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

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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 carcharodontosaurids had already evolved by the mid Cretaceous. The presence of a close relative of the North American genus *Acrocanthosaurus* on Africa suggests that carcharodontosaurids had already achieved a trans-Tethyan distribution by the mid Cretaceous.

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

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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 carcharodontosaurids (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 carcharodontosaurids 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 along the western edge of the Ténéré Desert in Niger in a place known as "Gadoufaoua" (Taquet 1976; Sereno et al. 1999, 2001; Fig. 1A). Like the Tegama Group to which it belongs, the Elrhaz Formation consists almost exclusively of cross-bedded fluvial sandstones of low relief, much of which are intermittently obscured by migrating sand dunes. The formation has yielded a diverse terrestrial fauna including the spinosaurid theropod *Suchomimus tenerensis*, the diplodo-

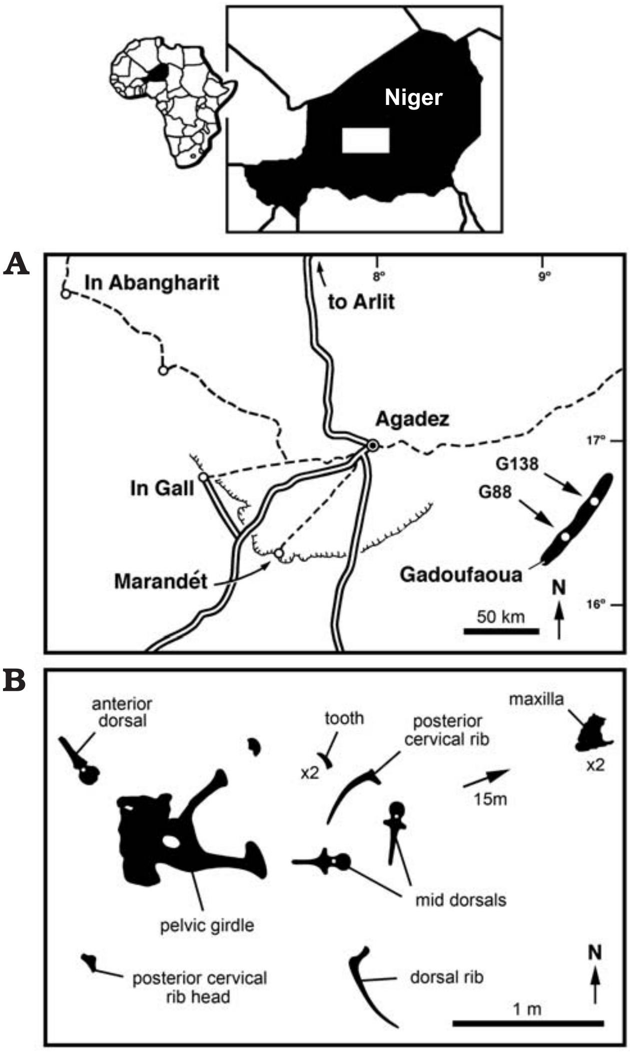

Fig. 1. **A**. The region of central Niger known as Gadoufaoua (black) and the sites (white dots) where the holotypic specimens of *Kryptops palaios* gen. et sp. nov. (site G88) and *Eocarcharia dinops* gen. et sp. nov. (site G138) were discovered. **B**. Site map for *Kryptops palaios* (MNN GAD1) gen. et sp. nov. with cranial elements shown at twice natural size. The maxilla, located 15 m from the other bones, was not in place and probably was originally closer to the other bones.

coid sauropod *Nigersaurus taqueti*, the ornithopods *Ouranosaurus nigeriensis* and *Lurdusaurus arenatus*, several crocodilians 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 diagnostic 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

Table1. The archosaurian fauna of the Elrhaz Formation in the Gadoufaoua region of the Ténéré Desert in central Niger.

Higher taxon		Species
Dinosauria	Theropoda	*Kryptops palaios* gen. et sp. nov. *Eocarcharia dinops* gen. et sp. nov. *Suchomimus tenerensis* undescribed noasaurid
	Sauropodomorpha	*Nigersaurus taqueti* undescribed titanosaurian
	Ornithischia	*Ouranosaurus nigeriensis* *Lurdusaurus arenatus* *Valdosaurus nigeriensis*
Pterosauria	Ornithocheiridae	undescribed taxa
Crocodylomorpha	Notosuchia	*Anatosuchus minor* *Araripesuchus wegneri*
	Pierosauridae	*Stolokrosuchus*
	Neosuchia	*Sarcosuchus imperator*

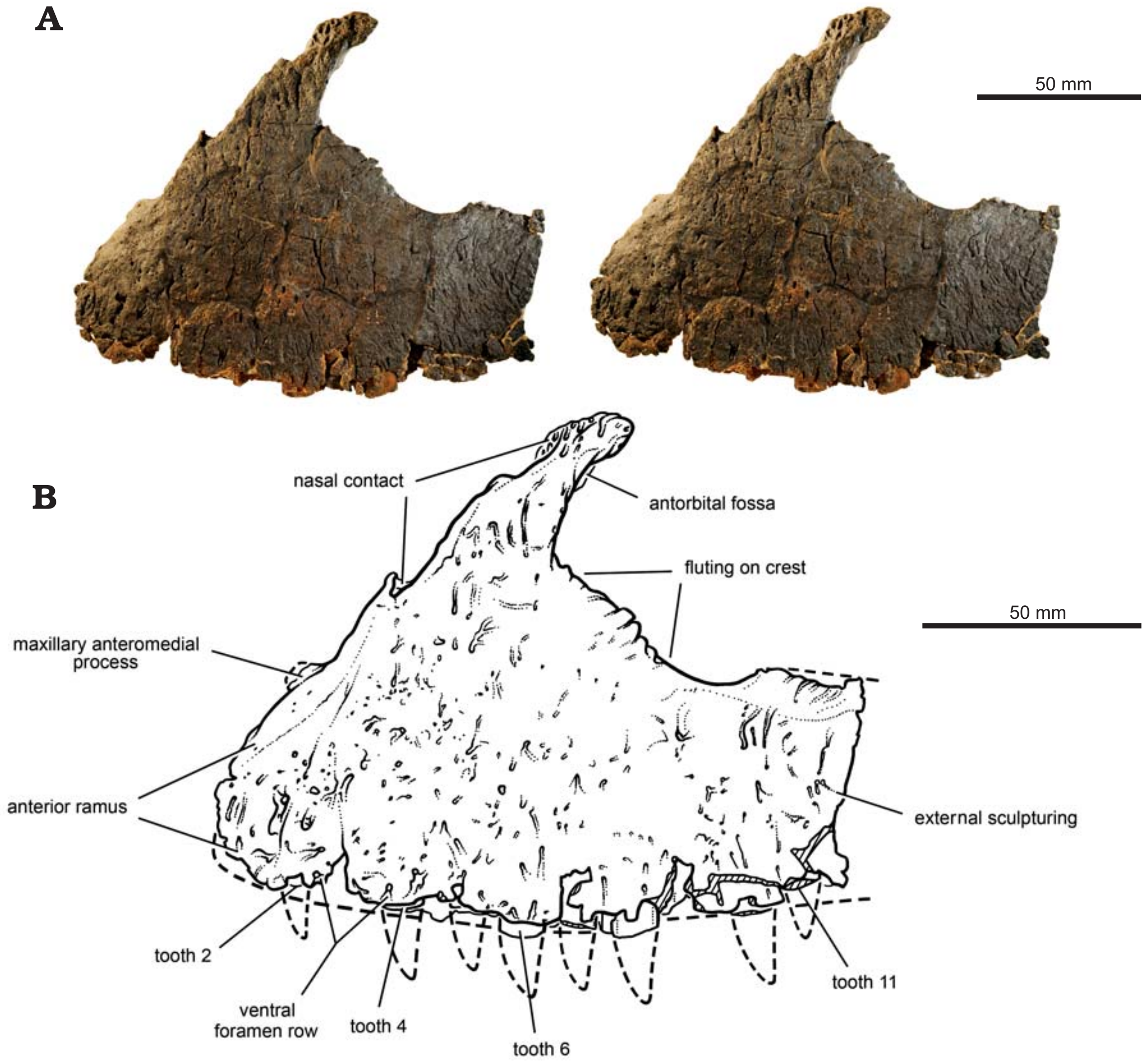

Fig. 2. Abelisaurid theropod *Kryptops palaios* gen. et sp. nov. MNN GAD1-1 from the Lower Cretaceous Elrhaz Formation of Niger. Left maxilla in lateral view; stereopair (**A**) and line drawing (**B**). Cross-hatching indicates broken bone; dashed lines indicate estimated edges.

Naturales, Buenos Aires, Argentina; MIWG, Museum of Isle of Wight Geology, Sandown, U.K.; MNN, Musée National du Niger, Niamey, Republique du Niger; OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA; UCRC, University of Chicago Research Collection, Chicago, Illinois, USA.

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

Table 2. Measurements (cm) of the maxilla (MNN GAD1-1), fourth and fifth sacral vertebrae, and right side of the pelvic girdle (MNN GAD1-2) in *Kryptops palaios* gen. et sp. nov. Parentheses indicate estimation.

Maxilla	
Length of preserved tooth row	15.0
Depth at level of sixth alveolus	6.8
Length of base of posterodorsal ramus	9.5
Sacrum	
Sacral 4, centrum length	11.0
Sacral 4, centrum width	4.8
Sacral 5, maximum depth of vertebra	44.7
Sacral 5, centrum length	11.0
Sacral 5, centrum depth	9.4
Sacral 5, centrum width	9.8
Acetabulum	
Acetabulum, maximum anteroposterior length	18.3
Acetabulum, maximum dorsoventral length	16.4
Ilium	
Blade, length	65.0
Blade, depth above acetabulum	29.4
Preacetabular process, maximum length	17.0
Preacetabular process, maximum depth	(36.5)
Postacetabular process, maximum length	20.8
Postacetabular process, maximum depth	21.5
Pubic peduncle, maximum length	16.2
Ischial peduncle, maximum length	4.0
Ischium	
Shaft, maximum length from acetabulum	(58.0)
Shaft at mid length, maximum dorsoventral diameter	2.5
Shaft at mid length, maximum transverse diameter	2.5
Pubis	
Maximum length from acetabulum	(62.0)
Boot, maximum length	(28.0)
Boot, width near posterior end	3.0

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* than in other abelisaurids (Fig. 4), a primitive condition. Finally, the texturing of the external surface of the maxilla is composed of shorter grooves than typical of similar ornamentation on other abelisaurids. The sacrum and ilium are also more primitive than in *Majungasaurus* and *Carnotaurus* (Bonaparte et al. 1990; Carrano 2007); the sacrum is composed of only five vertebrae, and the ilium has a relatively deeper preacetabular process.

