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Brief report

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Evidence of a new carcharodontosaurid from the Upper Cretaceous of Morocco

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We report an isolated frontal of a large-bodied theropod from the Cenomanian "Kem Kem beds" of Morocco with an unusual morphology that we refer to a new carcharodontosaurid distinct from the sympatric *Carcharodontosaurus*. The specimen shows an unique combination of plesiomorphic and potentially autapomorphic features: very thick and broad bone with a complex saddle-shaped dorsal surface, and a narrow vertical lamina between the prefrontal and lacrimal facets. This study supports the hypothesis that a fourth large theropod was present in the Cenomanian of Morocco together with *Carcharodontosaurus*, *Deltadromeus*, and *Spinosaurus*.

Introduction

Although the Mesozoic fossil record of African theropods is poorly known in comparison to that of other continents, several specimens have been reported from the Cenomanian of Northern Africa, most of them of large size and referred to the Abelisauroidea, the Carcharodontosauridae, and the Spinosauridae (e.g., Stromer 1915, 1931, 1934; Russell 1996; Sereno et al. 1996; Mahler 2005; Brusatte and Sereno 2007; Sereno and Brusatte 2008). Here we report a new specimen that adds information on the diversity of the large-bodied African theropods.

The fossil here described comes from the southeastern surroundings of Taouz (Errachidia Province, Morocco) and was donated to the MPM by a donor who had purchased it from a Moroccan fossil dealer. A large number of fossils from the Tafilalt and Kem Kem regions (SE Morocco) collected by local inhabitants and fossil dealers currently form part of public collections all over the world (McGowan and Dyke 2009). Unfortunately, this specimen was collected by local people, and its exact horizon and locality remain unknown. However, some general information may be gleaned from the most recent and exhaustive summary on the stratigraphy of the Cretaceous dinosaur-bearing units of Tafilalt and Kem Kem (Cavin et al. 2010). Those units, corresponding to the Ifezouane Formation and the overlying Aoufous Formation, are known in the literature also as the "Kem-Kem beds" (Sereno et al. 1996), and are Cenomanian in age. They predate the late Cenomanian global marine transgression marked in northern Africa by a marine limestone unit (Akrabou Formation of southern Morocco, Cavin et al. 2010). These are the only dinosaur-bearing units in the surroundings of Taouz (Cavin et al. 2010), so, based on its provenance, the fossil here described belongs to the "Kem Kem compound assemblage" of Cavin et al. (2010). The aim of this study is to describe the specimen, to compare it to other African theropods, and to determine its phylogenetic relationships.

Institutional abbreviation.—MPM, Museo Paleontologico di Montevarchi, Arezzo, Italy.

Other abbreviations.—MPT, most parsimonious tree; OTU, Operational Taxonomic Unit.

Systematic palaeontology

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Carcharodontosauridae Stromer 1931

Genus et species indet.

Figs. 1, 2.

Locality and age: Southeastern of Taouz, Errachidia Province, Meknès-Tafilalet Region, Morocco; Cenomanian, Upper Cretaceous (Cavin et al. 2010).

Material.—Left frontal.

Description

The fossil, MPM 2594, is an isolated and almost complete left frontal (Fig. 1, Table 1). The middle part of the interfrontal suture, most of the supratemporal fossa, the posterolateral margin of the postorbital process and most of the parietal facet are eroded away. Compared to other theropods (e.g., Currie and Zhao 1993; Coria and Currie 2002), the bone is markedly thick, with a maximum depth at the anteromedial margin of the supratemporal fossa that is about 40% of bone length. A marked thickening of the frontal is shared with the abelisaurids (Carrano and Sampson 2008). In dorsal view (Figs. 1A, 2A), the bone is triangular, and is mediolaterally widest at the posterior end. The width to length ratio of the bone is approximately 70%, as in abelisaurids and carcharodontosaurids (Sereno and Brusatte 2008). The dorsal surface of the bone is slightly concave in the central part, bordered medially by a slightly elevated convexity oriented anteroposteriorly, laterally by a distinctly convex and rounded domed area that in life was confluent with the orbital brow, and posteriorly by the dorsally raised anteromedial margin of the supratemporal fossa. The dorsal surface between the

