Rivista Italiana di Paleontologia e Stratigrafia | volume 117 | no. 3 | pp. 463-472 | December 2011

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

SIMONE D'ORAZI PORCHETTI [1], UMBERTO NICOSIA[1],
ATTILIO BIAVA [2] & SIMONE MAGANUCO [3]

Received: *June 6, 2011; accepted*: *October 27, 2011*

Key words: Theropoda, Abelisauridae, maxillae, 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 north-western Africa at the base of the Late Cretaceous.

Institutional abbreviations

FMNH, Field Museum of Natural History, Chicago, Illinois, United States of America; **MNN**, Musée 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 Hammada 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 claystone (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

---

[1] Dipartimento di Scienze della Terra, "Sapienza" Università di Roma, P.le Aldo Moro, 5, 00185, Roma, Italy.
E-mail: simone.dorazi@uniroma1.it (Corresponding Author); umberto.nicosia@uniroma1.it
[2] Via della Giuliana 35, 00195 Roma, Italy. E-mail: att.biava@libero.it
[3] Sezione di Paleontologia dei Vertebrati, Museo di Storia Naturale di Milano, C.so Venezia 55, 20121, Milano, Italy.
E-mail: simonemaganuco@iol.it

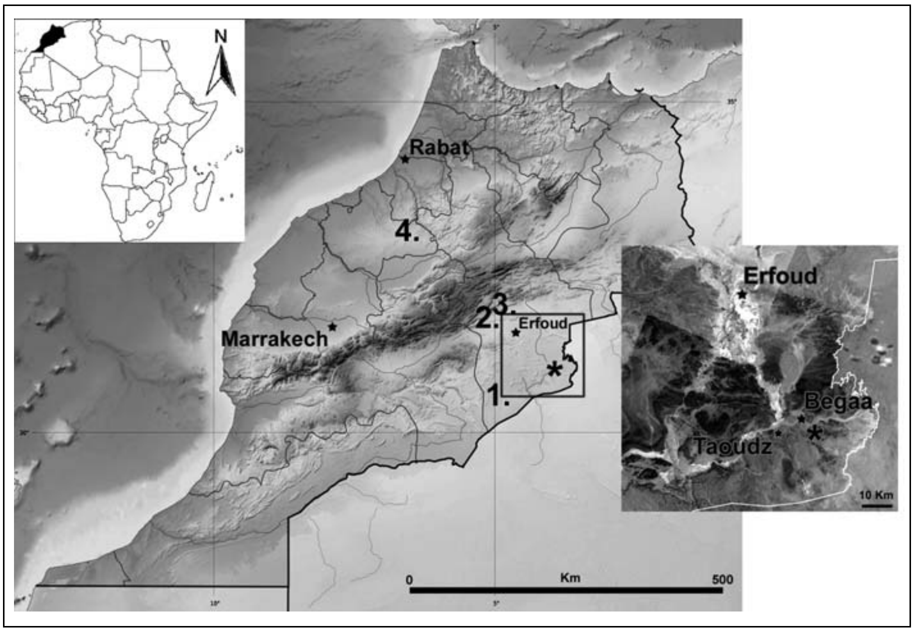


Fig. 1 - Geographic location of the new abelisaurid material along with previous abelisauroid findings from Morocco; *) MPUR NS 153/01 and MPUR NS 153/02, Cenomanian, Kem Kem beds, village of Begaa, east of Taouz (this work). 1) early Cenomanian, Kem Kem beds, Tafilalt region (Russell 1996). 2) Cenomanian, Kem Kem beds, Erfoud area, Tafilalt region, southern Morocco (Sereno et al. 2004; Mahler 2005). 3) Cenomanian, Erfoud area, Tafilalt region, southern Morocco (Novas et al. 2005). 4) Maastrichtian, Ouled Abdoun Basin, Oued Zem town, northwestern Morocco (Buffetaut et al. 2005). (Base map by Eric Gaba).

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
Abelisauroidea Bonaparte, 1991
Abelisauridae Bonaparte & Novas, 1985
Abelisauridae gen. et sp. indet.