Description

Maxilla.—The left maxilla is missing the distal portion of the posterior ramus and some of the alveolar margin and crown tips (Figs. 2, 3). The preserved portion of the tooth row is 15 cm long and contains 11 alveoli. Compared to the similar-sized maxilla of *Rugops primus* (MNN IGU1), there are probably six to seven posterior alveoli that are missing for a similar total of 17 or 18 maxillary teeth. In medial view, most of the medial lamina that encloses the maxillary antrum is broken away along with the distal portion of the anteromedial process (Fig. 3).

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 abelisauroid 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 than medially (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

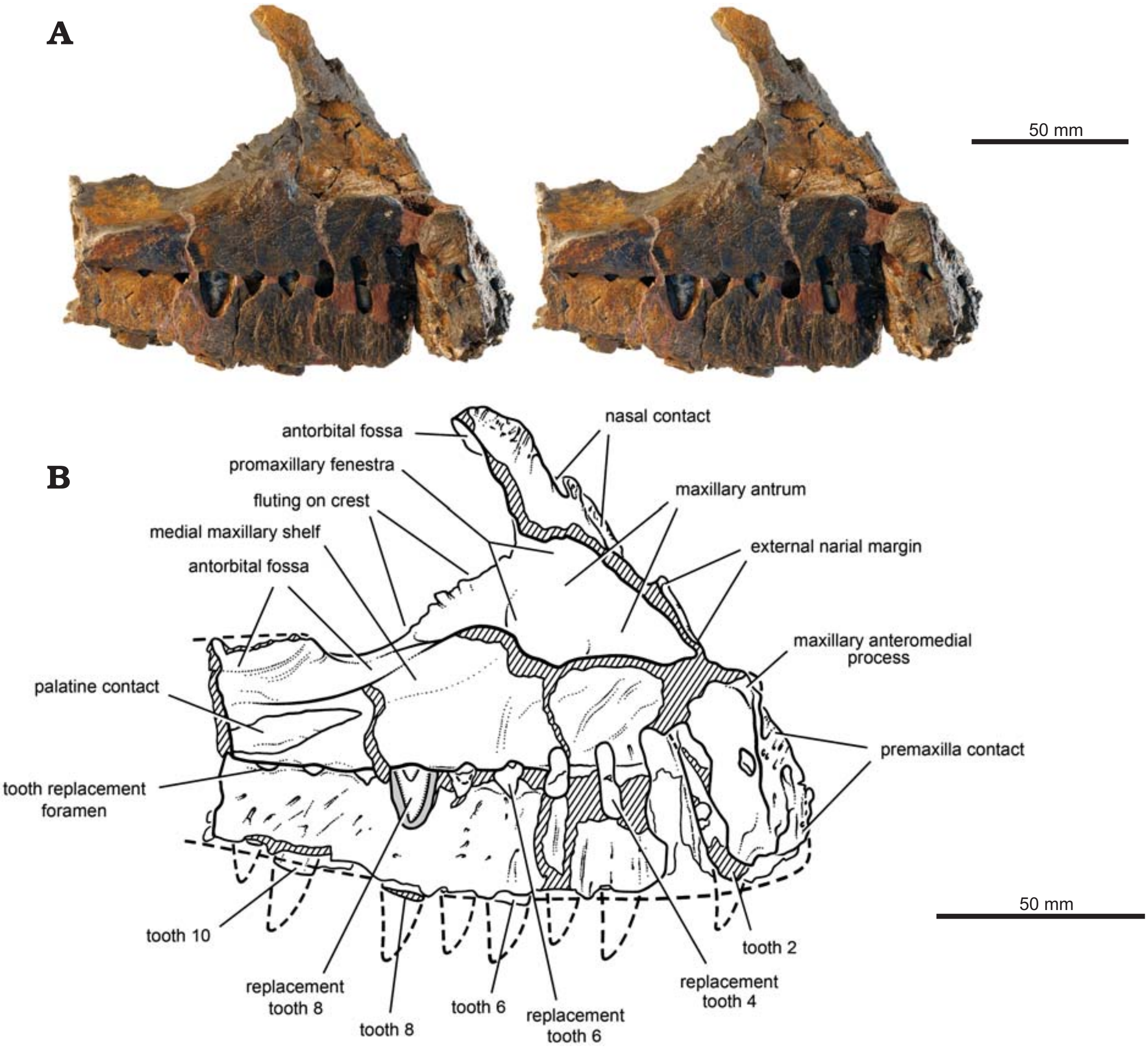

Fig. 3. Abelisaurid theropod *Kryptops palaios* gen. et sp. nov. MNN GAD1-1 from the Lower Cretaceous Elrhaz Formation of Niger. Left maxilla in medial view; stereopair (**A**) and line drawing (**B**). Cross-hatching indicates broken bone; dashed lines indicate estimated edges; grey tone indicates matrix.

(Sereno et al. 2004). 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;

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.

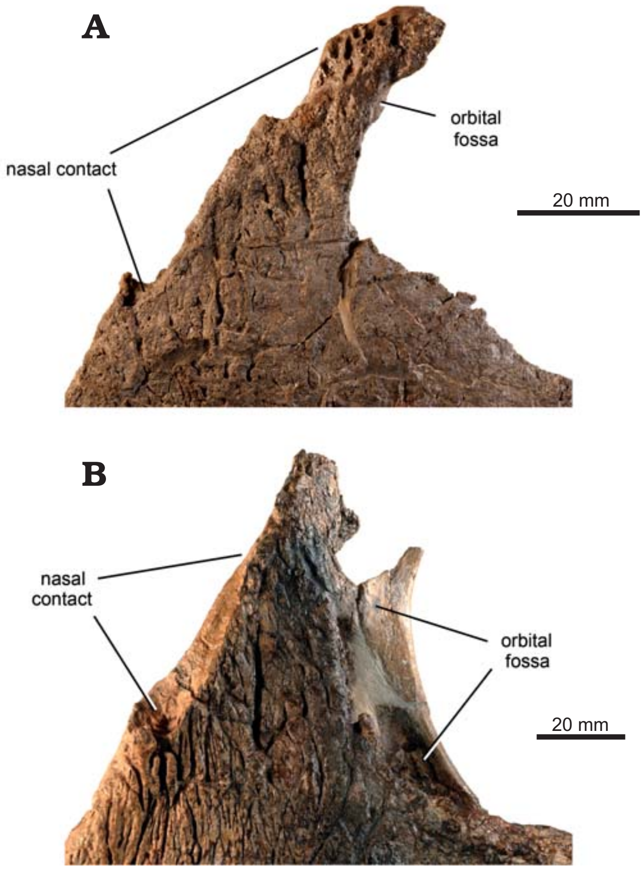

Fig. 4. Abelisaurid theropods from the Cretaceous of Niger. Comparison of posterodorsal ramus of the left maxilla in lateral view. **A**. *Kryptops palaios* gen. et sp. nov. (MNN GAD1-1) from the Lower Cretaceous Elrhaz Formation. **B**. *Rugops primus* (MNN IGU1) from the Upper Cretaceous Echkar Formation.

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-

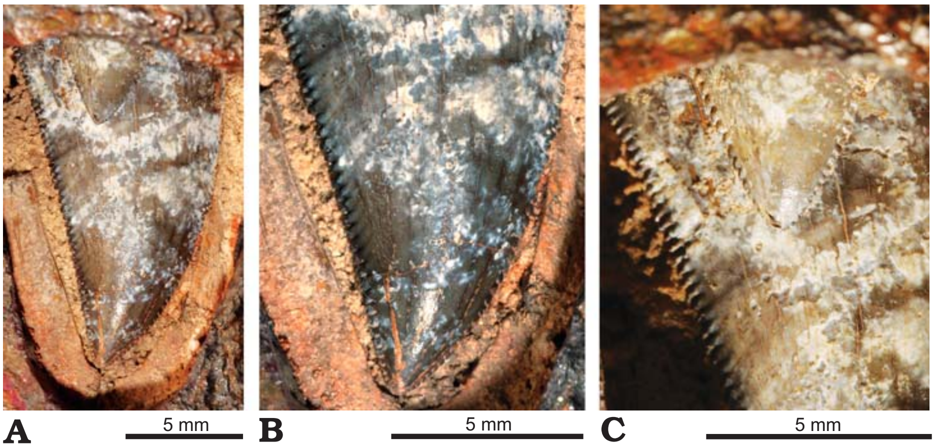

Fig. 5. Abelisaurid theropod *Kryptops palaios* gen. et sp. nov. MNN GAD1-1 from the Lower Cretaceous Elrhaz Formation of Niger. Erupting replacement crowns in medial view (**A**–**C**) in the eighth crypt of the left maxilla.

