described from a rich Cenomanian-age vertebrate fauna initially discovered by Lapparent near the oasis at In Abangharit in Niger. This vertebrate fauna has begun to document regional differentiation on Africa during the early Late Cretaceous.

ACKNOWLEDGMENTS

We thank J. Harris (Dixie State College) and T. Carr (Carthage College) for critical comments that improved the paper; P. Currie, D. Dutheil, J. Franzosa, S. Hutt, H.-D. Sues, M. Webster, and L. Witmer for discussion and historical information; C. Abraczinskas for guidance on all figures and construction of Figure 1; T. Keillor for extensive preparation and B. Masek and R. Vodden for minor preparation; and R. Cifelli (OMNH) and R. Coria (Museo Carmen Funes) for access to specimens in their care. English translations of Rauhut (1995) and Taquet and Welles (1977) are available at The Polyglot Paleontologist (http://ravenel.si.edu/paleo/paleoglot/index.cfm). This research was supported by the Howard Hughes Institute Undergraduate Education Initiative Grant at the University of Chicago and the University of Chicago Behrens Fund (to S.L.B.) and NSF (to P.C.S.).

LITERATURE CITED

Allain, R. 2002. Discovery of megalosaur (Dinosauria, Theropoda) in the Middle Bathonian of Normandy (France) and its implications for the phylogeny of basal Tetanurae. Journal of Vertebrate Paleontology 22:548–563.

Benton, M. J., S. Bouaziz, E. Buffetaut, D. Martill, M. Ouaja, M. Soussi, and C. Trueman. 2000.

Dinosaurs and other fossil vertebrates from fluvial deposits in the Lower Cretaceous of southern Tunisia. Palaeogeography, Palaeoclimatology, Palaeoecology 157:227–246.

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

Brochu, C. A. 2002. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. Society of Vertebrate Paleontology Memoir 7:1–138.

Brusatte, S., and P. Sereno. 2006. Basal abelisaurid and carcharodontosaurids from the Elrhaz Formation (Aptian-Albian) of Niger. Journal of Vertebrate Paleontology 26(3):46A.

Calvo, J. O., and R. Coria. 2000. New specimen of *Giganotosaurus carolinii* (Coria & Salgado, 1995), supports it as the largest theropod ever found. Gaia 15:117–122.

Carrano, M. T., S. D. Sampson, and C. A. Forster. 2002. The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 22:510–534.

Chure, D. J., and J. H. Madsen. 1996. Variation in aspects of the tympanic pneumatic system in a population of *Allosaurus fragilis* from the Morrison Formation (Upper Jurassic). Journal of Vertebrate Paleontology 16:63–66.

Chure, D. J., and J. H. Madsen 1998. An unusual braincase (?*Stokesosaurus clevelandi*) from the Cleveland-Lloyd Dinosaur Quarry, Utah (Morrison Formation; Late Jurassic). Journal of Vertebrate Paleontology 18:115–125.

Clark, J. M., P. Altangerel, and M. A. Norell. 1994. The skull of *Erlicosaurus andrewsi*, a Late Cretaceous "segnosaurs" (Theropoda: Therezinosauridae) from Mongolia. American Museum Novitates 3115:1–39.

Coria, R. A., and P. J. Currie. 2002. The braincase of *Giganotosaurus carolinii* (Dinosauria: Theropoda) from the Upper Cretaceous of Argentina. Journal of Vertebrate Paleontology 22:802–811.

Coria, R. A., and P. J. Currie 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. Geodiversitas 28:71–118.

Coria, R. A., and L. Salgado. 1995. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. Nature 377:224–226.

Currie, P. J. 1985. Cranial anatomy of *Stenonychosaurus inequalis* (Saurischia, Theropoda) and its bearing on the origin of birds. Canadian Journal of Earth Sciences 22:1643–1658.

Currie, P. J. 1995. New information on the anatomy and relationships of *Dromaeosaurus albertensis* (Dinosauria: Theropoda). Journal of Vertebrate Paleontology 15:576–591.

Currie, P. J. 1997. Braincase anatomy; pp. 81–85 *in* P.J. Currie and K. Padian (eds.), The Encyclopedia of Dinosaurs. Academic Press, New York.