Material: MPUR NS 153/02 (NS 153/02 hereafter) is reposited in the collections of the Museo di Paleontologia 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 Taouz, 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 palatine. The paradental 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

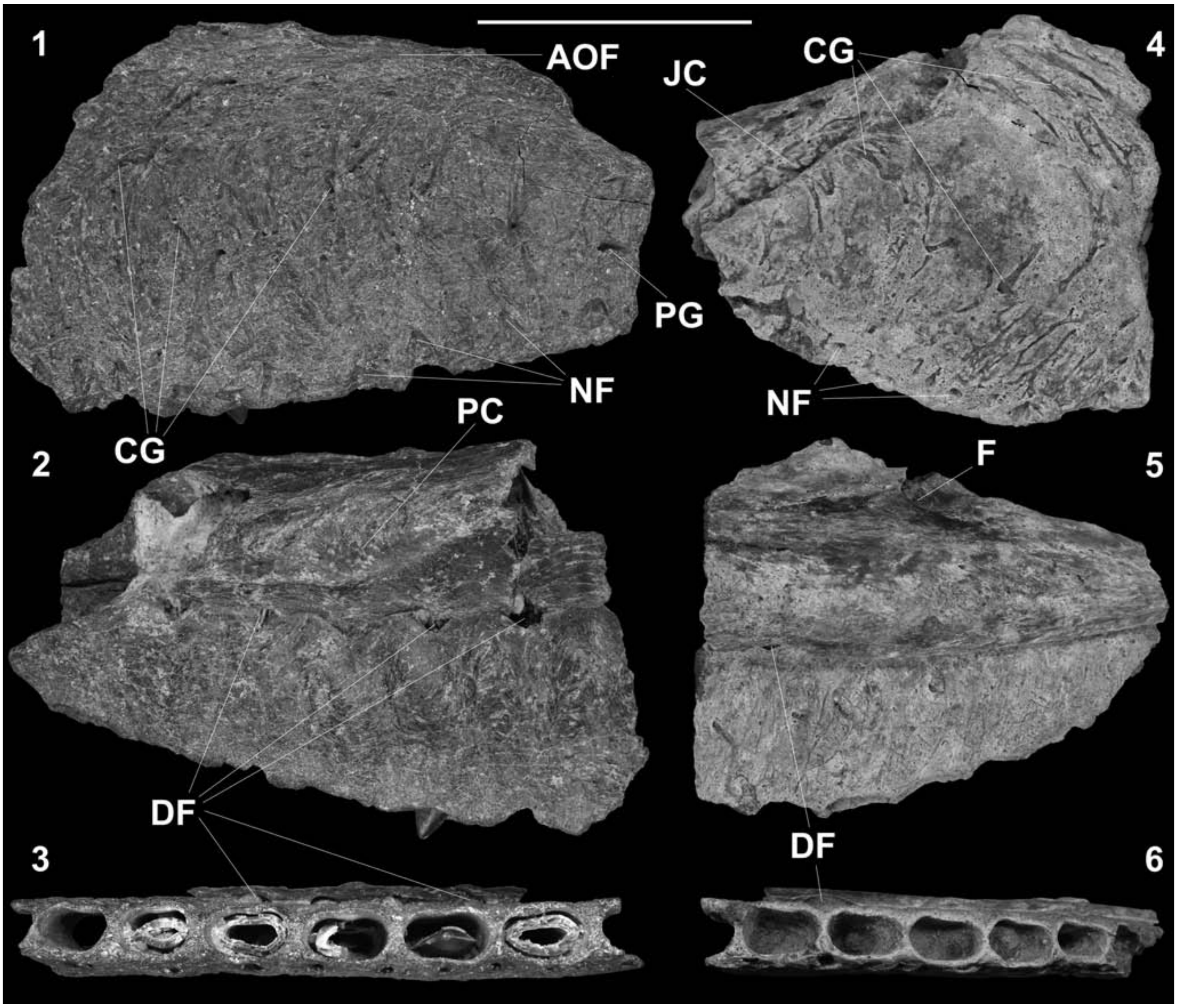


Fig. 2 - Abelisaurid maxillae, MPUR NS 153/02 (1, 2, 3) and MPUR NS 153/01 (4, 5, 6) in lateral (1, 4) medial (2, 5) and ventral view (3, 6). Abbreviations: AOF: antorbital fossa; CG: curved grooves; DF: dental foramina; F: foramen; JC: jugal contact; NF: neurovascular foramina; PC: palatine contact;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

Measurements (mm)	NS 153/01	NS 153/02
Maximum rostrocaudal length	82,5	108,3
Maximum dorsoventral depth	67,5	65
Maximum medio-lateral thickness shelf	17	19
Maximum medio-lateral thickness maxilla at the alveoli	11	11,2

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.

