NEW ABELISAUROID MATERIAL FROM THE UPPER CRETACEOUS (CENOMANIAN) OF MOROCCO

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Key words: Theropoda, Abelisauridae, maxillæ, Cenomanian, Northwestern Africa, Morocco.

Abstract. Fragmentary cranial bones of dinosaur origin have been recently recovered from the Kem Kem beds (Upper Cretaceous, Cenomanian) of Morocco. They include two incompletely preserved maxillary bones evidencing diagnostic features of abelisaurid theropods. These new finds provide further evidence of Abelisauridae in the Late Cretaceous of Morocco.

Riassunto. Resti frammentari di ossa craniche di dinosauro sono state recentemente rinvenute nei Kem Kem beds (Cretaceo Superiore, Cenomaniano) del Marocco. Il materiale consta di due mascellari incompleti con caratteristiche morfologiche riconducibili a teropodi abelisauridi. Il nuovo materiale fornisce una ulteriore prova della presenza di Abelisauridae in questa regione sin dalla base del Cretaceo Superiore.

Introduction

In the last decade new discoveries of abelisaurian dinosaurs have greatly improved the knowledge about their global distribution (e.g., Novas 1997; Sampson et al. 1998; Carrano et al. 2002; Sereno et al. 2002, 2004; Wilson et al. 2003; Novas et al. 2004; Canale et al. 2009). Yet, the abelisauroid record from the Upper Cretaceous of Morocco is rather fragmentary and sometimes controversial (Russell 1996; Amiot et al. 2004; Sereno et al. 1996, 2004; Buffetaut et al. 2005; Mahler 2005; Novas et al. 2005, Carrano & Sampson 2008), and each new discovery is potentially very informative under palaeoecological and palaeogeographical respects. Although incomplete, the material presented here helps to confirm and define the occurrence of Abelisauridae in northwestern Africa at the base of the Late Cretaceous.

Institutional abbreviations

FMNH, Field Museum of Natural History, Chicago, Illinois, United States of America; MNN, Museé National du Niger, Niamey, Niger MPUR NS, Museo di Paleontologia Università di Roma Nuova Serie, Rome, Italy; UCPC, University of Chicago Paleontological Collection; Illinois, United States of America; UNPSJB, Universidad Nacional de Patagonia “San Juan Bosco”, Comodoro Rivadavia, Argentina.

Geological Setting

The specimens were discovered by local searchers at the Hammad des Kem Kem area, close to the Begaa village, about 10 km north-east of Taouz (Morocco) (Fig. 1), in alluvial deposits referred to the Kem Kem beds (an informal unit), a succession of red sandstones and mudstones (e.g., Garassino et al. 2006), subdivided into a lower sandstone unit with cross-bedded stratification and an upper sequence of sandstone and claysone (Amiot et al. 2004). The exact stratigraphic position of the findings is not well-documented but features of the matrix embedding the bones are consistent with the lithology of the lower portion of the Kem Kem beds.
beds. On the basis of the palaeoichthyological record (Sereno et al. 1996), the age of these deposits has been assigned to the Late Cretaceous (Cenomanian).

Systematic Palaeontology

**Theropoda** Marsh, 1881

**Ceratosauria** Marsh, 1884

**Abelisauridae** Bonaparte, 1991

**Abelisauridae gen. et sp. indet.**

Material: MPUR NS 153/02 (NS 153/02 hereafter) is reposited in the collections of the Museo di Palaeontologia of the Sapienza Università di Roma and consists of a partial left maxillary bone, lacking the ascending process, and preserving a partially erupted tooth and several erupting teeth (see Tab. 1 for measurements).

Locality and Age: Hammada des Kem Kem, close to the village of Begaa, about 10 km north-east of Tazouz, Morocco, Kem Kem beds, Late Cretaceous (Cenomanian).