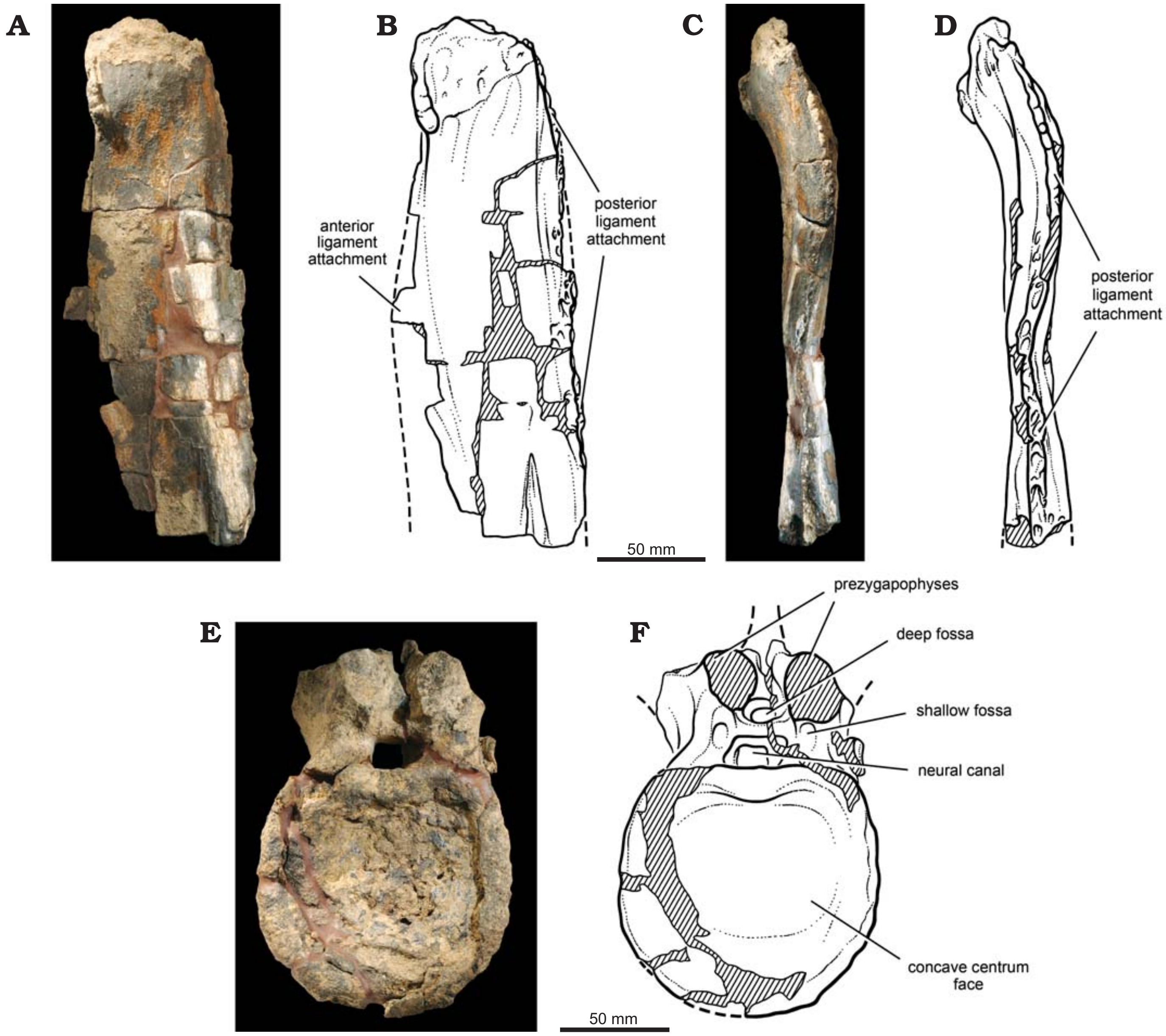

Fig. 6. Abelisaurid theropod *Kryptops palaios* gen. et sp. nov. MNN GAD1-5 from the Lower Cretaceous Elrhaz Formation of Niger. Mid dorsal vertebra, spine in left lateral (**A**, **B**) and posterior (**C**, **D**) views, and centrum in anterior view (**E**, **F**). Photographs (**A**, **C**, **E**) and line drawings (**B**, **D**, **F**). Cross-hatching indicates broken bone.

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).

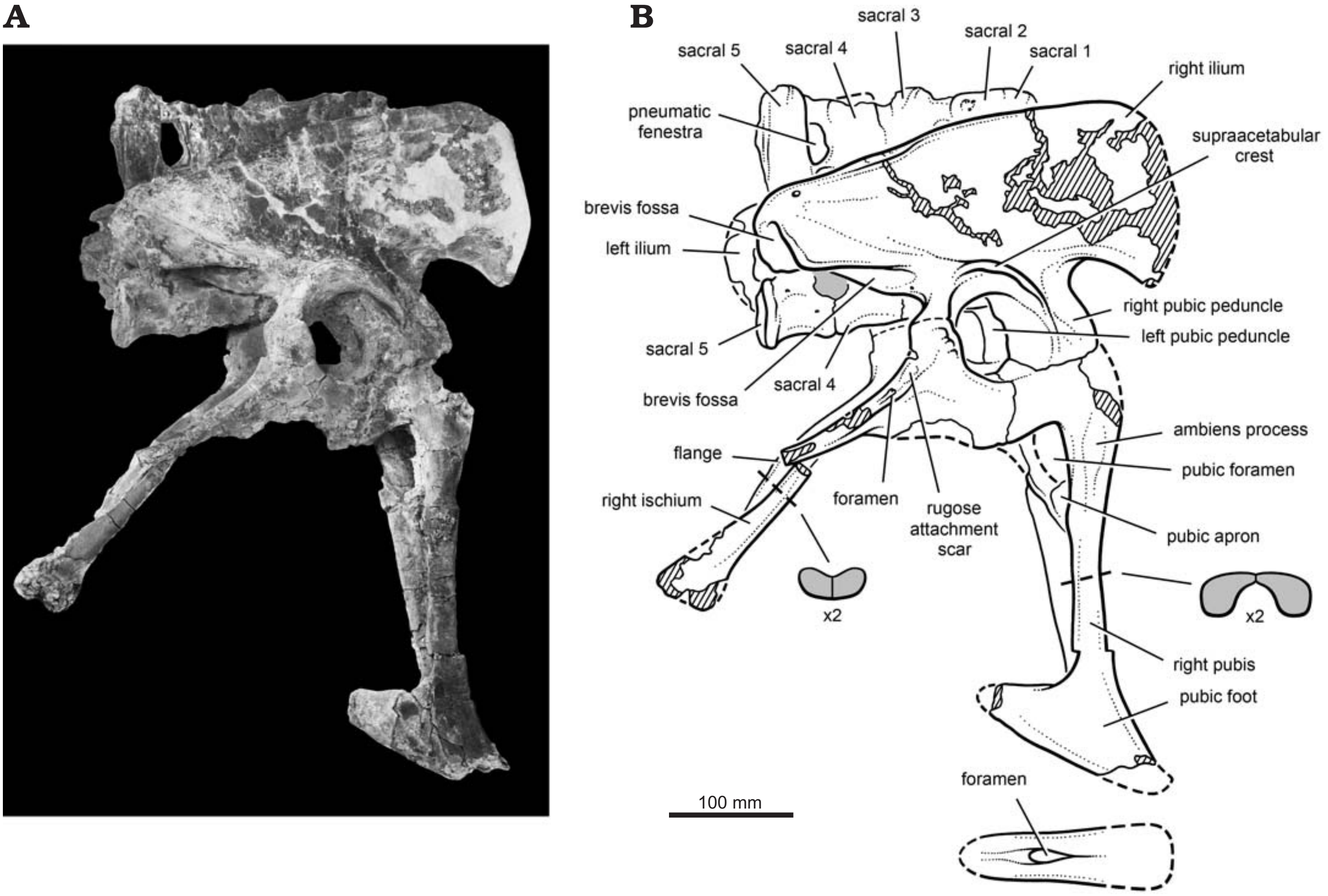

Fig. 7. Abelisaurid theropod *Kryptops palaios* gen. et sp. nov. MNN GAD1-2 from the Lower Cretaceous Elrhaz Formation of Niger. Pelvic girdle in right lateral view; photograph (**A**) and line drawing with two cross-sections and ventral view of the pubic foot (**B**). Cross-hatching indicates broken bone; dashed lines indicate estimated edge; grey tone on specimen indicates matrix.

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-

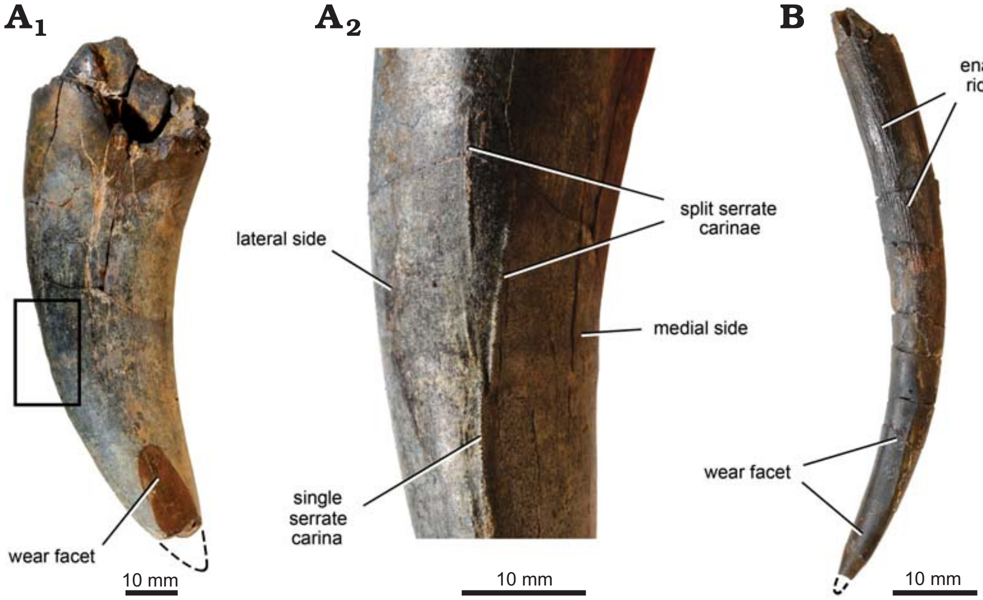

Fig. 8. Archosaurian teeth associated with the holotype of *Kryptops palaios* gen. et sp. nov. **A**. Carcharodontosaurid tooth MNN GAD15 in lateral (A_1) and anterior (A_2) views, with box (A_1) showing the location of the split carina (A_2). **B**. Ornithocheiroid pterosaur tooth MNN GAD16 in probable mesial view.

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 abelisaurids coossify with maturity.

Ilium.—The ilium is strikingly primitive in shape compared to that in the more derived abelisaurids *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-

