

RECORD OF ABELISAUROIDAE (DINOSAURIA: THEROPODA) FROM THE CENOMANIAN OF MOROCCO

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Abelisauroid theropods have¹ been used as evidence of land connections between several southern continents and Europe during the Late Cretaceous. Abelisauroids (abelisaurids and noasaurids) have been described from South America (Bonaparte and Powell, 1980; Bonaparte and Novas, 1985; Martínez et al., 1986; Bonaparte et al., 1990; Coria et al., 2002; Lamanna et al., 2002), Madagascar (Krause and Hartman, 1996; Sampson et al., 1996, 1998, 2000, 2001; Carrano et al., 2002), India (Chatterjee, 1978; Wilson et al., 2003), and southern Europe (Buffetaut et al., 1988; Le Loeuff and Buffetaut, 1991; Accarie et al., 1995). Their presence in Africa has been in dispute.

Russell (1996) referred dentary fragments from the Kem Kem beds of Morocco (Cenomanian; Sereno et al., 1996) to the Abelisauridae based on small size and the subrectangular shape of the alveoli. This assignment, however, has been questioned (Sampson et al., 1998; Carrano et al., 2002). Smith et al. (2001) have speculated that various isolated teeth from the Bahariya Formation (Cenomanian) of Egypt are abelisaurid, but this also remains a tentative assignment. Recently, Sereno et al. (2002, 2004) have described a noasaurid and an abelisaurid from the Aptian-Albian of Niger, and have reinterpreted *Deltadromeus agilis*, of the Cenomanian of Morocco (upper Kem Kem), as a possible basal noasaurid. A new maxilla, described below, establishes without doubt the presence of abelisaurids on the northwestern shores of Africa during the Cenomanian.

Institutional Abbreviations—FMNH, Field Museum of Natural History, Chicago; UCPC, University of Chicago Paleontological Collection, Chicago; UNPSJB, Universidad Nacional de Patagonia “San Juan Bosco,” Comodoro Rivadavia, Argentina.

SYSTEMATIC PALEONTOLOGY

THEROPODA Marsh, 1881

ABELISAUROIDEA Bonaparte, 1991

ABELISAUROIDEA Bonaparte, 1991

ABELISAUROIDEA Bonaparte and Novas, 1985

gen. et sp. indet.

Referred Specimen—UCPC 10, a partial right theropod maxilla.

Locality and Stratigraphic Horizon—Specimen UCPC 10 was collected by locals in the Kem Kem beds, probably near Erfoud in western Morocco. The Kem Kem beds record alternating delta and nearshore marine environments and consist of channel deposits of red sandstone (Russell, 1996; Sereno et al., 1996) identical to the matrix that encrusted the specimen.

Geological Age—Cenomanian, based on teeth recording the presence of nine elasmobranchs in this formation, five of which are known exclusively from the Cenomanian (Sereno et al., 1996).

Description—The specimen, consisting of the anterior half of the right maxilla, is missing posterior and ascending rami, as well as the antero-medial process (Figs. 1, 2). The anteromedially beveled articular surface for the premaxilla is present. The preserved portion of the ventral margin is complete, and includes the first six alveoli, all with erupting teeth. Dorsally, the surface is nearly entirely broken, revealing the interior of the promaxillary fossa (promaxillary recess of Whitmer, 1997), an en-

closed pneumatic cavity that extends anteriorly from the anteroventral corner of the antorbital fenestra. The broken posterior margin has exposed an alveolus in cross-section, which occupies more than half of the depth of the ramus. Both the lamina medialis and lamina lateralis are preserved in the posterodorsal corner of this specimen. As is typical of abelisaurids, these laminae are of nearly equal height and show no external infolding or depression (Figs. 1A, 2A). In non-abelisaurid theropods, the lamina medialis is generally significantly taller than the lamina lateralis, and a marked depression, the antorbital fossa, is present on the dorsal margin of the lamina lateralis. In UCPC 10, the smooth dorsal edge of the lamina lateralis indicates that the maxilla lacked a maxillary fenestra. The maxilla is very dorsoventrally deep, as its vertical height at the anterior corner of the antorbital fenestra is approximately 75% of the horizontal length of the first six alveoli.