Theropoda Marsh, 1881
Ceratosauria Marsh, 1884
Abelisauroidea 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

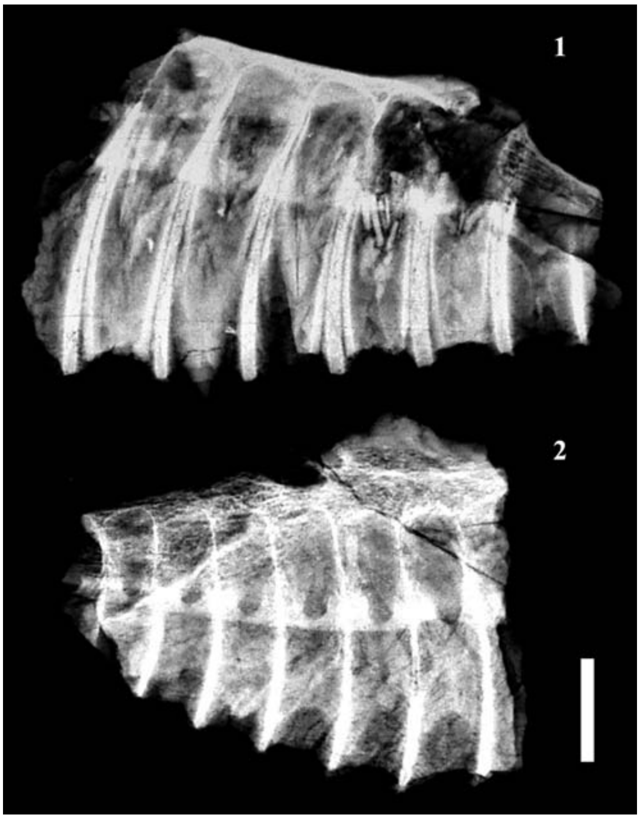


Fig. 3 - X-ray sheet of MPUR NS 153/02 1) and MPUR NS 153/01 2) in lateral view. Scale bar: 2 cm.

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 abelisauroid 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 Abelisauroidea (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).

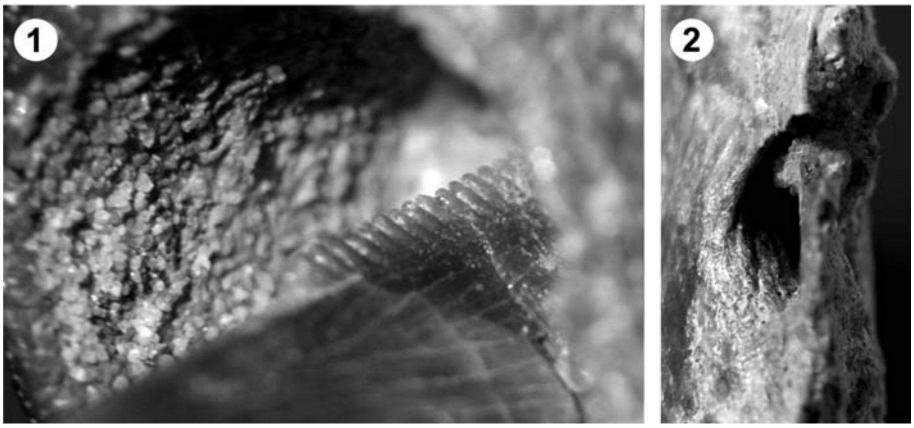


Fig. 4 - 1) MPUR NS 153/02, close-up of the serration on the *in situ* tooth. 2) close-up of the foramen on the dorsal margin of MPUR NS 153/01.

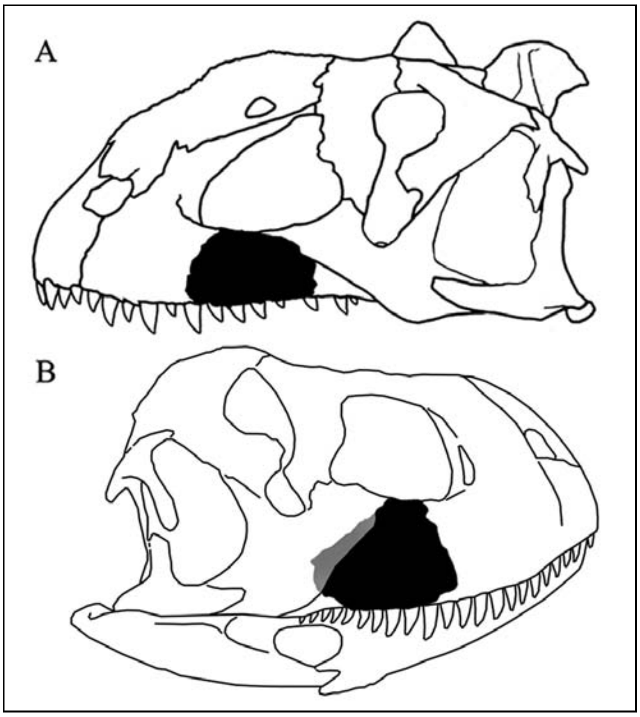


Fig. 5 - A) NS 153/02 and B) NS 153/01; position of the new material on the skull; base drawing modified from Sampson & Witmer (2007) and Canale et al. (2009).