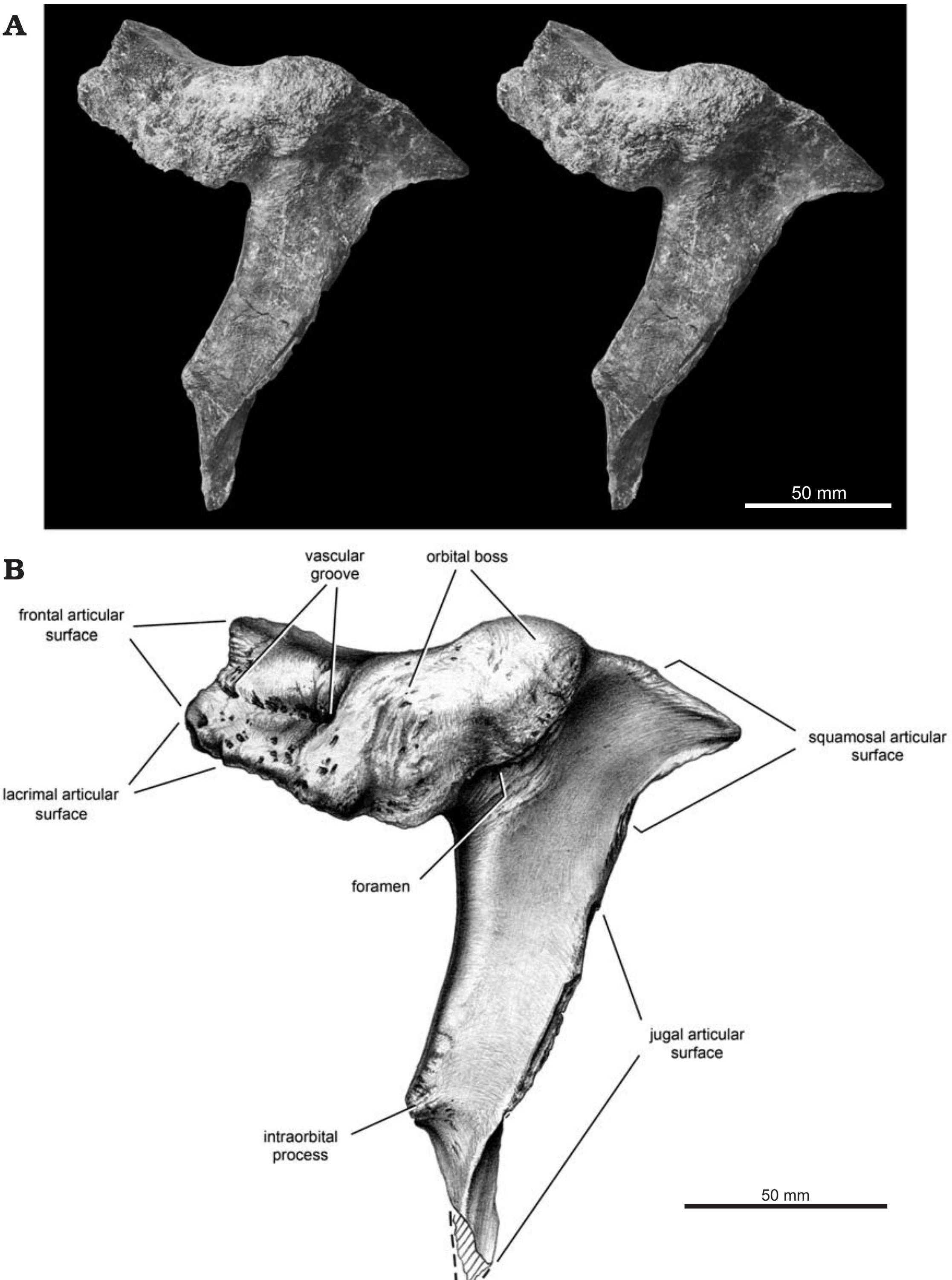

Fig. 9. Carcharodontosaurid theropod *Eocarcharia dinops* gen. et sp. nov. MNN GAD2 from the Lower Cretaceous Elrhaz Formation of Niger. Left postorbital (holotype) in lateral view; stereopair (**A**) and pencil drawing (**B**). Cross-hatching indicates broken bone; dashed lines indicate estimated edge.

velopment 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.

Pubis.—In lateral view the pubis has a shaft that is vertical in orientation and gently concave anteriorly. In cross-section of the shaft, the anterior surface is flat and a posterior fossa is present throughout most of its length. A substantial distal foot is present, although not as well developed as in allosauroids (Fig. 7). The shaft and foot are straighter and relatively smaller, respectively, in *Carnotaurus* (Bonaparte et al. 1990), *Aucasaurus* (Coria et al. 2002), *Pycnonemosaurus* (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 postcranial 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 allosauroids 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* is estimated to be about 25 cm in length, from which we infer an approximate skull length of skull 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.

Table 3. Measurements (cm) of the left maxilla (MNN GAD7), left frontal (MNN GAD10), and left postorbital (MNN GAD2) in *Eocarcharia dinops* gen. et sp. nov.

Maxilla	
Maximum length	52.8
Maximum depth	25.0
Anterior extremity to antorbital fenestra, length	19.8
Antorbital fossa margin, anterior end, depth from fenestra	6.2
Antorbital fossa margin, posterior end, depth	2.6
Frontal	
Maximum length	10.2
Maximum width	7.1
Prefrontal	
Maximum length in dorsal view	5.5
Maximum width	3.8
Maximum Depth	3.0
Postorbital	
Maximum depth	16.3
Brow rugosity, maximum length	6.2
Anterior process, length	6.8
Ventral process, length	11.4
Posterior process, length	2.0

Tetanurae Gauthier, 1986

Allosauroidea 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.

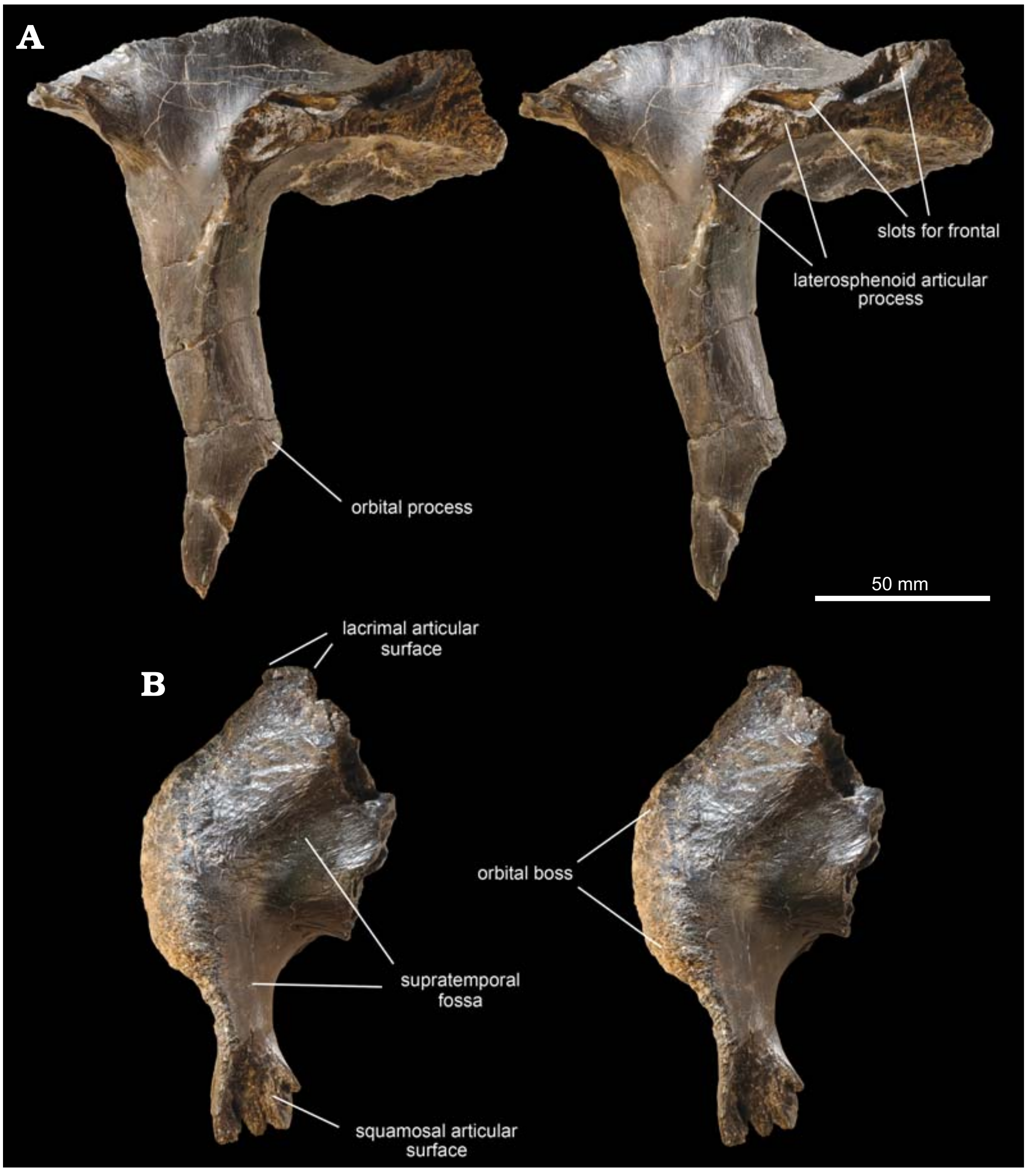

Fig. 10. Carcharodontosaurid theropod *Eocarcharia dinops* gen. et sp. nov. MNN GAD2 from the Lower Cretaceous Elrhaz Formation of Niger. Stereopairs of left postorbital (holotype) in medial (**A**) and dorsal (**B**) views.

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°88' and E 9°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 posterodorsal 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 posterodorsal 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

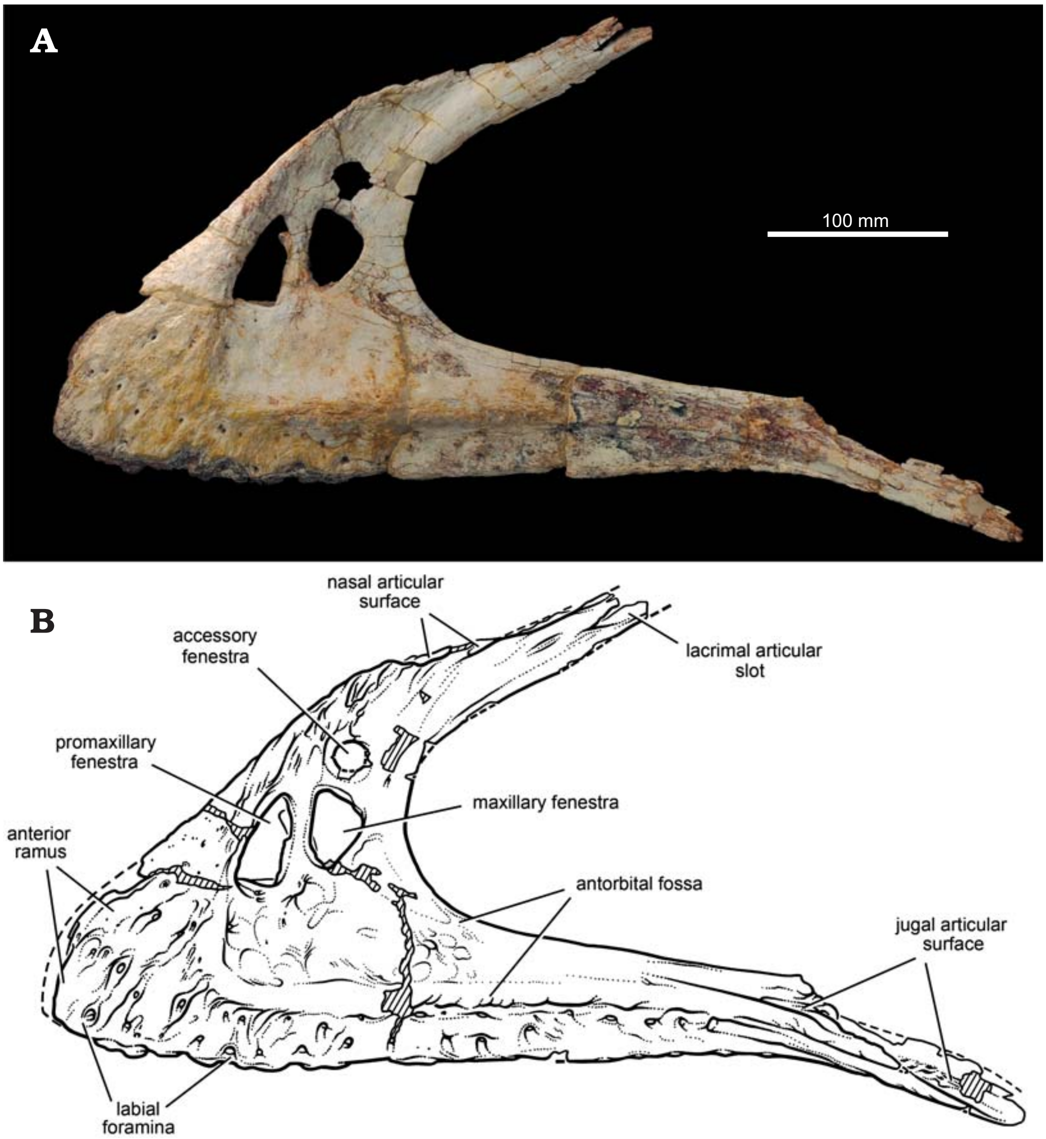

Fig. 11. Carcharodontosaurid theropod *Eocarcharia dinops* gen. et sp. nov. MNN GAD2 from the Lower Cretaceous Elrhaz Formation of Niger. Left maxilla in lateral view; photograph (**A**) and line drawing (**B**). Cross-hatching indicates broken bone; dashed lines indicate estimated edge; grey tone indicates matrix.