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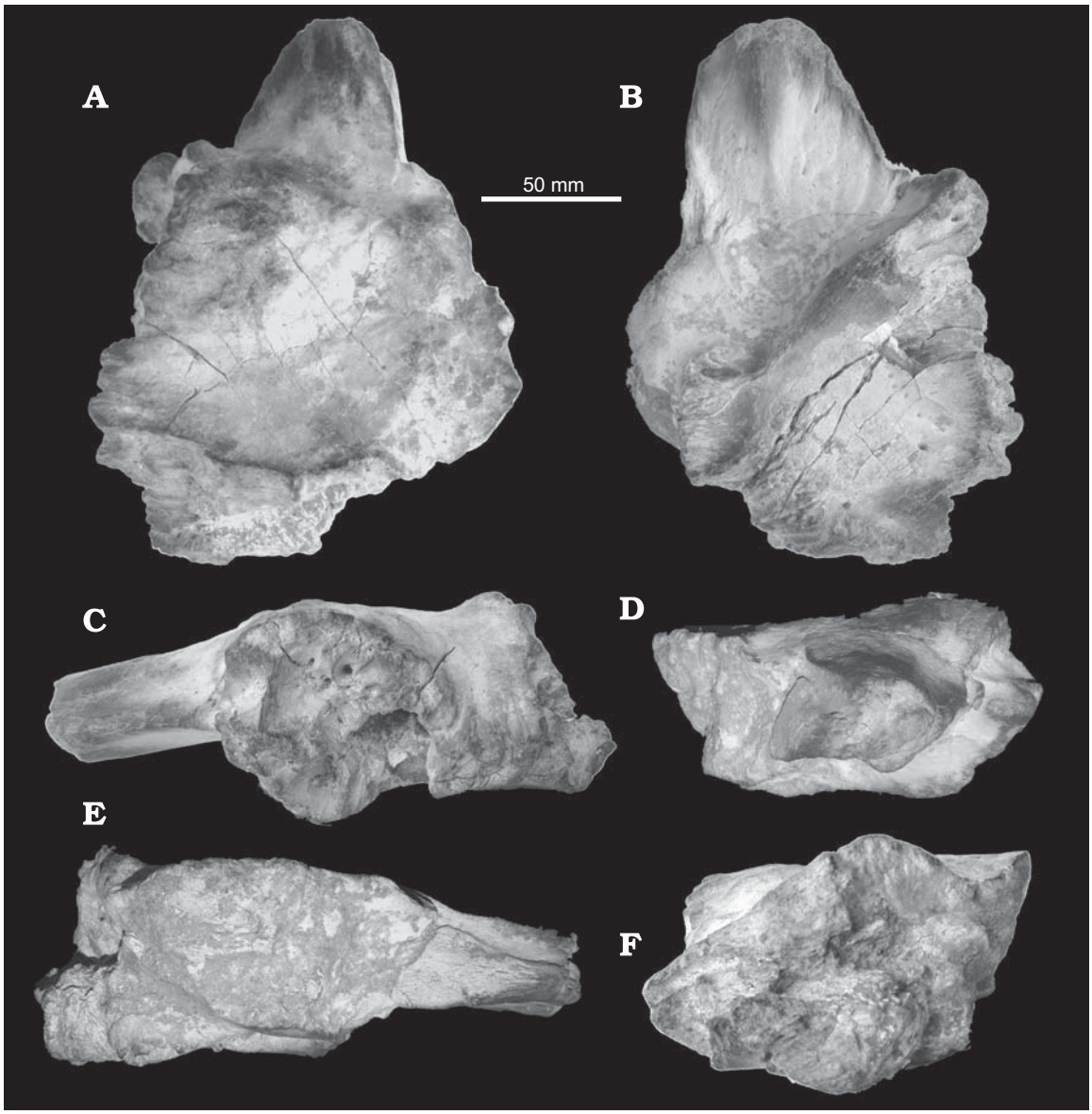

Fig. 1. Carcharodontosaurid from the Cenomanian "Kem Kem beds" of Morocco, left frontal (MPM 2594), in dorsal (**A**), ventral (**B**), lateral (**C**), anterior (**D**), medial (**E**), and posterior (**F**) views.

antromedial margin of the supratemporal fossa and the raised lacrimal facet is saddle-shaped. The dorsal surface of the postorbital process is flat and horizontally oriented.

The nasal process is elongate and gently convex dorsally (Fig. 1A). The smooth dorsal half of the medial surface of the nasal process probably contacted the posterior end of the nasal, indicating that the nasal processes of the frontals did not contact along the midline of the skull (Fig. 1E). A shallow dorsal depression placed posteromedial to the nasal process may indicate the posterior limit of the nasal articulation.

