Basal abelisaurid and carcharodontosaurid theropods from the Lower Cretaceous Elrhaz Formation of Niger

PAUL C. SERENO and STEPHEN L. BRUSATTE


We report the discovery of basal abelisaurid and carcharodontosaurid theropods from the mid Cretaceous (Aptian–Albian, ca. 112 Ma) Elrhaz Formation of the Niger Republic. The abelisaurid, *Kryptops palaios* gen. et sp. nov., is represented by a single individual preserving the maxilla, pelvic girdle, vertebrae and ribs. Several features, including a maxilla textured externally by impressed vascular grooves and a narrow antorbital fossa, clearly place *Kryptops palaios* within Abelisauridae as its oldest known member. The carcharodontosaurid, *Eocarcharia dinops* gen. et sp. nov., is represented by several cranial bones and isolated teeth. Phylogenetic analysis places it as a basal carcharodontosaurid, similar to *Acrocanthosaurus* and less derived than *Carcharodontosaurus* and *Giganotosaurus*. The discovery of these taxa suggests that large body size and many of the derived cranial features of abelisaurids and carcharodontosaurs had already evolved by the mid Cretaceous. The presence of a close relative of the North American genus *Acrocanthosaurus* on Africa suggests that carcharodontosaurs had already achieved a trans-Tethyan distribution by the mid Cretaceous.

Key words: Theropoda, Abelisauridae, Allosauroida, Carcharodontosauridae, *Kryptops*, *Eocarcharia*, Cretaceous, Africa.

Paul C. Sereno [dinosaur@uchicago.edu], Department of Organismal Biology and Anatomy, University of Chicago, 1027 E. 57th Street, Chicago, Illinois, 60637, USA; Stephen L. Brusatte [brusatte@uchicago.edu], Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen’s Road, Bristol BS8 1RJ, United Kingdom.

Introduction

Large-bodied theropods of very distinctive form have long been known from southern, or Gondwanan, continents and include the short-snouted abelisaurids (Bonaparte et al. 1990; Coria et al. 2002; Wilson et al. 2003; Sampson and Krause 2007), long-snouted spinosaurids (Stromer 1915; Sereno et al. 1998; Sues et al. 2002), and large-skulled carcharodontosaurs (Stromer 1931; Coria and Salgado 1995; Sereno et al. 1996; Coria and Currie 2006; Brusatte and Sereno 2007). All three of these clades are now known to have northern representatives (Charig and Milner 1997; Harris 1998; Currie and Carpenter 2000; Accarie et al. 1995), and so understanding their origins and interrelationships carries particular biogeographic significance (Rauhut 2003; Holtz et al. 2004; Sereno et al. 2004; Brusatte and Sereno in press). Their position within Neotheropoda nevertheless, must be considered tentative, in part because basal representatives are poorly known.

We report the discovery of two new species, a basal abelisaurid and carcharodontosaurid, from the Elrhaz Formation of Niger, which is regarded as Aptian–Albian in age (ca. 112 Ma; Gradstein et al. 2004). The spinosaurid *Suchomimus tenerensis* is the most common large theropod in the fauna (Sereno et al. 1998). The new taxa, which are among the earliest known members of their respective clades, indicate that large body size and some of the cranial features that diagnose their respective groups had already evolved by the mid Cretaceous.

The basal abelisaurid provides new evidence for the early appearance of the textured, short-snouted skull form within this clade, as well as unequivocal proof of the presence of abelisaurids on Africa before the close of the Early Cretaceous. Its axial column and pelvic girdle retain a number of primitive features. The new carcharodontosaurid, based on skull bones and teeth from several individuals, shows many similarities to *Acrocanthosaurus*, a North American genus that has been re-interpreted as a carcharodontosaurid (Sereno et al. 1996; Harris 1998; Brusatte and Sereno in press). The new taxon adds to previous evidence suggesting that carcharodontosaurs flourished and had achieved a trans-Tethyan distribution before the close of the Early Cretaceous (Sereno et al. 1996; Krause et al. 2006).

Geologic setting

The fossils in this report were recovered from the Elrhaz Formation of Niger, which is regarded as Aptian–Albian in age (ca. 112 Ma; Gradstein et al. 2004). The spinosaurid *Suchomimus tenerensis* is the most common large theropod in the fauna (Sereno et al. 1998). The new taxa, which are among the earliest known members of their respective clades, indicate that large body size and some of the cranial features that diagnose their respective groups had already evolved by the mid Cretaceous.
coid sauropod *Nigersaurus taqueti*, the ornithopods *Ouranosaurus nigeriensis* and *Lurdusaurus arenatus*, several crocodylians and chelonians, as well as bony fish, a hybodont shark, and freshwater bivalves (Taquet 1975; Sereno et al. 1998, 1999, 2001, 2007; Taquet and Russell 1999; Table 1). 

**Material and methods**

The bones attributed to the holotype and only known specimen of the new abelisaurid likely belong to a single disarticulated adult individual (Figs. 1B, 2–7). The maxilla was eroded free of matrix and transported approximately 15 meters distant from the other bones, all of which were partially exposed but preserved in place (Fig. 1B). Except two teeth from disparate species (Fig. 8), there were no other vertebrate remains in the immediate area of the holotype. This association is key, as the pelvic girdle is more primitive in form than any other known abelisaurid. Like the maxilla, nevertheless, there are features in the pelvic girdle indicative of abelisaurid affinity as described below.

All of the remains of the new carcharodontosaurid, in contrast, were found in isolation (Figs. 9–17). An isolated postorbital was chosen as the holotype, as this roofing bone is diagnostically of the species and also allows referral to Carcharodontosauridae (Figs. 9, 10). The orientation, length, unusual slot-and-groove form of its articulation with the frontal, and surface of the supratemporal fossa clearly matches the opposing articular surfaces and continuation of the fossa on two frontals from the same formation (Figs. 9, 10, 18A). One of these frontals is articulated with a prefrontal (Figs. 14, 15) and the other with a parietal (Fig. 16), suggesting that all of these bones pertain to the same species. The more tenuous association of the maxilla is based on similarity to the maxillae and maxillary teeth of other carcharodontosaurids, and its distinction from the same in other large theropods from the Elrhaz Formation, namely the new abelisaurid and the spinosaurid *Suchomimus tenerensis* (Sereno et al. 1998). The exposed erupting crown in the maxilla (Fig. 17A) matches several isolated teeth found in the formation (Fig. 17B), suggesting that they may well pertain to the new carcharodontosaurid.

To avoid potentially confusing phrases, we use traditional, or “Romerian”, terms of orientation (e.g., anterior, posterior) versus their veterinarian equivalents (e.g., rostral, caudal) (Wilson 2006). Our phylogenetic analyses use maximum parsimony as implemented by PAUP* 4.0 (Swofford 1998).

**Institutional abbreviations.**—AMNH, American Museum of Natural History, New York, New York, USA; BMNH, Natural History Museum, London; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People’s Republic of China; MACN, Museo Argentino de Ciencias
Systematic paleontology

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Ceratosauria Marsh, 1884

Abelisauroidea Bonaparte and Novas, 1985

Abelisauridae Bonaparte and Novas, 1985

Genus Kryptops nov.

Type species: Kryptops palaios gen. et sp. nov.

Derivation of the name: From Greek krypto, covered; ops, face; in reference to the pitted surface and impressed vessel tracks on the maxilla, which is indicative of a firmly attached, possibly keratinous, integument or covering.

Diagnosis.—Same as for only known species.

Kryptops palaios sp. nov.

Figs. 1A, 2, 3, 4A, 5–7, Table 2.

Derivation of the name: From Greek palaios, old; in reference to its Early Cretaceous age.

Holotype: MNN GAD1, partial skeleton including a left maxilla (MNN GAD1-1: Figs. 1B, 2, 3, 4A, 5), several partial vertebrae and ribs (MNN GAD1-3 to GAD1-8; Figs. 1B, 6), and an articulated pelvic girdle and sacrum (MNN GAD1-2; Fig. 7).

Type locality: “Gadoufaoua” on the western edge of the Ténéré Desert (Fig. 1A), coordinates N 16°26’, E 9°7’.

Type horizon: Elrhaz Formation (Aptian–Albian, ca. 112 Ma).

Diagnosis.—Abelisaurid theropod characterized by the following two autapomorphies: (1) a deep secondary wall in the anteroventral corner of the antorbital fossa that completely...
obscures the antorbital fossa and that has a scalloped and fluted dorsal margin and (2) external texture on the maxilla, which is composed of short linear grooves.

It differs most obviously from other abelisaurids and nearly all other theropods in the marked development of a secondary wall on the maxilla that completely obscures the antorbital fenestra in lateral view (Fig. 2). In addition, the derived abelisaurid articular trough for the nasal on the maxilla is narrower and less developed in *K. palaios* gen. et sp. nov. Parentheses indicate estimation.

In lateral view the external surface of the maxilla is rugose and textured with small pits and short vascular grooves that course in several directions (Fig. 2). This ornamentation is similar to that in other abelisaurids and some carcharodontosaurids (Sereno et al. 1996; Sampson et al. 1998; Sereno et al. 2004; Sampson and Krause 2007) and may indicate that much of the face that was underlain by bone had more of a keratinous, than scaled, integument (Goodwin et al. 2006). The grooves in *Kryptops* are relatively short compared to those in *Rugops* (Fig. 4). A larger ventral row of neurovascular foramina, a few of which are preserved (Fig. 2), are located immediately above the alveolar margin, an abelisaurid synapomorphy (Wilson et al. 2003; Sereno et al. 2004). In carcharodontosaurids and most other theropods, this row of foramina is separated farther from the ventral alveolar edge, the intervening margin of which is usually smooth. This suggests that the fleshy edge or labial scales at the margin of the mouth was narrower in abelisaurids than in most other theropods.

The maxilla arches medially toward the premaxillary articulation, which is beveled at about 45° and fully exposed in medial view (Fig. 3). In most theropods including carcharodontosaurids, the premaxillary articulation faces more anteriorly (e.g., *Allosaurus*; Madsen 1976). The inward curve of the maxilla and beveled premaxillary articulation suggest that the snout in *Kryptops* was quite broad, one of the unusual structural features of the abelisaurid cranium (Bonaparte et al. 1990; Sampson et al. 1998; Sampson and Witmer 2007). The articular surface is rugose and dorsally may preserve portions of pneumatic diverticulae, as occur in several other abelisaurids (Wilson et al. 2003).

The anterior ramus is particularly short with a length to depth ratio of about 0.33. The ramus is also shorter in length than depth in other abelisaurids, *Allosaurus* and carcharodontosaurids, in contrast to many basal tetanurans (e.g., *Torvosaurus*, *Afrovenator*, Britt 1991; Sereno et al. 1994). The posterodorsal ramus is particularly short and narrow in lateral view (Fig. 2). The principal reason for its narrow proportions is the very narrow lamina bordering the antorbital fossa. In most other theropods, including other abelisaurids, the antorbital fossa forms a broad band along the trailing edge of the posterodorsal ramus.

The well preserved nasal articulation is exposed in lateral view, a derived condition shared with other abelisaurids
In *Kryptops*, the articulation is developed as a narrow slot with a tapered ventral end (Fig. 4A). Other abelisaurids show a more derived condition, in which the slot broadens in width distally and terminates in a concave socket as in *Rugops* (Fig. 4B).

The proximal portion of the posterior ramus of the maxilla has subparallel dorsal and ventral margins as in other abelisaurids and the carcharodontosaurid *Giganotosaurus* (Coria and Salgado 1995). The unusual feature in *Kryptops* is that the dorsal margin is scalloped rather than smooth. The raised and fluted margin forms a secondary lateral wall enclosing the antorbital fossa (Figs. 2, 3). The absence of the posterior portion of the ramus precludes determining if *Kryptops* also had the derived, laterally-facing jugal articulation as in other abelisaurids (Wilson et al. 2003; Calvo et al. 2004; Sereno et al. 2004).

