

A LARGE ABELISAUROID THEROPOD DINOSAUR FROM THE EARLY CRETACEOUS OF LIBYA

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ABSTRACT—Despite increasingly intensive paleontological sampling, Cretaceous terrestrial vertebrates from continental Africa remain relatively poorly known, frustrating efforts to characterize paleoecosystems in the region, as well as the paleobiogeography of the southern continents during this interval. Here we describe the partial skeleton of a large-bodied theropod dinosaur from the Early Cretaceous (early Aptian, ~125–120 Ma) of Libya. The specimen consists of associated elements (two incomplete dorsal vertebrae, a proximal caudal centrum, a partial proximal caudal neural arch, the distal right femur, and the mostly complete right tibia) and is referable to the widespread ceratosaurian clade Abelisauroidea. The discovery adds to the growing record of abelisauroids from mainland Africa, and firmly establishes the presence of the clade on the continent prior to its final separation from South America. Indeed, the age of the Libyan theropod predates or is penecontemporaneous with the accepted timing of fragmentation of most major Gondwanan landmasses, supporting the hypothesis that abelisauroids could have dispersed throughout the southern continents before land connections between these areas were severed. Moreover, the considerable size of the Libyan form challenges assertions that abelisauroids were ecologically subordinate to basal tetanuran theropods in Early and middle Cretaceous paleoenvironments of Gondwana.

INTRODUCTION

ALTHOUGH RECENT years have witnessed a dramatic increase of paleontological activity within the Cretaceous of the African mainland (e.g., Sereno et al., 1994, 1996, 2004; J. B. Smith et al., 2001; O’Leary et al., 2004; Gomani, 2005; Jacobs et al., 2006; O’Connor et al., 2006; Sereno and Brusatte, 2008), terrestrial vertebrates from this interval remain poorly known (see Sereno et al., 1994; Russell, 1995; O’Connor et al., 2006; Krause et al., 2007), impeding efforts to understand late Mesozoic Afro-Tethyan paleoecosystems (e.g., J. B. Smith et al., 2001) and the evaluation of paleobiogeographic hypotheses related to Gondwanan fragmentation (see Sampson et al., 1998; Krause et al., 1999, 2006, 2007; Lamanna et al., 2002; Wilson et al., 2003; Sereno et al., 2004; Sereno and Brusatte, 2008). This is particularly true of Libya, which has produced only a handful of Cretaceous terrestrial vertebrate remains thus far.

Lapparent’s (1960) monograph on fossil vertebrates of the Saharan “Continental Intercalaire” briefly mentioned fish and dinosaur material from the Jabal Nafusah region of northwestern Libya (Fig. 1). Lapparent referred several Libyan dinosaur fossils (a tooth and a vertebra) to *Elaphrosaurus iguidiensis* Lapparent, 1960, a theropod taxon he named (in the same publication) on the basis of remains from Algeria, Tunisia, and Niger. Unfortunately, the stratigraphic provenance of the Libyan specimens is uncertain: whereas they were most likely recovered from the Upper Jurassic–Lower Cretaceous Cabao Formation or the overlying Lower Cretaceous Chicla Formation (see El-Zouki, 1980), it is also possible that they came from the Upper Cretaceous Sidi as Sid Formation. Moreover, *E. iguidiensis* lacks discernible autapomorphies and is currently considered a *nomen dubium* (see Dalla Vecchia, 1995; Makovicky et al., 2004; Carrano and Sampson, 2008). We regard the material assigned to this taxon as Theropoda indet. Additional dinosaur remains have been recorded from the Cabao (El-Zouki, 1980) and Chicla

formations (Dalla Vecchia, 1995; Duffin, 2001; J. B. Smith and Dalla Vecchia, 2006), and have also been briefly noted from younger rocks in Libya (Nessov et al., 1998; Rage and Cappetta, 2002). However, little of this material has been formally described, and none of it appears diagnostic to the genus level (contrary to previous reports [see Glut, 1997; Weishampel et al., 2004], there appears to be no definitive record of the allosauroid theropod *Carcharodontosaurus* Stromer, 1931, in Libya). Thus, although Cretaceous terrestrial sediments are common in Libya, dinosaurs from the nation remain virtually unknown.