Nonetheless, a comparison between the specimens, which represent more or less the same maxillary area (Fig 5.A, 5.B), has revealed clear differences. For instance, the ornamentation of NS 153/02 is more complex and dense relative to NS 153/01, with several anastomosed grooves, channels and small creases. Additionally, the "posterior groove" over the lateral surface in NS 153/02 is not present in NS 153/01. In medial view, the palatal shelf is corrugated, with distinct bulges over the alveoli and interalveolar depressions in NS 153/02 but not in NS 153/01, and in the latter the medial surface of the ventral alveolus does not extend as far ventrally as the lateral surface (the medial and lateral ventral surfaces of the alveoli are equally developed on NS 153/02). The height of the maxillae is proportionally different and NS 153/01 is slightly higher than NS 153/02 (4,75 for NS 153/01 versus 4,57 of NS 153/02, as deduced from the maxillary maximum height/length of the rostralmost alveolus ratio). Additionally, the angle between the ventral margin of the maxilla and the surface for the contact with the jugal is higher in NS 153/01 than in NS 153/02. In NS 153/02 the dorsal and the ventral edges are straight and subparallel, whereas in NS 153/01 the ventral margin is bent upward; this feature is probably exaggerated by preservational bias, the maxillary caudal end being slightly eroded or partially broken. As noticed above, the lateral surface of the antorbital fossa is little developed in NS 153/02 and is lacking in NS 153/01.

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.

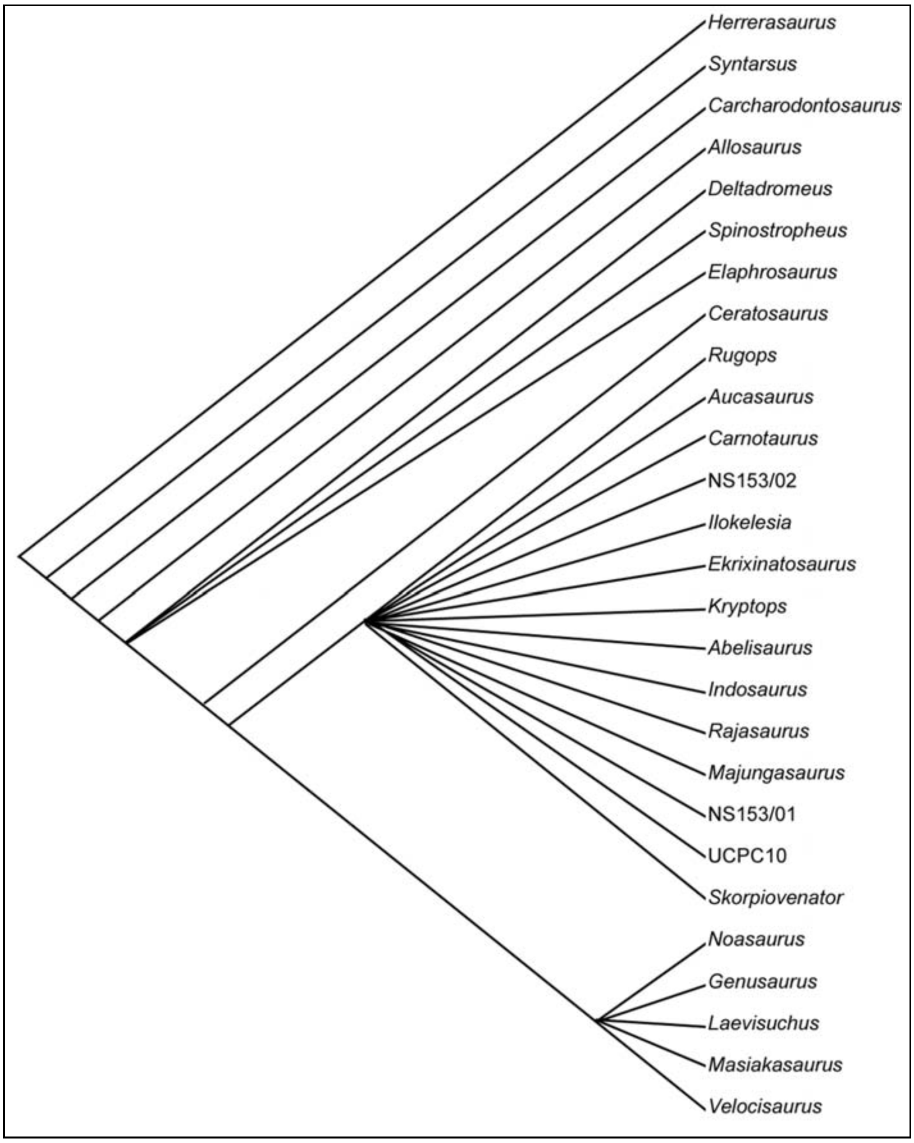
Comparison

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 paradental 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 paradental 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 paradental plates in UCPC 10, and other features (e.g., subrectangular alveoli) that according to Carrano & Sampson (2008) occur homoplastically in other tetanurans, 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 paradental 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. iguidensis* (Echkar Formation, Cenomanian, Niger) have curved furrows and crests in the rostralmost 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 paradental plates shows only a subtle vertical texture in *Carcharodontosaurus*. Although present also in carcharodontosaurids, 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 MNN 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 Abelisauridae. For instance, *Rugops*