The openings into the antorbital sinus system are incomplete, because much of the medial lamina is broken away. Dorsal and ventral margins of a transversely narrow oval fenestra, nevertheless, are discernable opening anteriorly into the maxillary antrum. This fenestra is hidden in lateral view by the secondary wall of the antorbital fossa (Fig. 3). A very similar configuration is present in the more completely preserved maxillae of *Rugops*, *Ekrixinatosaurus*, *Abelisaurus*, *Majungasaurus*, and *Carnotaurus* (Bonaparte and Novas 1985; Bonaparte et al. 1990; Calvo et al. 2004; Tykoski and Rowe 2004; Sampson and Witmer 2007). Given its location, shape and direction, this opening has been identified as the promaxillary fenestra (Witmer 1997). There is no trace of any other external fenestrae in this region of the antorbital fossa, nor is there any available fossa margin for a maxillary fenestra in the more common posterolateral location. The aforementioned abelisaurids also lack a maxillary fenestra.

In medial view, the deep interdental plates are fused and textured with subtle striations coursing in different directions as in other abelisaurids (Rauhut 2004; Novas et al. 2004; Sereno et al. 2004).
Sampson and Witmer 2007). These striations appear to shift from a predominantly subvertical orientation anteriorly to one angled at about 45° in the middle of the tooth row. The groove for the dental lamina is invaginated and associated with a row of replacement foramina (Fig. 3). Some breakage of the medial wall shows that the entire body of the maxilla is packed with replacement teeth. A strong maxillary shelf projects medially, its posterior end located just above a marked attachment scar for the palatine (Fig. 3). Dorsal to this ridge, the antorbital fossa is well exposed, walled laterally by the secondary crest. The medial shelf continues anteriorly to join the posteromedial margin of the maxillary antrum, which is fully exposed due to the loss of its medial wall.

In ventral view, portions of 11 eroded alveoli are visible. As is characteristic of abelisaurids, these are subrectangular rather than elliptical, as in noasaurids and most other theropods (Carrano et al. 2002; Wilson et al. 2003; Sereno et al. 2004; Sampson and Witmer 2007). The roots of the teeth reflect this alveolar shape and are subrectangular in cross-section.

Although all fully erupted maxillary teeth are broken, several complete teeth are preserved within the alveoli. We exposed two replacement teeth within the eighth alveolus, the crowns of which are exposed in medial view (Fig. 5). As mentioned above, there were likely 17 or 18 teeth in a complete maxillary series, so these crowns are located at mid length along the tooth row. The crowns are relatively flat, such that the serrations of both mesial and distal carinae are visible in lateral view (Fig. 5). Broken crowns have an average basal length of 10 mm and basal width of 6 mm, resulting in a length-to-width ratio similar to that in other abelisaurid teeth (Chatterjee and Rudra 1996; Lamanna et al. 2002; Bittencourt and Kellner 2002; Smith and Dodson 2003).

The posterior margin, which is only slightly concave, has more prominent serrations that are separated by noticeable interserrational sulci (Fig. 5B, C). Each wedge-shaped serration appears to expand toward its straight outer edge. The distal corner of the serration is prominent, forming a short hook-like projection, which points toward the apex of the tooth. Hooked serrations of similar form are present in Rugops. At mid length along the crown in Kryptops, there are about 15 serrations every 5 mm. This serration count is similar to that in teeth from poorly known Moroccan and Egyptian abelisaurids (Mahler 2005; Smith and Lamanna 2006), whereas Rugops, the younger abelisaurid from Niger, has only about 10 serrations every 5 mm.

The body of the maxilla is packed with replacement teeth, three to a column as seen in the eighth alveolus; very small replacement crowns are present near the root of near-full size replacement crowns in the sixth and eighth alveoli. As pre-
served it is not possible to discern a particular replacement pattern for the tooth row.

Axial skeleton.—The axial skeleton is represented by one fragmentary anterior dorsal vertebra (MNN GAD1-3), two partial mid dorsal vertebrae (MNN GAD1-4, 5), an articulated sacrum (MNN GAD1-2), and two ribs (MNN GAD1-6, 7; Figs. 1B, 6). Only the sacrum and ribs are complete; the dorsal vertebrae preserve only a portion of the centrum and lack transverse processes and complete zygapophyses. Enough of these vertebrae are preserved, nevertheless, to demonstrate the less modified condition of the axial column compared to later abelisaurids.

The spool-shaped anterior dorsal centrum is proportionately short. Its anteroposterior length of approximately 7 cm is less than the height or width of the posterior centrum face (9 cm, 11 cm, respectively). An oval pleurocoel is centrally located on the side of the centrum below the neurocentral suture, its exact shape and internal passages obscured by erosion. The vertical neural spine is relatively narrow and tall, its width (6 cm) less than one-third its preserved height (18 cm). A rugose ligament process projects from each side fore and aft, and a spinodiapophyseal lamina extends as a web of bone from mid height on the lateral aspect of the spine to the base of each transverse process. The taller proportions of the centrum and neural spine differ substantially from the squat, low-spined anterior dorsal vertebrae of Carnotaurus and Majungasaurus, which also do not have noticeable development of a spinodiapophyseal lamina (Bonaparte et al. 1990; O’Connor 2007).
Two vertebrae are identified as mid dorsals, based on their relatively large size, presence of a hyposphene-hypantrum articulation, absence of a parapophysis on either the centrum or ventral portion of the neural arch, and absence of a strong ventral keel and chevron facets (Fig. 6E, F). The centrum is hollowed, although it is not possible to determine if a pleurocoel was present. The anterior centrum face is gently concave (Fig. 6E, F). The associated neural spine, like that of the anterior dorsal, is anteroposteriorly narrow and tall, measuring 8 cm and 24 cm, respectively (Fig. 6A–D). Both spines curve away from the midline (Fig. 6C, D), reminiscent of natural spinal variation present in the taller-spined Acrocanthosaurus (Harris 1998), Suchomimus (Sereno et al. 1998), and Ceratosaurus (Madsen and Welles 2000). Unlike Acrocanthosaurus, the ligament processes and edges of the spine are not invaded by pneumatic diverticulae. The bases of robust prezygapophyses are preserved that seem to indicate the presence of hypantral articular surfaces medially. Several other ceratosaurs such as Ceratosaurus, Spinostropheus, and Carnotaurus have a pneumatic fossa below each prezygapophysis, but there is no development of such a depression in dorsal vertebrae in Kryptops. The relatively large size of the neural canal and prezygapophyses and tall proportions of the neural spine differ strongly from that in Carnotaurus and Majungasaurus; Kryptops had much taller erect neural spines along the dorsal series.

A complete sacrum, composed of a coossified series of five vertebrae, narrows in width and disappears between the blades of opposing ilia (Fig. 7). The reduction in the width of the central portion of the series also characterizes Carnotaurus and several other ceratosaurs (e.g., Ceratosaurus, Gilmore 1920; O’Connor 2007). The ventral margin of the sacral series may also be slightly arched, because the middle sacrals are not visible through the acetabulum. This margin, however, is not nearly as arched as in Carnotaurus (Bonaparte et al. 1990). Sacral 5, the best exposed of the series, has a spool-shaped centrum 11 cm in length with a nearly circular posterior articular face (10.5 cm wide, 9.5 cm deep). Although the junction between sacrals 4 and 5 is distinct, the centra appear to be coossified, in contrast to the free posteriormost sacral articulation in the Indian abelisaurid Rajasaurus (Wilson et al. 2003). A small pleurocoel may have been present in sacral 5, but the side of the centrum is poorly preserved. A low median crest marks the ventral side of the centra of sacrals 4 and 5. Given the degree of coossification present in the sacral series, it is un-
likely that there were any further sacral vertebrae. In Carnotaurus, in contrast, a dorsosacral is incorporated into the sacrum (Bonaparte et al. 1990; O’Connor 2007).

The sacral neural spines, like those in the dorsal series, are tall. In the sacral series, however, they are coossified into a single unit. The smooth, rounded borders of a large D-shaped fenestra separate a section of the neural spines of sacrals 4 and 5 (Fig. 7). Pneumatic foramina open into the neural spines along the anterior and posterior margins of the fenestra, which may have housed a paramedian pneumatic diverticulum. Pneumaticity of the neural arches in general and of the sacral series in particular is common among abelisauroids, such as Masiakasaurus (Carrano et al. 2002), Carnotaurus (Bonaparte et al. 1990; Bonaparte 1991; Tykoski and Rowe 2004), and Majungasaurus (Sampson et al. 1998; O’Connor 2007). The postzygapophyses of sacral 5 have a well developed hyposphene, stabilizing the articulation with the first caudal vertebra.

The preserved ribs are similar in form and compare most closely to the third dorsal rib in Allosaurus (Madsen 1976). They are slender, solid and lack any pneumatic invasion. Their length is between 50 and 60 cm. A web of bone bridges the gap between the capitulum and head and would have approached the ventral edge of the transverse process.

An articulated pelvic girdle is preserved, the more complete right side of which was facing downward (Fig. 7; Table 2). Pelvic remains are poorly known for most abelisauroids. The pelvic girdle and sacrum were preserved as a unit most likely because the bones of the pelvic girdle are coossified, although sutural traces remain between the ilium and pubis. Coossification of the pelvic girdle is common at maturity among coelophysoids and ceratosaurs. Both peduncles of the free ilium of Majungatholus have well developed articular pegs for a secure, and potentially fused, attachment to the ischium and pubis (Carrano 2007). The pelvic girdle of an unidentified abelisaurid from Argentina shows fusion of both iliopubic and puboischiadic articulations (Coria et al. 2006); probably the articulations of the pelvic girdle in abelisauroids coossify with maturity.

Ilium.—The ilium is strikingly primitive in shape compared to that in the more derived abelisauroids Ekrixinatosaurus, Majungasaurus, and Carnotaurus (Bonaparte et al. 1990; Calvo et al. 2004; Carrano 2007). The preacetabular process is more than twice as deep as the postacetabular process in lateral view (Fig. 7), the anterior margin of the preacetabular process is nearly vertical, the posterior margin of the postacetabular process is subrectangular or convex, the supraacetabular crest and the prominent lateral margin of the brevis shelf are not joined as a unified shelf overhanging the ischial peduncle, and the pubic peduncle is massive and significantly longer than the ischial peduncle (Fig. 7). In more derived abelisauroids, the preacetabular process is only moderately deeper than the postacetabular process, the anterior margin of the preacetabular process is angled posteroventrally at about 45° from the more prominent anterodorsal corner, the posterior margin of the postacetabular process is concave, the supraacetabular crest and lateral margin of the postacetabular process join to form a single prominent ridge, and the pubic peduncle is extremely short with a distal margin that is near vertical in orientation (Coria et al. 2006; Carrano 2007).

A robust supraacetabular crest overhangs the nearly circular acetabulum. The rim probably would have obscured more of the acetabulum in lateral view were it not for some dorsal crushing of the pelvic girdle that has displaced the right side dorsal to the left (Fig. 7). The pubic peduncle is massive with a broad acetabular margin visible in lateral view and near horizontal distal margin. Its anterior margin does not show any de-
Development of a fossa ventral to the preacetabular process (cuppedicus fossa), as occurs in allosauroids and most tetanurans (Hutchinson 2001). The ischial peduncle, which is completely fused with the ischium, is separated from the remainder of the ilium by a notch. The brevis fossa is transversely broad but does not flare distally as occurs in coelophysoids (Rauhut 2003). Much of the fossa is exposed in lateral view, which may have been enhanced somewhat by upward displacement of the right ilium. Lateral exposure of the brevis fossa seems to vary among abelisauroids.
The shaft and foot are straighter and relatively smaller, respectively, in *Carnotaurus* (Bonaparte et al. 1990), *Aucasaurus* (Coria et al. 2002), *Pycnomemosaurus* (Kellner and Campos 2002), *Masiakasaurus* (Carrano et al. 2002), and an unnamed abelisaurid from India (Chatterjee and Rudra 1996). The pubis in noasaurids also has a more limited distal expansion (*Masiakasaurus*, unnamed Niger noasaurid; Carrano et al. 2002; Sereno et al. 2004). In *Kryptops* the foot is expanded equally anteriorly and posteriorly in lateral view, and is transversely broader anteriorly than posteriorly in ventral view. In the region of the foot, the symphysis in anterior view appears continuous with no median fenestra. A foramen is present, in contrast, between the pubes in distal view (Fig. 7B).