Here we describe associated axial and appendicular remains (two incomplete dorsal vertebrae, a proximal caudal centrum, a partial proximal caudal neural arch, the distal right femur, and the mostly complete right tibia) of a large-bodied theropod dinosaur from the Early Cretaceous of Libya that is referable to the ceratosaurian clade Abelisauroidea. Representatives of Abelisauroidea were widely distributed across the southern continents and Europe during the Cretaceous (see Carrano and Sampson, 2008, and references therein), and have figured prominently in hypotheses of Gondwanan paleobiogeography (e.g., Bonaparte, 1986; Sampson et al., 1998; Lamanna et al., 2002; Sereno et al., 2004; J. B. Smith and Lamanna, 2006; Krause et al., 2007; Sereno and Brusatte, 2008; Ali and Aitchison, 2009; Canale et al., 2009; Fanti, 2009). However, these animals remain relatively poorly known from mainland Africa (see Sereno et al., 2004; Mahler, 2005; Novas et al., 2005a; J. B. Smith and Dalla Vecchia, 2006; J. B. Smith and Lamanna, 2006; Carrano and Sampson, 2008; Sereno and Brusatte, 2008). The new Libyan find thus contributes to the sparse record of Abelisauroidea in Cretaceous deposits of the African continent.

Materials.—Specimens referred to herein are housed in the Centro de Pesquisas Paleontológicas “Llewellyn Ivor Price,” Peirópolis, Brazil (CPP), the Field Museum of Natural History, Chicago (FMNH), the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires (MACN),

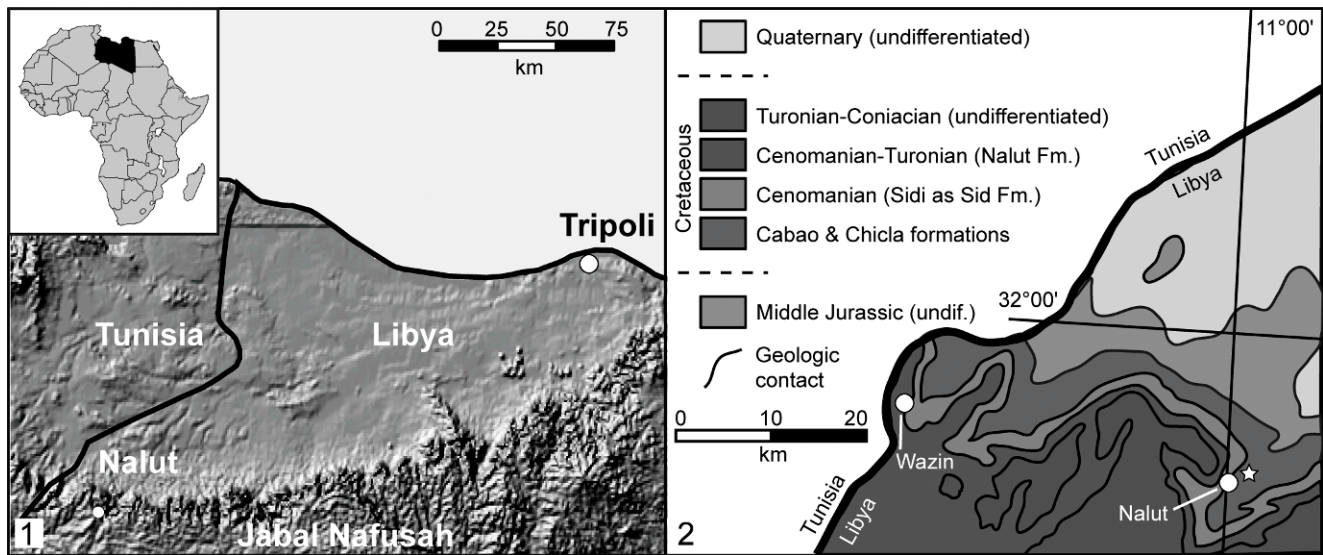


FIGURE 1—1, Location of the study area, near the town of Nalut along the Jabal Nafusah escarpment, northwestern Libya; 2, Simplified bedrock geology of the Nalut area, including the outcrop belt of the Tithonian to Aptian-Albian aged Cabao and Chicla formations. Star indicates approximate location of PRC NF001. (After J. B. Smith and Dalla Vecchia, 2006, fig. 1).

the Museo Provincial “Carlos Ameghino,” Cipolletti, Argentina (MPCA), the Muséum National d’Histoire Naturelle, Paris (MNHN), the Petroleum Research Centre (Nafusah Region), Tripoli (PRC.NF), the Museo de Ciencias Naturales de la Universidad Nacional del Comahue, Neuquén, Argentina (MUCPv), the Université d’Antananarivo, Antananarivo, Madagascar (UA), and the Universidad Nacional de la Patagonia “San Juan Bosco,” Comodoro Rivadavia, Argentina (UNPSJB).

AGE AND STRATIGRAPHIC CONTEXT

The specimen (PRC.NF.1.21), was discovered near the town of Nalut, ~30 km east of the Tunisian border, at locality PRC NF001 (Fig. 1). The find constitutes the initial results of a joint Libyan-American expedition to Jabal Nafusah that took place in August of 2005. Stratigraphic nomenclature employed here follows El-Zouki (1980).