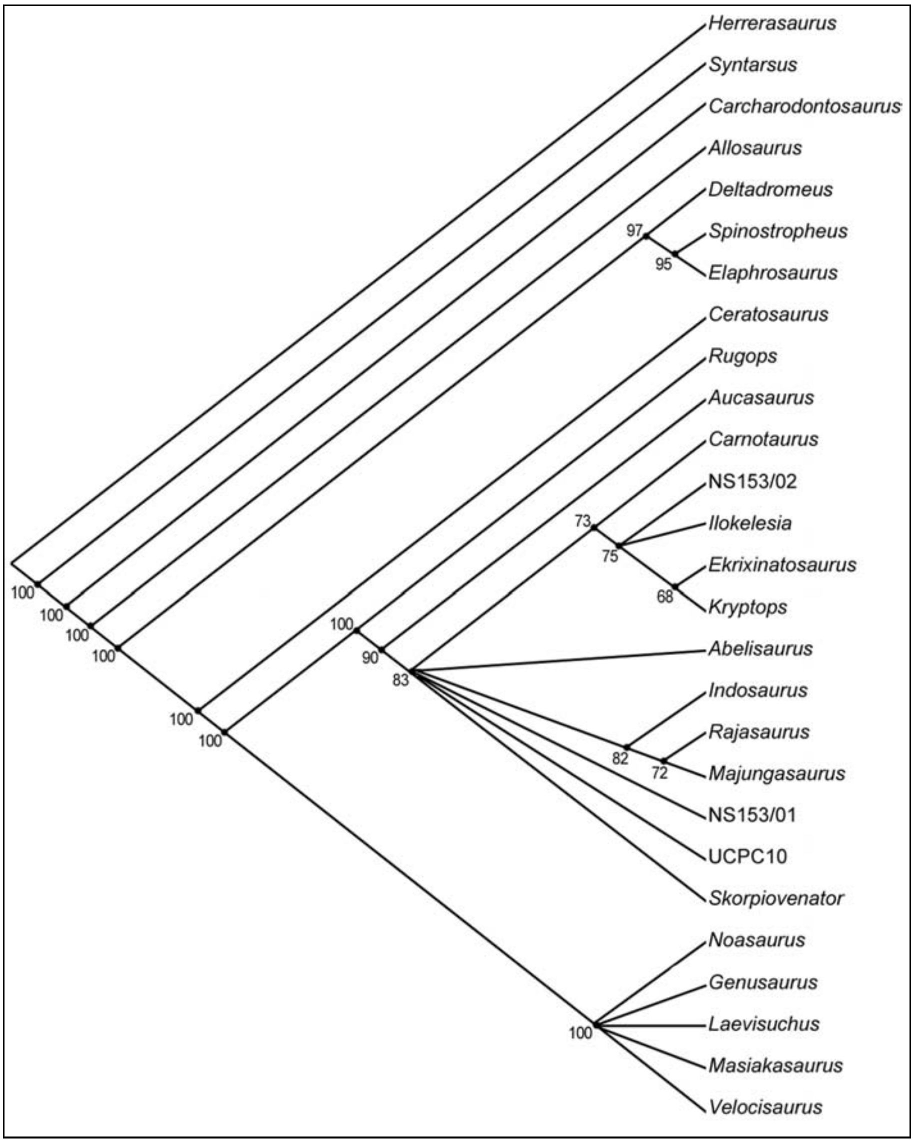


Fig. 6 - 1) Street consensus tree (previous page) of 10.000 most parsimonious trees (MPTs) generated by PAUP 4.0b10 (Swofford 2002) based on data matrix in Appendix. 2) Majority-rule consensus tree (this page) of 10.000 most parsimonious trees (MPTs) generated by PAUP 4.0b10 (Swofford 2002) based on data matrix in Appendix. Percentages at nodes are indicated only for groups appearing on more than 60% of the MPTs.

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 Ceratosauria, 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* (Canale 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 Abelisauroidea (Fig. 6.1), whereas *Carcharodontosaurus* 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 Carnotaurinae: although overlooked in the cladogram, the differences may represent a differentiation in morphological terms.

Conclusions

The new specimens are nested inside the Abelisauridae 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 Maevarano Formation of Madagascar: this variability may be reconducted 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 searchers (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.

