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A thick-skulled theropod (Dinosauria, Saurischia) from the Upper Cretaceous of Morocco with implications for carcharodontosaurid cranial evolution

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ABSTRACT

In this study, we erect *Sauroniops pachytholus* gen. et sp. nov., a large-bodied theropod dinosaur from the Cenomanian (Upper Cretaceous) of Morocco, on the basis of an almost complete frontal showing a unique combination of features including a naso–frontal suture extended along 40% of the frontal length, a thick dome in the anterolateral corner of the dorsal surface, a trapezoidal prefrontal facet that is restricted to the anterodorsal margin of the lateral surface of the frontal with no participation in the orbital roof and separated from the lacrimal facet by a narrow vertical lamina, a hypertrophied 'D-shaped' lacrimal facet that is four times the anterior depth of the postorbital facet, and a raised posteromedial margin of the dorsal surface describing a saddle with the anterolateral dome and confluent with a series of anteromedial rugosities. Phylogenetic analysis found robust support for placing *Sauroniops* among the basal carcharodontosaurids and related to *Eocarcharia*, showed that some of the unusual features of the new theropod were convergently acquired by abelisaurids, and revealed a mosaic pattern in the evolution of the carcharodontosaurid skull table. The frontals of *Sauroniops* and *Carcharodontosaurus*, both from the 'Kem Kem compound assemblage' of Morocco, show comparable size but differ in the extent of the naso–frontal articulation, the shape and disposition of the prefrontal and lacrimal articulations, the development of dorsal ornamentation and the morphology of the supratemporal fossa. Among carcharodontosaurids, the skull table developed unique configurations among each lineage and appears diagnostic at the species-level. The dome-like frontal in *Sauroniops* may indicate head-butting behaviour in this taxon or evolved for visual display.

1. Introduction

Carcharodontosauridae is a clade of theropod dinosaurs mainly known from the Aptian–Turonian of Africa, South America, North America and Asia, including among the largest-known hypercarnivorous terrestrial vertebrates (Stromer, 1931; Stovall and Langston, 1950; Coria and Salgado, 1995; Sereno et al., 1996; Coria and Currie, 2002, 2006; Novas et al., 2005b; Brusatte and Sereno, 2007; Sereno and Brusatte, 2008; Brusatte et al., 2010b). Carcharodontosaurids probably originated in the Late Jurassic (Rauhut, 2011) and reached a cosmopolitan distribution no later than the Early Cretaceous (Brusatte et al., 2010b). Carcharodontosaurids possess a highly distinctive, apomorphic skeletal morphology relative to related non-coelurosaurian tetanuran lineages (Carrano et al., 2012), showing lateral sculpturing of the facial bones, extensive fusion among the skull roof and braincase elements, blade-like teeth with distinctive enamel ornamentation, extensive pneumatization of the axial skeleton, and the reorganisation of the pelvis and hind limb as probable load-bearing adaptation (Sereno et al., 1996; Coria and Currie 2002, 2006; Novas et al., 2005b; Eddy and Clarke, 2011; Bates et al., 2012). Due to the numerous autapomorphies in their skeletons, carcharodontosaurids can be identified even from isolated bones (e.g., Russell, 1996; Rauhut, 2011).

Cau et al. (2012) described an isolated frontal of a large-sized theropod dinosaur from the Cenomanian (Upper Cretaceous) of Morocco and interpreted it as belonging to a carcharodontosaurid distinct from the sympatric *Carcharodontosaurus*, based on its unique morphology and on the result of a phylogenetic analysis placing the new specimen in a basal lineage of the Carcharodontosauridae. A comparison with the other theropod lineages known from the Cenomanian of Morocco was provided (Cau et al., 2012), and no support for alternative interpretations was recovered. A re-examination of the specimen led us to review both its

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taxonomic status and phylogenetic affinities, and to add new information on the cranial evolution of the Carcharodontosauridae.

2. Material and methods

A description of the specimen discussed herein is provided by Cau et al. (2012). Therefore, here we have discussed those features that were not analysed in depth by Cau et al. (2012) but are significant in both the phylogenetic affinities of the new taxon and in the context of carcharodontosaurid skull evolution. Cau et al. (2012) included the new specimen in a novel phylogenetic analysis of the Theropoda focussing on North African clades. Here, we have modified some characters, updated or corrected some codings present in the previous analysis and added new character statements to the analysis that further elucidate the phylogenetic affinities of the specimen discussed herein (see Appendices 1 and 2). The resulted data matrix includes 37 Operational Taxonomic Units (OTUs) and 817 characters, and was analysed with TNT vers. 1 (Goloboff et al., 2008) performing 5000 heuristic search replicates and saving all shortest trees found. The nodal support was determined performing 5000 heuristic search replicates and saving all trees no more than ten steps longer than the shortest trees found. Taxonomy followed Cau et al. (2012) and references therein. In this study, the terms 'preorbital facet' refers to the combined prefrontal and lacrimal facets of the frontal, while 'frontal body' refers to the frontal with the exclusion of the nasal process.

