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Integrating palaeoecology and morphology in theropod diversity estimation: A case from the Aptian-Albian of Tunisia

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ABSTRACT

Current knowledge of theropod dinosaurs of northern Africa and their diversity during the Early Cretaceous is deceptively fragmentary and commonly associated with inadequate stratigraphic and palaeoecological data. Thereby, confused taxonomic affinities of theropod remains, represented primarily by isolated teeth and fragmentary skeletal remains, resulted in speculations on the number of genera and their stratigraphic, geographic and ecological distribution. In this study, we introduce a discussion on the theropod diversity in the Aptian–Albian of southern Tunisia based on a multidisciplinary approach that combines detailed sedimentological analyses with canonical morphological and phylogenetic analyses. This study indicates the presence of three theropod clades, Spinosauridae, Abelisauroidea, and Carcharodontosauridae. Relevant for the identification of isolated specimens from the Saharan regions, carcharodontosaurids are not represented in the Aptian-Albian teeth record and thus relatively less abundant than spinosaurids and abelisauroids. Five ziphodont tooth morphotypes are referred to ontogenetic and/or positional differences among a single abelisauroid taxon. The other three teeth morphotypes most likely represent two distinct spinosaurid taxa. Finally, the calibrated stratigraphic distribution of discussed elements indicates a clear ecological partition between theropod taxa. In particular, abelisauroids and carcharodontosaurids are commonly found in inland, fluvial deposits together with titanosauriform and rebbachisaurid sauropods, and rare crocodilians. Conversely, spinosaurids are limited to estuarine to coastal deposits dominated by a rich and diverse crocodilian fauna along with actinopterygians and sarcopterygians, including large-sized coelacanthiforms.

1. Introduction

Fossil vertebrates from the deposits marking the Aptian-Albian in the Saharan region play a fundamental role in understanding the stratigraphic and geographic distribution of several dinosaur lineages in continental Africa and neighbouring regions. Although a number of different dinosaur clades are now recognized in the fossil record, fragmentary and isolated skeletal remains combined with largely understudied stratigraphic sections commonly limit the potential of such discoveries to a regional meaning. In the last decade, detailed revisions of both stratigraphic and palaeontological data from the well-known successions of southern Tunisia have yielded evidences of a diverse, late Early Cretaceous ecosystem composed of bony fish, sharks, turtles, crocodiles, pterosaurs, as well as several vertebrate tracksite (Bouaziz et al., 1988; Benton et al., 2000; Buffetaut and Ouaja, 2002; Cuny et al., 2004; Srarfi et al., 2004; Srarfi, 2006; Contessi and Fanti, 2012a,b; Fanti et al., 2012; Contessi, 2013a,b, and references therein). Dinosaurs are represented by skeletal remains of titanosauriforms and rebbachisaurid sauropods, whereas ornithopods and theropods are to date represented by isolated teeth, with the exception of fragmentary and poorly preserved cranial and post-cranial material (Lapparent, 1951; Buffetaut and Ouaja, 2002; Fanti et al., 2013, 2014; F.F., pers. obs.). In this study, we discuss the taxonomic potential of isolated theropod teeth and fragmentary, non-dental materials collected from the Dahar escarpment of southern Tunisia and extend taxonomic analyses and comparisons to a rich collection of isolated theropod teeth from other Saharan localities (Fig. 1). As tooth assemblages give important insights into faunal constituents otherwise poorly represented by skeletal remains, a detailed analysis of isolated theropod teeth offers the opportunity to (1) evaluate theropod taxonomical diversity in the Aptian-Albian of southern Tunisia, and (2) compare the data from Tunisia with currently known theropod diversity in coeval deposits of northern Africa. As such, the results of this research improve general understanding of the Lower Cretaceous Tunisian ecosystems and have important implications for Gondwanan and peri-Mediterranean palaeobiogeography.