PRC.NF.1.21 was found within a thick sequence of buff-white colored, poorly cemented, medium to coarse-grained, tabular cross-bedded sandstone near the top of the Cabao Formation (~17 m below the unconformable contact with the Chicla Formation). The associated bones were preserved in a ~3 m wide lens of pebbly sandstone and vertebrate fossil clasts that we interpret as a channel deposit.

The age of the Cabao Formation has received limited treatment in the literature, but the unit is considered equivalent to the Asfer Group (Barale and Ouaja, 2002 [=“Merbah el Asfer Formation”]) of neighboring Tunisia (see El-Zouki, 1980; Mateer et al., 1992). Due to its stratigraphic position, the level of the Cabao Formation that produced PRC.NF.1.21 is here regarded as correlative with the Douiret Formation, the uppermost unit of the Asfer Group. The Douiret Formation is currently assigned a Lower Cretaceous age (lower Aptian, see Ben Ismaïl, 1991; Barale and Ouaja, 2002; Anderson et al., 2007). The Chicla Formation, which overlies the Cabao Formation at PRC NF001, is considered to be Aptian-Albian in age on the basis of its stratigraphic relationships (El-Zouki, 1980; Fatmi et al., 1980; Mateer et al., 1992) as well as its micro- and macrofloral assemblages (Nairn, 1978; Tekbali, 1987; Fatmi and Sbeta, 1991). The contact between the Cabao and Chicla formations is

unconformable (see El-Zouki, 1980; Fatmi et al., 1980), indicating some passage of time between the deposition of the two units. Therefore, the balance of evidence indicates that the horizon of the Cabao Formation that yielded PRC.NF1.21 is of early Aptian age (~125–120 Ma [after Ogg et al., 2008]).

Vertebrate fossils (teeth of the hybodont shark *Priohybodus* d’Erasmus, 1960; teeth and scales of the actinopterygian *Lepidotes* Agassiz, 1832; indeterminate turtle and crocodylomorph fragments; a purported spinosaurid theropod vertebra) have previously been used to support a “Neocomian” (=Berriasian-Barremian) age for the Cabao Formation (El-Zouki, 1980). However, because the stratigraphic ranges of these taxa extend beyond the Berriasian-Barremian, they do not necessarily indicate that the Cabao Formation was deposited during that interval. Incidentally, we note that the supposed spinosaurid vertebra appears to consist only of a centrum (see El-Zouki, 1980, pl. 2) that is not definitively referable to Spinosauridae or any other lower-level theropod taxon.

DESCRIPTION

Vertebrae.—The preserved vertebrae of PRC.NF.1.21 are incomplete. One dorsal, here assigned to the caudal portion of the series (Fig. 2.1, 2.2), and the proximal caudal centrum (Fig. 2.3) exhibit clear neurocentral sutures. This suggests that, despite its large size (see Table 1), the individual represented by PRC.NF.1.21 was not fully mature at death (see Brochu, 1996; Irmis, 2007).

All of the preserved vertebral centra are craniocaudally short, amphiplatyan to slightly amphicoelous, and lack pneumatic fossae or foramina. The caudal edge of the centrum of the caudal dorsal extends far ventrally, rendering the ventral margin of this centrum strongly concave in lateral view (Fig. 2.1). This vertebra possesses shallow infraprezygapophyseal, infradiapophyseal, and infrapostzygapophyseal fossae and a “heart-shaped” neural canal with a maximum diameter 35% that of the centrum, proportionately larger than in most basal neotheropods (Fig. 2.2). The caudally projecting hyposphene of this bone is situated immediately dorsal to the neural canal. The overall morphology of the proximal caudal centrum is similar to those of the abelisaurids *Aucasaurus* Coria et al., 2002, *Carnotaurus* Bonaparte, 1985, and

