

Joshua B. Smith · Matthew C. Lamanna

An abelisaurid from the Late Cretaceous of Egypt: implications for theropod biogeography

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Abstract Recent paleogeographic scenarios postulate the isolation of continental Africa during the Late Cretaceous. The absence of abelisaurid theropods from Upper Cretaceous African strata was offered as support of hypothesized African isolation with the acknowledgement that the paucity of African abelisaurids may be mostly an issue of sampling. Here we report on a shed theropod tooth from the Upper Cretaceous (Maastrichtian, ~70 Ma) Duwi Formation of Egypt. The tooth was referred to the Malagasy abelisaurid “*Megalosaurus*” *crenatissimus* (= *Majungasaurus crenatissimus*) in 1921. A discriminant function analysis was run to test for morphological congruence between the Egyptian tooth and the dentitions of 24 theropod taxa. The analysis correctly classified 96.6% of the teeth in the sample and assigned the tooth to *Majungasaurus*. As current paleogeographic reconstructions posit Madagascar had attained its current position relative to Africa before the Late Cretaceous, it is unlikely that the Egyptian tooth actually pertains to *Majungasaurus*. Nevertheless, its classification as an abelisaurid supports its

referral to the clade. This tooth thus constitutes defensible evidence of an abelisaurid from the post-Cenomanian Cretaceous of mainland Africa. Combined with recent discoveries of abelisaurids in Niger and Morocco, the result indicates that Abelisauridae was a diverse group in Africa during the Cretaceous, existing in multiple places for at least ~25 Ma and weakens support for hypotheses of an isolated Africa during the Late Cretaceous.

Introduction

Although the effects of the fragmentation of Gondwana on terrestrial vertebrate evolution remain poorly understood, one paleogeographic scenario (Hay et al. 1999) led to the hypotheses of the faunal isolation of continental Africa throughout the Late Cretaceous (Krause et al. 1997; Sampson et al. 1998). The observed absence of abelisaurid theropod dinosaurs from post-Cenomanian (Upper Cretaceous) African strata and the presence of this clade in coeval sediments of other Gondwanan landmasses was interpreted to be consistent with a Late Cretaceous isolation of Africa with the acknowledgement that the paucity of post-Cenomanian African abelisaurids may be more due to incomplete sampling than to their actual absence from the continent (Sampson et al. 1998; Krause et al. 1999). Indeed, until very recently (Serenó et al. 2004; Mahler 2005), postulated occurrences of African abelisaurids (Russell 1996) were contested (Sampson et al. 1998; Carrano et al. 2002).

Here we discuss a tooth from Maastrichtian-aged (~70 Ma, see Gradstein et al. 2005) deposits of the Duwi Formation near Idfu in the Nile Valley of Egypt (Fig. 1, exact locality data are unknown; research in Palermo did not reveal a more accurate location). The tooth (Fig. 2) described by Gemmellaro (1921) is morphologically very similar to the teeth of the carnosaurine abelisaurid *Majungasaurus* from the latest Cretaceous of Madagascar (Sampson et al. 1998) and is referable to Abelisauridae. This, the first defensible abelisaurid from Egypt and the

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J. B. Smith (✉)
Earth & Planetary Sciences, Washington University,
1 Brookings Drive,
Box 1169, St. Louis, MO 63130, USA
e-mail: smithjb@wustl.edu
Tel.: +1-314-9357033
Fax: +1-314-9357361

M. C. Lamanna
Vertebrate Paleontology, Carnegie Museum of Natural History,
4400 Forbes Avenue,
Pittsburgh, PA 15213, USA
e-mail: LamannaM@CarnegieMNH.org

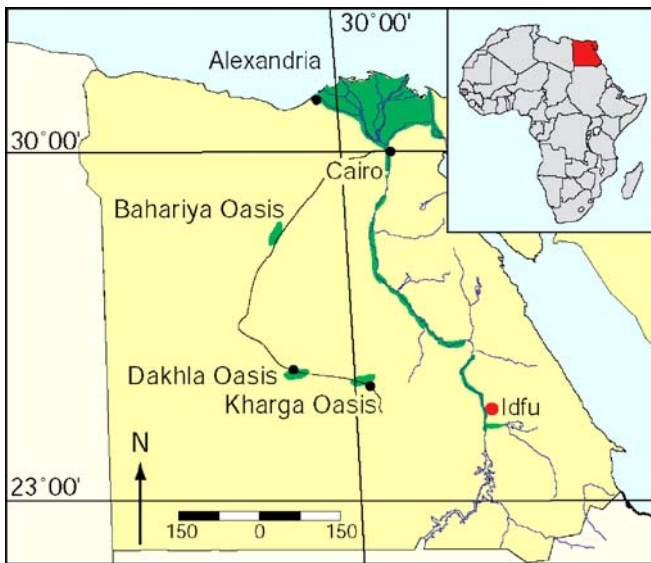


Fig. 1 Location of the Idfu area of Egypt (modified from Smith et al. 2001)

post-Cenomanian of continental Africa,¹ demonstrates that the clade inhabited the African mainland during the latest Cretaceous and weakens the support for a Cretaceous faunal isolation of Africa.