Description. NS 153/02 (Fig. 2.1-2.3) has been identified as the incomplete main body of a left maxilla. The lateral surface is covered with deep elaborate sculpturing made of several intersecting pits, arched grooves and channels typical of abelisaurid theropods. The lower margin of the antorbital fossa contains in a smooth-textured area on the dorsal edge of the maxilla, which is placed close to an incomplete elliptical foramen, at the caudal end of the specimen. NS 153/02 has 13 neurovascular foramina lying extremely close to the lower margin of the ventral ramus and placed both between and over the alveoli. Caudally, the area for the jugal contact is poorly preserved and most of it is missing. On the caudalmost part of the lateral surface, a distinctive and deep ornamentation is identified as the rostralmost portion of the "posterior groove", as described by Sereno et al. (2004, fig. 3). In medial view, the dorsal portion of the specimen preserves part of the palatal process of the maxilla that we will call as shelf for brevity hereafter. The ventral surface of the palatal shelf preserves a row of 5 dental foramina lying below this shelf (*sensu* Lamanna et al. 2002). The medial surface of the shelf is rather smooth, except for several small ridges gathered in a lanceolate area, where the maxilla joined the palate. The parapetal plates (*sensu* Carrano & Sampson 2008) are fused and heavily furrowed by oblique grooves, which are oriented rostroventrally. The medial wall of the alveoli sinks over the sockets, and two contiguous hollows are generally separated by triangular medial bulges. As noted by Lamanna et al. (2002), these ridges could be related to the presence of underlying replacement teeth. X-ray analysis (Fig. 3.1) reveals rows of erupting teeth on the specimen at the position of these triangular medial bulges. The ventral margin of the maxilla of NS 153/02 preserves eight rectangular alveoli but only one partially erupted tooth. Four other alveoli contain broken teeth and two are missing teeth.

The erupted tooth (see Smith & Dodson 2003 and Smith et al. 2005 for terminology) is symmetrical in cross-section with an ovoid outline, mesially rounded and distally pointed. Its surface is smooth and lacks any evidence of enamel wrinkles. The tooth is lingually compressed with mesial and distal denticulate carinae. The mesial apical denticles are as high as long, with narrow cellae lacking any evidence of blood
Measurements (mm)

<table>
<thead>
<tr>
<th>Measurements</th>
<th>NS 153/01</th>
<th>NS 153/02</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum rostrocaudal length</td>
<td>82.5</td>
<td>108.3</td>
</tr>
<tr>
<td>Maximum dorsoventral depth</td>
<td>67.5</td>
<td>65</td>
</tr>
<tr>
<td>Maximum medio-lateral thickness shelf</td>
<td>17</td>
<td>19</td>
</tr>
<tr>
<td>Maximum medio-lateral thickness maxilla at the alveoli</td>
<td>11</td>
<td>11.2</td>
</tr>
</tbody>
</table>

Tab. 1 - Measurements (mm) of the specimens (MPUR NS 153/01, MPUR NS 153/02).

grooves, which are indeed preserved on the central and basal portion of the mesial carina. The mesial apical serration density is 3 per mm. Most of the distal denticles are broken, yet the portion of the tooth inside the alveolus shows longer denticles relative to the mesial side, with narrow cellae and definite blood grooves (Fig. 4.1). The distal apical serration density is 3.5 per mm.

**Fig. 2** - Abelisaurid maxillae, MPUR NS 153/02 (1, 2, 3) and MPUR NS 153/01 (4, 5, 6) in lateral (1, 4) medial (2, 5) and ventral view (3, 6). Abbreviations: AOF: antorbital fossa; CG: curved grooves; DF: dental foramina; J: jugal contact; NF: neurovascular foramina; PC: palatine contact; PG: posterior groove. Scale bar: 5 cm.

**Theropoda** Marsh, 1881

**Ceratosaurus** Marsh, 1884

**Abelisauridae** Bonaparte, 1991

**Abelisauridae** Bonaparte & Novas, 1985

Abelisauridae gen. et sp. indet.

**Material**: MPUR NS 153/01 (NS 153/01 hereafter) is reposited at the Museo di Paleontologia of the Sapienza Università di Roma and consists of a right maxillary body, missing both the rostral and the ascending process and lacking any teeth (see Tab. 1 for measurements).

**Locality and Age**: Hammada des Kem Kem, close to the village of Begaa, about 10 km north-east of Taouz, Morocco, Kem Kem beds, Late Cretaceous (Cenomanian).