The anterior border of a large obturator foramen is preserved, which unlike the condition in tetanurans was probably completely enclosed by bone as in *Carnotaurus* and an unnamed Argentine abelisaurid (Bonaparte et al. 1990; Coria et al. 2006). The bone tapers posteriorly to a thin lamina as it extends toward the ischium. On the pubic shaft nearby is a raised area, the ambiens process, which likely represents the attachment area for a muscle by that name (Romer 1923; Hutchinson 2001).

**Ischium.**—The iliac peduncle of the ischium is coossified with the ilium (Fig. 7). The broader pubic peduncle thins to a plate ventrally where it meets its opposite in the midline. Although some of this ventral border is broken away, there is no indication that there existed a discrete obturator process that characterizes many tetanurans (e.g., *Allosaurus*, *Sinraptor*; Madsen 1976; Currie and Zhao 1993). The ischial border of the acetabulum is divided into a dorsal portion that forms a raised, rounded articular rim and a ventral portion that is non-articular. The articular rim is subtle and is not developed as a raised platform as in *Allosaurus* or prominent trochanter as in coelophysoids (Madsen 1976; Raath 1977; Tykoski and Rowe 2004; Munter and Clark 2006). An attachment scar with a nearby foramen is present on the posterior margin of the base of the ischium.

A prominent crescent-shaped flange is present on the ischial shaft at mid length on the left side (Fig. 7). The right ischial shaft is broken at mid length with the upper end twisted posteriorly. The natural ventral curve of the ischial shaft is preserved on the left side. The shafts broaden toward their distal ends to about twice their mid shaft width and terminate in a modest foot with a flat, partially coossified symphysis.

**Maturity and body size.**—The maturity of the holotype and only known specimen of *Kryptops palaios* is indicated by the coossification of all neural arches and respective centra, sacral centra, and bones of the pelvic girdle. The maxilla and post-craniad bones of *Kryptops palaios* have an absolute size comparable to those of *Majungasaurus* (Sampson and Krause 2007), suggesting a comparable body length of roughly 6 to 7 meters. The best known abelisaurids appear to have proportionately short skulls, with skull/femur ratios less than 1.00 as estimated in *Majungatholus* (0.88; Krause et al. 2007: fig. 1) and *Carnotaurus* (0.58; Calvo et al. 2004). Calvo et al. (2004) calculated a higher ratio for *Ekrixinatosaurus* (1.08), but this was based on more fragmentary remains. Skull/femur ratios for allosaurids are generally greater than 1.00 (e.g., 1.20 for *Acrocanthosaurus*; Currie and Carpenter 2000), although particular taxa have relatively smaller skulls such as *Allosaurus* (0.76–1.00; Currie and Carpenter 2000). In *Majungatholus* and *Carnotaurus*, maxilla length is close to 50% skull length (Bonaparte et al. 1990; Sampson and Witmer 2007). The maxilla in *Kryptops palaios* estimated to be about 25 cm in length, from which we infer an approximate skull length of 50 cm. Judging from the length of the pubis (approximately 62 cm), femur length in *Kryptops* would have been at least 65 cm, which generates an estimated skull/femur ratio of 0.77. Skull length in *Kryptops palaios* thus was likely significantly shorter than femur length as in better known abelisaurids.

**Tetanurae Gauthier, 1986**

**Allosauroida Marsh, 1878**

**Carcharodontosauridae Stromer, 1931**

**Genus Eocarcharia nov.**

Type species: *Eocarcharia dinops* sp. nov.

Derivation of the name: From Greek eos, dawn; karcharias, shark (Greek); in reference its basal position in the “shark-toothed” theropod clade Carcharodontosauridae.

Diagnosis.—Same as for only known species.
Eocarcharia dinops sp. nov.

Figs. 9–17, 19A, Table 3.

Derivation of the name: From Greek dinops, fierce-eyed; in reference to the massive ornamented brow above the orbit.

Holotype: MNN GAD2, a complete left postorbital (Figs. 9, 10).

Referred material: MNN GAD3, complete left postorbital; MNN GAD4, partial right postorbital; MNN GAD5, partial right postorbital; MNN GAD6, partial right postorbital; MNN GAD7, nearly complete left maxilla (Figs. 11–13); MNN GAD8, right maxillary fragment; MNN GAD9, left maxillary fragment; MNN GAD10, left frontal and prefrontal (Figs. 14, 15); MNN GAD11, frontoparietal (Fig. 16); MNN GAD12, three teeth; MNN GAD13, tooth fragment; MNN GAD14, complete crown (Fig. 17B).

Type locality: “Gadoufaoua” on the western edge of the Ténéré Desert, Niger; type locality has coordinates N 16°31′88″ and E 9°38′88″; referred specimens come from a 10 km stretch of richly fossiliferous outcrop (Fig. 1A; Taquet 1975; Sereno et al. 1998; Sereno et al. 1999; Taquet and Russell 1999).

Type horizon: Elrhaz Formation (Aptian–Albian, ca. 112 Ma).

Diagnosis.—Large-bodied carcharodontosaurid with enlarged subtriangular laterally exposed promaxillary fenestra larger in size than the maxillary fenestra, a circular accessory pneumatic fenestra on the postero-dorsal ramus of the maxilla, dorsoventral expansion of the antorbital fossa ventral to the promaxillary and maxillary fenestrae, postorbital brow accentuated by a finely textured ovoid swelling, or boss, positioned above the postero-dorsal corner of the orbit, postorbital medial process with a plate-shaped projection fitted to an articular slot on the frontal, postorbital articulation for the jugal that includes a narrow laterally-facing facet, an enlarged prefrontal lacking the ventral process with subquadrate exposure on the dorsal skull roof and within the orbit (limiting the anterior

Fig. 10. Carcharodontosaurid theropod Eocarcharia dinops gen. et sp. nov. MNN GAD2 from the Lower Cretaceous Elrhaz Formation of Niger. Stereopairs of left postorbital (holotype) in medial (A) and dorsal (B) views.
ramus of the frontal to the roof over the olfactory bulbs), and a low protuberance on the frontoparietal suture.

*Eocarcharia dinops* also differs from other carcharodontosaurs such as *Acrocanthosaurus*, *Giganotosaurus*, and *Carcharodontosaurus* by the low proportions of the suborbital flange on the postorbital and from *Mapusaurus*, *Giganotosaurus*, and *Carcharodontosaurus* by the absence of extensive external neurovascular grooves on the maxilla and blade-shaped crowns with prominently developed, marginal, arcuate enamel wrinkles in upper and lower tooth rows. Unlike these advanced carcharodontosaurs, *Eocarcharia* retains the pre-frontal as a separate element and has only a rudimentary lacrimal-postorbital suture. Finally, *Eocarcharia* has a relatively small planar sutural surface on the postorbital for the squamosal, rather than the more complex spiral articulation observed in *Carcharodontosaurus*, *Mapusaurus*, and *Giganotosaurus*.

**Description**

*Maxilla.*—The maxilla is represented by one nearly complete specimen (Figs. 11–13, Table 3; MNN GAD7) and two that preserve only the central portion of the bone. The maxilla is approximately twice as long as deep and has 15 alveoli (Table 3). Articular surfaces include the premaxilla, nasal, lacrimal, jugal and palatine. The partially preserved premaxillary contact has a fairly steep, slightly arched profile, resembling that in *Acrocanthosaurus* (Currie and Carpenter 2000) more so than the straight suture in *Mapusaurus* (Coria and Currie 2006) or *Carcharodontosaurus* (Sereno et al. 1996). The middle portion of the nasal contact is exposed in lateral view, where it clearly forms the border of the antorbital fossa, as in other carcharodontosaurs and most allosaurids. There is no slot anteriorly for the anteroventral process of the nasal as in abelisaurids. The jugal contact is well preserved along the pos-
terior ramus and faces dorsolaterally (Figs. 11, 12C, D). The anteriormost end of the jugal contact, however, is more superficial and overlaps the posterior end of the antorbital fossa (Fig. 12C, D). The jugal thus would have formed the posteroventral corner of the antorbital fossa as in other carcharodontosaurids and most allosauroids. The anterior ramus of the lacrimal articulates in a beveled, V-shaped slot at the end of the posterodorsal ramus of the maxilla (Fig. 11). The ventral ramus of the lacrimal contacts the maxilla medial to the jugal suture, as best exposed in medial view (Fig. 13). Just anterior to the lacrimal contact lies a well marked, elongate scar for the lateral ramus of the palatine.

The maxilla is a relatively flat bone. Most probably in consequence the snout was relatively narrow in transverse width as in other carcharodontosaurids. In lateral view the maxilla has a gently sinuous alveolar margin (Fig. 11). The anterior ramus is shorter anteroposteriorly than deep, as in Carcharodontosaurus, Giganotosaurus, Allosaurus, and abelisaurids. In other basal tetanurans, such as Neovenator, Afrovenator, and spinosaurids, this ramus is longer than deep. The posterodorsal ramus in Eocarcharia tapers in width once it relinquishes the edge of the antorbital fossa to the nasal. This margin in Eocarcharia and other carcharodontosaurids is gently curved. In some basal tetanurans (Dubreuillosaurus, “Megalosaurus” hesperis, Afrovenator), there is an angular bend at this point along the margin.

The posterior ramus is tapered throughout its length (Fig. 11). The posterior portion that contacts the jugal is deflected posteroventrally at an angle of 20° from a horizontal line established along the alveolar margin, a condition very similar to that in Acrocanthosaurus (Currie and Carpenter 2000). A few other basal tetanurans, namely Afrovenator, also exhibit this condition. Other basal tetanurans exhibit posteroventral deflection of only the very tip of this ramus (e.g., Torvosaurus, Suchominus, Monolophosaurus, Allosaurus, Carcharodontosaurus, Sinraptor, Yangchuanosaurus; Madsen 1976; Dong and Zhang 1983; Britt 1991; Currie and Zhao 1993; Zhao and Currie 1993; Sereno et al. 1996, 1998).

The external surface of the maxilla is textured with neurovascular foramina and associated channels but lacks the pervasive pits and grooves of Carcharodontosaurus and abelisaurids. Two rows of neurovascular foramina pierce the lateral surface dorsal to the alveolar margin. The ventral, or labial, row is situated about 5 mm above the alveolar margin and has larger foramina (Figs. 11, 12C, D). The upper row of foramina curves dorsally above the second alveolus.

The antorbital fossa in Eocarcharia is particularly deep anteriorly under the fenestrae (Fig. 11). Unlike most theropods the ventral rim of the antorbital fossa parallels the alveolar margin rather than rising anteriorly, and the fossa wall below the fenestrae is deeper than the remaining ventral margin of the maxilla (Fig. 12A, B). The anteroventral corner of the fossa is squared rather than gently arched, a condition close to that in Acrocanthosaurus (Currie and Carpenter 2000), Neovenator (Brusatte et al. in press), Afrovenator (Sereno et al. 1994), Dubreuillosaurus (Allain 2002), and coelophysids.

Fig. 12. Carcharodontosaurid theropod Eocarcharia dinops gen. et sp. nov. MNN GAD2 from the Lower Cretaceous Elrhaz Formation of Niger. Left antorbital region in left lateral view (A, B) and posterior ramus in lateral view (C, D); photographs (A, C) and line drawings (B, D). Cross-hatching indicates broken bone; dashed lines indicate estimated edge; grey tone indicates matrix.
The antorbital fossa is bordered ventrally by a raised, somewhat swollen and rounded rim that flattens posteriorly (Figs. 11, 12A, B). Some carcharodontosaurs, such as *Mapusaurus* and *Carcharodontosaurus saharicus*, have an everted and swollen ventral margin (Sereno et al. 1996; Coria and Currie 2006). In *Giganotosaurus* and *Acrocanthosaurus*, in contrast, most of the ventral margin is not raised (Coria and Salgado 1996; Currie and Carpenter 2000).