The lateral surface of the maxilla is rugose, with large numbers of pits as well as adjacent grooves and broader channels with rounded edges (Figs. 1A, 2A). These grooves and channels are not uniform in direction but generally trend dorsoventrally. The pits open into foramina that pass into the body of the maxilla. Despite the extensive pitting, there is no canal along the floor of the antorbital rim for vascular supply. The sutural contact surface with the premaxilla is near vertical in orientation, although laterally, a flange of the lateral lamina extends forward to overlap the premaxilla. The ventral edge of the maxilla is gently convex under the first and second alveoli. The position of each alveolus is marked by a slight embayment in the lateral wall of the alveolus. Distinctive vascular pits are present on the ventral margin between each pair of alveoli.

Medially, the thicker dorsal portion of the maxilla overhangs the thinner alveolar housing, creating a horizontal palatal shelf (Figs. 1B, 2B). The medial surface below and above the palatal shelf is marked by faint, shallow striations. Below the shelf, the laminar surface is characterized by a series of medial convexities that overlie the crypts for replacement teeth. They are more pronounced anteriorly. Although this surface exhibits convexities, there is no separation of interdental plates; they are fused seamlessly. Because the medial lamina does not extend as far ventrally as the lateral lamina, more of the tooth sockets are visible in medial aspect. As with the lateral lamina, the medial lamina is gently ventrally concave over each alveolus. The palatal shelf itself is largely broken, and has been reconstructed. As with the lower surface, this shelf shows an undulating alternation of convexities and concavities that correspond with tooth replacement series. The palatal shelf is higher anteriorly, sloping ventrally as it extends posteriorly. In the anterodorsal corner of this specimen, the base of the anteromedial process is present. The edge of a shallow depression or fossa is apparent immediately posterior to this process.

In anterior view, the maxilla is slightly laterally convex just above the tooth row (Fig. 1D). The remainder of the body of the maxilla is flat. Several small foramina are visible on the anterior surface of the maxilla where it joined the premaxilla.

In occlusal aspect (Fig. 1C), tooth sockets 1 and 3 house fully developed but unerupted replacement teeth, sockets 4 and 5 contain newly erupting teeth, socket 6 has a fully erupted tooth, and socket 2 holds a broken crown. The sockets themselves are subrectangular or reniform, with a slight inward curving of the medial wall of the socket. These sockets are wider anteriorly than posteriorly. In addition, they become longer posteriorly: socket 1 is 150 mm, and socket 6 is 180 mm long. The ventral halves of the tooth crowns are symmetric in lateral view; only fully erupted tooth number 6 is slightly recurved posteriorly. Denticles, spaced at 2.3–3.0 per millimeter, adorn the entire anterior and posterior carinae of each tooth, fading only at the very tip.