Acknowledgements. We thank A. Cillari for in depth discussions of the material. We are deeply indebted to M. Carrano for his helpful advices on an early version of the manuscript. C. Dal Sasso also helped refine the manuscript. G. Pavia, from the "Umberto I Policlinico di Roma", is kindly acknowledged for providing the X-ray analysis. Thanks goes to F. Di Vincenzo for helping us with a preliminary cladistic analysis. Authors would also like to thank M. Auditore, who added his art for implementing visual quality of selected illustrations. M.A. Loewen and A. Cau are acknowledged for reviewing the manuscript and for helpful suggestions.

REFERENCES

Amiot R., Buffetaut E., Tong H., Boudad L. & Kabiri L. (2004) - Isolated theropod teeth from the Cenomanian of Morocco and their palaeobiogeographical significance. *Rev. Paléobiol.*, 9: 143-149.

Bonaparte J.F. (1991) - The Gondwanian theropod families Abelisauridae and Noasauridae. *Hist. Biol.*, 5:11-25.

Bonaparte J.F. & Novas F.E. (1985) - *Abelisaurus comahuensis*, n.g., n.sp., Carnosauria del Crétacico Tardio de Patagonia. *Ameghiniana*, 21(2-4): 259-265.

Brusatte S.L. & Sereno P.C. (2007) - A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and a revision of the genus. *J. Vert. Paleontol.*, 27(4): 902-916.

Buffetaut E., Escuillié F. & Pohl. B. (2005) - First theropod dinosaur from the Maastrichtian phosphates of Morocco. *Kaupia*, 14: 3-8.

Buscalioni A.D., Gasparini Z., Perez-Moreno B.P. & Sanz J.L. (1997) - Argentinean theropods: first morphological analysis on isolated teeth. DFG Online Series, 1st European Workshop on Vertebrate Palaeontology (Copenhagen, 1996).

Canale J.I., Scanferla C.A., Agnolin F.L. & Novas F.E. (2009) - New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. *Naturwissenschaften*, 96: 409-414.

Carrano M.T. & Sampson S.D. (2008) - The phylogeny of Ceratosauria (Dinosauria: Theropoda). *J. Syst. Paleontol.*, 6(2): 183-236.

Carrano M.T., Sampson S.D. & Forster C.A. (2002) - The osteology of *Masiakasaurus knopfleri*, a new abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. *J. Vert. Paleontol.,* 22: 510-534.

Cau A. & Maganuco S. (2009) - A new theropod dinosaur, represented by a single unusual caudal vertebra, from the Kem Kem Beds (Cretaceous) of Morocco. *Atti Soc. It. Sci. Nat. Mus. Civico St. Nat. Milano,* 150(II): 239-257.

Coria R.A. & Currie P.J. (2006) - A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas*, 28: 71-118.

Garassino A., Pasini G. & Dutheil D.B. (2006) - *Cretapenaeus berberus* n. gen., n. sp. (Crustacea, Decapoda, Penaeidae) from the Late Cretaceous (Cenomanian) of southeastern Morocco. *Atti Soc. It. Sci. Nat.,* 147(1): 3-17.

Ibrahim N. (2010) - A unique ancient ecosystem: the theropod dominated Late Cretaceous Kem Kem dinosaur assemblage of South East Morocco. *Soc. Vert. Paleontol., Abstr. Pap.,* 109A.

Lamanna M.C., Martinez R.D. & Smith J.B. (2002) - A definitive abelisaurid theropod dinosaur from the early Late Cretaceous of Patagonia. *J. Vert. Paleontol.,* 22: 58-69.

Lapparent A. F. de (1960) - Les dinosauriens du “continental intercalaire” du Sahara central. *Mém. Soc. Géol. France,* 88A.

Maganuco S., Cau A. & Pasini G. (2008) - New information on the abelisaurid pedal elements from the Late Cretaceous of NW Madagascar (Mahajanga Basin). *Atti Soc. it. Sci. Nat. Mus. Civico St. Nat. Milano,* 149(II): 239-252.

Mahler L. (2005) - Record of Abelisauridae (Dinosauria: Theropoda) from the Cenomanian of Morocco. *J. Vert. Paleontol.,* 25: 236-239.

Marsh O.C. (1881) - Classification of the Dinosauria. *Am. J. Sci.,* 23: 81-86.

Marsh O.C. (1884) - Principal characters of American Jurassic dinosaurs. Part VIII. The order Theropoda. *Am. J. Sci., ser.* 327:329-340.

McGowan A.J. & Dyke G.J. (2009) - A surfeit of theropods in the Moroccan Late Cretaceous? Comparing diversity estimates from field data and fossil shops. *Geology,* 37(9): 843-846.

Novas F.E. (1997) - Abelisauridae, p. 1-2. In: Currie P. J. & Padian K. (Eds) - Encyclopedia of Dinosaurs. Academic Press, San Diego, California.