Three fenestrae are present on the wall of the fossa. The promaxillary and maxillary fenestrae are subtriangular, the former the larger of the two and measuring 52 mm in height and 29 mm across its base. *Sinraptor* also has a promaxillary fenestra that is larger than the maxillary fenestra (Witmer 1997; contra Currie and Zhao 1993), although this is rare among theropods. Only the anterior margin of the promaxillary fenestra is concealed in lateral view by the rim of the antorbital fossa. A small subcircular accessory fenestra posterodorsal to the maxillary fenestra measures approximately 18 mm in diameter. Other basal neotheropods exhibit an accessory fossa in this region, including *Ceratosaurus*, *Sinraptor*, and some specimens of *Allosaurus* (Witmer 1997; Rauhut and Fechner 2005). These accessory depressions, however, are variable in size and form and their homology is less certain than the promaxillary and maxillary fenestrae.

The internal sinuses of the maxilla are preserved in part despite erosion of the medial aspect of the maxilla (Fig. 13). The promaxillary fenestra opens medially into a large cavity, the promaxillary recess, which extends anteriorly into the anterior ramus (Witmer 1997). The maxillary fenestra opens medially into a separate chamber, the maxillary antrum, the medial wall of which has broken away. A transverse septum...
separates promaxillary and maxillary recesses. The rim of the antorbital fossa is exposed posterior to the fifth alveolus. Swellings for each tooth crypt are visible on the floor of the antorbital fossa.

The interdental plates are fused forming a continuous lamina, as in many basal neotheropods including *Carcharodontosaurus*, *Giganotosaurus*, *Neovenator*, *Allosaurus*, *Torvosaurus*, and *Ceratosaurus*. Weathering of the entire medial alveolar region has artificially enlarged several of the replacement foramina along the groove for the dental lamina and partially opened several of the anterior crypts in medial view (Fig. 13). The seventh crypt has been opened to expose a complete replacement crown. The maxillary medial shelf dorsal to the row of replacement foramina is low and beveled by a long palatine articular scar that extends as far forward as the seventh alveolus. The anterior end of the shelf and the anteromedial maxillary process are not preserved. The row of replacement foramina is located approximately at mid height along the ramus, which is not proportionately as deep as in advanced carcharodontosaurids such as *Carcharodontosaurus* (Brusatte and Sereno 2007) and abelisaurids (Fig. 3). Ventrally, the anteroposteriorly broad alveoli are separated by narrow troughs throughout most of the tooth row, as in *Carcharodontosaurus* (Brusatte and Sereno 2007) but unlike most other basal neotheropods.

There are 15 teeth in the maxillary tooth row (Fig. 13), posterior to which the maxilla is declined posteroventrally as in *Acrocanthosaurus* (Currie and Carpenter 2000). Fully erupted teeth were present in positions 2, 5, 6, 10, and 13 but were eroded away. Replacement teeth are exposed in most alveoli medial to the functioning crown as in other theropods (Edmund 1960). We opened the crypt of the seventh alveolus to fully expose an erupting crown (Fig. 17A). Based on comparison to this tooth, we have tentatively referred several isolated teeth from the field area to *Eocarcharia dinops* (MNN GAD12–14; Fig. 17B). Although these crowns are more transversely compressed than those of most theropods (Smith et al. 2005), they are not strongly blade-shaped or characterized by a straight posterior carina or high relief enamel wrinkles (Brusatte et al. 2007), as occurs in *Tyrannosaurus*, *Mapusaurus*, *Giganotosaurus*, *Carcharodontosaurus*, and an isolated tooth from Japan (Cora and Salgado 1995; Sereno et al. 1996; Chure et al. 1999; Novas et al. 2005; Coria and Currie 2006).

The distal carina extends much further basally than the mesial carina, a common condition in theropods that also occurs in *Allosaurus*, *Acrocanthosaurus*, and a large carcharodontosaur tooth from Patagonia (Vickers-Rich et al. 1999). In contrast, both carinae extend basally to the same level in maxillary teeth of *Carcharodontosaurus* and *Giganotosaurus*. Serrations are present across the tip of the crown, as in *Acrocanthosaurus* (Harris 1998), *Carcharodontosaurus*, and most coelurosaurs (Currie and Carpenter 2000). The serrations are fine and unilobate, rather than bilobate, as in *Tyrannosaurus* (Novas et al. 2005).

Using descriptive metrics by Smith et al. (2005), the best-preserved referred tooth (Fig. 17B) exhibits crown-base length (CBL) of 24 mm, crown base width (CBW) of 11 mm, crown height (CH) of 48 mm, apical length (AL) of 57 mm, crown base ratio (CBR = CBW/CBL) of 0.46, crown height ratio (CHR = CH/CBL) of 2.0, average mesial serration density (MAVG) of 13 per 10 mm, average distal serration density (DAVG) of 15 per 10 mm, and serration (= denticle) size density index of 0.87 (DSDI = MAVG/DAVG). Only one replacement crown is exposed in situ on the maxilla, and average mesial serration density (MAVG) is the only measure possible. This tooth has 11 serrations per 5 mm near its apex and 17 per 5 mm toward the base, resulting in a MAVG of 28 serrations per 10 mm, a serration size considerably smaller than those in the isolated crown. We have no explanation for this difference except to note that serration count may be subject to individual variation and also variation along the tooth row.

Prefrontal.—The prefrontal (Figs. 14, 15) articulates in a deep, squared notch in the frontal. The posterosmedial corner is more deeply inset on the ventral side, where the frontal process for the nasal is narrower transversely than the prefrontal. A process of the prefrontal extends posteriorly from the posterosmedial corner into a pit in the frontal; the pit is exposed only on the anterior margin of a disarticulated frontal (Fig. 16C, D). The prefrontal is absent in advanced carcharodontosaurids, such as *Carcharodontosaurus* (Fig. 18B). This region of the skull roof is occupied by the lacrimal, which like the prefrontal in *Allosaurus* and many other neotheropods has a cone-shaped posterior process that inserts into a deep pit in the frontal. For this reason, it seems likely that the “lacrimal” in advanced carcharodontosaurids is actually a coossified lacrimal-prefrontal.

The prefrontal and frontal are joined by an interdigitating suture posteriorly and posterolaterally, which is doubtless why they have remained in contact (Fig. 14). The anterolateral suture with the lacrimal, in contrast, is pitted and sinuous but not interdigitating. Just before the suture reaches the lacrimal laterally, it opens into a narrow vertical fissure (Fig. 14C, D). Toward the anterior end, the anteromedially facing nasal articulation is developed as a vertical butt joint (Fig. 14C, D).

In most theropods that retain the prefrontal as a separate element, the bone is exposed on the skull roof as a relatively small, subtriangular element with a narrow anterior apex that tapers to a point between the nasal and lacrimal. A slender ventral process extends along the posterosmedial aspect of the lacrimal just medial to the lacrimal foramen. By contrast, the form of the prefrontal in *Eocarcharia* is very unusual. First, there is no development of a ventral process, which is present in *Acrocanthosaurus* (Currie and Carpenter 2000), *Allosaurus* (Madsen 1976), *Sinraptor* (Currie and Zhao 1993), *Monolophosaurus* (Zhao and Currie 1993), and other theropods. There are no broken areas that might otherwise account for the absence of this process via postmortem damage. Second, the prefrontal is enlarged relative to the frontal, its transverse width is fully one-half the maximum width of the frontal, and its area nearly one-third that of the frontal in ventral
view (Fig. 14C, D). Third, it has a subrectangular rather than subtriangular shape on the dorsal skull roof (Fig. 14A, B). And fourth, it is considerably thickened, especially its posterior margin, which is swollen and pitted similar to the adjacent surface of the frontal (Figs. 14, 15). The anterior portion of the prefrontal angles anteroventrally at about 45° in lateral view (Fig. 15). In *Eocarcharia*, thus, the prefrontal is not only retained as a separate ossification in contrast to advanced carcharodontosaurs, but it is enlarged relative to the condition in *Acrocanthosaurus* (Currie and Carpenter 2000).

**Frontal.**—A complete left frontal is preserved as well as a pair of similar-sized coossified frontals (Figs. 14–16; Table 3). Coossification of the frontals and their firm attachment posteriorly to the parietals in the second specimen suggests that it had achieved maturity. Both specimens have an articular surface for the postorbital that receives the slots and grooves on the opposing postorbital articular surface. When the frontal-prefrontal and holotypic postorbital are joined, furthermore, the articular slots and processes accommodate one another and the margin of the supratemporal fossa runs
continuously across both, strongly suggesting that they belong to the same species. Articular contacts on the frontal also include the nasal, lacrimal, parietal, laterosphenoid and orbitosphenoid.

In dorsal view the frontal is particularly broad at mid length (Figs. 14A, B). Although frontals that are at least one-half as broad as long characterize some abelisaurids, allosauroids, and tyrannosaurids, the frontal in carcharodontosaurids is especially broad. In *Carcharodontosaurus* maximum transverse width of the frontal is approximately 60% its length. In *Eocarcharia* the frontal is broader still, with a maximum transverse width 70% its maximum length. The frontal is thickened throughout and has an interdigitating interfrontal suture that fuses with maturity, as in other carcharodontosaurids and several other theropods (Fig. 16). Anteriorly the fluted nasal suture angles steeply at about 45° when the body of the frontal is held horizontal (Figs. 15C, D). On the skull roof, the frontal-nasal suture appears to angle posteromedially to the midline without a median frontal reentrant (Figs. 14A, B). The prefrontal, as described in detail above, inserts into a squared notch in the frontal, which is deeper ventrally than dorsally (Fig. 12). The lateral portion of the frontal, which is swollen, rugose, and marked by a well defined vascular groove and foramen, forms the medial portion of the brow (Figs. 14A, B, 15).

Posteriorly, the supratemporal fossa is broadly exposed, the rim of which rises as a rounded ridge as it passes medially and joins the parietal suture not far from the midline (Figs. 14A, B). In advanced carcharodontosaurids such as *Carcharodontosaurus*, in contrast, the supratemporal fossa has negligible exposure dorsally, is displaced laterally far from the midline, and extends under the ridge so that both the frontal and parietal overhang the anteromedial corner of the fossa (Fig. 18). *Acrocanthosaurus* (OMNH 10146) has an intermediate condition, in which the fossa on the frontal is invaginated with a low overhanging rim, whereas the fossa on the parietal is developed only as a near vertical wall.

In ventral view, the transversely narrow proportion of the anterior ramus of the frontal is well exposed and is devoted entirely to roofing the olfactory portion of the endocranium (Figs. 12C, D, 14C). In *Eocarcharia*, *Carcharodontosaurus*, and other tetanurans (e.g., *Sinraptor*; Currie and Zhao 1993), the broader anterior ramus of the frontal extends to each side of the endocranial roof. The narrow anterior ramus of the frontal is a very unusual feature of the skull roof of *Eocarcharia*, which clearly identifies the conjoined fronto-parietal as pertaining to the same species (Fig. 14C, D). In this specimen, the arcuate articular trough for each orbitosphenoid is well preserved tapering to an end at mid orbit.