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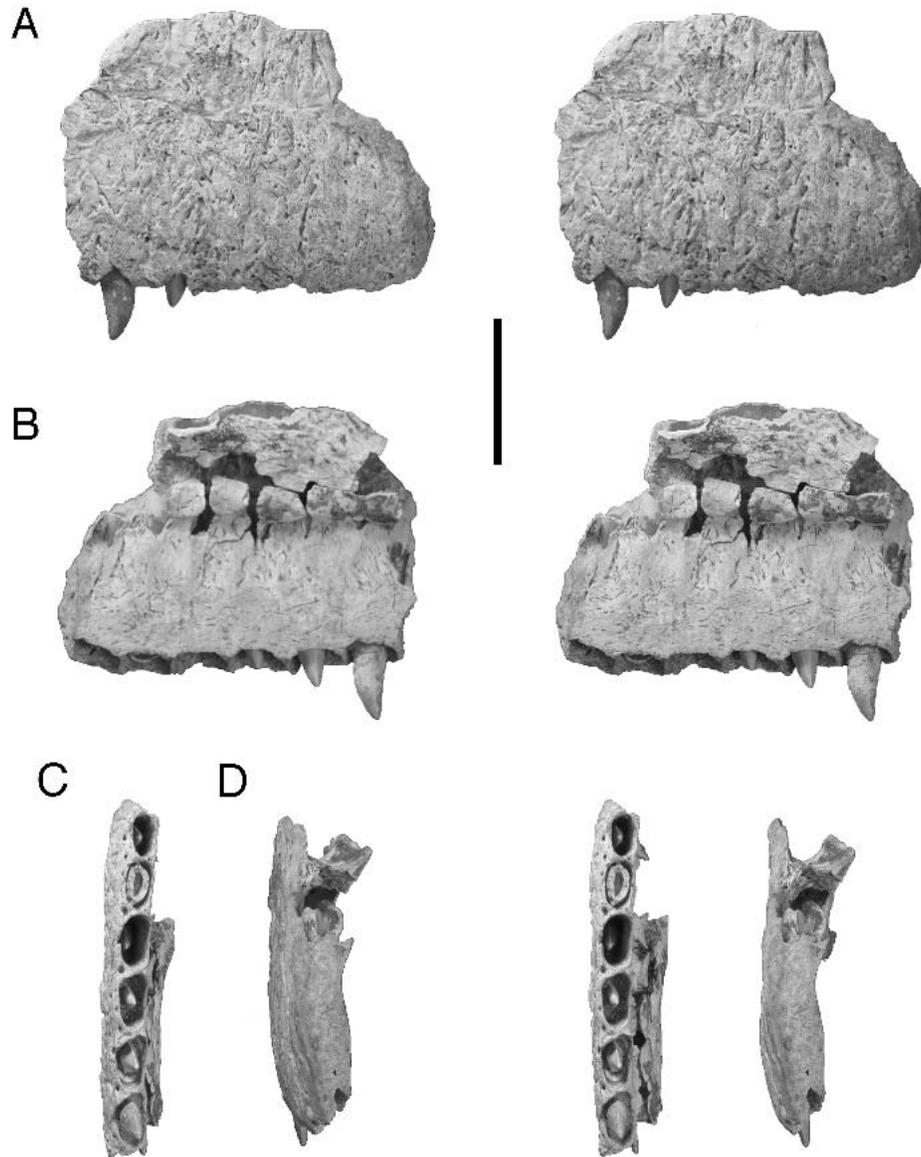


FIGURE 1. Specimen UCPC 10, stereoscopic pairs. **A**, lateral view. **B**, medial view. **C**, occlusal view. **D**, anterior view. Scale bar equals 5 cm.

DISCUSSION

Comparisons

UCPC 10 can be readily diagnosed as a theropod maxilla based on its pneumatized antorbital rim, and its teeth, which are serrated, labiolingually compressed, and slightly recurved. UCPC 10 exhibits several characters that suggest it as a primitive member of the Abelisauridae, a basal group of Cretaceous theropods with a Gondwanan distribution. These consist of a dorsoventrally deep maxillary body, a near vertical articular edge for the premaxilla, pneumaticity limited to an uninflated promaxillary fossa, fully fused interdental plates, rather small teeth with little or no recurvature, subrectangular alveoli in ventral view, and pitted sculpturing of the lateral surface (Bonaparte and Novas, 1985; Holtz, 1998; Sampson et al., 1998; Lamanna et al., 2002; Sereno et al., 2004). In these respects, UCPC 10 is similar to the known abelisaurids *Rugops primus*, UNPSJB-PV247 (an abelisaurid maxilla from Argentina), *Abelisaurus comahuensis*, *Rajasaurus narmadensis*, *Majungatholus atopus*, and *Carnotaurus sastrei*. Abelisaurid skull bones from the latest Cretaceous are thicker and more ornamented in the more derived taxa, such as *Majungatholus* (FMNH PR2100) and *Carnotaurus* (FMNH PR1950). The lighter build and unornamented medial aspects of UCPC 10 suggest it to be more primitive.

