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A new specimen of *Spinosaurus* (Dinosauria, Theropoda) from the Lower Cretaceous of Tunisia, with remarks on the evolutionary history of the Spinosauridae

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Key words. – Dinosauria, Spinosauridae, Early Cretaceous, Tunisia.

Abstract. – A newly discovered incomplete dinosaur dentary from the Chenini Sandstones (early Albian) of Jebel Miteur (Tataouine Governorate, southern Tunisia) is extremely similar to the corresponding part of the type of *Spinosaurus aegyptiacus* STROMER, 1915, and is identified as *Spinosaurus* cf. *aegyptiacus*. A review of African spinosaurids shows that baryonychines were present in the Aptian, and apparently became replaced by spinosaurines in the Albian and Cenomanian, perhaps as part of a more general faunal change between the Aptian and Albian. Spinosaurines may have been derived from the less advanced baryonychines. Several alternative hypotheses about the biogeographical history of the Spinosauridae are discussed.

Un nouveau spécimen de *Spinosaurus* (Dinosauria, Theropoda) du Crétacé inférieur de Tunisie. Remarques sur l'histoire évolutive des Spinosauridae

Mots clés. – Dinosauria, Spinosauridae, Crétacé inférieur, Tunisie.

Résumé. – Un dentaire de dinosaure incomplet récemment découvert dans les Grès de Chenini (Albien inférieur) du Jebel Miteur (Gouvernorat de Tataouine, Sud tunisien) est très semblable à la partie correspondante du type de *Spinosaurus aegyptiacus* STROMER, 1915, et est donc identifié comme *Spinosaurus* cf. *aegyptiacus*. Un examen des Spinosauridae d'Afrique montre que les Baryonychinae y étaient présents à l'Aptien, et y furent apparemment remplacés par des Spinosaurinae à l'Albien et au Cénomanien, peut-être dans le cadre d'un changement faunique plus général entre l'Aptien et l'Albien. Les Spinosaurinae dérivent peut-être des Baryonychinae, qui sont moins évolués. Plusieurs hypothèses alternatives au sujet de l'histoire biogéographique des Spinosauridae sont discutées.

INTRODUCTION

Although reptile remains from the Lower Cretaceous of southern Tunisia were first mentioned by Pervinquière in 1912, and the occurrence of dinosaurs there was first reported by Lapparent in 1951 [see also Lapparent, 1960], spinosaurid remains were first identified in 1988 by Bouaziz *et al.* Isolated spinosaurid teeth are in fact very common in the Lower Cretaceous (mainly Albian) of southern Tunisia, but they seem to have often been mistaken for teeth of other reptiles because of their peculiar shape. This is well illustrated by the paper by Schlüter and Schwarzhans [1978] on vertebrates from a bone-bed at Ksar Krerachfa, in which typical *Spinosaurus* teeth are described and illustrated as those of plesiosaurs. Until recently, however, the only identifiable spinosaurid material from southern Tunisia consisted of isolated teeth. A lower jaw fragment recently discovered by one of us (M.O.) provides new evidence about the affinities of the Tunisian spinosaurids, and the evolutionary history of the spinosaurid theropods. One of the main interests of this specimen is that it allows direct comparisons with the type of *Spinosaurus aegyptiacus* (which have to be based on Stromer's careful description [Stromer, 1915] since the original specimens, kept in Munich, were destroyed by an Allied air raid in 1944).

GEOLOGICAL SETTING

The new specimen (palaeontological collection of Office National des Mines, n° BM231) is a surface find from the summit of the flat-topped hill known as Jebel Miteur, which is part of the Dahar escarpment, near the town of Ghoumrassen, in the Governorate of Tataouine (southern Tunisia) (fig. 1). The top of Jebel Miteur is formed by a bone-bed corresponding to the lower part of the Chenini Sandstones (the lower member of the Ain el Guettar Formation) [see stratigraphic columns in figure 1 and in Barale *et al.*, 1997]. Vertebrate specimens found in the bone-bed at Jebel Miteur include shark teeth, lungfish toothplates, *Lepidotes*-like teeth and scales, crocodilian teeth, sauropod bones, and teeth referred to the theropods *Carcharodontosaurus* and *Spinosaurus*. This assemblage is extremely sim-