In lateral view the articular edge of the frontal has a subtriangular articular surface anteriorly for the lacrimal, the broadest portion of which is near the prefrontal (Fig. 13A, B). This is opposite the condition in more advanced carcharodontosaurids, such as *Acrocanthosaurus* and *Carcharodontosaurus*, in which the articular surface on the frontal for the lacrimal (or lacrimal-prefrontal) is broadest posteriorly. Although the frontal is removed from the orbital margin by the lacrimal-postorbital contact, there appears to be a short nonarticular notch where these lateral bones join (Fig. 15A, B). The frontal-postorbital suture in *Eocarcharia* differs in detail from that in *Acrocanthosaurus* (OMNH 10146) and *Carcharodontosaurus* (SGM-Din 1). It features a deep

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**Fig. 15.** Carcharodontosaurid theropod *Eocarcharia dinops* gen. et sp. nov. MNN GAD2 from the Lower Cretaceous Elrhaz Formation of Niger. Frontal and prefrontal in lateral (A, B) and medial (C, D) views; photographs (A, C) and line drawings (B, D).
articulat slot for a long, thin process of the postorbital (Fig. 15A, B).

In medial view the rugose interfrontal suture (Fig. 15C, D) fuses with maturity (Fig. 16). The dorsal surface of the frontal near the midline is gently concave (Fig. 14A, B), in contrast to the condition in Acrocanthosaurus (OMNH 10146) and Carcharodontosaurus (SGM-Din 1), in which the dorsal surface is gently convex.

Parietal.—The parietal, the anterior portion of which is preserved, has an interdigitating frontoparietal suture marked by a protuberance where the suture intersects the rim of the supratemporal fossa (Fig. 16). This frontal portion of the protuberance is also present on the isolated frontal (Fig. 14A, B), suggesting again that these bones represent individuals of the same species. The supratemporal fossae are separated from the midline by a flat skull table, which is much narrower than that in Carcharodontosaurus (Fig. 18). Acrocanthosaurus again shows an intermediate condition (OMNH 10146). In ventral view, the anterior portion of the parietal forms the roof over the endocranial cavity. Near the midline, the roof is flat across the frontal and parietal (Fig. 16A, B).

Lacrimal.—Although the lacrimal is not preserved, some of its unusual features can be ascertained from articular scars on the prefrontal, frontal, and postorbital. First, the lacrimal extended posteriorly along the orbital margin to contact the postorbital and exclude the frontal from that margin; this is

Fig. 16. Carcharodontosaurid theropod Eocarcharia dinops gen. et sp. nov. MNN GAD2 from the Lower Cretaceous Elrhaz Formation of Niger. Frontals, parietal and fragmentary right and left orbitosphenoids in dorsal (A, B) and ventral (C, D) views; photographs (A, C) and line drawings (B, D). Cross-hatching indicates broken bone.
shown by the small, but well defined, articular facet for the lacrimal on the postorbital (Figs. 9, 10B). Second, the lacrimal thus would likely have contributed to the robust orbital brow as in other carcharodontosaurids; this is indicated by the broad and rugose articular area for the lacrimal on the frontal. And third, the lacrimal was likely strengthened to sustain considerable stress; this is indicated by the broad and rugose articulation with the prefrontal.

Postorbital.—The postorbital exhibits diagnostic features for *Eocarcharia dinops* for the referral to Carcharodontosauridae and for its relationships within that clade. The robust brow appears to resist breakdown, which may account for the preservation of four similar-sized postorbitals (MNN GAD3–6) in addition to the holotype (MNN GAD2; Figs. 9, 10). The postorbital contributes to the border of the orbit, laterotemporal fenestra, and supratemporal fenestra (Figs. 9, 10, 18A; Table 3). The most prominent feature of the postorbital in lateral view is the thickened brow, which is divisible into an anterior portion with subquadrilateral proportions that is canted anterodorsally and a posterior portion with an ovate shape, here termed the orbital boss, that is canted postero-dorsally (Fig. 9). The anterior portion of the brow is divided by a horizontal vascular groove that leads to a foramen that enters the central portion of the brow. The most prominent portion of the brow, the orbital boss, is weakly divided into two parts, anteroventral and postero-dorsal. All of the referred postorbitals show these structural details.

Contact between the postorbital and lacrimal is important to establish, given the absence of the latter among preserved bones. A small but definitive lacrimal articular surface is present at the anterior end of the orbital ramus, measuring 9 mm deep and 12 mm long (Figs. 9, 10B). Although this contact excludes the frontal from the orbital margin, its surface is absolutely and proportionately smaller than in other carcharodontosaurids (*Acrocanthosaurus, Mapusaurus, Giganotosaurus, Carcharodontosaurus*) (Fig. 19A1, B1). Removal of the frontal from the orbital margin (Fig. 18), an initial stage of which is preserved in *Eocarcharia*, evolved independently in abelisaurids and later within Coelurosauria (*Tyrannosauroidae*).

The texturing of the brow in *Eocarcharia* and other carcharodontosaurids suggests it was covered in keratin. The large and complex postorbital-frontal suture provides great stability against lateral impact. In advanced carcharodontosaurids, the already elaborated postorbital-lacrimal and post-orbital-squamosal sutures, likewise, become even larger and more complex. The head of the laterosphenoid, which braces the postorbital medially, is set in a socket in the postorbital, which is particularly deep in advanced carcharodontosaurids (Fig. 19B2). All of these contacts seem enhanced to handle increased stress (Byron et al. 2004).

The brow is clearly overbuilt for were primarily for display. We speculate here that the carcharodontosaurid brow may have been used for intraspecific lateral head-buttting. Most large-bodied theropods such as allosauroinds and spinosauroinds do not have bony orbital swellings, or bosses, on the orbit margin. In those that do, such as abelisaurids and some large tyrannosauroids, the swelling differs in structural detail from that of *Eocarcharia* and other carcharodontosaurids. Although the swollen postorbital brow in *Tyrannosaurus* is solid (Brochu 2003: fig. 17), it does not form a prominent lateral feature along the skull margin (Brochu 2003: fig. 3) as in carcharodontosaurids (Fig. 18). In *Carcharodontosaurus saharicus*, furthermore, there is a nonarticular, pitted pyramidal projection on the lateral aspect of the ventral ramus of the postorbital (Fig. 19B1). Both the brow and this ornamental feature project laterally, and both may have played a role in lateral head-buttting.

Coria and Currie (2006: 80) describe a portion of the orbital brow in *Giganotosaurus* and *Mapusaurus* as a separate "palpebral" ossification distinct from the postorbital. No trace of such an accessory element is present in any of the well preserved postorbitals of *Eocarcharia dinops* or *Carcharodontosaurus saharicus* (Fig. 19B). The presence of the element in two taxa suggests that it is not an anomaly or artifact of preservation. Either these elements are already fused without trace in *Eocarcharia* and *Carcharodontosaurus*, or the accessory ossification in *Giganotosaurus* and *Mapusaurus* is a shared derived character.

The ventral ramus has a subrectangular cross-section at mid shaft in contrast to the derived U-shaped cross-section in spinosaurids (*Afrovenator, Torvosaurus, Dubreuillosaurus*; Sereno et al. 1994; Allain 2002). A small, rugose, distally positioned infraorbital process is present, which differs from the larger, subtriangular, more proximally positioned process in *Acrocanthosaurus* and advanced carcharodontosaurids (*Mapusaurus, Giganotosaurus, Carcharodontosaurus*; Figs. 9, 19). In *Eocarcharia*, other carcharodontosaurids and abelisaurids, the suborbital process is formed solely by the
postorbital, whereas in tyrannosaurs it is often joined ventrally by the jugal (Chure 2000; Brochu 2003).

Medially the articular contacts with the frontal, parietal, and laterosphenoid are clearly demarcated (Figs. 10A, 19A₂). The rugose frontal contact, which is canted along an antero−dorsal−posteroventral axis, has a distinctive plate−shaped process that inserts into a matching slot on the frontal. This plate−shaped process, an autapomorphy of Eocarcharia dinops gen. et sp. nov., is not present in Carcharodontosaurus. More posteriorly a deep notch accommodates the remainder of the frontal and anterior end of the parietal. Posteroventral to the parietal contact, a shallow oval concavity accommodated the articular head of the laterosphenoid. In Carcharodontosaurus this cavity is deeper and bounded by a thin rim (Figs. 10A, 19A₂).

Articular contact with the jugal and squamosal is exposed in medial and lateral views (Figs. 9, 19A₂). The postorbital articulates with the jugal along an elongate, articular surface that begins at mid length on the medial aspect of the ventral ramus and twists to face laterally at its ventral tip (Fig. 9). Unlike any other theropod described to date, the jugal wraps around the posterior margin of the ventral ramus, where it lies in a narrow inset along its posterior edge. This inter−locking postorbital−jugal articulation constitutes an autapomorphy for Eocarcharia dinops. The short posterior ramus of the squamosal splits to accommodate dorsal and ventral sides of this articular wedge. The dorsal articulation is subtriangular and inset. The ventral articulation extends anteroventrally just beyond the base of the posterior ramus of the postorbital, its tip exposed in lateral view near the margin of the laterotemporal fenestra (Figs. 9, 19A₁). In advanced carcharodontosaurs, the postorbital−squamosal articulation is developed as a more elaborate spiral articulation involving a lengthened posterior ramus of the postorbital (Sereno et al. 1996; Fig. 19B).

In dorsal view (Figs. 10B, 19A₃) the postorbital forms the anterolateral corner of the supratemporal fossa as in most theropods but unlike abelisaurids, in which the supratemporal fossa does not reach the postorbital (Wilson et al. 2003).

Orbitosphenoid.—The edge of the right and left orbitosphenoid is preserved in articulation within an articular trough on the frontal (Fig. 16C, D). It is clear from the limited extent of the orbitosphenoid and absence of articular scars farther anteriorly on the frontal that the olfactory tracts and bulbs were not surrounded by bone. Several independent lineages of theropods, in contrast, have enclosed the anterior end of the endocranial cavity by extending the ossified orbitosphenoid anteriorly between the orbits and by ossifying a median mesethmoid (or “interorbital septum”) between the olfactory tracts and bulbs. This has occurred in larger, more derived species within Ceratosauria (Sampson and Witmer 2007), Allosauroida (Larson 2001; Franzosa and Rowe 2005), and Tyrannosauroidea (Brochu 2003). Among basal allosauroids such as Sinosaurus (Currie and Zhao 1993) and Allosaurus (Hopson 1979), it is clear that the anterior end of the endocranium remains unossified. Eocarcharia exhibits this basal condition, as shown by the limited anterior ossification of the orbitosphenoid of a mature individual (Fig. 14C, D). Acrocanthosaurus (Franzosa and Rowe 2005), Giganotosaurus (Coria and Currie 2002), and Carcharodontosaurus (Lars−son 2001), on the other hand, exhibit the fully−ossified derived condition.

Maturity and body size.—The cranial bones attributed to Eocarcharia pertain to mature, or near mature, individuals. Among the referred cranial bones are fused frontals (Fig. 16), and these articulate well with the holotypic postorbital (Fig. 9). Adult skull size appears to have been attained. The maxilla of Eocarcharia is approximately 70% and 50% of the linear dimension of the maxilla in adult specimens of Acrocanthosaurus (NCSM 14345) and Carcharodontosaurus (SGM−Din 1), respectively. This serves as a rough approximation of the
Fig. 19. Left postorbital in two carcharodontosaurids. A. Basal carcharodontosaurid *Eocarcharia dinops* gen. et sp. nov. MNN GAD2 from the Lower Cretaceous Elrhaz Formation of Niger. B. Advanced carcharodontosaurid *Carcharodontosaurus saharicus* (Deperet and Savornin, 1927) SGM-Din 1 from the Upper Cretaceous Kem Kem beds of Morocco. Line drawings in lateral (A₁, B₁), medial (A₂, B₂), and dorsal (A₃, B₃) views.
size differential between these genera. Adult *Eocarcharia* thus appears to be about one-half of the linear dimensions of the derived carcharodontosaurids *Giganotosaurus*, *Mapusaurus*, and *Carcharodontosaurus*, and therefore would have had a body length of about 6 to 8 meters.

**Phylogenetic analysis**

Several suprageneric taxa, such as Ceratosauria and Carcharodontosauria, are used in the phylogenetic analysis to determine the relationships of the new species. Our usage and phylogenetic definitions (Fig. 20A, B; Appendix 1) follow Wilson et al. (2003), Sereno et al. (2004, 2005) and Sereno (2005). Background on their usage in the phylogenetic literature is available on-line (Sereno et al. 2005).

