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An abelisaurid (Dinosauria: Theropoda) tooth from the Lower Cretaceous Chicla formation of Libya

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Abstract

An isolated theropod dinosaur tooth discovered in 1984 near Nalut in northwestern Libya is the only known dinosaur record from the Aptian–Albian (Lower Cretaceous) Chicla Formation in the Jabal Nafusah region of the country. The tooth was re-examined in an effort to better ascertain its taxonomic affinities. A stepwise discriminant function analysis compared the Libyan tooth to the dentitions of 24 other theropods and classified the tooth with cranial material from the Late Cretaceous of India previously referred to the abelisaurid *Indosuchus*. The temporal and paleogeographic "distance" separating the Libyan specimen from "*Indosuchus*" indicates that the former cannot pertain to that genus. However, the results of the analysis and synapomorphies of Abelisauridae present on the Libyan crown indicate that it can be referred to the clade, thus contributing to the growing record of Abelisauridae in the Cretaceous of mainland Africa.

Keywords: Libya; Dinosauria; Theropoda; Abelisauridae; Teeth; Morphometrics

1. Introduction

Despite the interval having been relatively well-sampled, the nature of the Cretaceous terrestrial vertebrate faunas of mainland Africa remains poorly known (Sereno et al., 1994; Sampson et al., 1998). This situation is particularly pronounced in Libya, where Mesozoic invertebrates have received more study than vertebrates due to the prominence of the petroleum industry (e.g., El Mehaghag, 1996; El-Mehdawi, 1998; Imam, 2001; Troeger, 2003). Fossils of dinosaurs, for example, are currently known from only a few localities (Lapparent, 1960; El-Zouki, 1980; Dalla Vecchia, 1995; Nessov et al., 1998; Duffin, 2001; Rage and Cappetta, 2002) and the materials which have been described are poorly informative, isolated elements.

In 1984, an amateur geologist, Umberto Lenuzza, collected an isolated predatory dinosaur (theropod) tooth crown from a locality near the town Nalut, along Jabal Nafusah (Fig. 1). Thought at the time to be the second occurrence of a dinosaur reported from Libya (it was apparently the third, see El-Zouki, 1980), the tooth (and associated fish and crocodyliform remains) was briefly described by Dalla Vecchia (1995) and mentioned by Duffin (2001). As is common with isolated theropod teeth, Dalla Vecchia (1995) found classifying the crown problematic. While researching the Jabal Nafusah region and its fossils in preparation for an August 2005 expedition (see Smith et al., in press), one of us (JBS) erected the hypothesis that the tooth might pertain to an abelisaurid. The Abelisauridae is a clade of ceratosaurian theropods with a widespread Gondwanan distribution (e.g., Bonaparte and Novas, 1985; Martínez et al., 1986; Sampson et al., 1998; Forster, 1999; Coria et al., 2002; Lamanna et al., 2002; Wilson et al., 2003), and which has been reported (e.g., Buffetaut et al., 1988, 1999; Buffetaut, 1989; Astibia

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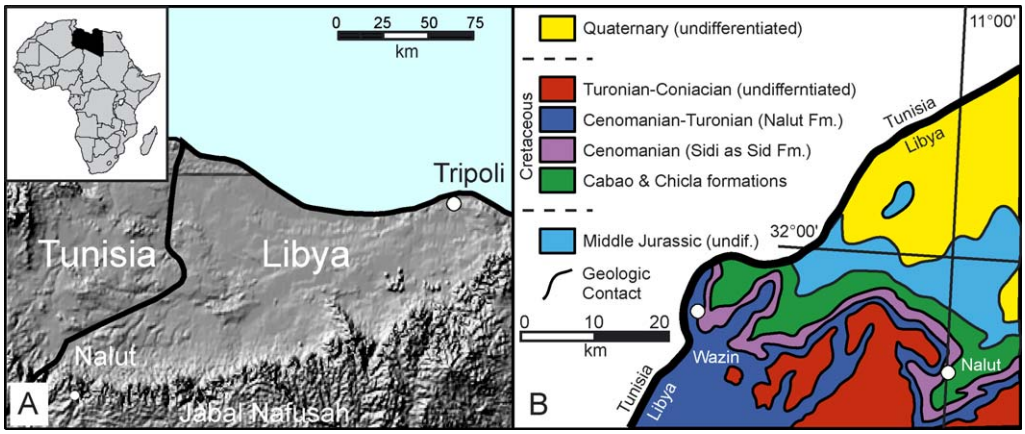