Materials and methods

The tooth, Museo di Geologia e Paleontologia (MGUP, Università di Palermo) MEGA002, was originally referred (Gemmellaro 1921) to “*Megalosaurus*” *crenatissimus* (an abelisaurid from the Late Cretaceous of Madagascar currently identified as *Majungasaurus crenatissimus* Krause and Sampson, *in press*). Since 1921, it was virtually ignored in the literature (but see Sampson et al. 1996) and its affinities were never verified. Recent advances in theropod dental morphometrics (Smith et al. 2005b) and progress in dental character identification (Smith 2005; Smith and Krause, *in press*) facilitated the rigorous testing of taxonomic identification hypotheses for isolated theropod teeth (beyond the untested referrals which are common in the literature, e.g., Buffetaut et al. 2004). Accordingly, these elements may now be utilized with increased confidence to inform paleobiogeographic hypotheses in a manner similar to that which is common for mammalian teeth (Krause et al. 1997; Krause 2001). As such, theropod teeth can now be used with greater confidence to help answer important questions confounded by a poorly resolved fossil record.

¹Buffetaut et al. (2005) noted a comparable abelisaurid tooth from Maastrichtian-aged rocks in Morocco, but while the hypothesis for the specimen is reasonable, it has yet to be rigorously tested and remains tentative, as do other possible abelisaurid remains (Stromer and Weiler 1930) now lost (Smith et al. 2005b) from the Nile Valley.

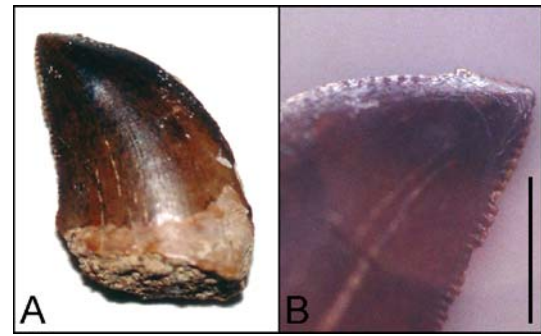


Fig. 2 Theropod crown (MGUP MEGA002) from Egypt in left lateral view (a) and in right lateral view showing denticles (b). Scale bars equal to 10 mm in subpanel a and 5 mm in subpanel b

Following Smith (2005) and Smith and Krause (*in press*), we evaluated the referral of the tooth to *Majungasaurus*. We additionally tested the hypothesis with a stepwise discriminant analysis (DA) using squared Mahalanobis distances (D^2) to examine morphological congruence between MGUP MEGA002 and a standard dataset comprised of data from the teeth of 24 other theropods. Data from MGUP MEGA002 (Table 1) were compared against data (see electronic supplementary material S1) from:

- basal Theropoda (*Eoraptor*);
- basal Neotheropoda (*Dilophosaurus wetherilli*, *Liliensternus liliensterni*);
- basal Ceratosauria (*Ceratosaurus dentisulcatus*);
- Noasauridae (*Masiakasaurus*);
- Abelisauridae (an unnamed form from Morocco (Mahler 2005), *Rugops*, premaxillae and a maxilla from India previously referred to *Indosuchus*², *Majungasaurus*);
- ?Spinosauroida incertae sedis (“*Megalosaurus*” *hesperis*);
- Spinosauridae (*Baryonyx*, *Suchomimus*);
- Allosauridae (*Allosaurus fragilis*);
- Carcharodontosauridae (*Acrocanthosaurus*, *Carcharodontosaurus*);
- Tyrannosauridae (*Daspletosaurus*, *Gorgosaurus*, *Tyrannosaurus rex*);
- Troodontidae (*Saurornithoides junior*, *Troodon*); and
- Dromaeosauridae (*Bambiraptor*, *Deinonychus*, *Dromaeosaurus*, *Velociraptor*).

Metrics (electronic supplementary material S2) and procedure follow Smith et al. (2005b). Crown base length (CBL), crown base width (CBW), crown height (CH), and apical length (AL) describe crown size. CBL and CBW were measured in a horizontal plane referenced to the base of the distal carina. Crown basal shape was

²The specimens of the Indian abelisaurid (S1) cannot be referred to *Indosuchus* (Lamanna et al. 2002; Novas et al. 2004). However, as the teeth are morphologically consistent with a single genus (Fig. 10 in Smith et al. 2005b) and the remains might have come from one individual (Wilson et al. 2003), the teeth are grouped together here pending additional study.