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 carcharodontosaurids 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 carcharodontosaurids, *Eocarcharia* retains the prefrontal 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 carcharodontosaurids and most allosauroids. There is no slot anteriorly for the anteroventral process of the nasal as in abelisaurids. The jugal contact is well preserved along the pos-

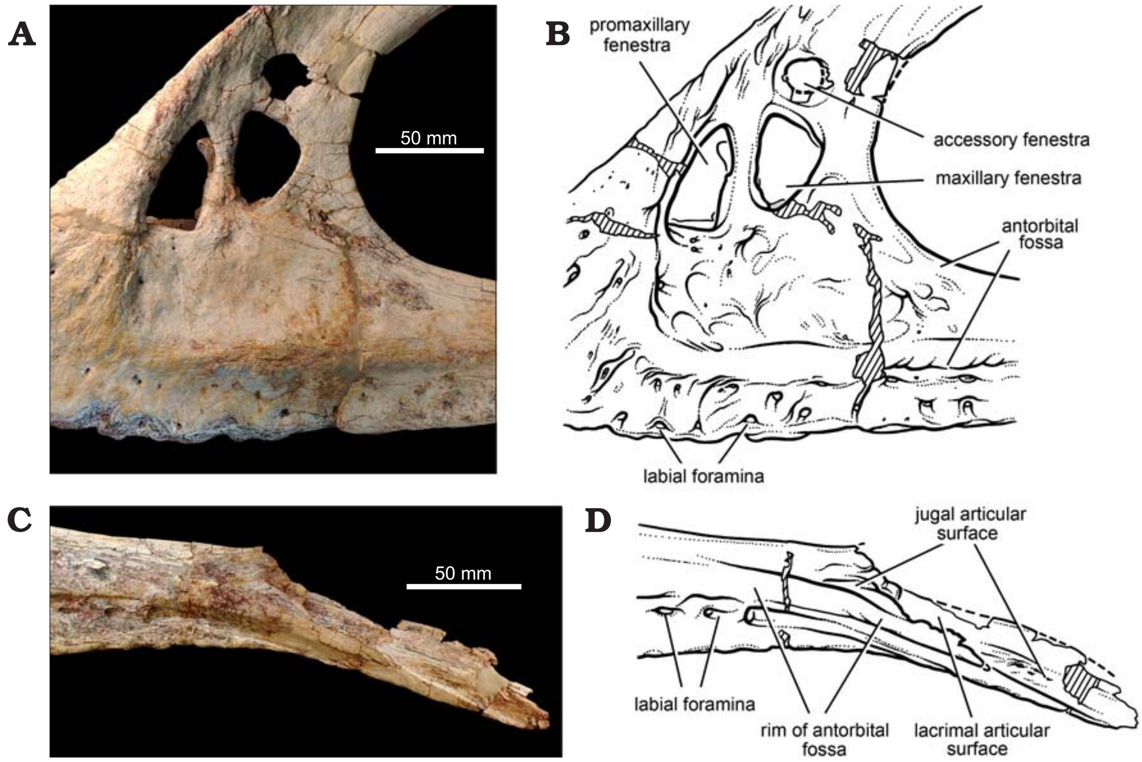

Fig. 12. Carcharodontosaurid theropod *Eocarcharia dinops* gen. et sp. nov. MNN GAD2 from the Lower Cretaceous Elrhaz Formation of Niger. Left antorbital region in left lateral view (**A**, **B**) and posterior ramus in lateral view (**C**, **D**); photographs (**A**, **C**) and line drawings (**B**, **D**). Cross-hatching indicates broken bone; dashed lines indicate estimated edge; grey tone indicates matrix.

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*, *Acrocanthosaurus*, *Allosaurus*, and abelisaurids. In other basal tetanurans, such as *Neovenator*, *Afrovenator*, and spinosauroids, 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*, *Suchomimus*, *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

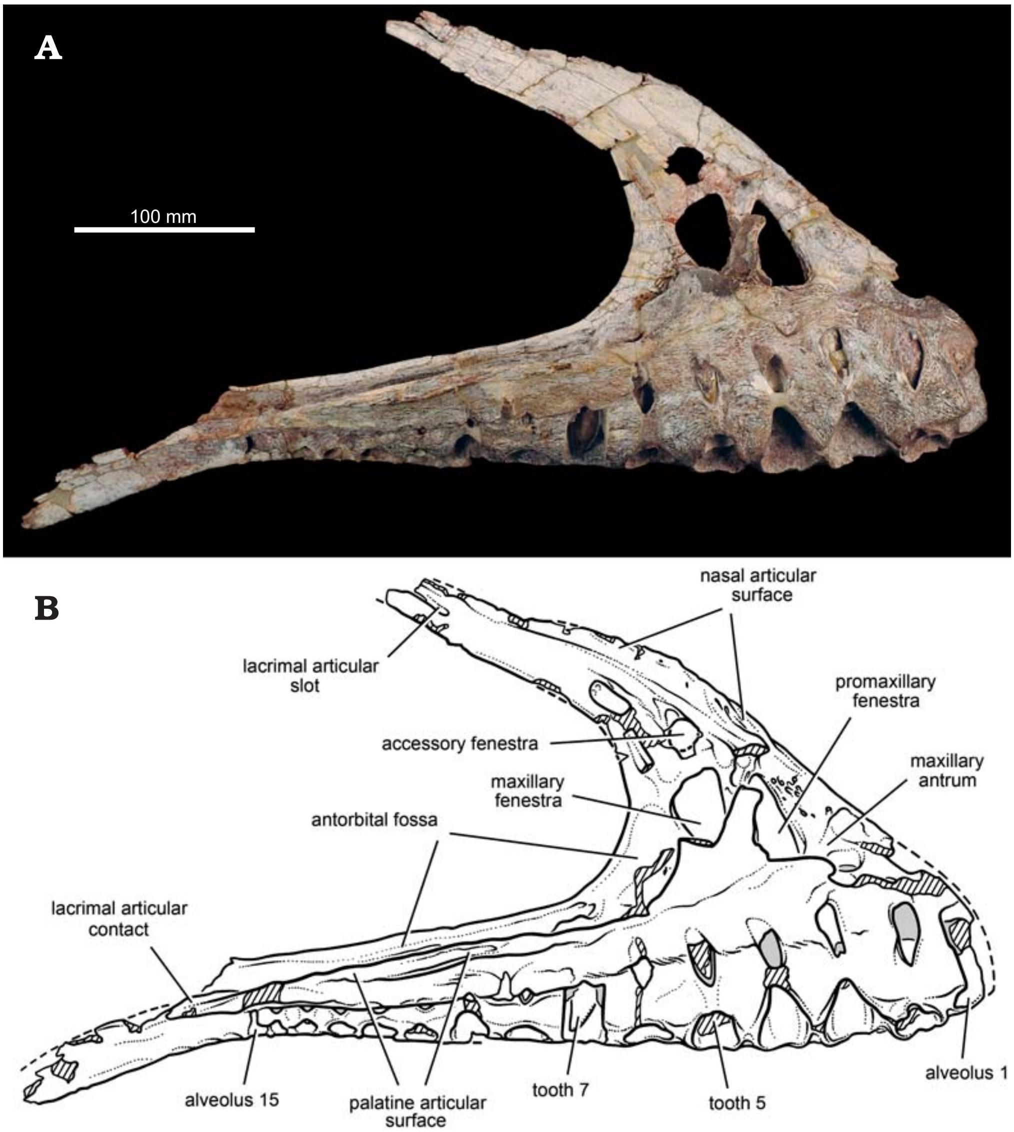

Fig. 13. Carcharodontosaurid theropod *Eocarcharia dinops* gen. et sp. nov. MNN GAD2 from the Lower Cretaceous Elrhaz Formation of Niger. Left maxilla in medial view; photograph (**A**) and line drawing (**B**). Cross-hatching indicates broken bone; dashed lines indicate estimated edge; grey tone indicates matrix.