Currie, P. J., and K. Carpenter. 2000. A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. Geodiversitas 22:207–246.

Currie, P. J., and X.-J. Zhao. 1993a. A new large theropod (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. Canadian Journal of Earth Sciences 30:2037–2081.

Currie, P. J., and X.-J. Zhao 1993b. A new troodontid (Dinosauria, Theropoda) braincase from the Dinosaur Park Formation (Campanian) of Alberta. Canadian Journal of Earth Sciences 30:2231–2247.

de Klerk, W. J., C. A. Forster, S. D. Sampson, A. Chinsamy, and C. F. Ross. 2000. A new coelurosaurian dinosaur from the Early Cretaceous of South Africa. Journal of Vertebrate Paleontology 20: 324–332.

Depéret, C., and J. Savornin. 1925. Sur la découverte d'une faune de Vertébrés albiens à Timimoun (Sahara occidental). Comptes Rendus de l'Academic de Sciences 181:1108.

Depéret, C., and J. Savornin. 1927. La faune de reptiles et de poisons albiens de Timimoun (Sahara algérien). Bulletin de la société géologique de France 27:257–265.

Ferrandini, M., J. Philip, J. F. Babinot, J. Ferrandini, and G. Tronchetti. 1985. La plate-forme carbonatée du Cénomano-Turonien de la région d'Erfoud-Errachidia (Sud-est marocain): stratigraphie et paléoenvironnements. Bulletin de la société géologique de France 8, t. I (4):559–564.

Franzosa, J., and T. Rowe. 2005. Cranial endocast of the Cretaceous theropod dinosaur *Acrocanthosaurus atokensis*. Journal of Vertebrate Paleontology 25:859–864.

Harris, J. D. 1998. A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and Paleobiogeographic implications, based on a new specimen from Texas. New Mexico Museum of Natural History and Science Bulletin 13:1–75.

Holtz, T. R. 2000. A new phylogeny of the carnivorous dinosaurs. Gaia 15:5–61.

Holtz, T. R., R. E. Molnar, and P. J. Currie. 2004. Basal Tetanurae; pp. 71–110 in D. B. Weishampel, P. Dodson, and H. Osmolska (eds.), The Dinosauria (2nd ed.). University of California Press, Berkeley, California.

Hopson, J. A. 1979. Paleoneurology; pp. 39–146 *in* C. Gans (ed.), Biology of the Reptilia. Academic Press, New York.

Huene, F. von. 1907–1908. Die Dinosaurier der Europaischen Triasformation. Geologische und Palaeontologische Abhandlungen, Jena. Supplement Band 1:1–419.

Hutt, S., D. M. Martill, and M. J. Barker. 1996. The first European allosaurid (Lower Cretaceous, Wealden Group, England). Neues Jahrbuch für Geologie une Paläontologie, Monatshefte 1996: 635–644.

Kirkland, J. I., L. E. Zanno, S. D. Sampson, J. M. Clark, and D. D. DeBlieux. 2005. A primitive therizinosauroid dinosaur from the Early Cretaceous of Utah. Nature 435:84–87.

Kurzanov, S. M. 1976. Braincase structure in the carnosaur *Itemirus* n. gen. and some aspects of the cranial anatomy of dinosaurs. Paleontological Journal 10:361–369.

Lamanna, M. C., R. D. Martínez, and J. B. Smith. 2002. A definitive abelisaurid theropod dinosaur from the Early Late Cretaceous of Patagonia. Journal of Vertebrate Paleontology 22:58–69.

Lapparent, A.F. de 1953. Reconnaissance de gisements à dinosauriens du Tamesna (Sahara méridional). Travail de l'Institut de Recherche saharienne 10:7–17.

Lapparent, A. F. de 1960. Les dinosauriens du "continental intercalaire" du Sahara central. Mémoires de la Société Géologique de France 88A.

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

Larsson, H. C. E., P. C. Sereno, and J. A. Wilson. 2000. Forebrain enlargement among nonavian Theropod dinosaurs. Journal of Vertebrate Paleontology 20:615–618.

Linnaeus, C. 1758. Systema Naturae per Raegna Tria Naturae.Vol. 1.Regnum Animale. [photographic facsimile]. Trustees of the British Museum of Natural History, 823 pp.