Novas F.E., Agnolin F.L. & Bandyopadhyay S. (2004) - Cretaceous theropods from India: a review of specimens described by Huene and Matley (1933). *Rev. Mus. Argentino Cie. Nat., nuevo serie,* 6: 67-103.

Novas F.E., Dalla Vecchia F. & Pais D.F. (2005) - Theropod pedal unguals from the Late Cretaceous (Cenomanian) of Morocco, Africa. *Rev. Mus. Argentino Cie. Nat., nuevo serie,* 7: 167-175.

Russell D.A. (1996) - Isolated dinosaur bone from the middle Cretaceous of Tafilalt, Morocco. *Bull. Mus. Nat. Hist. Nat., Paris, 4^{e} series, section C,* 18: 349-402.

Sampson S.D. & Witmer L.M. (2007) - Craniofacial anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Soc.Vert. Paleontol. Mem. 8* (*J. Vert. Paleontol.,* 27 *Suppl.* 2): 32-102.

Sampson S.D., Witmer L.M., Forster C.A., Krause D.W., O’Connor P.M., Dodson P. & Ravoavy F. (1998) - Predatory dinosaur remains from Madagascar: implication for the Cretaceous biogeography of Gondwana. *Science,* 280: 1048-1051.

Sereno P.C. & Brusatte S.L. (2008) - Basal abelisaurid and carcharodontosaurid theropods from the Lower Cretaceous Elrhaz Formation of Niger. *Acta Palaeontol. Pol.,* 53(1): 15-46.

Sereno P.C., Conrad J. & Wilson J.A. (2002) - Abelisaurid theropods from Africa: Phylogenetic and biogeographic implications. *J. Vert. Paleontol.,* 22(3): 106A.

Sereno P.C., Wilson J.A. & Conrad J.L. (2004) - New dinosaurs link southern landmasses in the mid-Cretaceous. *Proc. Roy. Soc. London B,* 271: 1325-1330.

Sereno P.C., Dutheil D., Iarochene M., Larsson H., Lyon G., Magwene P., Sidor C., Varricchio D. & Wilson J. (1996) - Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science,* 272: 986-991.

Smith J.B. (2007) - Dental morphology and variation in *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Soc. Vert. Paleontol. Mem. 8* (*J. Vert. Paleontol.,* 27 *Supp.* 2): 103-126.

Smith J.B. & Dodson P. (2003) - A proposal for standard terminology of anatomical notation and orientation in fossil vertebrates dentitions. *J. Vert. Paleontol.,* 23(1): 1-12.

Smith J.B., Vann D.R. & Dodson P. (2005) - Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. *Anatomical Record A,* 285: 699-736.

Stromer E. (1934) - Ergebnisse der Forschungsreisen Prof E. Stromer in den Wüsten Ägyptens. II. Wirbeltierreste der Baharje-Stufe (unterstes Cenoman). 13. Dinosauria von E. Stromer. *Abh. Bayer. Ak. Wiss., them. Naturwissen. Abt., Neue Folge* 22: 1-79.

Swofford D.L. (2002) - PAUP*: phylogenetic analysis using parsimony (*and other methods). Version 4.0b10. Sinauer Associates, Sunderland, MA.

Wilson J.A., Sereno P.C., Srivastava S., Bhatt D.K., Khosla A. & Sahni A. (2003) - A new abelisaurid (Dinosauria: Theropoda) from the Lameta Formation (Cretaceous, Maastrichtian) of India. *Contr. Mus. Paleontol., Univ. Michigan,* 31:1-42.

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

Herrerasaurus

00000 00001 00000 00000 00000 00000 00000 00?00 00000 00000 00000 00100 00000 00000 00000 00000 00000 00000 01000 00000 00001 00000 00000 00000 00000 00000 00000 00000 00000 00000 0

Syntarsus
00000 10010 00000 00000 00000 00000 00000 00000 00000 00100 00000
01000 00000 00000 00100 00100 00001 11010 00100 01000 01000 01000
00000 11011 00000 00000 10110 00000 00100 00100 0

INGROUP

Abelisaurus
11111 21?01 ?1011 11021 11110 1011? 111?1 1?111 ?10?? ?1001 1??1?
??1?? 1???? ???10 1???? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ?

Allosaurus
00000 10000 00000 00001 00000 00000 00000 00000 00111 01100 01101
01001 10000 01000 00111 11000 10010 00000 01100 00000 00001 00000
01000 00000 10110 01000 01000 12001 21011 00000 1

Aucasaurus
11?11 21?01 1??1? ?1?2? ???0? ????1 10?1? ????? ????? ????? ????? ?????
????? ??0?? ????? ???1? ????? ?1??? ??(12)?? ???11 1???0 10111 11111
?1111 ?111? ??1?0 ?1?11 1?1?1 111?? 00111 1

*Carcharodontosaurus**
110?? 10000 00001 ?1001 00011 10000 01000 00??? ?1??? 01100 ?????
????? ???0? ??0?0 ?0??? ????? 0???? 00??? ????? ????? ????? ????? ?????
0???? ???0? ????? ?1??0 ????? ????? ????? ?