Most of the medial surface of the bone posterior to the nasal process is broken off (Figs. 1E, 2E). The prefrontal facet is a sub-triangular concavity opening anteriorly. It has no lateral component (Fig. 1A, C, D), is bordered posterodorsally by a low shelf of bone confluent with the dorsal margin of the lacrimal facet, and is separated from the lacrimal facet by a narrow lamina running vertically (Fig. 2A, C). The ventral margin of the prefrontal facet shows an interdigitate suture (Fig. 2B) that suggests a strong interlocking joint with the prefrontal.

The dorsal surface of the lacrimal facet is markedly convex dorsally, rising well above the level of the nasal and postorbital processes (Fig. 1C). That feature is cited as an autapomorphy of *Carcharodontosaurus saharicus* that differentiates it from *Carcharodontosaurus iguidensis* (see Brusatte and Sereno 2007). Nevertheless, a similar condition is present also in *Giganotosaurus carolinii* (see Coria and Currie 2002), and recalls the condition in some abelisaurids (e.g., *Carnotaurus*; Carrano and Sampson 2008) suggesting that it may be a homoplastic feature among large-bodied theropods. The posterior half of the lacrimal facet below the dorsal convexity is eroded. The lacrimal articulation is about 75 mm dorsoventrally deep near the prefrontal margin. A deep pit penetrates the bone in the posterior half of the lacri-