(Tykoski and Rowe 2004). The antorbital fossa is bordered ventrally by a raised, somewhat swollen and rounded rim that flattens posteriorly (Figs. 11, 12A, B). Some carcharodontosaurids, 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 medial maxillary 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 *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 *Tyrannotitan*, *Mapusaurus*, *Giganotosaurus*, *Carcharodontosaurus*, and an isolated tooth from Japan (Coria 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 carcharodontosaurid 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 *Tyrannotitan* (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 10mm, 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 posteromedial 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 posteromedial 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 posteromedial 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

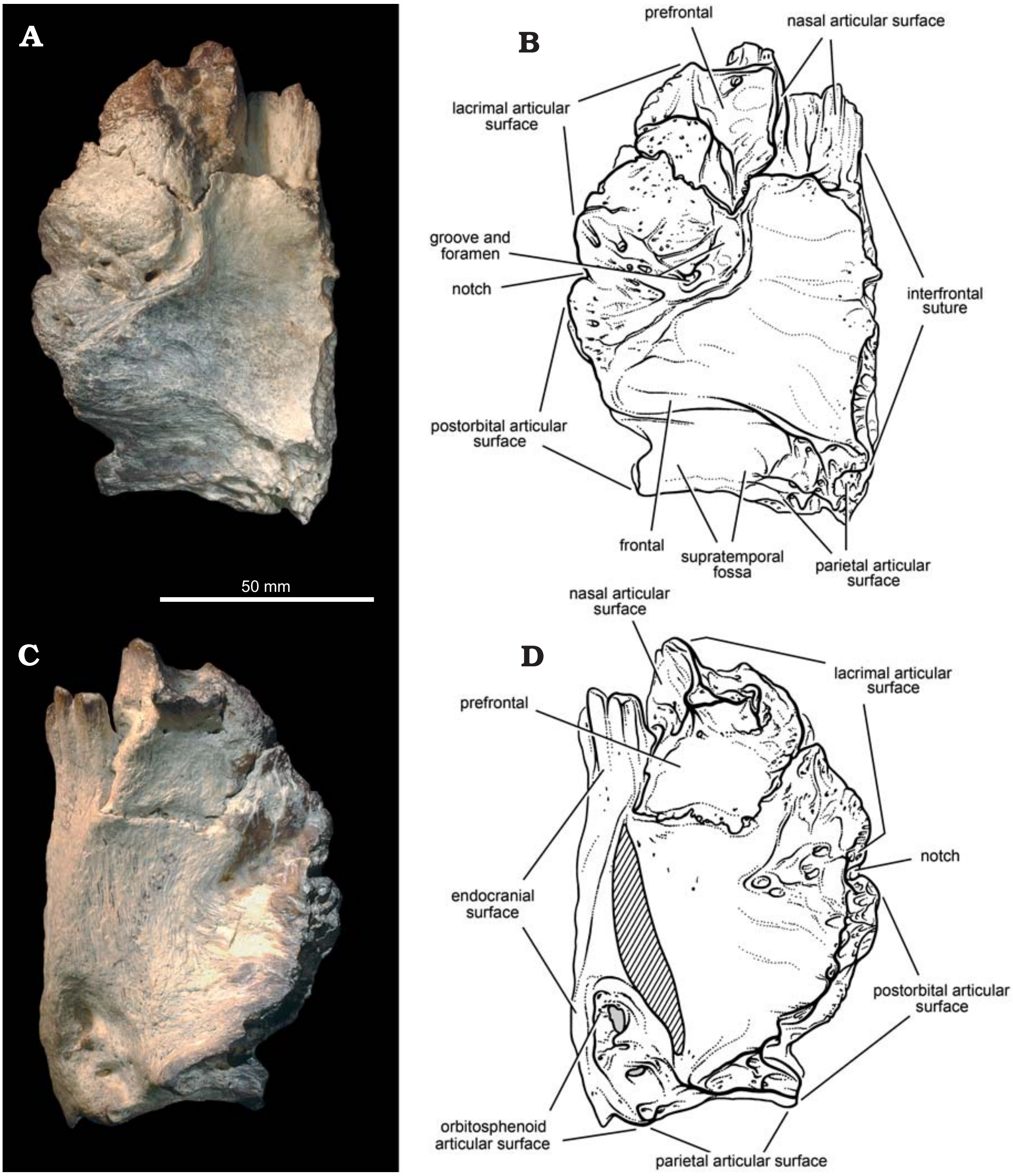

Fig. 14. Carcharodontosaurid theropod *Eocarcharia dinops* gen. et sp. nov. MNN GAD2 from the Lower Cretaceous Elrhaz Formation of Niger. Frontal and prefrontal in dorsal (**A**, **B**) and ventral (**C**, **D**) views; photographs (**A**, **C**) and line drawings (**B**, **D**). Cross-hatching indicates broken bone; grey tone indicates matrix.

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 carcharodontosaurids, 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

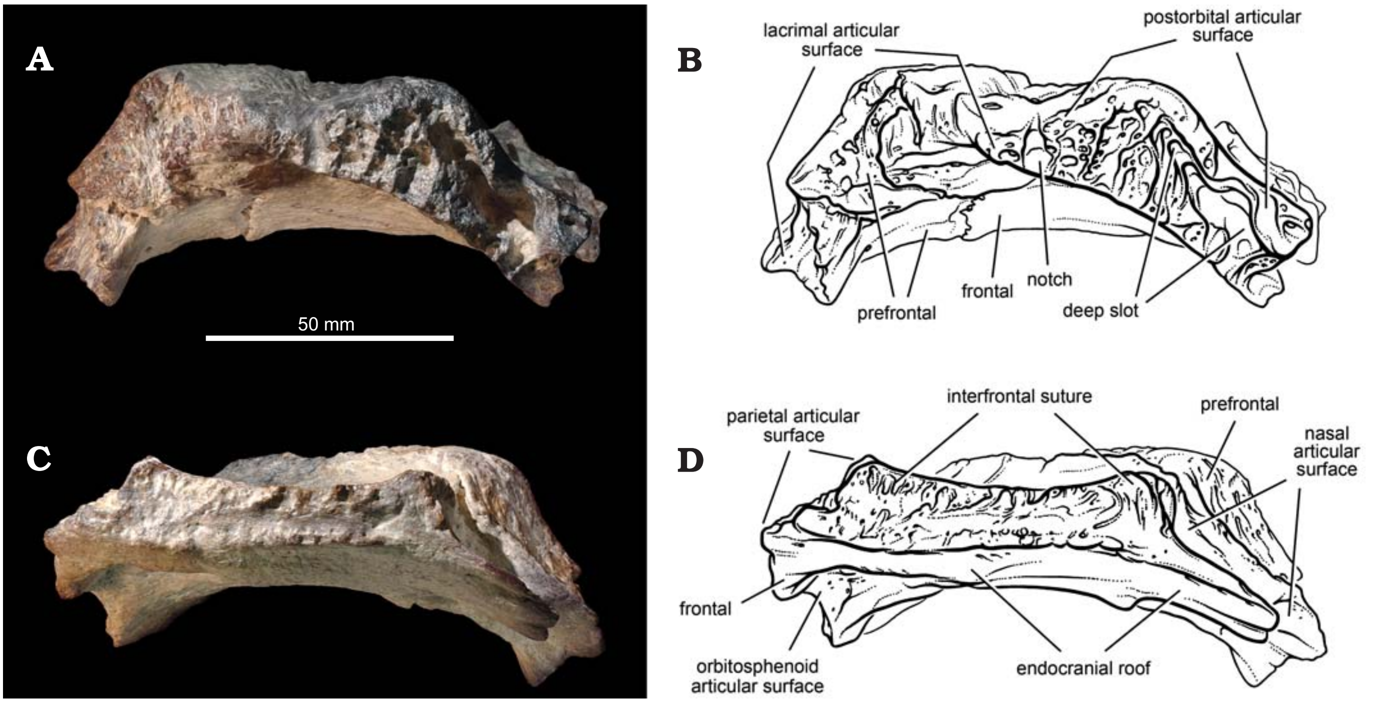

Fig. 15. Carcharodontosaurid theropod *Eocarcharia dinops* gen. et sp. nov. MNN GAD2 from the Lower Cretaceous Elrhaz Formation of Niger. Frontal and prefrontal in lateral (**A**, **B**) and medial (**C**, **D**) views; photographs (**A**, **C**) and line drawings (**B**, **D**).

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, 18A). 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, D). In *Acrocanthosaurus*, *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 frontoparietal 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

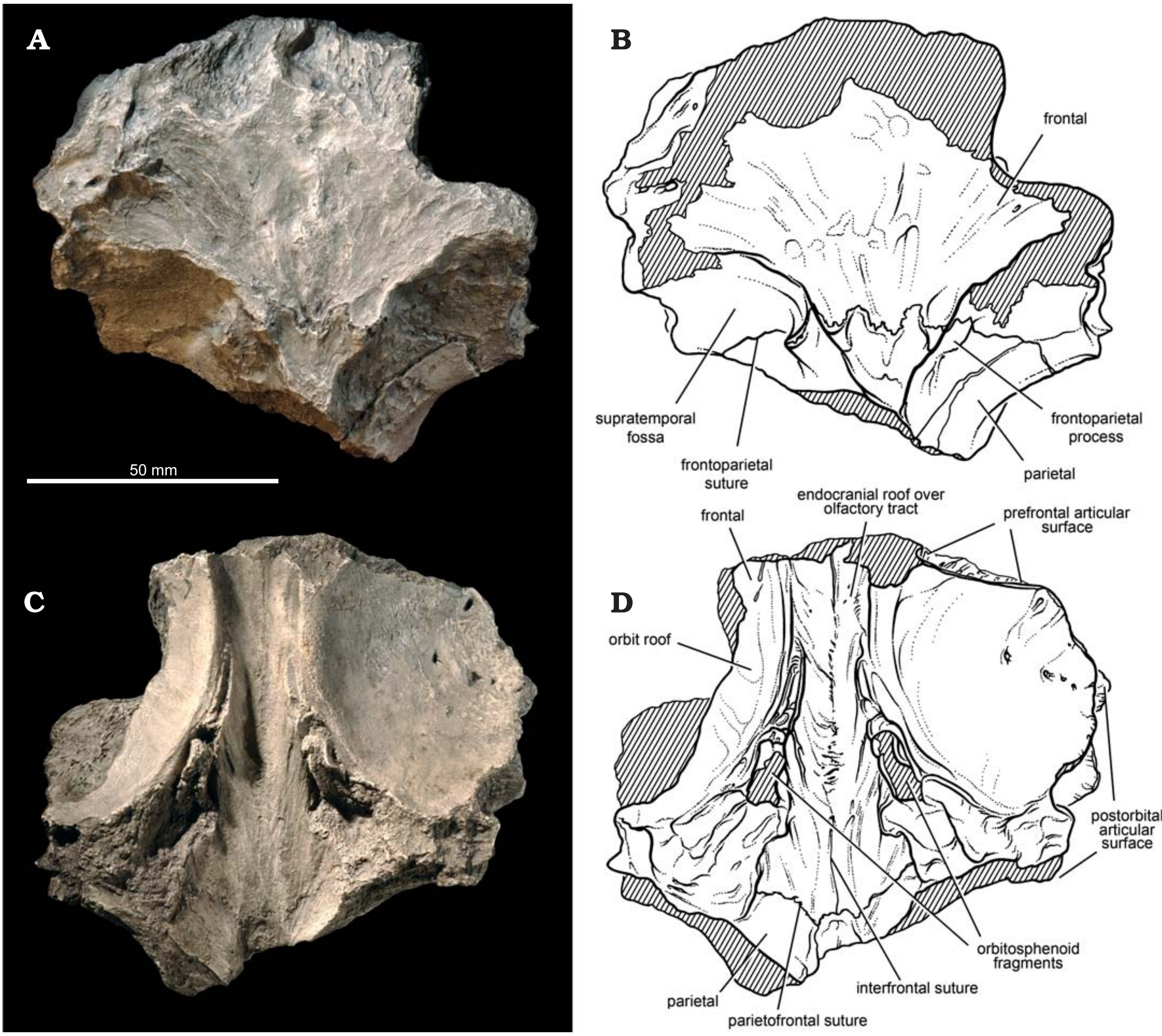

Fig. 16. Carcharodontosaurid theropod *Eocarcharia dinops* gen. et sp. nov. MNN GAD2 from the Lower Cretaceous Elrhaz Formation of Niger. Frontals, parietal and fragmentary right and left orbitosphenoids in dorsal (**A**, **B**) and ventral (**C**, **D**) views; photographs (**A**, **C**) and line drawings (**B**, **D**). Cross-hatching indicates broken bone.