Fig. 1. (A) Location of the town of Nalut along the Jabal Nafusah escarpment, near the Tunisian border, northeastern Libya. (B) Simplified bedrock geology of the Nalut area, including the outcrop belt of the Cabao and Chicla formations (the Cabao Formation is a time transgressive unit (?Tithonian–Neocomian) which underlies the Chicla Formation). Figure modified from Smith et al. (in press).

et al., 1990; Le Loeuff and Buffetaut, 1991) from the Late Cretaceous of Europe (although these records have been strongly challenged (see Coria and Rodrigues, 1993; Coria and Salgado, 1998; Sampson et al., 1998, but see rebuttal by Buffetaut et al., 2005)), but which remains poorly known from mainland Africa (Sereno et al., 2004; Mahler, 2005; Smith and Lamanna, 2006). Given the paucity of information on African abelisaurids in general and Libyan dinosaurs in particular, and as the Lenuzza tooth is currently the only dinosaur fossil definitively known from the Chicla Formation in Libya, a test of the hypothesis that this tooth might be referable to Abelisauridae is warranted. As advances in morphometrics (Smith et al., 2005a) and research in dental anatomy (Smith, 2005; Smith and Krause, in press) have facilitated testing taxonomic identification hypotheses for isolated theropod teeth, thus making it possible to use these elements with greater confidence in resolving paleobiogeographic and paleoecological questions, we used these methods here to evaluate the taxonomy of the Libyan specimen.

2. Study area

The tooth, which is held in the collections of the Museo Paleontologico Cittadino in Monfalcone, Italy (MPCM 13693), was discovered in a sand quarry near the town of Nalut, in the western Jabal Nafusah region, near the Tunisian border (Fig. 1, see Dalla Vecchia, 1995; Duffin, 2001). Dalla Vecchia (1995) reported that the crown was recovered from sandstones of the Chicla Formation. This unit (as well as the same rocks across the border in Tunisia, which in that region are called the Chenini Formation) is dated to the Aptian–Albian of the Lower Cretaceous (~99–125 Ma, see Gradstein et al., 2005) based on the macrofloral assemblage (e.g., Barale et al., 1997; Barale and Ouaja, 2002) preserved therein. Most of the data favor an early Albian age (~110 Ma) but there is some indication (Imam, 2000) that the rocks could be Aptian (~120 Ma).

3. Materials and methods

The morphology of MPCM 13693 was examined (nomenclature follows Smith and Dodson, 2003) as in Smith (2005) to determine if it possesses abelisaurid dental characteristics (see Smith and Krause, in press). The hypothesis that the crown came from an abelisaurid was additionally tested, after Smith et al. (2005a), with a stepwise discriminant analysis (DA) using squared Mahalanobis distances (D^2), to examine morphological congruence between MPCM 13693 and the teeth of 24 other theropods. The premise of the analysis is that if MPCM 13693 pertains to an abelisaurid, its morphology should be more congruent with an abelisaurid in the dataset than a non-abelisaurid. Data from MPCM 13693 (Table 1) were compared against data (see Smith and Lamanna, 2006) from basal Theropoda (*Eoraptor*), basal Neotheropoda (*Dilophosaurus wetherilli*; *Liliensternus liliensterni*), basal Ceratosauria (*Ceratosaurus dentisulcatus*), Noasauridae (*Masiakasaurus*), Abelisauridae (*Majungasaurus*; *Rugops*; a maxilla and premaxillae previously referred to *Indosuchus*; an unnamed form from Morocco (Mahler, 2005)), ?Spinosauroidea incertae sedis ('*Megalosaurus*' *hesperis*), Spinosauridae (*Baryonyx*; *Suchomimus*), Allosauridae (*Allosaurus fragilis*), Carcharodontosauridae (*Acrocanthosaurus*; *Carcharodontosaurus*),

Table 1
Morphometric data measured from the theropod tooth (MPCM 13693) from Nalut, Libya

CBL	CBW	CH	AL	MAVG	DAVG	DAVG2	CBR	CHR	CA	CA2
16.20	9.80	27.50	29.50	12.5	8.5	−0.37	0.61	1.82	81.9	0.035

Abbreviations for metrics as in the text. See Smith et al. (2005a) for units.