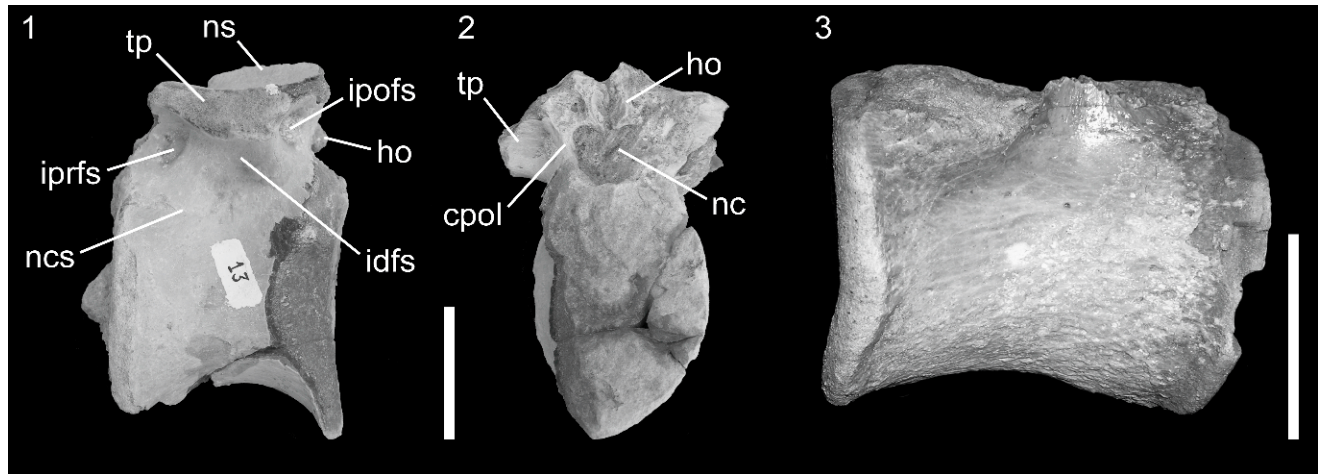


FIGURE 2—Vertebrae of an abelisauroid theropod (PRC.NF.1.21) from the Early Cretaceous of Libya. Caudal dorsal vertebra in differing views: 1, left lateral; and 2, caudal; 3, proximal caudal centrum in left lateral view. Scale bars equal 5 cm. Abbreviations: **cpol**, centropostzygapophyseal lamina; **ho**, hyposphene; **idfs**, infradiapophyseal fossa; **ipofs**, infrapostzygapophyseal fossa; **iprfs**, infraprezygapophyseal fossa; **nc**, neural canal; **ncs**, neurocentral suture; **ns**, neural spine; **tp**, transverse process.

Majungasaurus Lavocat, 1955 (see Bonaparte et al., 1990; Coria et al., 2002; O'Connor, 2007), being ventrally concave in lateral view (Fig. 2.3). Haemal arch facets appear less developed than in the proximal caudals of *Majungasaurus* (O'Connor, 2007, fig. 16); they more closely resemble those of *Aucasaurus* (Coria et al., 2002) in this regard. The proximal caudal neural arch fragment preserves only the postzygapophyses and the ventral extreme of the neural spine.

Femur.—The distal portion of the right femur is preserved (Fig. 3.1). It measures 405 mm in maximum proximodistal length (Table 1). Based on comparisons with more complete femora of the abelisauroids *Carnotaurus*, *Ekrixinatosaurus* Calvo et al., 2004, *Genusaurus* Accarie et al., 1995, *Ligabueino* Bonaparte, 1996, *Majungasaurus*, *Masiakasaurus* Sampson et al., 2001, and *Xenotarsosaurus* Martínez et al., 1986, the bone appears to be roughly 40–50% complete (see Martínez et al., 1986; Bonaparte et al., 1990; Accarie et al., 1995; Bonaparte, 1996; Carrano et al., 2002; Calvo et al., 2004; Carrano, 2007). We therefore estimate the total femoral length of PRC.NF.1.21 to be approximately 800–1,000 mm. Assuming that the skeletal proportions of the Libyan form were similar to those of other abelisauroids, we estimate its total body length at 7–9 m (see Table 1). PRC.NF.1.21 thus appears to represent one of the largest abelisauroids yet discovered, and probably the largest member of the clade known from the Early Cretaceous.

The femoral shaft is bowed caudally (Fig. 3.2, 3.4) and is subcircular in cross-section, with mediolateral and craniocaudal diameters of 127 and 111 mm, respectively. The incomplete medial epicondylar crest (Fig. 3.1, 3.4) resembles that of *Xenotarsosaurus* (Martínez et al., 1986) in being less developed than in many other abelisauroids (e.g., *Carnotaurus* [Bonaparte et al., 1990]; *Masiakasaurus* [Carrano et al., 2002]; *Quilmesaurus* Coria, 2001 [Coria, 2001; Juárez Valieri et al., 2007]; CPP 174 [an indeterminate abelisauroid from the Maastrichtian of Brazil, see Novas et al., 2008]). There is no indication of the subtle “lateral prominence” on the distal femoral shaft that has been reported in *Carnotaurus*, *Ekrixinatosaurus*, *Quilmesaurus*, CPP 174, and probably *Elaphrosaurus bambergi* Janensch, 1920 (see Novas et al., 2008). The damaged distal condyles are separated by cranial and caudal intercondylar sulci, the former of which is expanded into a shallow fossa. As in other abelisauroids, the

tibiofibular (=tibiofibularis) crest is mediolaterally broad, and its long axis is oriented proximolaterally-distomedially (Fig. 3.3), rather than proximodistally as in most non-ceratosaurian theropods (Carrano and Sampson, 2008). The fibular condyle is larger than its tibial counterpart.