**Description**: NS 153/01 (Fig. 2.4–2.6) is the caudal half of the main body of a right maxilla preserving an almost complete, laterally-facing rostrodorsally inclined contact surface for the jugal bone. The lateral
surface is covered by conspicuous ornamentation consisting of distinctive rostrally convex, crescent-shaped grooves, associated with pits and furrows. The ventrolateral margin is bordered by a row of 9 neurovascular foramina. Medially, the palatal process of the maxilla runs horizontally dorsal to the alveolar wall for the entire length of the specimen; this inflated band decreases in height (from 2.1 cm to 0.9 cm) moving caudally. The dorsal and ventral surfaces of the shelf are smooth whereas it becomes rather irregular and wrinkled in the middle portion of the medial surface, where the maxilla contacts the palatine. Between the shelf and the paradental plates, the medial wall of the shelf folds to cover a row of dental foramina. The interdental plates (sensu Carrano & Sampson 2008) run all over the height of the maxillary main body as is visible in the broken rostral margin and by X-ray analysis (Fig. 3.2). An elliptical foramen (Fig. 4.2), here interpreted as a probable vascular channel, pierces the dorsal edge of NS 153/01, just behind the craniodorsal end of the maxillary-jugal contact. A thin lamina obscures this foramen in lateral view, but the inner edge is clearly visible in medial view as a gentle embayment in the medial profile of the shelf. The paradental plates are clearly fused to one another, forming a deep and wrinkled medial alveolar wall. The paradental plates are covered with obliquely oriented furrows that are oriented rostroventrally. Rostrally, the medial surface of the maxilla is hollow over the alveoli and prominent over the interalveolar areas, whereas it flattens caudally in correspondence of the caudalmost-preserved alveoli. The dorsoventral height of the alveolar portion of the maxilla narrows caudally as the size of each individual alveolus decreases. In ventral view, five complete and two incomplete rectangular alveoli are preserved, all of which lack teeth.

**Remarks**

These new specimens are consistent with other abelisaurid dinosaurs due to several features. Other abelisaurids also exhibit the longitudinal grooves on fully fused paradental plates, the rectangular alveoli and a sculptured lateral surface. Additionally, both NS 153/01 and 02 have neurovascular foramina bordering the ventral margin of the ventral ramus, a condition which has been considered synapomorphic for Abelisauroida (Wilson et al. 2003), and a rostrally inclined contact on the lateral surface of the maxilla for articulation with the jugal, regarded as a derived condition for abelisaurid dinosaurs (Sereno et al. 2004; Sereno & Brusatte 2008).
These differences are significant and likely represent the presence of two taxa, even though the specimens are not complete enough for a specific taxonomic assignment.

Comparison

NS 153/01 and 02, although incomplete, can be compared to some extent with other abelisaurid taxa. Similarities in age and locality between NS 153/02 and NS 153/01 are compared with UCPC 10, also from the Kem Kem beds of Morocco (Mahler 2005). UCPC 10 consists of a maxillary fragment referred to the Abelisauridae. It shares abelisaurid synapomorphies as sculptured surface of the ventral ramus, a dorsoventrally deep maxillary body with lateral and medial surfaces of subequal depth, deep fused parodental laminae, and subrectangular alveoli (Sereno et al. 2004; Carrano & Sampson 2008; Cau & Maganuco 2009). However, UCPC 10 lacks the crescent-shaped grooves of NS 153/01 and 02 and has faint shallow striations along the medial surface of the parodental plates. In this feature UCPC 10, NS 153/01 and 02 all differ from the strongly furrowed plates of the derived Campanian and Maastrichtian taxa (Carrano & Sampson 2008). The faint ornamentation on the parodental plates in UCPC 10, and other features (e.g., subrectangular alveoli) that according to Carrano & Sampson (2008) occur homoplastically in other tetanuran, led those Authors to question the abelisaurid affinities of UCPC 10.

Regardless, UCPC 10 shows further abelisaurid features (Sereno & Brusatte 2008; Cau & Maganuco 2009) including: a subvertical rostral end of the rostral ramus, a rostromedially directed premaxillary facet, and a row of foramina located in proximity to the alveolar border, and differs from carcharodontosaurids maxillae, that show a caudodorsally inclined rostral ramus, a rostrally directed premaxillary facet, and the row of ventral foramina located more dorsally (Brusatte & Sereno 2007). Therefore, following Cau & Maganuco (2009), we support Mahler’s (2005) interpretation and consider UCPC 10 an abelisaurid maxilla.

Although Carrano & Sampson (2008) consider the bone ornamentation as a non-distinctive character for abelisaurid dinosaurs, other authors pointed out a determinative and diagnostic role for this feature (Sereno et al. 2004; Sereno & Brusatte 2008). The development of both lateral striations and medial parodental furrows may be ontogenetically-related in the Abelisauridae (Cau & Maganuco 2009), as well as skull roof thickening and elaboration (e.g., horns or knobs) in this taxon (Carrano & Sampson 2008; and references therein), and sculpturing of the facial bones in carcharodontosaurids (Coria & Currie 2006). An alternative expla-
nation is that such a kind of ornamentation was not yet particularly developed in basal members of the group, as is the case in *Kryptops*, which does not show the marked ornamentation on the medial surface of the maxilla (Sereno & Brusatte 2008) visible in most derived abelisaurids. Sampson & Witmer (2007) pointed out that ‘in *Majungasaurus* and other abelisaurids, metaplastic ossification of the dermis and the resulting sculpturing may reflect a more general systemic propensity for the mineralization of soft tissues that extended to other systems’.