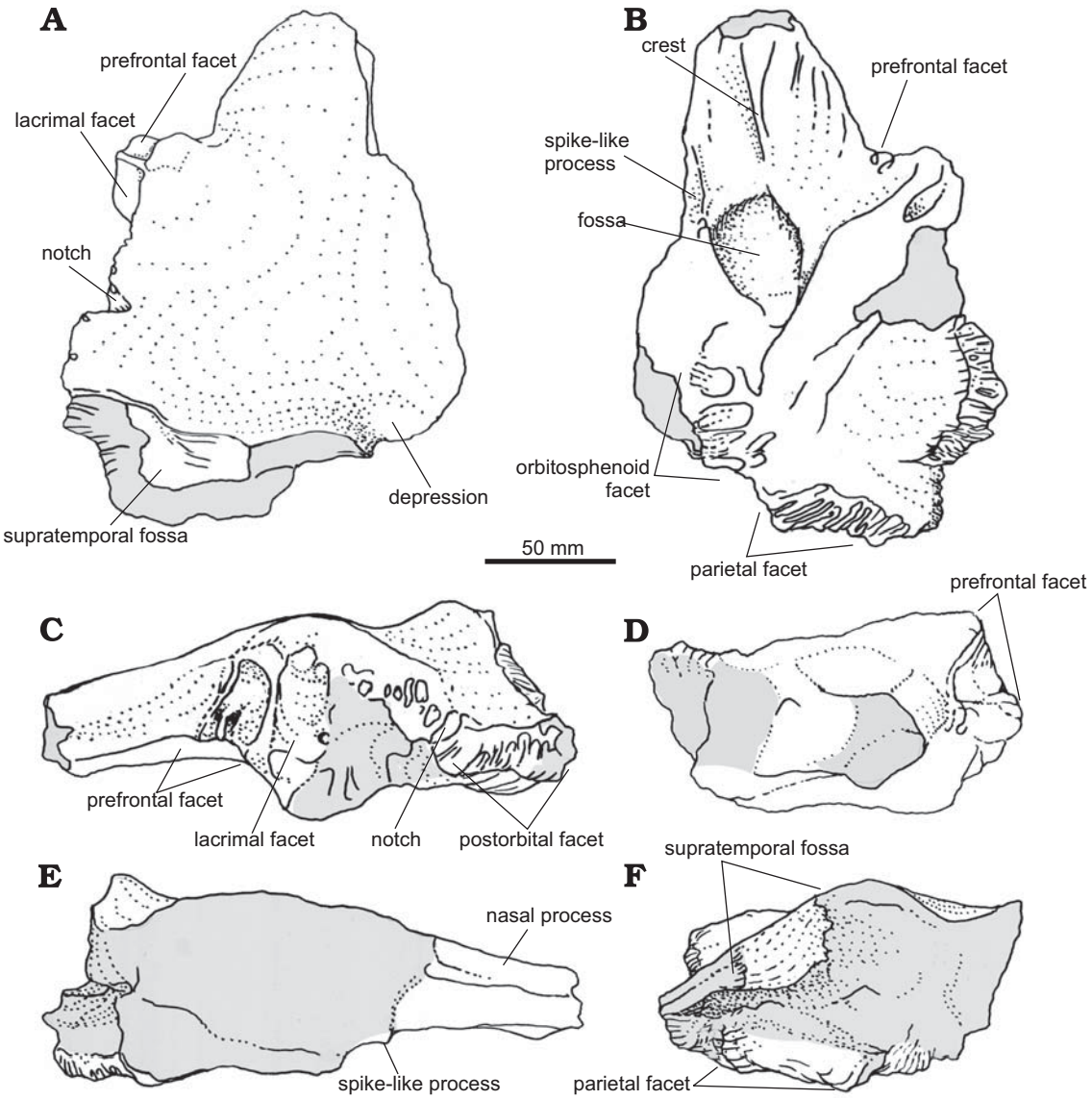

Fig. 2. Carcharodontosaurid from the Cenomanian "Kem Kem beds" of Morocco, drawing of the left frontal (MPM 2594), in dorsal (**A**), ventral (**B**), lateral (**C**), anterior (**D**), medial (**E**), and posterior (**F**) views. Grey areas indicate weathered or damaged surfaces.

mal articulation. A narrow non-articular notch, oriented posterodorsally, is present between the lacrimal and postorbital facets (Fig. 2A), as in abelisaurids and carcharodontosaurids.

Only the anterior half of the postorbital facet is preserved. It is long and low, rectangular in lateral view and extensively pitted. Only the anteromedial half of the supratemporal fossa is preserved on the posterior edge of the frontal. The anteroposterior length of the supratemporal fossa is no more than 30–35% of the frontal length. The dorsal surface of the bone just anterior to the fossa is raised and inclined posterodorsally. As a consequence, the anteroventral surface of the supratemporal fossa is sloped posteroventrally, as in carcharodontosaurids and the abelisaurid *Rajasaurus* (Wilson et al. 2003; Sereno and Brusatte 2008). The fossa is transversely concave and faces almost posteriorly in the medialmost preserved part. The anterior margin of the fossa is marked by a low lip. In posterior view, when the dorsal surface of the frontal is oriented horizontally, the margin of the bone just anterior to the supratemporal fossa is directed dorsomedially, then curves steeply ventrally just medial to its tallest point (Fig. 2F). A dorsally facing depression is placed medially to the raised anteromedial margin of the supratemporal fossa. This morphology indicates that the two supratemporal fossae were widely separated, as in derived carcharodontosaurids (Sereno and Brusatte 2008). Only the lateroventral margin of the parietal articulation is preserved. It is a slightly rough surface with no sign of fusion with the parietal.

In ventral view (Figs. 1B, 2B), an elongate ventral ridge running along the middle of the nasal process marks the lateral margin of the impression of the olfactory bulb. The latter merges posteriorly into a moderately deep elliptical fossa. A small spike-like process in a shallow fossa is placed anteromedially to the elliptical fossa. There is no evidence of an ossified interorbital septum, nor of an ossified sphenethmoid or mesethmoid. Laterally, the elliptical fossa is bounded by the

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Table 1. Measurements (in mm) of MPM 2594.

Maximum preserved length	186
Maximum preserved width	135
Depth at lacrimal facet	73
Depth at mid-length of the medial surface	52
Depth at the level of the anteromedial margin of supratemporal fossa	75
Lacrimal facet, length	59
Nasal process, posterior width	54
Nasal process, maximum anterior depth	30
Nasal process, preserved length	61
Postorbital facet, depth	18
Prefrontal facet, length	30

15 mm-thick anterior margin of the orbit. The anterolateral end of the latter is confluent with the ventral margin of the prefrontal articulation. The orbital roof is flat anteromedially and slightly concave at the level of the postorbital process. The orbitosphenoid and parietal facets are placed medially and posteriorly to the orbital roof.

Phylogenetic analysis

In order to test the affinities of MPM 2594, we included it in a phylogenetic analysis evaluating the distribution of 808 morphological characters among 35 neotheropods (see Supplementary Online Material, SOM available at http://app.pan.pl/SOM/app57-Cau_etal_SOM.pdf for details and method).