Tibia.—The straight-shafted, craniocaudally compressed right tibia (Fig. 4) is well preserved but incomplete cranially and distally. Based on comparisons with more complete abelisauroid tibiae (i.e., those of *Aucasaurus*, *Masiakasaurus*, *Pycnonemosaurus* Kellner and Campos, 2002, *Quilmesaurus*, *Velocisaurus* Bonaparte, 1991, and *Xenotarsosaurus*), it appears to preserve approximately 60% of the bone's original length (Fig. 4.1). As with other elements of PRC.NF.1.21, the size of the tibia suggests that the taxon it represents is only slightly smaller than *Carnotaurus* (Bonaparte et al., 1990), again indicating that the Libyan form is one of the largest known members of Abelisauroidea.

Interestingly, despite the overall size of the individual, the tibia of PRC.NF.1.21 is considerably less robust than those of the abelisauroids *Lametasaurus* Matley, 1924 (see Novas et al., 2004) and *Pycnonemosaurus* (Kellner and Campos, 2002), more closely resembling *Aucasaurus* (Coria et al., 2002), *Masiakasaurus* (Carrano et al., 2002), *Quilmesaurus* (Coria, 2001; Juárez Valieri et al., 2007), and *Xenotarsosaurus* (Martínez et al., 1986) in this aspect. The poorly differentiated lateral condyle (Fig. 4.3) is located at the same proximodistal level as the medial. Proximally, the cranial edge of the tibia expands into a large, laterally curving cnemial crest that arises from the medial surface of the shaft. Although incomplete cranially, the crest is strongly developed, extending far cranially and further proximally than the proximal condyles. The fibular crest is well developed proximally, with its distal terminus situated at the level of the base of the cnemial crest (Fig. 4.1). Distally, the fibular crest is oriented parallel to the long axis of the tibial shaft, with its cranial edge caudally bounding a large lateral fossa. Proximally (~45 mm distal to the proximal end of the tibia), the fibular crest bifurcates into cranial and caudal rami. The cranial ramus curves cranially, paralleling the craniodistal margin of the cnemial crest and forming the proximal boundary of the lateral fossa. The caudal ramus continues to the tibial proximal margin, in the same craniocaudal plane as the distal fibular crest. The bifurcate fibular crest thus encloses a proximally positioned

TABLE 1.—Femoral and body length (mm) and geological age of abelisauroid from Libya (PRC.NF.1.21) and other representatives of Abelisauroidea, demonstrating the large dimensions of the Libyan form despite its relative antiquity. Femoral completeness (column D) was estimated through qualitative comparison of the specimen in question with complete abelisauroid femora. Complete femoral length (column E) was estimated by multiplying preserved length (column C) by (100/percentage complete [column D]). Note that, in all sampled abelisauroid specimens for which body lengths have been published (column F), complete femoral length (column E)/body length (column F) = 0.11 (column G). Estimated body length (column H) was therefore calculated by multiplying complete femoral length (column E) by (1/0.11). Sources: 1, Novas et al., 2008; 2, this study; 3, Bonaparte et al., 1990; 4, Ardolino and Delipino, 1987; 5, Calvo et al., 2004; 6, Leanza et al., 2004; 7, Accarie et al., 1995; 8, Carrano, 2007; 9, Rogers et al., 2002; 10, Carrano et al., 2002; 11, Coria, 2001; 12, Ruben. D. Martinez pers. comm., 2006; 13, Bridge et al., 2002; 14, Lamanna et al., 2002. Geological abbreviations: **EK**, Early Cretaceous; **LK**, Late Cretaceous. Institutional abbreviations see Materials.