*Kryptops palaios.*—*Kryptops palaios* exhibits several derived characters clearly indicative of relationships among abelisaurid theropods. In the skull these include features of the maxilla such as the extensive external neurovascular texturing, reduction of the antorbital fossa, and highly inclined posterodorsal ramus. Knowledge of abelisaurids has increased dramatically after description of the first well preserved skeleton (*Carnotaurus*; Bonaparte et al. 1990) and more recent discovery of additional remains from Argentina (Coria and Salgado 2000; Lamanna et al. 2002; Coria et al. 2002; Calvo et al. 2004). Africa (Sereno et al. 2004), India (Wilson et al. 2003), and Madagascar (Sampson et al. 1998; Sampson and Krause 2007). Many phylogenetic analyses have been conducted that have included various abelisaurids, the most significant being those of Carrano et al. (2002), Wilson et al. (2003), Novas et al. (2004), Tykoski and Rowe (2004), Sereno et al. (2004), and Carrano and Sampson (2007). As is well seen in the recent analyses by Sereno and colleagues (Wilson et al. 2003; Sereno et al. 2004) and Carrano and Sampson (2007), little character support exists within Abelisauridae at most nodes, which collapse with one additional step. Missing data is a major issue. Cranial or postcranial data are lacking for several species. These analyses, nevertheless, agree that the African genus *Rugops* is in a basal position within Abelisauridae (Fig. 20A).

We added *Kryptops palaios* to a cladistic analysis of basal neotheropods by Sereno et al. (2004) and were able to score this species for 29 of 169 characters (17%). We modified one character (character 16) to code for a new condition of the articular slot on the maxilla for the anteroposterior process of the nasal (Appendix 1). As in Sereno et al. (2004), we removed three very poorly known genera (*Laevisuchus*, *Genusaurus*, *Illokelesia*) to reduce tree number and ordered multistate characters with overlapping states of magnitude. We obtained two minimum length trees of 213 steps with *Kryptops* positioned as the basalmost abelisaurid (Fig. 20A).

Characters supporting the basal position of *Kryptops* include the narrow articular slot on the maxilla for the anteroventral process of the nasal; later abelisaurids have elaborated this characteristic suture (Fig. 4). In *Kryptops* the iliac blade and sacrum more closely resemble the condition in *Allosaurus* than the lengthened iliac blade and increased sacral count in abelisaurids such as *Carnotaurus* or *Majungasaurus* (Bonaparte et al. 1990; Carrano 2007). The condition in *Rugops*, however, remains unknown (Sereno et al. 2004), and so these synapomorphies may be positioned at more than a single node. Phylogenetic resolution among abelisaurids breaks down with a single additional step in tree length, as character data remains very incomplete for several genera (Appendix 1).

Based on these results, we tentatively regard *Kryptops palaios* as an early basal abelisaurid and infer that abelisaurids had evolved a proportionately short, textured snout and relatively large body size (at least 6 m body length) before the close of the Early Cretaceous some 100 Ma. Some of their characteristic postcranial features, however, may have evolved during the early Late Cretaceous, because *Kryptops* maintains proportionately long neural spines in cervico-dorsal vertebrae, a deeper iliac blade, and a sacral series limited to five vertebrae.

*Eocarcharia dinops.*—The holotypic postorbital shares several synapomorphies with carcharodontosaurid theropods, most notably the robust overhanging brow with an expanded postorbital-frontal suture, the exclusion of the frontal from the orbital margin by lacrimal-postorbital contact, the broadened immobile nature of the postorbital-squamosal suture, and a modest intraorbital flange (Figs. 18, 19).

To more specifically determine its phylogenetic position, we examined the relationships of *Eocarcharia dinops* and other carcharodontosaurids based largely on data in a recent phylogenetic study of allosaurid theropods (Brusatte and Sereno in press). Taxa were pruned to include only seven carcharodontosaurids and a pair of proximate outgroups (*Allosaurus*, *Sinraptor*). Several characters were reevaluated and some were rescored for clarity and testability following Sereno (2007). New information on *Eocarcharia* was incorporated as well. In sum, 73 of the original 99 characters in Brusatte and Sereno (in press) remained informative after the analysis was restricted to carcharodontosaurids. Of these 73 characters, 54 survived further scrutiny, to which we added 6 new cranial characters. The final dataset, the aim of which is to evaluate carcharodontosaurid interrelationships, involves 9 terminal taxa and 60 characters (Tables 5 and 6).

We obtained four minimum length trees of 84 steps (CI = 0.74; RI = 0.74), which when summarized by a strict consensus tree (Fig. 20B) is similar to that in the analysis of Brusatte and Sereno (in press). Ingroup resolution, however, completely collapses with one additional step as a result of rogue taxa with high levels of missing data. Only 25 and 32% of character states, for example, are known for *Tyrannotitan* and *Eocarcharia*, respectively.

When *Eocarcharia* and *Tyrannotitan* are removed, a stable arrangement emerges with *Acrocanthosaurus* and *Neovenator* positioned as successive outgroups to Carcharodontosaurinae (Fig. 20B). This arrangement is maintained in trees with as
many as six additional steps. The more derived position of Acrocanthosaurus with respect to Neovenator is supported by several unambiguous synapomorphies including the deep proportions of the premaxilla (1), squared anteroventral corner of the dentary (34), the U-shaped symphyseal region of the conjoined dentaries (36), and the presence of sacral and caudal pleurocoels (50, 51). Placement of Eocarcharia and Tyrannotitan within Carcharodontosauridae will remain problematic until both genera are better documented. A more detailed description of the available remains of Tyrannotitan (Novas et al. 2005) may allow a better resolution of its position.

Discussion

Abelisaurids have played a prominent role in biogeographic hypotheses ever since they first came to light in the mid 1980s (Bonaparte 1985; Bonaparte and Novas 1985). Initially, when abelisaurid fossils were known only from Gondwanan landmasses, they were considered an endemic clade (Bonaparte and Kielan-Jaworowska 1987; Bonaparte 1991). More recently, Sampson et al. (1998: fig. 1) suggested that the absence of abelisaurids on Africa and their presence on South America, India, and Madagascar provided evidence of the early separation of Africa “circa 120 Ma”, which later was dubbed the “Africa-first” hypothesis (Sereno et al. 2004: 1327).

Central to this hypothesis was a paleogeographic reconstruction that shows the early separation of Africa from South America prior to other landmasses sometime between 140–120 Ma (Hay et al. 1999). By 120 Ma they show a continuous mid Atlantic seaway and claim that Africa was geographically isolated “throughout most of the Cretaceous” (Hay et al. 1999: 18, fig. 15). This early separation of Africa from South America is contradicted by many lines of logic and paleontologic evidence, which have consistently suggested a later date—around 100 Ma—for the establishment of deep circulation in the mid Atlantic (Rabinowitz and LaBrecque 1979; Reyment and Dingle 1987; Nürnberg and Müller 1991; Pittman et al. 1993; Azevedo 2004; Arai et al. 2007; Bengston et al. 2007; Jacobs et al. 2007).

Although Hay et al. (1999) was cited as the source for the paleogeographic sketch map at 120 Ma, Sampson et al. (1998: fig. 1) and Krause et al. (2007: fig. 11) used maps available on-line from the Ocean Drilling Stratigraphic Network (http://www.odsn.de/odsn/services/paleomap/paleomap.html; Krause et al. 2007: 15–16). Their maps of 120 Ma (Sampson et al. 1998: fig. 1; Krause et al. 2007: fig. 11), for example, show a narrow mid Atlantic seaway on either side of a tenuous land connection, whereas the map for the same time in Hay et al. (1999) shows a continuous mid Atlantic seaway. Hay et al. (1999) openly admitted that one of the inspirations for the mapping project was to explain the similarities long noted by paleontologists between the dinosaurian faunas South America and Indo-Madagascar. Circularity in reasoning, however, is something to eschew in the assessment of fossil evidence and paleogeography.

The “pan-Gondwana” hypothesis of Sereno et al. (2004: 1328), in contrast, suggests that an age of about 100 Ma “pinpoints the final separation of South America and Africa in the latest Albanian (ca. 100 Ma), significantly later than proposed by the ‘Africa-first’ model (ca. 120–140 Ma)”. This central theme of this hypothesis is that there may not have been enough time during the early Late Cretaceous, between the final opening of the Atlantic and the severing of one or more high-latitude land connections (Fig. 20C), to have allowed the evolution a distinctive biotic pattern on non-African Gondwanan landmasses (e.g., South America, India, Madagascar).
“About 100 Ma” (Sereno et al. 2004: 1328), of course, is an age estimate or midpoint of a range. For any biogeographic model of land-seaway interaction, uncertainty is introduced by eustatic fluctuation in sea level, which has been estimated to have been as high as 40–50 meters during the Albian (Bengston et al. 2007). Ammonites and foraminifera provide key fossil evidence for an incursion of surface waters from the north into the mid Atlantic Sergipe Basin north of Rio Grande-Walvis Ridge (Bengston et al. 2007) by the mid Albian (ca. 106 Ma), which would have significantly reduced land connections between South America and Africa. In the latest Albian (ca. 100 Ma), a deep water connection between the north and south Atlantic was established, which corresponds closely to the current boundary between Early and Late Cretaceous (Gradstein et al. 2004). Sereno et al. (2004: 1328) remarked that “trans-Atlantic interchange may have been operative as late as 95 Myr ago”, the upper bound of an interval (±5 My) from 105 to 95 Ma, when dispersal overland or across a narrow channel may well have been intermittently limited or impossible. The midpoint of that range, 100 Ma remains the best single age estimate for the biogeographic separation of the terrestrial faunas of South America and Africa.

The latest version of the Africa-first hypothesis (Krause et al. 2006, 2007) now also accepts 100 Ma as the best median age estimate for continental separation of South America and Africa, abandoning the principal difference upon which the hypothesis was named. In this regard, their diagrammatic depiction of Africa-first and pan-Gondwana models at 100 Ma is intentionally misleading (Krause et al. 2007: fig. 12); a mid Atlantic seaway between South America and Africa is shown only for their revised Africa-first hypothesis, although this was the age of separation proposed by the pan-Gondwana hypothesis (Sereno et al. 2004). By reducing this critical age of separation to 20 My, the Africa-first hypothesis is now restricted to the early Late Cretaceous (Krause et al. 2006, 2007). This more restricted proposition already had been outlined by Sereno et al. (2004: 1324), who referred to it as a “temporally restricted version” of the Africa-first hypothesis.

The major problems continue to be, first, that the terrestrial fossil record for the Late Cretaceous on several southern continents is patchy (Lamanna et al. 2002; Sereno et al. 2004; Carrano and Sampson 2007) and, second, that the geologic record for potential land connections between South America, India, and Madagascar is poorly known. Regarding the former, the terrestrial fossil record is most complete on South America during the mid and Late Cretaceous. Although abelisaurid teeth have been recorded recently on Africa in the latest Cretaceous (Smith and Lamanna 2006), more diagnostic remains of this group have yet to be recorded in post-Cenomanian rocks (Lamanna et al. 2002; Sereno et al. 2004). The Late Cretaceous African record is extremely sketchy at present and precludes well-constrained biogeographic hypotheses involving Africa during this interval. Absence of evidence in paleobiogeography simply cannot substitute for positive evidence of absence. Regarding the geologic record, land connections between South America and Africa are well documented by local terrestrial and marine sections and fossils (Fig. 20C). For the critical east Antarctic land bridge (Fig. 20C, number 3), in contrast, there is only meager geologic information for the Late Cretaceous. Uncertainty even exists as to which land areas were connected to Antarctica (India by the Kerguelen Plateau; Madagascar by the Gunnerus Ridge; Case 2002).