The Moroccan maxilla is particularly comparable to that of the Nigerian *Rugops primus* in tooth morphology, alveolar shape, rugose lateral texture, the straight border with the premaxilla, and the position of the palatal shelf. The two maxillae differ in that the Moroccan specimen shows more pitting on the lateral surface, while the *Rugops* maxilla has more pronounced lateral channels and grooves. Also, the lower medial surface of the Moroccan maxilla shows a series of convexities and is only lightly striated; the medial surface of the Nigerian maxilla is flatter and more heavily striated. In addition, the lamina medialis is slightly taller than the lamina lateralis in *Rugops*, whereas these walls are approximately the same height in the Moroccan maxilla. Because many currently known abelisaurids exhibit subtle differences in maxillary ornamentation (e.g., *Majungatholus atopus*, *Carnotaurus sastrei*, and *Rajasaurus narmadensis*), these differences may indicate that the two maxillae represent distinct species, as is the case with Cenomanian carcharodontosaurid material from Morocco and Niger (Sereno, pers. comm.).

Like *Rugops* (Sereno et al., 2004), UCPC 10 is close in form to Argentine maxilla UNPSJB-PV247, especially in its degree of antorbital pneumatization, and its subvertical premaxillary articulation, palatal shelf, and rugose lateral sculpturing. UCPC 10 differs primarily in its slightly smaller size and smooth, undulating medial surface.

The Moroccan maxilla shares some similarities with carcharodonto-

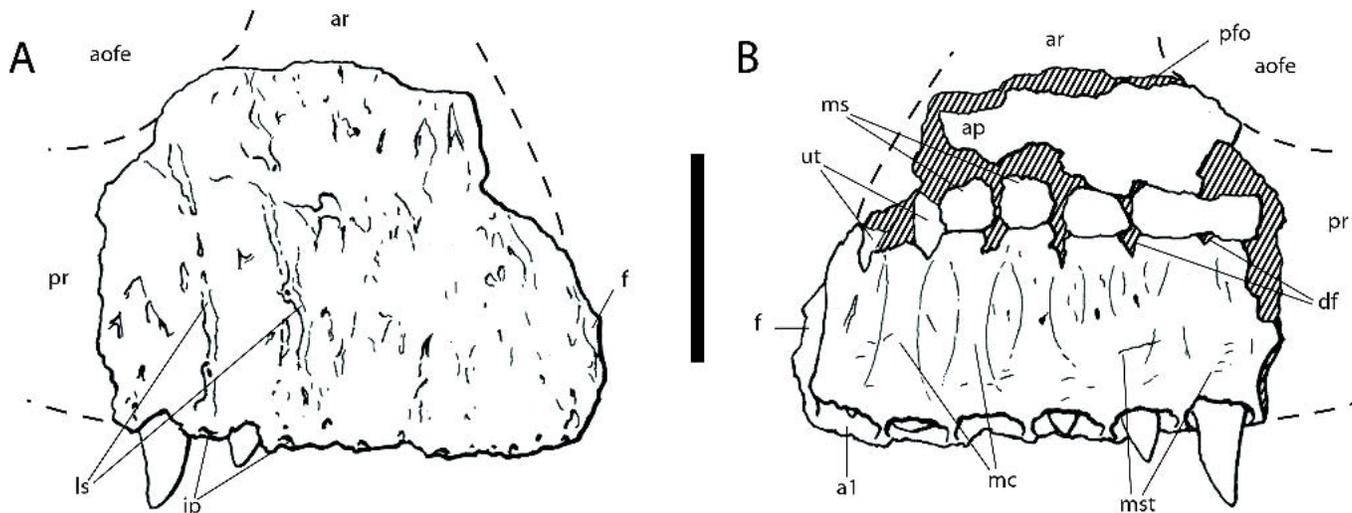


FIGURE 2. Line drawing of UCPC 10. **A**, lateral view. **B**, medial view. **Abbreviations:** **al**, alveolus 1; **aofe**, antorbital fenestra; **ap**, anteromedial process; **ar**, ascending ramus (broken); **df**, dental foramina; **f**, flange (overlaps premaxilla); **ip**, interalveolar pits; **ls**, lateral sculpturing; **mc**, medial convexities; **ms**, medial shelf (broken); **mst**, medial striations; **pfo**, promaxillary fossa; **pr**, posterior ramus (broken); **ut**, unruptured teeth. Scale bar equals 5 cm.