A. Taxon	B. Specimen	C. Femur, preserved length	D. Femur, % complete (estimated)	E. Femur, complete length (estimated)	F. Body length	G. Femur, complete length/body length	H. Body length (estimated)	I. Source, dimensions	J. Geological age	K. Source, age
Abelisauroidea indet.	CPP 174	270	50	540	?	N/A	4,909	1	Maastrichtian (LK)	1
Abelisauroidea indet.	PRC.NF.1.21	405	40-50	810-1,013	?	N/A	7,364-9,209	2	early Aptian (EK)	2
<i>Carnotaurus sastrei</i>	MACN-CH-894	1,030	100	1,030	9,000	0.11	9,364	3	Campanian-Maastrichtian (LK)	4
<i>Ekrixinatosaurus novasi</i>	MUCPV-294	770	100	770	7,000	0.11	7,000	5	early Cenomanian (LK)	6
<i>Genusaurus sisteronis</i>	MNH, Bev. 1	380	100	380	?	N/A	3,455	7	mid. Albian (EK)	7
<i>Majungasaurus crenatissimus</i>	FMNH PR 2278	568	90	631	6,000	0.11	5,736	8	Maastrichtian (LK)	9
<i>Mastakosaurus knopfleri</i>	FMNH PR 2123	203	100	203	1,800	0.11	1,845	10	Maastrichtian (LK)	9
<i>Mastakosaurus knopfleri</i>	UA 8681	203	100	203	1,800	0.11	1,845	10	Maastrichtian (LK)	9
<i>Quilmesaurus curriei</i>	MPCA-PV-100	350	40-50	700-875	?	N/A	6,364-7,955	11	Campanian-Maastrichtian (LK)	11
<i>Xenotarsosaurus bonapartei</i>	UNPSJB-PV 184/612	603	100	603	?	N/A	5,482	12	mid. Cenomanian-Turonian (LK)	13, 14

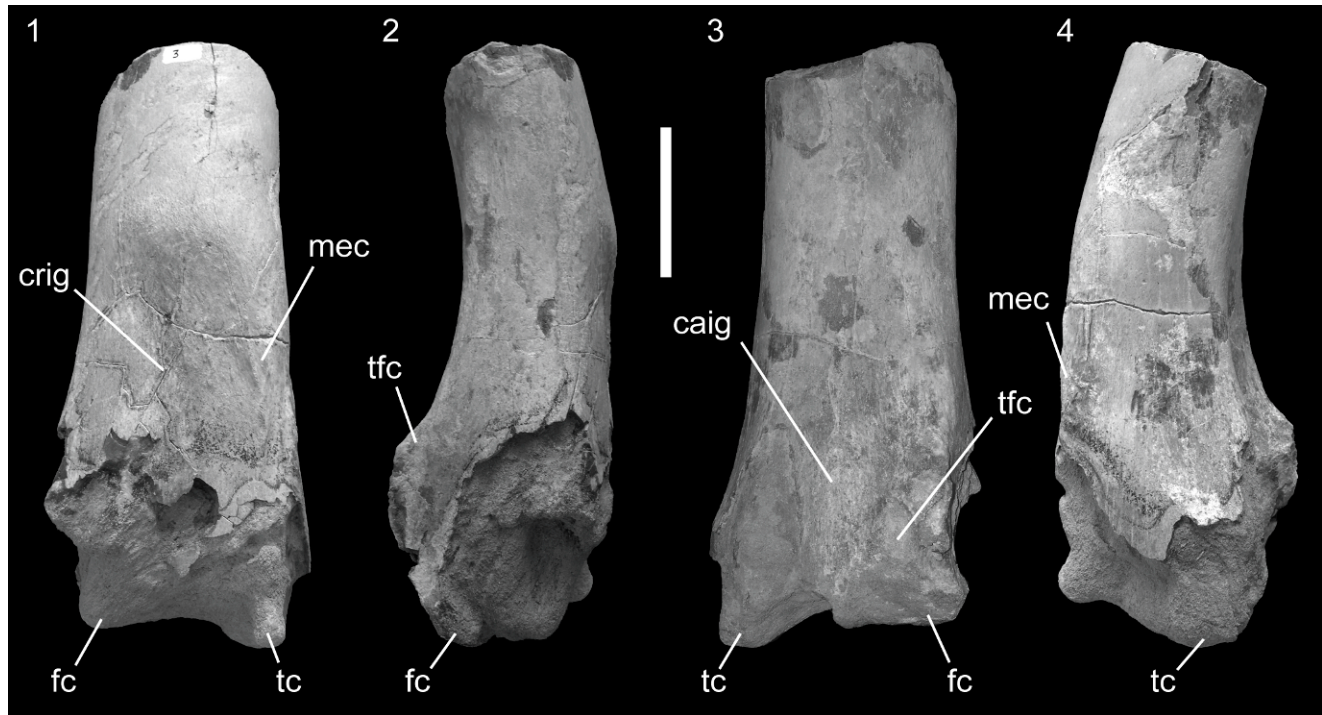


FIGURE 3—Distal portion of the right femur of PRC.NF.1.21 in differing views: 1, cranial; 2, lateral; 3, caudal; 4, and medial. Scale bar equals 10 cm. Abbreviations: **caig**, caudal intercondylar groove; **crig**, cranial intercondylar groove; **fc**, fibular condyle; **mec**, medial epicondylar crest; **tc**, tibial condyle; **tfc**, tibiofibular crest.

subtriangular fossa, a condition not observed in other theropods. Caudal to this crest, on the tibial shaft, there is an ovoid scar, possibly for the insertion of the *M. flexor tibialis internus* 2–4 (Tarsitano, 1983). As in *Masiakasaurus* (Carrano et al., 2002), a sulcus pierced by a small foramen separates the distal end of the fibular crest from the more caudally positioned proximal end of the fibular facet. The cranial tibial incisure occupies less than 50% of the tibial medial surface (Fig. 4.2).