Recently Carrano and Sampson (2007: 30) have agreed that preference for a particular paleobiogeographic scenario is mitigated by the African record, but they go farther to suggest that the newly described African abelisauroids (abelisaurids, noasaurids) have “no impact on existing biogeographical scenarios.” Prior to 2004 Africa lacked positive evidence of either abelisaurids or noasaurids, and thus it was easier for Sampson and co-authors to construct a biogeographic scenario linking southern continents that had abundant fossil remains of both groups (South America, India, Madagascar). Two factors have complicated that argument.

First, the presence of both abelisauroid groups on Africa in mid Cretaceous rocks eliminates the strongest potential argument favoring the Africa-first hypothesis—the shared presence of groups that are entirely absent on Africa. Now the argument depends on the monophyly of non-African noasaurids and abelisaurids. For noasaurids, no such phylogenetic case has emerged, as their interrelationships are uncertain (Sereno et al. 2004; Carrano and Sampson 2007). Among abelisaurids, there is a subclade of non-African genera, as discussed by Sereno et al. (2004) and Carrano and Sampson (2007: figs. 4, 9). This subclade, however, is united by very weak character support and increasingly is home to species from earlier horizons in the Cretaceous that eventually may predate the opening of the Atlantic.

Second, acceptance by authors of the Africa-first hypothesis that South America and Africa separated closer to 100 Ma than 120 Ma compresses by about one half the available interval to establish a common terrestrial biota on non-African landmasses, before they as well were isolated by seaways. There are two narrow, high latitude sweepstakes routes (Fig. 20C, numbers 2, 3), both of which must have been functional for long distance dispersal among non-African landmasses. The main question regarding Gondwana’s high-latitude sweepstakes route is the duration over which at least two land bridges on either side of Antarctica were operative after the opening of the Atlantic.

At the opposite pole, considerable phylogenetic and geologic evidence exists during the mid and Late Cretaceous for an even higher-latitude sweepstakes route within the Arctic Circle across the Bering region between Asia and western North America (Sereno 1997). High-latitude sweepstakes routes are possible during the Mesozoic given the absence of polar ice. In our view, however, the Africa-first hypothesis—that a common, distinctive biota exclusive of Africa arose over a relatively short interval of time using a multi-bridge, Antarctic route—has yet to be convincingly established on the basis of either fossil or living organisms.
Conclusions

*Kryptops palaios* adds to increasing evidence pointing to a diversity of abelisaurids on Africa by mid Cretaceous time. It joins the slightly younger (Cenomanian) taxon *Rugops* from Niger (Sereno et al. 2004), an unnamed abelisaurid maxilla of similar age from Morocco (Mahler 2005), and isolated teeth from latest Cretaceous rocks in Egypt (Smith and Lamanna 2006). *Kryptops* is the oldest African abelisaurid and the oldest indisputable abelisaurid on any continent. Potentially older abelisaurid remains have been suggested for a pair of Early Cretaceous (Hauterivian–Barremian) vertebral from South America (Rauhut et al. 2003) and Late Jurassic (Kimmeridgian–Berriasian) vertebral and limb bones from Africa (Rauhut 2005), although their referral remains tentative.

*Kryptops palaios* indicates that abelisaurids with derived cranial features were present on Africa before the close of the Early Cretaceous (Aptian–Albian). The more inclusive clades to which abelisaurids belong (Abelisauroidia, Ceratosaursia) are now better represented on Africa than elsewhere and include an articulated noasaurid (Sereno et al. 2004) and the basal ceratosaursians *Spinolestes, Berberosaurus*, and *Elaphrosaurus* (Sereno et al. 2004; Allain et al. 2007; Carrano and Sampson 2007).

*Eocarcharia*, a contemporary of *Kryptops*, and *Neoovenator* from the Barremian of Isle of Wight (Hutt et al. 1996) constitute the oldest known carcharodontosaurids. Nearly equal in age are non-African genera *Acrocanthosaurus* from the Late Aptian–Early Albian of North America (Harris 1998) and *Tyranannosaurus* from the ?Aptian of South America (Novas et al. 2005). Mid Cretaceous theropods from Africa suggest that abelisaurids, carcharodontosaurids, and spinosaurids had come to the fore as the principal large-bodied predators in several faunas. Fossils from later Cretaceous horizons on Africa are needed to learn if this predatory triumvirate survived to the end of the period and, if so, how they compare to relatives on other continents.

Acknowledgements

We thank Carol Abraczinskius (University of Chicago, USA) for her skillful renderings from bones and for the arrangement and labeling of all figures. We also thank the members of the 2000 Expedition to Niger for discovering the specimens, Andrew Gray, Ray Vodden, Hannah Moots, Sara Burch, and Caitlin Wylie (University of Chicago, USA) for skillful preparation of the material, Martin Munt and Steve Hutt (Isle of Wight Museum of Geology, Sandown, UK), Angela Milner and Sandra Chapman (Natural History Museum, London, UK), Zhao Xijin and Xing Xia (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, PRC), Rich Cifelli, Nick Czaplewski, and Jeff Person (Sam Noble Oklahoma Museum of Natural History, Norman, OK), and Rodolfo Coria (Museo Carmen Funes, Plaza Huincul, Argentina) for permission to study material in their care, Mark Webster, Michael LaBarbara, Lawrence Heaney, David Rowley, Matt Friedman, Tom Rothfus (University of Chicago, USA), Roger Benson (University of Cambridge, Cambridge, UK), Matt Lamanna (Carnegie Museum of natural History, Pittsburgh, USA), and Francois Therrien (Royal Tyrrell Museum of Palaeontology, Drumheller, Canada) for their comments on the manuscript. This research was supported by two Howard Hughes Institute Undergraduate Education Initiative Grants and the Behrens Fund at the University of Chicago (to SB) and the National Geographic Society and National Science Foundation (to PS).

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Appendix 1

Phylogenetic taxonomy

Six higher level taxa that are used in the text and cladograms (Fig. 20A, B) have variant phylogenetic definitions in the recent literature. We use the definitions and definitional authors listed below and do not present any emendations (additional information available on-line at www.taxnonsrch.org; Sereno 2005; Sereno et al. 2005):

Ceratosauria Marsh, 1884; The most inclusive clade containing Ceratosaurus nasicornis Marsh, 1884 but not Passer domesticus (Linnaeus, 1758). (Sereno 2005)


Noasauridae Bonaparte and Novas, 1985: The most inclusive clade containing Allosaurus fragilis Marsh, 1877 but not Passer domesticus (Linnaeus, 1758). (Sereno 2005)

Carcharodontosauridae Stromer, 1931: The most inclusive clade containing Carcharodontosaurus saharicus Depéret and Savornin, 1927 but not Allosaurus fragilis Marsh, 1877, Sinraptor dongi Currie and Zhao, 1993, Passer domesticus (Linnaeus, 1758). (Sereno 2005)

Carcharodontosaurinae Stromer, 1931: The most inclusive clade containing Carcharodontosaurus saharicus Depéret and Savornin, 1927 and Giganotosaurus carolinii Coria and Salgado, 1995. (Brusatte and Sereno in press)

Table 4. Character state scores for Kryptops palaios for 169 characters in the analysis of basal tetanuran theropods by Sereno et al. (2004).

Table 5. Taxon-character matrix for carcharodontosaurids including Eocarcharia dinops and with Sinraptor dongi and Allosaurus fragilis as outgroups.
Table 6. Character list associated with the taxon-character matrix in Table 5. Parenthetical character numbers refer to the character number in Brusatte and Sereno (in press). Citations following a given character refer to the original author of the character (Sereno 2007).

**Cranial**

1(3). Premaxilla, main body, anteroposterior length relative to dorso-ventral depth: longer (0); subequal (1); deeper (2) (modified from Holtz 2000).

2(4). Premaxilla, anterior margin immediately above alveolar rim, inclination from vertical (lateral view): 0–9° (0); 10–20° (1) (modified from Brusatte and Sereno in press).

3(5). Maxilla, ventral anterior fossa, position of medial rim relative to the lateral rim: ventral (0); level (1) (modified from Holtz et al. 2004).

4(7). Maxilla, promaxillary fenestra, orientation of opening: posterior (0); lateral (1) (modified from Allain 2002).

5(8). Maxilla, maxillary fenestra, lateral exposure: partially or fully obscured by the edge of the antorbital fossa (0); fully exposed (1) (Holtz et al. 2004).

6(10). Maxilla, promaxillary recess, medial wall: solid (0); fenestrate (1) (modified from Allain 2002).

7(12). Maxilla, posterodorsal ramus, antorbital margin: rounded edge (0); flute over antorbital recess (1) (modified from Holtz et al. 2004).

8. Maxilla, posterior ramus, inclination of ventral margin under jugal articulation (lateral view): horizontal (0); declined by approximately 20° (new character).

9(13). Maxilla, extensive grooved sculpturing of external surface of main body: absent (0); present (1) (Forster 1999).

10(15). Maxilla, anterior interdental plates, depth: less (0), or more (1), than twice anteroposterior width (Brusatte and Sereno in press).

11(16). Nasal, dorsal surface, texture: low (0); rugose with relief (1) (modified from Holtz et al. 2004).

12(17). Nasal shape (dorsal view): expanding posteriorly (0); parallel-sided (1) (modified from Rauhut 2003).

13(19). Nasal, shape of the posterior suture: medial projection extends as far or farther posteriorly than the lateral projection (0); lateral projection extends farther posteriorly than the medial projection (1) (Holtz et al. 2004).

14(20). Lateral, dorsal edge of anterior ramus, form: level with, or slightly raised above, skull roof (0); prominent crest (1) (Harris 1998).

15(31). Prefrontal: present (0); absent (lost or coossified with the lacrimal) (1) (modified from Gauthier 1986).

16(33). Frontal-parietal, shelf over anteromedial corner of supratemporal fossa: absent (0); present (1) (modified from Forster 1999).

17(34). Frontal-frontal suture: open (0); coossified externally (1) (Holtz 2000).

18(35). Frontal-parietal suture: open (0); coossified externally (1) (Forster 1999).

19(26). Postorbital brow overhanging orbit: absent (0); present (1) (Brusatte and Sereno in press).

20(36). Postorbital-lacrimal contact: present (0); absent (1) (modified from Sereno et al. 1996).

21. Postorbital-lacrimal contact, size relative to postorbital-frontal contact: small, less than 20% (0); large, more than 50% (1) (new character).

22. Postorbital posterior process, length: shortest process (0); subequal to ventral process (1) (new character).

23. Postorbital-squamosal articulation: elongate scarf joint (0); transversely broad interlocking suture (1); spiral suture with long medial process (2) (new character).

24. Postorbital articulation for laterosphenoid head: rugose concavity (0); deep-rimmed socket (1) (new character).

25(23). Postorbital, intrarobital flange on ventral process: absent (0); present as a discrete projection (1) (Sereno et al. 1996).

26(40). Basioccipital-exoccipital, occipital condyle, shape: hemispherical (0); subospherial (1) (modified from Coria and Currie 2002).

27(41). Basioccipital, paired pannatoocyes with median commissure on neck of occipital condyle: absent (0); present (1) (modified from Coria and Currie 2002).

28(42). Basioccipital, axis of the occipital condyle with frontals held horizontal, angle from horizontal: 0–15° (0); more than 25° (1) (modified from Forster 1999).

29(46). Basioccipital-basisphenoid, composition of basal tubera: basioccipital posteriorly, basisphenoid anteriorly (0); basisphenoidal medially, basisphenoid laterally (1) (Sereno et al. 1996).

30. Basisphenoid fossa, form: shallow pocket (0); deep funnel approximately 30% depth of braincase (1) (modified from Sereno et al. 1996).

31(44). Laterosphenoid, trigeminal foramen, location relative to nuchal crest (with frontal roof horizontal): anterior or ventral (0); posterior (1) (Coria and Currie 2002).

32(43). Ossified sphenethmoid septum and orbitosphenoid walls between and around olfactory tract and bulbs: absent (0); present (1) (modified from Coria and Currie 2002).