articular 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

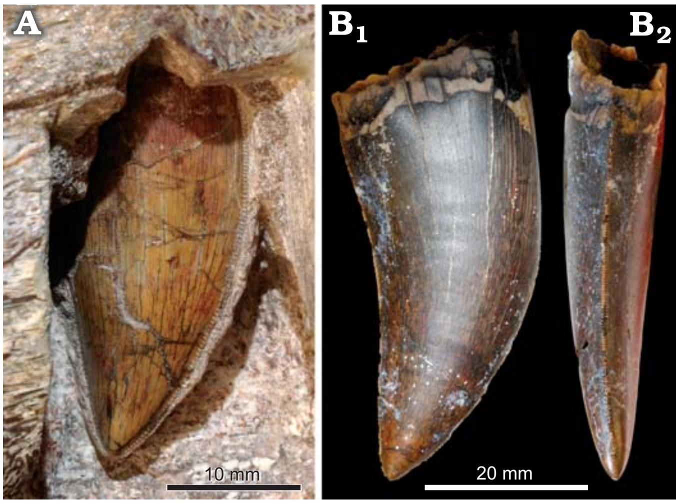

Fig. 17. Carcharodontosaurid theropod *Eocarcharia dinops* gen. et sp. nov. from the Lower Cretaceous Elrhaz Formation of Niger. **A**. Crown of a replacing tooth in the seventh alveolus of the left maxilla (MNN GAD7) in medial view. **B**. Isolated crown (MNN GAD14) in medial (B_1) and anterior (B_2) views.

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 subquadrate proportions that is canted anterodorsally and a posterior portion with an ovate shape, here termed the orbital boss, that is canted posterodorsally (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 posterodorsal. 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. 19A_3, B_3). 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 (Tyrannosauridae).

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 postorbital-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. 19B_2). 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-butting. Most large-bodied theropods such as allosauroids and spinosauroids do not have bony orbital swellings, or bosses, on the orbit margin. In those that do, such as abelisaurids and some large tyrannosaurids, 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. 19B_1). Both the brow and this ornamental feature project laterally, and both may have played a role in lateral head-butting.

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 spinosauroids (*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

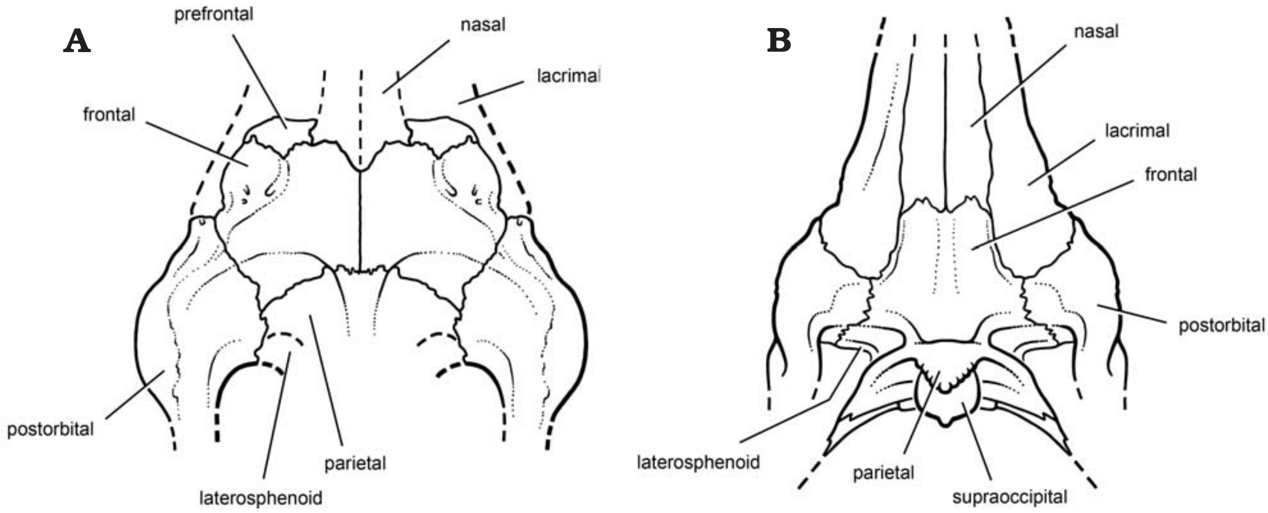

Fig. 18. Posterior skull roof in dorsal view reconstructed in two carcharodontosaurids. **A**. Basal carcharodontosaurid *Eocarcharia dinops* gen. et sp. nov. **B**. Advanced carcharodontosaurid *Carcharodontosaurus saharicus* (Deperet and Savornin, 1927).

postorbital, whereas in tyrannosaurids 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, $19A_2$). The rugose frontal contact, which is canted along an anterodorsal-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, $19A_2$).

Articular contact with the jugal and squamosal is exposed in medial and lateral views (Figs. 9, $19A_2$). 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 interlocking postorbital-jugal articulation constitutes an autapomorphy for *Eocarcharia dinops*. The short posterior ramus is triangular in lateral view and has a wedge-shaped articular process for the squamosal, which is best exposed in dorsal view (Figs. 10, $19A_3$). The anterior 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, $19A_1$). In advanced carcharodontosaurids, 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, $19A_3$) 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), Allosauroidea (Larson 2001; Franzosa and Rowe 2005), and Tyrannosauroidea (Brochu 2003). Among basal allosauroids such as *Sinraptor* (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* (Larsson 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

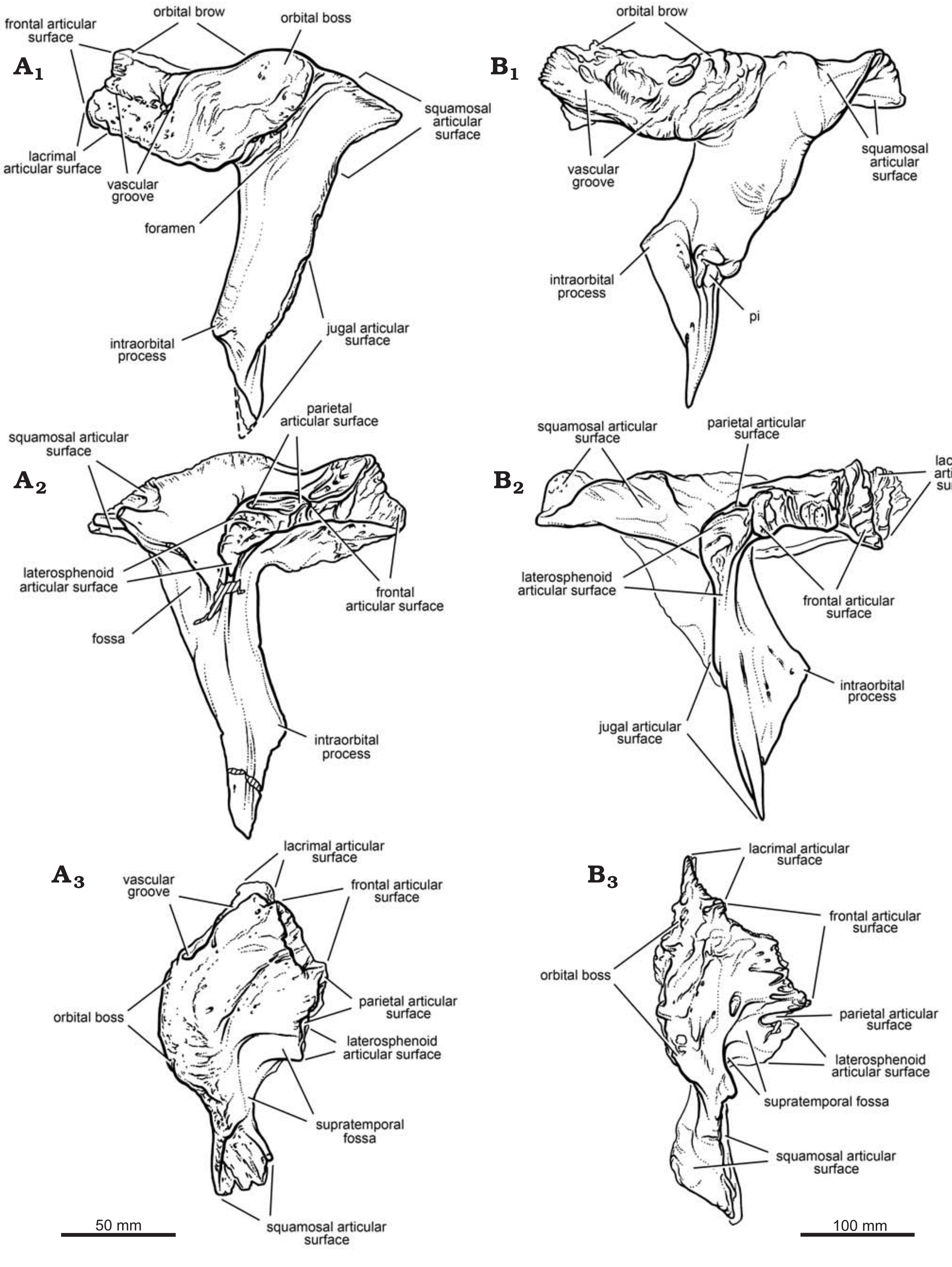

Fig. 19. Left postorbital in two carcharodontosaurids. **A**. Basal carcharodontosaurid *Eocarcharia dinops* gen. et sp. nov. MNN GAD2 from the Lower Cretaceous Elrhaz Formation of Niger. **B**. Advanced carcharodontosaurid *Carcharodontosaurus saharicus* (Deperet and Savornin, 1927) SGM-Din 1 from the Upper Cretaceous Kem Kem beds of Morocco. Line drawings in lateral (A_1, B_1), medial (A_2, B_2), and dorsal (A_3, B_3) 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 Carcharodontosauridae, 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 anteroventral process of the nasal (Appendix 1). As in Sereno et al. (2004), we removed three very poorly known genera (*Laevisuchus*, *Genusaurus*, *Ilokelesia*) 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 cervicodorsal 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 allosauroid 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