2. Geological setting

A recent revision of stratigraphic correlations and fossil occurrence in the Tataouine basin (Fig. 1) revealed that the strata exposed in the

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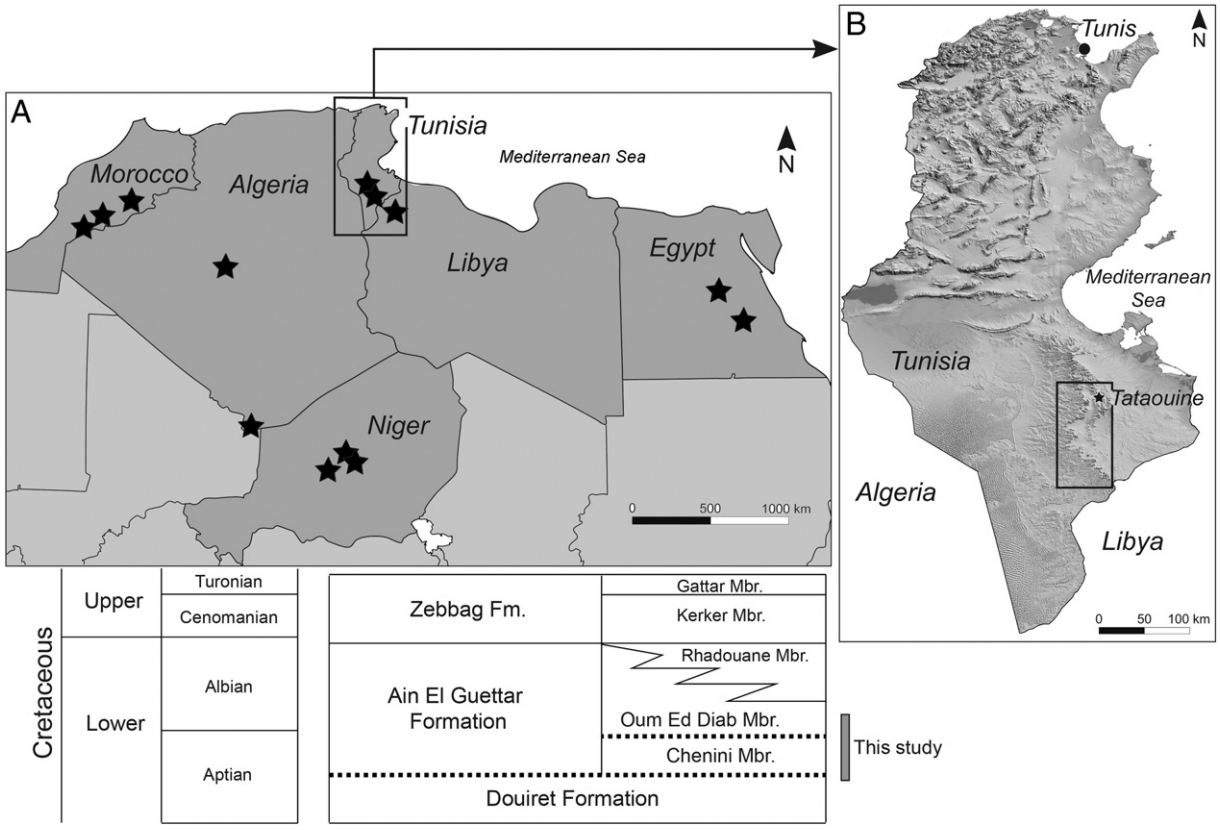

Fig. 1. A. Present day map of Africa showing the mid-Cretaceous localities from which isolate theropod teeth included in this study have been discovered. B. Reference map of Tunisia showing the position of the Tataouine Basin: the study area is located along the prominent Jeffara escarpment. C. Stratigraphic nomenclature for the mid-Cretaceous of southern Tunisia (after Fanti et al., 2012). Dashed lines indicate major unconformities.