*Nomenclatural acts*The electronic version of this published work has been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix 'http://zoobank.org/'. The LSID for this publication is: urn:lsid:zoobank.org:pub:107AE7B1-845B-4657-A140-4D6931F5ABAF.

3. Systematic palaeontology

Institutional abbreviations: MPM, Museo Paleontologico di Montevarchi, Arezzo, Italy.

Dinosauria Owen, 1842
Theropoda Marsh, 1878
Carcharodontosauridae Stromer, 1931
Sauroniops gen. nov.

Type species. *Sauroniops pachytholus* sp. nov.

Etymology. The genus name is formed by Sauron, fictional character created by J.R.R. Tolkien (1892–1973), and *ὀψη*, Greek, 'eye'.

Diagnosis. Large-bodied basal carcharodontosaurid dinosaur with the following unique combination of features (autapomorphies marked by asterisk): (1) dorsoventrally thickened frontal (with the depth of the body ranging between 28%, along the medial suture, and 38%, at the level of the anteromedial margin of the supratemporal fossa, of bone length); (2) nasal processes of the frontal with a transversely convex dorsal surface and completely separated medially by the posteromedial processes of nasal extended along 40% of the frontal length and reaching the frontal body; (3) thick dome-like eminence in the anterolateral corner of the dorsal surface of the frontal at the level of the prefrontal–lacrimal articulations*; (4) anterolateral margin of the lateral surface of the frontal with a narrow vertical lamina separating the prefrontal facet from an elliptical fossa in the lacrimal facet*; (5) prefrontal facet of the frontal trapezoidal, barely visible in ventral view, mostly restricted to the anterodorsal margin of the lateral surface of the bone, and not participating in the orbital fossa*; (6) frontal with interdigitate suture for prefrontal restricted to the anteroventral corner of the facet, formed by a low shelf running along the posterolateral margin of the nasal process and a small finger-like projection*; (7) hypertrophied, 'D-shaped' lacrimal facet of the frontal bordering the whole posterolateral exposure of the prefrontal facet and with maximum depth that is four times the depth of the anterior half of the postorbital facet*; (8) dorsal surface of the frontal anterior to the anteromedial margin of supratemporal fossa raised and facing anterodorsally, describing with the dorsal dome a posteromedially–anterolaterally directed saddle-shaped concavity, and confluent with a series of low rounded rugosities placed posteriorly to the nasal facet*.

Sauroniops pachytholus sp. nov.
(Figs. 1A–F, 2A, B)

Etymology. The species name is formed by *πάχους*, Greek for 'thick'; and *θόλος*, Greek for 'dome'; in reference to the thickened frontal dome above the orbit, diagnostic of this taxon.

Diagnosis. As for genus; currently monospecific.

Remarks. Among Carcharodontosauridae, *Sauroniops pachytholus* differs from the comparably-sized *Acrocanthosaurus atokensis* from the Aptian–Albian of the USA (Stovall and Langston 1950) in showing a thick dome in the anterolateral corner of the dorsal surface of the frontal, in showing a lacrimal–frontal articulation, a more posteriorly extended naso–frontal contact reaching the frontal body, a prefrontal facet of the frontal that is trapezoidal and restricted to the anterior margin of the lateral surface of the bone with reduced lateral exposition and lacking participation to the orbital margin, in showing the thickest point of the preorbital facet in its anterior end, and a relatively shallower anterior half of the postorbital facet of the frontal; from the comparably-sized *Carcharodontosaurus iguidensis* from the Cenomanian of Niger (Brusatte and Sereno, 2007) in showing a prefrontal facet of the frontal that is trapezoidal, separated from the lacrimal facet by a narrow vertical lamina, restricted to the anterior margin of the lateral surface of the bone with reduced lateral exposition and lacking participation to the orbital margin, in lacking a dorsomedially inclined anterior half of the dorsal surface of the frontal, in showing a lacrimal articular facet on the frontal that is proportionally twice as deep as in *C. iguidensis* with the thickest point in its anterior end, in lacking an anteriorly facing anterolateral corner of the postorbital facet of the frontal, and in showing a thick dome in the anterolateral corner of the dorsal surface of the frontal; from the sympatric and comparably-sized *Carcharodontosaurus saharicus* (Stromer, 1931; Sereno et al., 1996; Brusatte and Sereno, 2007, Fig. 2C) in showing a distinct anterolateral corner instead of a more gently curved anterolateral margin in dorsal view, more widely spaced nasal processes and a more posteriorly extended naso–frontal articulation reaching the dorsal surface of the frontal body, in lacking a dorsomedially inclined anterior half of the dorsal surface of the frontal, a deeply invaginated anterior margin of the supratemporal fossa, prominent frontal shelves overhanging the supratemporal fossa, and an extensively ossified interorbital septum; from *Eocarcharia dinops* from the Aptian–Albian of Niger (Sereno and Brusatte, 2008) in showing an elongate nasal process of the frontal with transversely convex dorsal surface not overlapped by the nasal, a trapezoidal and proportionally smaller prefrontal facet on the frontal with no ventral exposition, in lacking a sulcus running along the anterolateral margin of the dorsal