Madsen, J. H. 1976. *Allosaurus fragilis*: a revised osteology. Utah Geological Survey Bulletin 109:1–163.

Mahler, L. 2005. Record of Abelisauridae (Dinosauria: Theropoda) from the Cenomanian of Morocco. Journal of Vertebrate Paleontology 25:236–239.

Makovicky, P. J., and Norell, M. A. 1998. A partial ornithomimid braincase from Ukhaa Tolgod (Upper Cretaceous, Mongolia). American Museum Novitates 3247:1–16.

Marsh, O. C. 1877. Notice of new dinosaurian reptiles from the Jurassic Formation. American Journal of Science (Series 3) 14:514–516.

Marsh, O. C. 1878. Principal characters of American Jurassic dinosaurs. Pt. 1. American Journal of Science (Series 3) 16:411–416.

Marsh, O. C. 1881. Principal characters of American Jurassic dinosaurs. Part V. American Journal of Science (Series 3) 21:417–423.

Medeiros, M. A., and C. L. Schultz. 2002. A fauna dinossauriana da "Laje do Coringa," Cretáceo médio do nordeste do Brasil. Arquivos do Museu Nacional, Rio de Janeiro 60:155–162.

Monbaron, M., D. A. Russell, and P. Taquet. 1999. *Atlasaurus imelakei* n.g., n.sp., a brachiosaurid-like sauropod from the Middle Jurassic of Morocco. Comptes Rendus de l'Academie des Sciences 329: 519–526.

Naish, D., S. Hutt, and D. M. Martill. 2001. Saurischian dinosaurs 2: theropods; pp. 242–309 in D. M. Martill and D. Naish (eds.), Dinosaurs of the Isle of Wight. The Palaeontological Association, London.

Norell, M. A., P. J. Makovicky, and J. M. Clark. 2004. The braincase of *Velociraptor*; pp. 133– 143 in P. J. Currie, E. B. Koppelhus, M. A. Shugar, and J. L. Wright (eds.), Feathered Dragons: Studies on the Transition from Dinosaurs to Birds. Indiana University Press, Bloomington, Indiana.

Nothdurft, W., J. B. Smith, M. C. Lamanna, K. J. Lacovara, J. C. Poole, and J. R. Smith. 2002. The Lost Dinosaurs of Egypt. Random House, New York.

Novas, F. E., S. de Valais, P. Vickers-Rich, and T. Rich. 2005. A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. Naturwissenschaften 92:226–230.

Osmólska, H. 2004. Evidence on relation of brain to endocranial cavity in oviraptorid dinosaurs. Acta Palaeontologica Polonica 49:321–324.

Owen, R. 1842. Report on British fossil reptiles. Report of the British Association for the Advancement of Science 11 (1841):60–294.

Rauhut, O. W. M. 1995. Zur systematischen Stellung der afrikanischen Theropoden *Carcharodontosaurus* Stromer 1931 und *Bahariasaurus* Stromer 1934. Berliner Geowissenschaften Abhlandlungen E 16: 357–375.

Rauhut, O. W. M. 2003. The interrelationships and evolution of basal theropod dinosaurs. Special Papers in Palaeontology 69:1–213.

Rauhut, O. W. M. 2004a. Braincase structure of the Middle Jurassic theropod dinosaur *Piatnitzkysaurus*. Canadian Journal of Earth Sciences 41:1109–1122.

Rauhut, O. W. M. 2004b. Provenance and anatomy of *Genyodectes serus*, a large-toothed ceratosaur (Dinosauria: Theropoda) from Patagonia. Journal of Vertebrate Paleontology 24:894–902.

Reyment, R. A., and R. V. Dingle. 1987. Palaeogeography of Africa during the Cretaceous Period. Palaeogeography, Palaeoclimatology, Palaeoecology 59:93–116.

Rogers, S. W. 1999. Exploring dinosaur neuropaleobiology: computed tomography scanning and analysis of an *Allosaurus fragilis* endocast. Neuron 21:673–679.

Russell, D. A. 1996. Isolated dinosaur bones from the Middle Cretaceous of the Tafilalt, Morocco. Bulletin du Muséum national d'Histoire naturelle, série 4, 18:349–402.