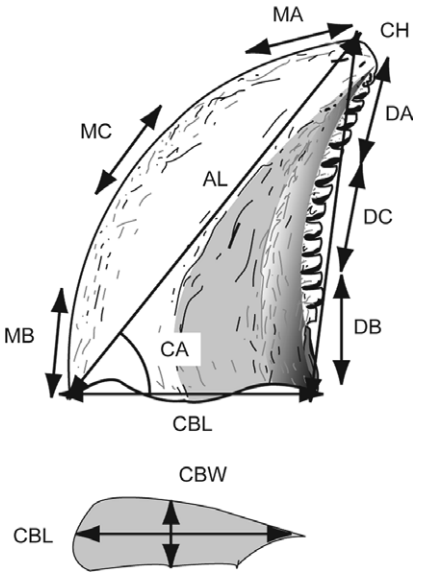

Fig. 2. Variables used in this study (modified from Smith et al., 2005a). (A) *Saurornitholestes* crown in lateral view showing CH (measured from apex to the base of the enamel); CBL, mesial apical (MA), mesial mid-crown (MC), and mesial basal (MB) denticle densities (measured along the length of the mesial carina); distal apical (DA), distal mid-crown (DC), and distal basal (DB) denticle densities (measured along the length of the distal carina). (B), the crown in (A) in basal view showing CBL and crown base width (CBW, measured perpendicular to CBL). CBL, CBW, CH, and AL are reported in mm. CA is the angle between CBL and AL. MA, MC, and MB are used to calculate MAVG; DA, DC, and DB are used to calculate DAVG. MAVG and DAVG are reported using a number and slash combination to indicate number of denticles per 5 mm of carina length (e.g., 10.5/5 mm). CBR is CBW:CBL; CHR is CH:CBL.

Tyrannosauridae (*Daspletosaurus*; *Gorgosaurus*; *Tyrannosaurus rex*), Troodontidae (*Saurornithoides junior*; *Troodon*), and Dromaeosauridae (*Bambiraptor*; *Deinonychus*; *Dromaeosaurus*; *Velociraptor*).

Crown size was assessed using crown base length (CBL), crown base width (CBW), crown height (CH), and apical length (AL). Crown basal shape was described using the crown base ratio (CBR) and "squatness" was assessed using the crown height ratio (CHR). Apex displacement (and indirectly, curvature) from the crown base center was described using the crown angle (CA). Size and spacing of denticles was assessed using the average distal denticle density (DAVG). See Smith et al. (2005a) for details on methods and metrics (Fig. 2). In the DA, raw data were used for CBL, CBW, CH, AL, CBR, and CHR. CA and DAVG data were compared after removing size as a confounding variable. This was accomplished by performing a principal components analysis of log-transformed data using AL, CA, CBL, CBW, CBR, CH, CHR, and DAVG. The data were then regressed on the factor scores (using orthogonal rotation) for the first principal component, which explained 84.4% of the variance (details of this analysis are available on request). The residuals from the regressions were used as new variables (size-corrected crown angle (CA2) and size-corrected average distal denticle density (DAVG2)) that were incorporated into the DA.

4. Results

MPCM 13693 (Fig. 3) possesses several features common to abelisaurids but distinct from other Theropoda. The mesial curvature profile (Smith et al., 2005a) describes a strong curve beginning at about the midpoint of the crown, as in *Majungasaurus*, the Indian specimens, and *Rugops*, rather than beginning basally and curving smoothly to the apex, as in most theropods. The distal curvature profile (Smith et al., 2005a) exhibits almost no curvature. Instead, it is straight and angles slightly mesially toward the apex, as in *Majungasaurus*, *Rugops*, and the Indian specimens, but in contrast to other theropods (this feature is convergently developed in the most distal dentary teeth of *T. rex* and perhaps some other tyrannosaurids (Smith, 2005), but it does not appear to be a typical aspect of non-abelisaurid dentitions as a whole (Smith and Krause, in press)). Interestingly, as in *Rugops*, but in contrast to the condition observed in *Majungasaurus* and the Indian specimens, the denticles of MPCM 13693 exhibit no traces