area preserve multiple fossil-bearing levels: all identifiable dinosaur remains, however, occur within the Oum ed Dhiab Member of the Ain el Guettar Formation (upper Aptian–Albian) (Fanti et al., 2012). Relevant to this study, theropod remains historically referred to the fluvial deposits of the Chenini Member (Benton et al., 2000) are instead representative of transgressive lag deposits on transgressive, erosional surface which mark the base of the overlying Oum ed Diab Member (Fanti et al., 2012, 2014). Therefore, the faunal assemblage in these coarse-grained beds preserves taxa that may originally pertained to the underlying Chenini Member deposits as well as taxa that relate to the Oum ed Diab Member. The coarse-grained Chenini beds are representative of high-energy fluvial deposits that accumulated on a low-gradient, distal alluvial plain similar to modern *wadi*-like drainage systems (Benton et al., 2000; Fanti et al., 2012). Differently, fine-grained, sandy deposits of the Oum ed Diab Member overlying the basal transgressive lag preserve estuarine to shoreface and tidal flat deposits interpreted as deposited in a vast embayment (Fanti et al., 2012, 2013). Although at the time of writing it is not possible to constrain the temporal gap represented by the unconformity that separates the Chenini and the Oum ed Diab members, the Chenini Member is referred to the uppermost Aptian-lowermost Albian, whereas the Oum ed Diab Member to the middle Albian (Ben Youssef et al., 1985; Bodin et al., 2010; Pons et al., 2010; Fanti et al., 2012, and references therein). Specimens described in this study were surface collected from the two above-mentioned lithostratigraphic intervals within the Oum ed Diab Member. From a taphonomic perspective, specimens collected from the basal, lag deposits are partly or completely covered with a solid, diagenetic crust and present clear evidences of abrasion on both enamel surface and serrations, indicative of intense pre-burial transportation within the coarse-grained sediments (i.e. coarse quartzarenite with centimetre- to decimetre-sized pebbles). Conversely, specimens collected from the juxtaposing, unconsolidated sandy deposits are in good preservation conditions although they were likely shed teeth, being found isolated and rootless. Significant differences in the taphonomic conditions and matrix associated with collected teeth allowed a robust stratigraphic discrimination of morphotypes discussed herein.

3. Material and methods

The relative paucity of well-preserved material from the Tataouine region and the lack of detailed classification of Saharan isolated teeth in the literature challenged the possibility for detailed study. Historically, all isolated elements, including teeth, have been referred to a 'typical' northern-Africa theropod fauna based on the very few skeletal material collected in these regions. This fauna includes three mid-Cretaceous theropod clades represented by a restricted number of taxa: carcharodontosaurids (*Carcharodontosaurus saharicus*, *C. iguidensis*, *Eocarcaria dinops*, *Sauroniops pachytholus*, Depéret and Savornin, 1925; Stromer, 1931; Lavocat, 1954; Russell, 1996; Sereno et al., 1996; Amiot et al., 2004; Brusatte and Sereno, 2007; Sereno and Brusatte, 2008; Cau et al., 2012, 2013), spinosaurids (*S. aegyptiacus* and its possible synonym *S. maroccanus*, *Cristatusaurus lapparenti*, and its possible synonym *Suchomimus tenerensis*, Stromer, 1915; Russell, 1996; Taquet and Russell, 1998; Smith et al., 2006; Sereno et al., 1998), and abelisaurids (*Rugops primus*, *Kryptos palaios*, Sereno et al., 2004; Sereno and Brusatte, 2008). A fourth lineage is represented by *Deltadromeus* (Sereno et al., 1996), a taxon lacking cranial and dental remains and with a controversial phylogenetic placement among Ceratosauria (see Carrano and Sampson, 2008). Recently, Amiot et al. (2004) and Richter et al. (2013) claimed the possible presence of dromaeosaurids in the Cenomanian of Morocco, the second report in continental Africa after the discovery of isolated teeth in the Wadi Milk Formation of Sudan (Rauhut and Werner, 1995). In continental Africa, Aptian–Cenomanian theropods are known primarily from the