33(50). Dentary, anterovelential corner, shape: convex (0); squared by projecting flange (1) (Sereno et al. 1996).

34(51). Dentary, anterior end of row of principal neurovascular foramina, form: parallel to (0), or arches ventrally away from (1), alveolar margin (modified from Brusatte and Sereno in press).

35(53). Dentary symphyseal region, shape (dorsal view): V-shaped (0); U-shaped (1) (Brusatte and Sereno in press).

**Dentition**

36(2). Premaxilla, number of teeth: 4 (0); 5 (1) (Harris 1998).

37(59). Mid maxillary and dentary teeth, profile of posterior margin (away from apex): concave (0); nearly straight (1) (modified from Holtz et al. 2004).

**Axial skeleton**

38(60). Axial intercentrum, orientation of ventral margin relative to that of the axial centrum: aligned (0); angled anterodorsally (1) (modified from Harris 1998).

39(61). Axis, ventral keel: present (0); absent (1) (Harris 1998).

40(62). Mid cervical centra, posterior articual face, width relative to height: subequal (0); 20% or more broader than tall (1) (Sereno et al. 1996).

41(63). Mid cervical centra, anterior articual face, orientation relative to a vertically-held posterior face: elevated (0); approximately level (1) (Sereno et al. 1996).

42(64). Cervicals, pneumatic structure of centrum: camerate (simple) (0); camellate (complex) (1) (Harris 1998).

43(65). Postaxial cervical pleurocoels, number of openings: one (0); two (1) (modified from Harris 1998).

44(66). Postaxial cervical zygosphenes, location in dorsal view: over centrum (0); lateral to centrum (1) (modified from Holtz 2000).

45(67). Dorsals, pleurocoels on posterior dorsal vertebrae: absent (0); present (1) (modified from Harris 1998).
46(68). Dorsals, posterior dorsal centra, length relative to height: sub−
equal (0); shorter (1) (modified from Holtz et al. 2004).
47(69). Dorsals, neural spines, height relative to centrum: less (0) or
more (1) than twice centrum height (Holtz 2000).
48(70). Mid dorsal centra, height at mid length in lateral view: more
(0), or less (1), than 60% of the height of the centrum face (modified
from Holtz 2000).
49(71). Sacral pleurocoels: absent (0); present (1) (Harris 1998).
50(72). Caudal pleurocoels: absent (0); present (1) (Sereno et al. 1996).
51(73). Distal caudal prezygapophyses, length: more (0), or less (1),
than 40% overlap of preceding centrum (Holtz 2000).

**Girdles and limbs**

52(97). Scapula, blade length relative to minimum width: less (0), or
more than (1), 8.0 (modified from Forster 1999).
53(81). Ischial shaft, distal expansion: subrectangular (0); foot with
discrete anterior and posterior projections (1) (modified from Har−
ris 1998).
54(82). Ischium, posteriorly directed flange on iliac peduncle: absent
(0); present (1) (Brusatte and Sereno in press).
55(83). Femur, orientation of central axis of head to shaft in anterior
view: approximately 90° (0); approximately 45° (1) (modified from
Harris 1998).
56(84). Femoral lateral condyle, shape: convex (0); cone−shaped
(1) (Brusatte and Sereno in press).
57(86). Femoral fourth trochanter, form: semicircular flange (0); low
crest (1) (modified from Harris 1998).
58(90). Tibial medial malleolus, medial expansion from shaft edge:
less (0), or more (1), than 40% tibial mid shaft width (modified
from Brusatte and Sereno in press).
59(91). Tibial lateral malleolus, distal extension beyond medial mal−
leolus: less (0), or 5% or more (1), tibial length (1) (modified from
Brusatte and Sereno in press).
60(92). Fibular length relative to femur: more (0), or less (1), than 70%
(Brusatte and Sereno in press).

Table 7. Rejected characters and modified character state scores from the analysis of Brusatte and Sereno (in press) are listed along with a brief expla−
nation of the modified character state scores, parenthetical character numbers are those used in Brusatte and Sereno (in press).

<table>
<thead>
<tr>
<th>Rejected characters</th>
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</table>
| 6. Maxilla, promaxillary fenestra, lateral exposure: partially or fully
| obscured by the edge of the antorbital fossa (0); fully exposed (1)
| (modified from Harris 1998). [Uninformative; all ingroups that
| preserve the promaxillary fenestra obscure at least the anterior margin
| of the opening in lateral view].
| 9. Maxilla, accessory antorbital pneumatic excavation or fenestra on
| the posterozdorsal ramus: absent (0); present (1) (Harris 1998: 2).
| [Uninformative; the condition in Allosaurus varies from absent to a
| subtle depression, and the condition in Sinraptor and Eocarcheria
| is difficult to identify with confidence as homologous].
| 11. Maxilla, articular surface with the premaxilla, inclination lateral
| view: angled strongly posteriorly (0); subvertical (1) (Brusatte
| and Sereno in press). [Ambiguous; the quantitative delineation of
| character states proved difficult to establish with a reasonable pro−
| tocol for assessment].
| 18. Nasal, lateral margin, form: offset with a small lateral crest (1); flat
| (0) (modified from Rauhut 2003). [Ambiguous; we cannot confi−
| dently score this subtle character, although some future modifica−
| tion may prove more effective].
| 22. Postorbital, ventral ramus, orientation: subvertical (0); angled anter−
| ventrally (1) (Holtz et al. 2004). [Uninformative; the axis of the ven−
| tral ramus of ingroup taxa are not substantially different but rather
| are oriented at 70 to 80° to a line through the anterior and posterior
| processes].
| 32. Frontal, supratemporal fossa, exposure in dorsal view: broadly ex−
| posed on frontal (0); mostly hidden, restricted by overhanging
| frontoparietal shelf (1) (modified from Coria and Currie 2002).
| [Potentially redundant; without more comparative evidence, this is
| regarded here as difficult to separate from character 33, which in−
| volves the overhanging frontoparietal shelf].
| 37. Parietal, nuchal crest, orientation: posterolateral (0); transverse (1)
| (modified from Coria and Currie 2002). [Variable; the orientation
| of the fragile crest appears to be variable and subject to preserv−
| ational factors].
| 45. Braincase, supratemporal fenestrae, orientation: dorsal (0); antero−
| lateral (1) (Coria and Currie 2002). [Ambiguous; measuring an ori−
| entation axis is often not an obvious procedure in this muscle bound space].
| 49. Dentary, anterior end in lateral view, depth: anteriorly tapering or
| parallel−sided (0); anteriorly expanding (1) (modified from Brus−
| atte and Sereno in press). [We rejected this character for the time
| being because it appears to overlap with the anteroventral expan−
| sion of the corner of the dentary (character 34)].
| 52. Dentary, external surface, texture: smooth (0); rugose, marked by
| pronounced lineations and ridges (1). [If there is distinguishable
| texture other than more foramina, it might well be correlated with
| the texture observed on the maxilla].
| 54. Dentary, orientation of dorsal and ventral margins of the tooth−bear−
| ing section: subparallel (0); caudally divergent (1) (Holtz et al.
| 2004: 219). [Uninformative; all of the theropods in the present anal−
| ysis that have a dentary show some expansion of depth toward the
| posterior end of the tooth row].
| 74. Gastral medial element, shape of distal end: tapered (0); club−
| shaped prominence (1) (Brusatte and Sereno in press). [Uncertain;
| this character is based on some unusually blunt−ended V−shaped
| gastral elements in Giganotosaurus and possibly similar straighter
| elements described in Acrocanthosaurus (Harris 1998: fig. 30B),
| although more detailed identification and description is lacking in
| these or any other taxa].
| 76. Ilium, posterior margin, shape: gently convex or caudally tapering
| (0); straight along its entire margin (1) [see 78 below].
| 77. Ilium, anterior margin, shape: gently convex (0); straight (1) [see 78
| below].
| 78. Ilium, pubic peduncle, form: anterior edge significantly posterior to
| the anterior margin of the preacetabular blade (0); curves strongly
| anteriorly such that the anterior edge is at the same level or anterior
| to the anterior margin of the preacetabular blade (1). [Ambiguous;
| characters 76–78 at this time are poorly documented in the litera−
| ture, the only reasonably complete ilium known in Mapusaurus
| (Coria and Currie 2006: fig. 26). Much of the ilium is preserved in
| Neovenator, and the posterior portion is known in Giganotosaurus.
| The short length and consistent shape of the iliac blades in Sin−
| raptor and Allosaurus may not adequately document potential
| more variable outgroup conditions].

87. Femoral extensor groove on distal end, form: deep and narrow (0); shallow and broad (1) (Harris 1998) [Ambiguous; the character is expressed as an incomplete ratio that leaves a much to interpretation].

88. Femoral ligament ridge in flexor groove: absent or indistinct (0); present (1) (Harris 1998) [Ambiguous; this character requires documentation and cannot be scored on the basis of literature figures or descriptions].

96. Scapula, acromion process, size: prominent (0); reduced or absent (1) (Holtz 2000) [Uninformative; the acromial proportions in Acrocanthosaurus (Currie and Carpenter 2000) and Mapusaurus (Coria and Currie 2006) look very similar to that in Sinraptor (Currie and Zhao 1993) and Allosaurus (Madsen 1976)].

99. Metacarpals, proximal articular ends, transverse width: less (0) or two times or more (1) than minimum transverse shaft width (Brusatte and Sereno in press) [Ambiguous; this would only apply to Acrocanthosaurus and then only to metacarpals 2 and 3. Mapusaurus (Coria and Currie 2006) preserves only the bases of metacarpals 2 and 3].

**Character state changes**

4(7). The promaxillary fenestra appears to be preserved as a narrow posteriorly-facing slit on the right maxilla in Giganotosaurus. No such slit is present on Carcharodontosaurus and Mapusaurus, and so its condition is scored as inapplicable (previously the opening was identified as the promaxillary fenestra).

18(34). The interfrontal suture is open in two available skulls for Eocarcharia as well as Acrocanthosaurus (Stovall and Langston 1950; Currie and Carpenter 2000) but were scored as coossified.

26(40). The character states were swapped so that a hemispherical, rather than dorsoventrally flattened, condyle is primitive (0), and Sinraptor is scored for the hemispherical condition, which can be seen in the various views of the braincase (Currie and Zhao 1993).

32(43). Acrocanthosaurus has an ossified sphenethmoid septum and orbitosphenoids that enclose the olfactory tract (Stovall and Langston 1950), whereas Eocarcharia clearly does not (Fig. 14).

33(50). Tyrannotitan has the anteroventral flange that forms a prominent corner on the dentary (Novas et al. 2005) but was scored as lacking this feature. The anterior end of the dentary of Carcharodontosaurus is well described in Brusatte and Sereno (2007), and we use their terminology for the flanges.

36(2). Premaxillary tooth count had been given a composite state “three or four.” As none of the terminal taxa have three premaxillary teeth, the state has been simplified to “4”.

42(64). Camellate or spongy bone, which is present in the cervical vertebrae of Acrocanthosaurus (Harris 1998), appears to be absent in several cervical vertebrae of Carcharodontosaurus but was scored as present.

6(68). Tyrannotitan has short posterior dorsal centra, rather than sub-equal to their height, as depicted in the available skeletal silhouette (Novas et al. 2005: fig. 1).

49(71). There are no sacral vertebrae preserved in Tyrannotitan, and so the presence or absence of sacral pleurocoels cannot be determined. Previously we followed (Novas et al. 2005) and scored sacral pleurocoels as absent.

52(97). We revised the ratio for scapular blade length from 7.5 to 8.0 to more clearly subdivide proportional lengths observed in basal tetanurans. Allosaurus and all carcharodontosaurids that preserve the scapular blade except Giganotosaurus have an elongate “strap-shaped” blade. Giganotosaurus and Sinraptor have proportionately shorter blades. We scored Tyrannotitan as unknown, although the base of the blade suggests it has strap-shaped propositions.