Summing up, the degree of ornamentation in fossilized bones may be affected by the ontogenetic stage of the individual and the phylogenetic affinities of the species. Brusatte & Sereno (2007), adopted the external sculpturing of maxillary bones as a distinctive feature of *Carcharodontosaurus*, and both *C. saharicus* from the Cenomanian (Kem Kem beds) and *C. iguudensis* (Echkar Formation, Cenomanian, Niger) have curved furrows and crests in the rostral most portion of the maxilla, and become straight and somewhat oriented rostroventrally in other sectors of the lateral surface of the caudoventral ramus. In any case, and differing in this from the abelisaurid specimens NS 153/01 and NS 153/02, the parodental plates show only a subtle vertical texture in *Carcharodontosaurus*. Although present also in carcharodontosaurs, it is apparent that rugosity of the external wall of the maxilla characterizes the abelisaurids in comparison to immediate outgroups such as the smooth-skulled *Ceratosaurus*.

In NS 153/01 and 02 the ornamentation is distinctive and considered therefore as an important tool for comparison and investigation of its ontogenetic and phylogenetic significance.

Much closer comparison can be made with UNPSJB–PV 247 (Lamanna et al. 2002) from the middle Cenomanian–Turonian Bajo Barreal Formation (Chubut, Argentina) and MNH IGU 1 (*Rugops primus* Sereno et al. 2004) from the Cenomanian of Niger. These taxa share with the new Moroccan specimens the curved grooves on the lateral surface and, at least with NS 153/02, the presence of a “posterior groove”. On the other hand, the orientation of ridges and furrows on the medial surface is in UNPSJB–PV 247 inverted respect to NS 153/01 and 02. The specimen of *Majungasaurus* FMNH PR 2100 (Sampson & Witmer 2007) from the Maastrichtian of Madagascar, shares with NS 153/01 and 02 the orientation of ridges and furrows on the lateral surface. The palatal shelf is corrugated in FMNH PR 2100 and in UCPC 10 as in NS 153/02, but is smooth in NS 153/01. NS 153/01 is too poorly preserved rostrally to evaluate the presence of an antorbital fossa, whereas the dorsal margin of NS 153/02 has a small area resembling the antorbital fossa of UNPSJB–PV 247. As previously mentioned, NS 153/01 shows a small dorsal crest at its rostral end, possibly as in the specimen MNN GAD 1-1 referred to *Kryptops* (Sereno & Brusatte 2008).

The presence of blood grooves on the teeth of NS 153/02 is remarkable, although this is not a consistent feature within Abelisauroidea. For instance, *Rugops*
lacks this character (Smith 2007) but other taxa such as *Kryptops* (even more basal than *Rugops*, according to Sereno & Brusatte 2008) and some derived forms such as *Majungasaurus* (Smith 2007) have blood grooves. Buscalioni et al. (1997) noticed that the “sulci-caudae complex” (i.e., blood grooves) should be considered convergent at least in Tetanurae, but the systematic importance of this character has not been completely assessed within the family Abelisauridae, and at present, there are no cladistic analyses merging this character.

Specimen NS 153/02 resembles *Rugops* based on the intense maxillary texture and the general pattern of pits and furrows with prevalence of crescent shaped grooves, reduction of the antorbital fossa (Sereno & Brusatte 2008). NS 153/02 differs from *R. primus* mainly by the presence of blood grooves and the absence of a projecting dorsal ridge on the margin of the antorbital fossa.

The paucity of features makes NS 153/01 hard to relate to other abelisaurid taxa and no close forms have been therefore identified below the family level.