The single most parsimonious tree (MPT) recovered by our analysis interprets MPM 2594 as a carcharodontosaurid bracketed by *Eocarcharia* and the clade including the other carcharodontosaurids. Forcing MPM 2594 as sister-taxon to the *Carcharodontosaurus* OTU, the resulting topology is five steps longer then the MPTs, a statistically significant difference (see SOM). Similar statistical differences result in those topologies where MPM 2594 is constrained as sister taxon to the other "Kem Kem OTUs", *Spinosaurus* and *Deltadromeus*, or as an abelisaurid (see SOM). Since the validity of the large Moroccan theropod *Sigilmassasaurus* is problematic (Russell 1996; Brusatte and Sereno 2007), we excluded it from the analysis.

Discussion

MPM 2594 is a theropod frontal based on the presence of both a supratemporal fossa and a lacrimal facet. It is unique among theropods in the combination of the raised anteromedial margin of the supratemporal fossa, saddle-shaped dorsal surface between lacrimal facet and supratemporal fossa, and presence of a narrow lamina between the prefrontal and lacrimal facets. Among "Kem Kem theropods" the frontal bone is known only in *Carcharodontosaurus*. Compared to the frontals of *Carcharodontosaurus* (see Stromer 1931; Brusatte and Sereno 2007), MPM 2594 differs in the following features: nasal processes completely separated medially; presence of distinct prefrontal and lacrimal facets (which suggests the presence of a non-vestigial prefrontal bone); lacrimal facet that is broadest anteriorly; subtriangular (instead of rounded) prefrontal articular facet (Eddy and Clarke 2011); saddle-shaped area between the lacrimal facet and the anteromedial margin of the supratemporal fossa; absence of deeply invaginated anterior surface of the supratemporal fossa (and corresponding shelf), absence of ossified sphenethmoid and mesethmoid. Comparison with the best-described craniofacial ontogenetic series among giant theropods (*Tyrannosaurus rex*; see Carr 1999; Carr and Williamson 2004) suggests that the differences between MPM 2594 and the known frontals of *Carcharodontosaurus* are beyond the expected ontogenetic or intraspecific variability for theropods. Since MPM 2594 is comparable in size to the adult frontals of Carcharodontosaurinae (Stromer 1931; Coria and Currie 2002; Brusatte and Sereno 2007), we consider it unlikely that these features in MPM 2594 reflect immaturity (e.g., Sereno and Brusatte 2008), and interpret them as a combination of potential autapomorphies and plesiomorphic states shared with the non-carcharodontosaurine allosauroids (Coria and Currie 2002; Brusatte and Sereno 2007; Sereno and Brusatte 2008; Eddy and Clarke 2011). Although Carrano and Sampson (2008: 222) and Coria and Currie (2006) reported a vestigial prefrontal fused to the posteromedial margin of the lacrimal in *C. saharicus* and in *Mapusaurus*, the frontals of the derived carcharodontosaurines lack a distinction between the prefrontal and the lacrimal facets (Brusatte et al. 2010). The presence of distinct prefrontal and lacrimal facets is reported in the basal carcharodontosaurid *Eocarcharia* (Sereno and Brusatte 2008). Among allosauroids, only the frontal of *Eocarcharia* shares with MPM 2594 the combination of a prefrontal facet restricted anteriorly and distinct from the laterally exposed lacrimal facet (Sereno and Brusatte 2008). MPM 2594 differs from *Acrocanthosaurus* and more basal allosauroids (e.g., *Sinraptor*, *Allosaurus*) because in these taxa the frontal articulates laterally only with the prefrontal and completely lacks a lacrimal facet (Madsen 1976; Currie and Zhao 1993; Eddy and Clarke 2011).

To date, the occurrence of more than one allosauroid genus has not been reported in North African formations (Sereno and Brusatte 2008), although these occurrences are known in other continents. At least two coeval allosauroid lineages are reported from the lowermost Upper Cretaceous in both Eastern Asia (Benson et al. 2010) and South America (Coria and Currie 2006), suggesting that the presence of a second large allosauroid in the Cenomanian of North Africa, coeval with *Carcharodontosaurus*, is plausible. The co-occurrence of two or more distinct tyrannosaurid species in uppermost Cretaceous formations from Asia and North America (Russell 1970; Brusatte et al. 2009) indicates that the presence of more than one large-bodied species of closely related theropods was common in Cretaceous ecosystems.

In conclusion, MPM 2594 indicates that a new carcharodontosaurid, sympatric with *Carcharodontosaurus*, *Deltadromeus*, and *Spinosaurus*, is present in the Cenomanian of Morocco. Although the combination of features present in MPM 2594 is unique and

should support the institution of a new species, pending more complete specimens we feel it would be inappropriate to erect a new taxon.

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