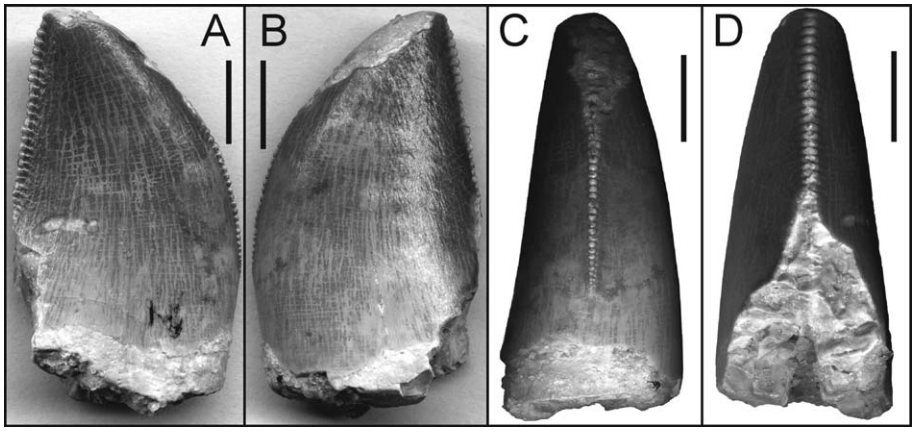

Fig. 3. Abelisaurid theropod tooth (MPCM 13693) from Nalut, Libya in left lateral (A), right lateral (B), mesial (C), and distal (D) views. Left and right defined looking at the mesial face. Scale bars = 5 mm.

of the caudae/interdenticular sulci complex (Smith and Krause, in press), which might suggest that the specimen is derived from a more basal member of the clade.

The DA correctly identified 95.4% of the teeth in the sample, and classified MPCM 13693 with the Indian material previously referred to the abelisaurid *Indosuchus* (26.39 D^2 units from MPCM 13693 to the "*Indosuchus*" centroid; $p < .0001$). The temporal and paleogeographic (see Storey et al., 1995; Krause et al., 1999) "distance" separating the Libyan specimen from the Indian form indicates that the former cannot pertain to the Indian taxon. However, coupled with the synapomorphies of Abelisauridae possessed by MPCM 13693, the results of the DA permit its referral to this clade.

5. Discussion

Although rocks equivalent (El-Zouki, 1980) to the Aptian–Albian Chicla Formation across the border in Tunisia (the Chenini Formation) have produced dinosaur material (e.g., Bouaziz et al., 1988; Benton et al., 2000; Buffetaut and Ouaja, 2002), MPCM 13693 is currently the only dinosaur element definitively known from this interval in Libya. The stratigraphic provenance of the Libyan fossils described by Lapparent (1960) is not certain (i.e., we cannot discount the possibility that, although not likely, these fossils could have come from the Cenomanian-aged Sidi as Sid Formation which overlies the Chicla Formation) and the other dinosaur material recovered from Libya so far is either older (El-Zouki, 1980) or younger (Nessov et al., 1998; Rage and Cappetta, 2002) than MPCM 13693.

Based on its possession of the features discussed above and given the results of the DA, we refer MPCM 13693 to Abelisauridae. This referral broadens the distribution of abelisaurids on continental Africa to include Niger (Sereno et al., 2004), Morocco (Mahler, 2005, and possibly Buffetaut et al., 2005), Egypt (Smith and Lamanna, 2006, and possibly Stromer and Weiler, 1930), and Libya. Buffetaut et al. (2005) described a putative abelisaurid tooth from the Late Cretaceous of Morocco, but although the specimen likely pertains to this clade, the hypothesis has yet to be rigorously tested (the existing meager literature on abelisaurid teeth is not sufficient to rigorously test this hypothesis). Similarly, likely abelisaurid remains from the Late Cretaceous of Egypt, described by Stromer and Weiler (1930), are difficult to resolve as they were fragmentary and were destroyed during World War II (Smith et al., 2005b). MPCM 13693 appears to be penecontemporaneous with the occurrence of the Aptian–Albian abelisaurid from Niger described by Sereno et al. (2004) and offers additional evidence that abelisaurids were probably well established on Africa by the late Early Cretaceous. Indeed, the age of these early African abelisaurids invites some speculation as to how early the group might have arrived on the African landmass (see hypotheses discussed by Buffetaut et al., 2005). As research continues in the Cretaceous of North Africa, it is becoming apparent that the spotty record of abelisaurids from the African mainland is probably the result of incomplete sampling more than a reflection of the actual abundance of this group (see comments by Sampson et al., 1998).

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