A cladistic analysis was performed in order to test the phylogenetic affinities of the new material. We adopted the phylogenetic data matrix of Carrano & Sampson (2008), which represents one of the most comprehensive phylogenetic analyses of the theropod clade Ceratosaurs, including 151 characters and 21 taxa. Six more taxa were added, thereby increasing the information content of the Carrano & Sampson (2008) matrix. They are specimens NS 153/01 and NS 153/02 (present study), the alleged abelisaurid UCPC 10 (Mahler 2005), the recently described abelisaurids *Kryptops* (Sereno & Brusatte 2008) and *Skorpiovenator* (Canales et al. 2009), and the tetanuran *Carcharodontosaurus* (Stromer 1934; Lapparent 1960; Sereno et al. 1996). The outgroup was composed by *Herrerasaurus* and *Syntarsus*. No changes were made to the Carrano & Sampson (2008) characters, which are equally weighted and unordered, with the exception of character 141, representing a clear transformation series according to these authors. The data matrix (see Appendix) was processed under the heuristic search option of PAUP 4.0b10 (Swofford 2002), setting to 10,000 the maximum trees command. The analysis produced 10,000 most parsimonious trees of 243 steps, with Consistency Index (CI) = 0.6626 and Retention Index (RI) = 0.7807. The strict consensus tree is consistent with the topologies proposed by Carrano & Sampson (2008), although the introduction of several fragmentary taxa led to a less resolved topology. Most of the taxa added, including the isolated maxillae (NS 153/01, NS 153/02, and UCPC 10), *Kryptops*, and *Skorpiovenator* are nested within Abelisauridae, which is the...
sister taxon of Noasauridae within a monophyletic Abelisauroida (Fig. 6.1), whereas Car不在乎dorontoanodon is found to be a non-ceratosaurian theropod unrelated to the studied specimens.

Different phylogenetic affinities emerged between NS 153/01 and NS 153/02 in the majority rule consensus tree (Fig. 6.2), with the latter specimen resulting more derived and nested within the taxon Carnosaurinae: although overlooked in the cladogram, the differences may represent a differentiation in morphological terms.

Conclusions

The new specimens are nested inside the Abeliauridae but no further determination can be attempted on this material based on the phylogenetic analysis by Carrano & Sampson (2008), its resolution being lowered by the fact that few of the features highlighted in the description of the specimens are formalised for cladistic analysis in Ceratosauria. For example, NS 153/02 differs from other forms (e.g., Rugops) by the presence of blood grooves in the teeth, but the taxonomic significance of this latter feature needs further evaluation. Although differences between the specimens are not translated in taxonomic terms, they seem to suggest some degree of differentiation (e.g. intraspecific variability, age classing, or even different taxa) between NS 153/02, NS 153/01, and UCPC 10. This may imply that NS 153/01 was not a fully grown individual at time of death, as well as UCPC 10.

Similarly, Maganuco et al. (2008) found a high morphological variability in abelisaurid pedal unguals and phalanges from the Maaswaver Formation of Madagascar: this variability may be retracted to some dimorphism in Majungasaurus crenatissimus, the only named species of abelisaurid up to today, or to variability above the species level.

Further fieldworks in the Kem Kem beds are needed to clear palaeoecological issues, such as the outnumbering theropods respect to other dinosaurs groups, probably reflecting a high number of feeding specializations in an unusual ecosystem (Ibrahim 2010) rather than the purported oversampling and selective collection by local searches (McGowan & Dyke 2009).

Although the erection of a new species is avoided due to the paucity of the material, our new specimens and the maxilla described by Mahler (2005), along with the isolated fragmentary bones described by Russell (1996) and recently reviewed by other authors (Cau & Maganuco 2009, and references therein), confirm that at least one abelisaurid species was present in the Cenomanian ecosystems of the Kem Kem and enlarge the distribution of the Abelisauridae from Niger to Morocco.

Albeit the exact stratigraphic position of NS 153/01 and NS 153/02 is unknown, morphological differences highlighted on the specimens may even support the presence of more than one taxon in the area during the early Late Cretaceous.

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**Appendix**

Phylogenetic data matrix. Ingroup taxa are listed in alphabetical order. Newly added taxa (this paper) are marked by an asterisk. See Carrano & Sampson (2008) for the complete list of characters.

**OUTGROUP**

<table>
<thead>
<tr>
<th>Heterodontosaurus</th>
<th>Avetheropoda</th>
<th>Ornithischia</th>
<th>Saurischia</th>
<th>Theropoda</th>
<th>Abelisauridae</th>
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Syntaxis

INGROUP

Abelisaurus

Allosaurus

Ankylosaurus

Carnotaurus

Ceratodus

Dilophosaurus

Eotitanosaurus

Elaphrosaurus

Gnathosaurus

Ikeleleosaurus

Indosaurus

Krytops

Leptosuchus

Majungasaurus

Noasaurus

NS153/01

NS153/02

Rajasaurus

Rugops

Skeliosaurus

Spinosaurus

UCPC106

Velociraptor

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