Table 1 Morphometric data measured or calculated from the theropod tooth (MGUP MEGA002) from Egypt

CBL	CBW	CH	AL	MAVG	DAVG	DAVG2	CBR	CHR	CA	CA2
13.01	6.69	16.63	20.97	11.2	13.43	0.006	0.52	1.28	76.4	0.029

Abbreviations for metrics as in the text. See Smith et al. 2005a,b for units

described using the crown base ratio, CBW:CBL (CBR); “squatness” was assessed using the crown height ratio, CH:CBL (CHR). Apex displacement (and indirectly, mesial curvature) from the crown base center (Smith et al. 2005b) was assessed using the crown angle (CA). Denticle size and spacing was assessed using the average distal denticle density (DAVG) reported with a number and slash indicating serrations per 5 mm (e.g., 10/5 mm).

In the DA, raw data were used for CBL, CBW, CH, AL, CBR, and CHR. As CA and DAVG values scale with tooth size (Farlow et al. 1991), CA and DAVG data were compared after removing size as a confounding variable (see Marko and Jackson 2001). A principal components analysis of log-transformed data was run 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. The regression residuals constitute new variables [size-corrected crown angle (CA2) and size-corrected average distal denticle density (DAVG2)], which were utilized in the DA.

Results

Several features support the referral of MGUP MEGA002 to Abelisauridae. Some are congruent with the condition observed in the derived abelisaurids *Majungasaurus* and the “*Indosuchus*” specimens (Smith and Krause, *in press*) and contrasted with that seen in the more basal *Rugops* and the Moroccan form (Serenó et al. 2004; Mahler 2005; this study), suggesting the tooth pertains to a derived, rather than basal, abelisaurid. The mesial curvature profile begins at a strong curve at about 1/3 the crown height basal to the apex, as in *Majungasaurus* and the Indian specimens (Smith and Krause, *in press*). As in the maxilla of *Majungasaurus*, *Rugops*, the Indian specimens, and an unnamed Patagonian taxon (Lamanna et al. 2002), but in contrast to most theropods (Smith and Krause, *in press*), the distal curvature profile exhibits almost no curvature and is tilted slightly toward the apex in lateral view. As in *Majungasaurus* and the Indian specimens but in contrast to *Rugops* and the Patagonian and Moroccan forms, the caudae/interdenticular sulci complex (Smith and Krause, *in press*) forms an intermediate condition between being absent and well developed.

The discriminant analysis (DA) correctly identified 96.6% of the teeth in the sample and classified MGUP

MEGA002 as *Majungasaurus* (29.44 squared Mahalanobis distance units from the *Majungasaurus* centroid, $p < 0.0001$). Although the assignment of the Egyptian tooth to the genus *Majungasaurus* in particular is unlikely given that Africa and Madagascar were separated by the Mozambique Channel throughout the Cretaceous (see Storey et al. 1995; Krause et al. 1999), the results of the analysis indicate that MGUP MEGA002 is more similar to the abelisaurids in the dataset than the nonabelisaurids, supporting the abelisaurid hypothesis. Also, that MGUP MEGA002 probably pertains to a derived form is reinforced by the fact that the tooth is more similar to *Majungasaurus*, a carnosaurine, than it is to the more basal abelisaurids in the dataset (e.g., *Rugops*).

Discussion

Previous definitive abelisaurids from mainland Africa are limited to Early and early Late Cretaceous occurrences in Morocco and Niger (Serenó et al. 2004; Mahler 2005). A derived abelisaurid from the Maastrichtian of Egypt documents the clade in the latest Cretaceous of Africa and opens the possibility that “faunal connections” between South America and Africa remained open later than the early Late Cretaceous. It indicates Abelisauridae was widespread and lived long on the African landmass with taxa occurring in several locations along the southern Tethyan margin spanning an interval of at least 15 Ma.

Interpreting occurrences of basal abelisaurids from ~95-million-year-old strata in Africa (Serenó et al. 2004) as weakening the possibility of Cretaceous African faunal isolation are confounded (see Krause and Sampson, *in press*) by the fact that the clade appears (Rauhut et al. 2003) to have evolved by at least the Neocomian of the Early Cretaceous (before ~125 Ma; see Gradstein et al. 2005). Abelisaurids could thus possibly have radiated into Africa before it separated from South America. However, as current data support an origination of Carnosaurinae after the separation of the two landmasses (see Fig. 4 in Sereno et al. 2004), a derived abelisaurid from Egypt does support the possibility, which is suggested by Sereno et al. (2004), that faunal communication between Africa and South America might still be possible into the Late Cretaceous and weakens the idea that Cretaceous African terrestrial tetrapods developed in isolation.

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