Sampson, S. D., L. M. Witmer, C. A. Forster, D. W. Krause, P. M. O'Connor, P. Dodson, and F. Ravoavy. 1998. Predatory dinosaur remains from Madagascar: implications for Cretaceous biogeography of Gondwana. Science 280:1048–1051.

Seeley, H. G. 1888. On the classification of the fossil animals commonly named Dinosauria. Proceedings of the Royal Society of London 43:165–171.

Sereno, P. C. 1998. A rationale for phylogenetic definitions, with application to the higher-level phylogeny of Dinosauria. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 210:41–83.

Sereno, P. C. 2005. Stem Archosauria—TaxonSearch. Available at: http://www.taxonsearch.org/dev/file_home.php [version 1.0, 2005 November 7, linked to Sereno et al. 2005 reference below]

Sereno, P. C., S. McAllister, and S. L. Brusatte. 2005. TaxonSearch: a relational database for documenting taxa and their phylogenetic definitions. Phyloinformatics 8:1–21.

Sereno, P. C., J. A. Wilson, and J. L. Conrad. 2004. New dinosaurs link southern landmasses in the Mid-Cretaceous. Proceedings of the Royal Society, Series B 271:1325–1330.

Sereno, P. C., D. B. Dutheil, M. Iarochene, H. C. E. Larsson, G. H. Lyon, P. M. Magwene, C. A. Sidor, D. J. Varricchio, and J. A. Wilson. 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. Science 272:986–991.

Sereno, P. C., A. L. Beck, D. B. Dutheil, H. C. E. Larsson, G. H. Lyon, B. Moussa, R. W. Sadleir, C. A. Sidor, D. J, Varricchio, G. P. Wilson, and J. A. Wilson. 1999.Cretaceous sauropods from the Sahara and the uneven rate of skeletal evolution among dinosaurs. Science 286:1342–1347.

Sereno, P. C., A. L. Beck, D. B. Dutheil, B. Gado, H. C. E. Larsson, G. H. Lyon, J. D. Marcot, O. W. M. Rauhut, R. W. Sadleir, C. A. Sidor, D. D. Varricchio, G. P. Wilson, and J. A. Wilson. 1998. A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. Science 282:1298–1302.

Smith, J. B., M. C. Lamanna, K. J. Lacovara, P. Dodson, J. R. Smith, J. C. Poole, R. Giegengack, and Y. Attia. 2001. A giant sauropod dinosaur from an Upper Cretaceous mangrove deposit in Egypt. Science 292:1704–1706.

Smith, J. B., D. R. Vann, and P. Dodson. 2005. Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. The Anatomical Record 285A: 699–736.

Stovall, J. W., and W. Langston. 1950. *Acrocanthosaurus atokensis*, a new genus and species of Lower Cretaceous Theropoda from Oklahoma. American Midland Naturalist 43:696–728.

Stromer, E. 1931. Ergebnisse der Forschungsrisen Prof. E. Stromers in den Wüsten Ägyptens.II. Wirbeltierreste der Baharje-Stufe (unterstes Cenoman). 10. Ein Skelett-Rest von Carcharodontosaurus no. gen. Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, Neue Folge 9: 1–23.

Stromer, E. 1934. Ergebnisse der Forschungsreisen Prof E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharje-Stufe (unterstes Cenoman). 13. Dinosauria von E. Stromer. Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, Neue Folge 22:1–79.

Sues, H.-D. 1997. On *Chirostenotes*, a Late Cretaceous oviraptorosaur (Dinosauria: Theropoda) from Western North America. Journal of Vertebrate Paleontology 17:698–716.

Sues, H.-D., E. Frey, D. M. Martill, and D. M. Scott. 2002. *Irritator challengeri*, a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. Journal of Vertebrate Paleontology 22: 535–547.

Taquet, P., and S. P. Welles. 1977. Redescription du crâne de dinosaure de Dives Normandie. Annales de Paléontologie 63:191–206.

Witmer, L. M. 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with analysis of the function of pneumaticity. Society of Vertebrate Paleontology Memoir 3:1–73.

Zhao, X.-J., and P. J. Currie. 1993. A large crested theropod from the Jurassic of Xinjiang, People's Republic of China. Canadian Journal of Earth Sciences 30:2027–2036.

Submitted August 22, 2006; accepted May 12, 2007.