Carnotaurus
11111 21?01 10110 11121 11111 11111 10111 11110 111?? ?1001 11?11
1?111 11111 11010 11211 11210 11112 01011 11211 11111 10110 10111
11111 11111 1111? 11110 ?111? ?11?? ??1?? ?0??? ?

Ceratosaurus
00001 21000 00010 00000 01000 00000 00000 00000 ?11?1 10000 11101
11001 11100 11000 11211 112?0 10012 00011 01210 ?1?00 01000 00101
1111? 111?0 10?11 11110 1(01)111 11101 11110 0010? ?

Deltadromeus
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ???0? ????? 10101 1???? ?????
????? ??1?0 ?1100 121?1 11?11 0110? ?

Ekrixinatosaurus
1??1? 0??00 1???? ?100? 1?11? ???1? ????? ?1??? ?1??? ????? ????? ?????
????1 ??0?0 ?1??? ??21? 0011? 01??? ?1(12)?? ?0?0? 10??? ????? ?????
1??11 1111? ????0 ?11?1 1???1 ??1?0 0???? ?

Elaphrosaurus
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ?1(12)?? ??100 1000? 11111 00210 11?00 ?1??0 11101 11100
11110 10110 ?0100 ?10?0 121?1 101?? 011?? ?

Genusaurus
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ?0(12)?? ????? ????? ????? ?????
1?1?1 1?1?? ????0 ?12?1 ?11?? ????? ????? ?

Ilokelesia
?1??? ????? ????? ????? ???11 1101? ????? ????? ????1 ????? ????? ?????
????? ????? ?1??? ??210 10112 010?1 11??? ????? 1011? ????? ?????
????? ????? ????? ????? ????? ????? ???11 ?

Indosaurus
????? ????? ????1 11111 111?? ????? ????? ????? ?11?? ???1? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ?

*Kryptops**
1???? 20000 ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ???10 1???? ????? ????? ????? ???11 ?11?? ????? ????? ????? 10001
1?111 ?0?1? ????? ????? ????? ????? ?

Laevisuchus
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ?1??? ???11 ?001? 010?? ?0??? ????? ?0??? ????? ????? ?????
????? ????? ????? ????? ????? ????? ?

Majungatholus
11111 21001 11011 11111 11111 10011 11011 11111 11111 11011 11111
12111 11111 11010 11211 11210 10112 01011 11(12)11 11111 00110
10111 111?1 ?1111 111?1 1??11 ?1??1 11111 11111 00111 ?

Masiakasaurus
01?1? 01110 ????0 00000 ???00 1000? 001?? ????? ???11 ?1001 ?????
??11? 11100 11101 11211 11211 10011 010?? ?0(12)01 11101 001?0
1?11? 1?1?0 111?? ???11 11?10 11211 11111 11111 11111 ?

Noasaurus
0??1? 01110 ????? ????? ????? ????? ????? ????? 1???? ????? ????? ?????
????? ??101 11(12)?? ???11 ?1011 0?0?? ????? ????? ?010? ????? ?????
????? ????? ????0 ????? ????? ????? 1???? ?

NS153/01*
1???? ????1 ????? ????? ????? ????? ???1? ????? ????? ????? ????? ?????
????? ???10 1???? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ?

NS153/02*
1???? ????0 ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ???10 1???? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ?

Rajasaurus
11??? ????? ????1 ?1111 111?? ????? ???1? ????? ?1111 ??01? ?????
?211? ???10 11010 112?? ??21? 1???? 0?011 11210 ?11?? ?0??? ?????
????? 0?0?? 1???1 ???11 ?1111 111?1 ????? 00??? ?

Rugops
11111 21001 11110 10001 110?? ????1 11111 ????? ????? ????? ?????
????? ????? ?1010 1???? ????? ????? ????? ????? ????? ?0??? ????? ?????
????? ????? ????? ????? ????? ????? ????? ?

*Skorpiovenator**
11?11 01?01 1?0?? ??121 ???11 11000 ?1011 1?111 1???? ????? ?????
??1?1 ????0 1?0?? ????? ????0 ?0??2 ?1??? ????? ????? 1??10 10011 ?????
???00 1?1?? ????1 ????1 ????? 1???0 0???? ?

Spinostropheus
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ?12?? ??100 10000 10111 102?? 111?? ?000? ???01 ?????
????? ???1? ????0 ????? 1???? ????? ????? ?

UCPC10*
1???? 2?0?1 ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ???10 1???? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ?

Velocisaurus
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????0 ????? 1???1 1111? 111?? ?