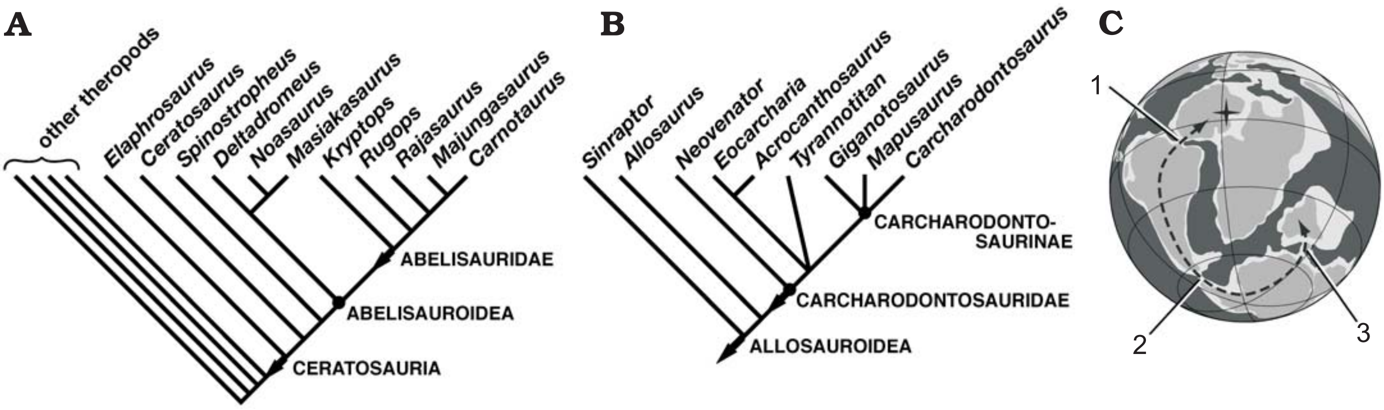

Fig. 20. Phylogenetic relationships of *Kryptops palaios* gen. et sp. nov. and *Eocarcharia dinops* gen. et sp. nov., with arrows and dots signifying stem and node-based definitions, respectively. **A**. Strict consensus tree derived from parsimony analysis (Swofford 1998) of character data in Sereno et al. (2004) with the addition of *Kryptops palaios* (see text and Appendix 1). The two minimum length trees represent alternative resolutions among outgroups. Cladogram depicts relationships within Ceratosauria only, with the fragmentary genera *Laevisuchus*, *Genusaurus*, and *Ilokelesia* removed to reduce tree number and with multistate characters ordered. **B**. Strict consensus tree of carcharodontosaurid relationships showing the phylogenetic position of *Eocarcharia dinops*. **C**. Paleogeographic reconstruction of the earliest Late Cretaceous (Cenomanian, ca. 97 Ma) showing key land bridges (1–3) for intercontinental land connections (map based on Scotese 2001). A cross marks the location of the fossils in this report. Abbreviations: 1, Walvis Ridge, Rio Grande Rise; 2, Palmer Land Block, South Georgia Island Terrane; 3, Kerguelan Plateau, Gunnerus Ridge.

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 geologic 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 Albian (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 by 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 Kerguelan 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 sweepstake 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) vertebrae from South America (Rauhut et al. 2003) and Late Jurassic (Kimmeridgian–Berriasian) vertebrae 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 (Abelisauroidea, Ceratosauria) are now better represented on Africa than elsewhere and include an articulated noasaurid (Sereno et al. 2004) and the basal ceratosaurians *Spinostropheus*, *Berberosaurus*, and *Elaphrosaurus* (Sereno et al. 2004; Allain et al. 2007; Carrano and Sampson 2007).

Eocarcharia, a contemporary of *Kryptops*, and *Neovenator* 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 *Tyrannotitan* 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.

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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.taxonsearch.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)

Abelisauroidea Bonaparte and Novas, 1985: The least inclusive clade containing *Carnotaurus sastrei* Bonaparte, 1985 and *Noasaurus leali* Bonaparte and Powell, 1980. (Wilson et al. 2003)

Abelisauridae Bonaparte and Novas, 1985: The most inclusive clade containing *Carnotaurus sastrei* Bonaparte, 1985 but not *Noasaurus leali* Bonaparte and Powell, 1980, *Coelophysis bauri* (Cope, 1889), *Passer domesticus* (Linnaeus, 1758). (Sereno 2005)

Allosauroidea 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)

Phylogenetic analysis

Abelisauroids.—We provide character state scores (Table 4) for *Kryptops palaios* gen. et sp. nov. as an addition to the taxon-character matrix for basal tetanuran theropods in Sereno et al. (2004). Twenty-nine of 169 characters (approximately 17%) were scored with an informative state based on the holotype of *Kryptops palaios*.

In addition, character 16 was modified as shown below from a two-state to an ordered three-state character, based on the intermediate condition observed in *Kryptops palaios*: Maxilla, form of articular surface for nasal anteroventral process, and form of nasal anteroventral process: shallow facet for tapered process (0); trough for tapered process (1); trough with terminal expansion as a pit or socket for blunt-tipped anteroventral process (2).

Re-analysis of the dataset with *Eocarcharia* included generated 2 minimum length trees of 213 steps (CI = 0.83; RI = 0.92). The phylogenetic structure shown within Abelisauroidea is tentative (Fig. 20A), given the high number of trees (112) and collapse of resolution that occurs with a single additional step or relaxation of the ordering of multistate characters. Missing data is a significant issue; many of the terminal taxa are known from fragmentary skulls or very incomplete postcranial skeletons (e.g., *Noasaurus*, *Kryptops*, *Rugops*, *Abelisaurus*). Greater stability will require additional character data and better documentation for several species.

Carcharodontosaurids.—Characters and character states are listed below along with citation of their first-use in the cladistic literature (Tables 5, 6). Most of the characters are from a previous analysis of Allosauroidea (Brusatte and Sereno in press) and sources cited therein. In that analysis, *Sinraptor* and *Allosaurus* are basal ingroup taxa and more remote theropods are used as outgroups. In the present analysis, *Sinraptor* and *Allosaurus* constitute successive outgroups to seven carcharodontosaurid genera. The analysis with this modification has been limited to carcharodontosaurid interrelationships.

Twenty-six of the 99 characters in Brusatte and Sereno (in press) were uninformative for analysis with the ingroup limited to carcharodontosaurids (original characters 1, 14, 21, 24, 25, 27–30, 38, 39, 47, 48, 55–58, 75, 79, 80, 85, 89, 93–95, 98). For remaining characters, we raised the bar regarding character description and coding from that in Brusatte and Sereno (in press), following recommendations in Sereno (2007) and incorporating additional information for *Eocarcharia* and *Neovenator*. For example, we required characters with relative dimensions, such as "broader than", to include a testable dimensional ratio. In several instances, character states could not be individuated as originally anticipated. Several characters were dropped because of ambiguity in their description, poor preservation, or high variability across available specimens. We rescored several characters, some of which then were uninformative in the present analysis. In sum, we rejected 19 characters from the analysis of Brusatte and Sereno (in press) (original characters 6, 9, 11, 18, 22, 32, 37, 45, 49, 52, 54, 74, 76–78, 87, 88, 96, 99), as listed with annotation below (Table 7). We also added six new characters involving the maxilla, postorbital, and basisphenoid (characters 8, 22–25, 31). In the end, our analysis of carcharodontosaurids involves 60 osteological characters, 37 of which are cranial (62%) and 23 postcranial (38%) (Table 6).

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

?1???	?????	??111	1????	?????	?????	?????	10???	?????	?????
?????	?????	?????	?????	?????	?????	?????	?????	?0???	11???
?????	?????	?????	????1	?1100	000?1	?0101	00001	1????	?????
?????	?????	?????	????						

Table 5. Taxon-character matrix for carcharodontosaurids including *Eocarcharia dinops* and with *Sinraptor dongi* and *Allosaurus fragilis* as outgroups.

	5	**10**	**15**	**20**	**25**	**30**	**35**	**40**	**45**	**50**	**55**	**60**
Sinraptor	00000	10000	00110	00000	X0000	00110	00000	00110	00010	01100	?0000	00000
Allosaurus	10000	11000	00010	00000	X0000	00010	0000010110		00010	10100	01010	00100
Neovenator	110?1	01000	010??	?????	X????	?????	??010	10010	01101	00100	01101	10010
Eocarcharia	??111	?0100	?????	01011	00101	?????	?0???	?0???	?????	?????	?????	?????
Acrocanthosaurus	21011	?010?	01110	01011	0?0?1	10001	01111	00001	11101	01011	11111	00111
Tyrannotitan	?????	?????	?????	?????	?????	?????	??111	?0???	??111	100?0	?10?1	????1
Mapusaurus	??1X0	?0011	11?01	???1?	1121?	?????	??1??	?1???	????1	1??11	11011	1111?
Giganotosaurus	21?00	?0011	11?11	11111	11211	111??	11111	01100	111?1	?00?1	10011	11101
Carcharodontosaurus	??1X0	00011	11001	11111	11211	11101	11111	?1??1	1000?	????1	???11	10??1

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 dorsoventral 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 antorbital 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 Holtz et al. 2004).

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); flange 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) (Forster 1999).

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). Lacrimal, 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 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 latersphenoid head: rugose concavity (0); deep-rimmed socket (1) (new character).

25(23). Postorbital, intraorbital 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); subspherical (1) (modified from Coria and Currie 2002).

27(41). Basioccipital, paired pneumatocoels 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); basioccipital 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, anteroventral 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 articular face, width relative to height: subequal (0); 20% or more broader than tall (1) (Sereno et al. 1996).

41(63). Mid cervical centra, anterior articular 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 zygapophyses, 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: subequal (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 Harris 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 distal 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 malleolus: 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 explanation. For the modified character state scores, parenthetical character numbers are those used in Brusatte and Sereno (in press).

Rejected characters

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 posterodorsal 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 *Eocarcharia* is difficult to identify with confidence as homologous].
11. Maxilla, articular surface with the premaxilla, inclination lateral view: angled strongly posterodorsally (0); subvertical (1) (Brusatte and Sereno in press). [Ambiguous; the quantitative delineation of character states proved difficult to establish with a reasonable protocol for assessment].
18. Nasal, lateral margin, form: offset with a small lateral crest (1); flat (0) (modified from Rauhut 2003). [Ambiguous; we cannot confidently score this subtle character, although some future modification may prove more effective].
22. Postorbital, ventral ramus, orientation: subvertical (0); angled anteroventrally (1) (Holtz et al. 2004). [Uninformative; the axis of the ventral 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 exposed 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 involves 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 preservational factors].
45. Braincase, supratemporal fenestrae, orientation: dorsal (0); anterolateral (1) (Coria and Currie 2002). [Ambiguous; measuring an orientation 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 Brusatte and Sereno in press). [We rejected this character for the time being because it appears to overlap with the anteroventral expansion 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-bearing section: subparallel (0); caudally divergent (1) (Holtz et al. 2004: 219). [Uninformative; all of the theropods in the present analysis 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 literature, 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 *Sinraptor* 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 subequal 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.