saurids, such as the rugose lateral surface and steep maxillary - premaxillary suture. Also, the degree of curvature of the medial wall in UCPC 10 is similar to that present in *Carcharodontosaurus saharicus*. However, in carcharodontosaurids, the maxillae are many times larger than that of UCPC 10, the anterior surface of the maxilla (maxillary - premaxillary suture as well as ascending process) is inclined to a greater degree, the lamina medialis is broadly exposed in lateral view, and the antorbital fossa is well developed. Also, the external rugosities on carcharodontosaurid maxillae are not as dense as those on UCPC 10, and carcharodontosaurid teeth are characterized by broader crowns with marginal wrinkles.

Biogeographic Implications—One hypothesis of Gondwanan dinosaur biogeography argues that Africa had completely separated from the rest of Gondwana prior to the abelisauroid radiation, and that abelisauroids spread from South America to India and Madagascar via circumferential land-bridge connections (Sampson et al., 1998, 2000; Krause et al., 1999; and Carrano et al., 2002). This hypothesis was previously supported by the late (Campanian-Maastrichtian) temporal range of abelisauroids (except the putative abelisauroid *Genusaurus sisteronis* from the Albian of France, which is considered indefinite by Carrano et al., 2002, and is ignored by other proponents of this hypothesis) and by the lack of abelisauroids in Africa.

UCPC 10, in combination with recent fossil discoveries of similar age in Africa and South America, establishes the presence of abelisauroids on Africa by the Cenomanian, weakening this hypothesis in favor of one that postulates sustained faunal contact between Africa and South America into the Late Cretaceous (Serenio et al., 2004). A disputed Moroccan abelisauroid dentary fragment (Russell, 1996) and a Patagonian abelisauroid maxilla (Lamanna et al., 2002) from the Cenomanian—Turonian (concurrent with geologic separation of Africa from Gondwana) cast doubt that Africa had wandered into isolation before the abelisauroid radiation. Discovery of a noosaurid and an abelisauroid from the Aptian-Albian of Niger (Serenio et al., 2004), and the presence of UCPC 10 in Cenomanian Morocco confirm an earlier abelisauroid radiation that included the African continent. The similarity of UCPC 10 to Argentine maxilla UNPSJB-PV247 and the maxilla of *Rugops primus* suggests very recent common ancestry of these three taxa, suggesting the possibility of faunal interchange between Africa and South America as late as the Aptian-Cenomanian.

Diversity—The Kem Kem beds have produced a disproportionately large number of large carnivores, whereas herbivores of any size remain extremely rare (Russell, 1996; Serenio et al., 1996). The confirmation of an abelisauroid in Morocco brings the total number of large carnivores to four, also including *Spinosaurus maroccanus*, *Carcharodontosaurus saharicus*, and *Deltadromeus agilis* (I consider *Stigilmassaurus brevicollis* material to be referable to *Spinosaurus maroccanus*).

Russell (1996) attributes the high abundance of theropods to deltaic piscivory. This hypothesis assumes that there was minimal transport of remains from upstream environments, which is difficult to maintain for a deltaic facies. Also, only one group of Kem Kem theropods, the spinosaurids, is adapted to catch and eat fish (reviewed in Charig and Milner, 1997; Serenio et al., 1998). While spinosaurid fossils are common in the Kem Kem, the confirmed presence of an abelisauroid adds another large predator to the fauna, making it even more enigmatic.

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