DISCUSSION

PRC.NF.1.21 clearly pertains to a ceratosaurian theropod, as evidenced by its possession of a proximolaterally-distomedially oriented tibiofibular crest on the femur (Carrano and Sampson, 2008) and tibial characters such as a hypertrophied cnemial crest (Rauhut, 2005), a lateral fossa, a fibular facet, and a craniocaudally compressed shaft (Serenio et al., 2004). Within Ceratosauria, the specimen is referable to Abelisauroida because the lateral condyle of the tibia is confluent with the cnemial crest (Fig. 4.3; see Rauhut, 2003). Among abelisauroids, PRC.NF.1.21 may be referable to Abelisauridae because the poorly differentiated lateral tibial condyle is located at the same proximodistal level as is the medial condyle (Novas et al., 2004), but we cannot conclusively refer the specimen to this more exclusive abelisauroid clade at this time.

Interestingly, the proximally bifurcate fibular crest of PRC.NF.1.21 appears unique to this specimen, indicating that the Libyan form probably pertains to a previously unrecognized genus or species. Nevertheless, we refrain from erecting a new taxon to receive the specimen pending the discovery of additional fossils or more conclusive character evidence.

The discovery of PRC.NF.1.21 holds significant implications for understanding the evolution and paleobiogeography of abelisauroid theropods. Along with records from the Hauterivian-Barremian of Argentine Patagonia (*Ligabueino andesi*

[Bonaparte, 1996] and an indeterminate form [Rauhut et al., 2003]), it represents one of the oldest known definitive occurrences of Abelisauroida, providing further evidence for the origin of the clade prior to the final separation of Africa and South America (Lamanna et al., 2002; Rauhut et al., 2003; Sereno et al., 2004; Rauhut, 2005; Sereno and Brusatte, 2008), and raising the possibility that abelisauroids originated on this conjoined landmass (we concur with Carrano and Sampson [2008:236] and Xu et al. [2009:Supplementary Information] in regarding the recently described Early Jurassic theropod *Berberosaurus* Allain et al., 2007 as a non-abelisauroid theropod rather than as an abelisauroid as originally proposed). Furthermore, the occurrence of PRC.NF.1.21 predates, or is approximately contemporaneous with, most major events in Gondwanan fragmentation (A. G. Smith et al., 1994; Hay et al., 1999; Scotese, 2004; Blakey, 2008; Ali and Aitchison, 2009), thus supporting the hypothesis that abelisauroids could have radiated throughout the supercontinent before it broke apart (Lamanna et al., 2002; Sereno et al., 2004). Therefore, although the observed Late Cretaceous distribution of Abelisauroida has previously been used in this context (see Sampson et al., 1998; Sereno et al., 2004), this distribution may actually be of limited utility in evaluating competing Gondwanan paleobiogeographic hypotheses, at least until low-level relationships within the clade are more conclusively resolved.

When coupled with other recent discoveries from Libya (J. B. Smith and Dalla Vecchia, 2006), Morocco (Russell, 1996; Mahler, 2005; Novas et al., 2005a, and probably Buffetaut et al., 2005), Egypt (J. B. Smith and Lamanna, 2006; Carrano and Sampson, 2008), Niger (Serenio et al., 2004; Sereno and Brusatte, 2008), and Kenya (Sertich et al., 2006), PRC.NF.1.21 provides additional evidence that, rather than being rare or absent as had previously been considered (e.g., Sampson et al., 1998), abelisauroids were taxonomically diverse, geographically widespread, and temporally long-lived on the African mainland

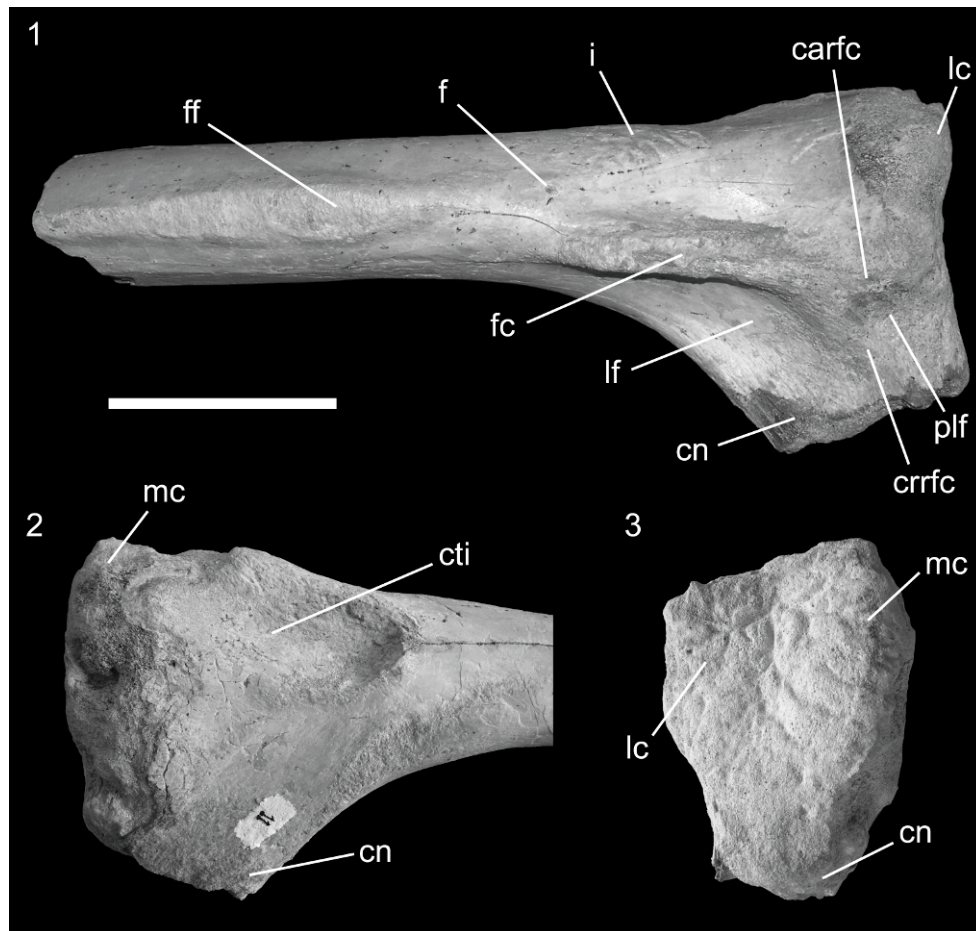


FIGURE 4—Partial right tibia of PRC.NF.1.21 in differing views: 1, lateral, 2, medial (proximal end only), and; 3, proximal views. Scale bar equals 10 cm. Abbreviations: **carfc**, caudal ramus of fibular crest; **cn**, base of cnemial crest; **crrfc**, cranial ramus of fibular crest; **cti**, cranial tibial incisure; **f**, foramen; **fc**, fibular crest; **ff**, fibular facet; **i**, insertion scar (of *M. flexor tibialis internus* 2–4?); **lc**, lateral condyle; **lf**, lateral fossa; **mc**, medial condyle; **plf**, proximolateral fossa.

(see Sereno et al., 2004; Novas et al., 2005a; J. B. Smith and Lamanna, 2006). Finally, the considerable dimensions of PRC.NF.1.21 (Table 1), combined with the geological age of the specimen, demonstrate that at least one abelisauroid lineage achieved very large body size by the late Early Cretaceous (early Aptian). Indeed, the estimated dimensions of the Libyan form are comparable to those of many coeval spinosaurid and carcharodontosaurid tetanurans, casting doubt on previous hypotheses (Apesteguía, 2002; Candeiro and Martinelli, 2005; Novas et al., 2005b) that abelisauroids were ecologically subordinate to such theropods in Gondwanan paleoenvironments during the Early and middle Cretaceous.

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NOTE ADDED IN PROOF

Le Loeuff et al. (in press) recently analyzed additional vertebrate fossils from the Cabao Formation of northwestern Libya. Among these are several further archosaurs, including a very large pholidosaurid crocodyliform, a baryonychine spinosaurid theropod, and a broad-toothed (probably macronarian) sauropod. Le Loeuff et al. (in press) also suggested that the abelisauroid tooth (Museo Paleontologico Cittadino [MPCM] 13693) described by Smith and Dalla Vecchia (2006), which was thought to be from the Chicla (= "Kiklah") Formation, was collected rather from the Cabao Formation. This raises the possibility that this specimen and PRC.NF.1.21 might be conspecific, although this cannot presently be confirmed. Le Loeuff et al. (in press) also present evidence that the Cabao Formation may be substantially more ancient than we have argued here, possibly as old as Berriasian or Valanginian. If so, PRC.NF.1.21 and possibly MPCM 13693 would likely be the oldest definitive abelisauroid specimens yet discovered from Africa.

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