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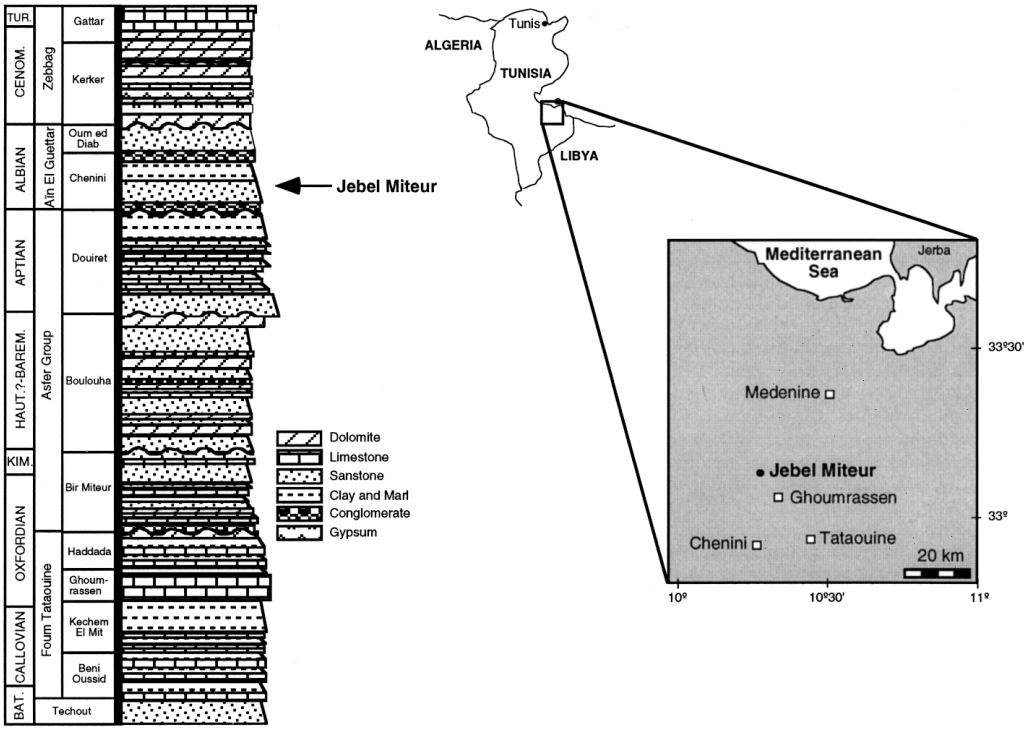

FIG. 1. – Sketch map of Tunisia showing geographical location of the Jebel Miteur locality (right) and synthetic log of the middle Jurassic to late Cretaceous sedimentary succession of southern Tunisia showing the position of the locality in the Albian Chenini Formation.
FIG. 1. – *Carte simplifiée de la Tunisie montrant la position géographique du gisement de Jebel Miteur (à droite), et coupe synthétique de la série sédimentaire du Jurassique moyen au Crétacé supérieur dans le Sud tunisien, montrant la position du site dans la formation Chenini (Albien).*

ilar to that reported by Bouaziz *et al.* [1988] from locality RH 45, also in the Chenini Sandstones, which is only a few kilometres away from Jebel Miteur. The bone-beds of the Chenini Sandstones were apparently deposited in a fluvial environment [see Benton *et al.*, 2000, for more details on their sedimentology and taphonomy].

The age of the Chenini Sandstones is now relatively well constrained [see also discussion in Benton *et al.*, 2000]. In the northern part of the Dahar escarpment, they are overlain by the so-called Vraconian bar, or Radouane Member, which is referred to the middle-late Albian on the basis of ammonites, including *Knemiceras* [Ben Youssef *et al.*, 1985 ; Bouaziz *et al.*, 1989]. They are underlain by the Douiret Clays, which are referred to the Aptian. Brachiopods indicating a Barremian to early Aptian age have been reported from beds underlying the Douiret Clays [Peybernès *et al.*, 1996]. In addition, palynological evidence suggests a late Aptian-early Albian age for the sandstones of the Ain el Guettar Formation [Ben Ismail, 1991]. Moreover, the vertebrate fauna from the Chenini Sandstones suggests an Albian age, because of the occurrence of selachians such as *Protolamna* [Bouaziz *et al.*, 1988]. The presence of the theropod dinosaur *Carcharodontosaurus*, which supposedly is not known to occur before the Albian [Taquet, 1976], was also considered as evidence for an Albian age, but recent unpublished finds in the Aptian of southern Tunisia may in fact indicate an earlier occurrence of this dinosaur (although identification of *Carcharodontosaurus* on the basis of teeth alone may be questionable). On the basis of the available evidence, it appears that the Chenini Sandstones are in all likelihood early Albian in age.

DESCRIPTION

The specimen (fig. 2), which is 115 mm long, consists of the rostral part of a left dentary, containing four alveoli ; it was largely encrusted in limonitic ironstone, like many fossils from the Chenini Sandstones. It is damaged rostrally and ventrally, and broken just caudal to the fourth alveolus. The specimen has been compared mainly with the types of *Spinosaurus aegyptiacus* STROMER, 1915 (on the basis of Stromer's description) and *Baryonyx walkeri* CHARIG & MILNER, 1986, which are currently the most thoroughly described spinosaurid specimens [Stromer, 1915, 1936 ; Charig and Milner, 1997], and which both include well preserved dentaries.

In dorsal view, the lingual edge is almost perfectly straight, whereas the labial edge is convex. The specimen reaches its greatest width (48 mm) at the level of the caudal rim of the third alveolus. More rostrally, the labial edge converges with the lingual edge. In cross-section, the bone is roughly triangular, being much broader dorsally than ventrally (fig. 3). This indicates that the rostral part of the mandible must have been V-shaped in cross-section. The labial surface of the bone has suffered some abrasion, and its dorsal (alveolar) region is partly damaged. It seems to have been rather smooth and sloping medioventrally. Several large foramina for nerves and/or blood vessels are visible on the labial surface. The lingual surface of the bone, corresponding to the mandibular symphysis, is flat and vertical. Apart from some depressions which may be due to abrasion or possibly to pathological processes, it is fairly smooth, and does not show any marked corrugations that would indicate a firm sutural union with the right dentary. In the type of *Spinosaurus aegyptiacus*, the condition was

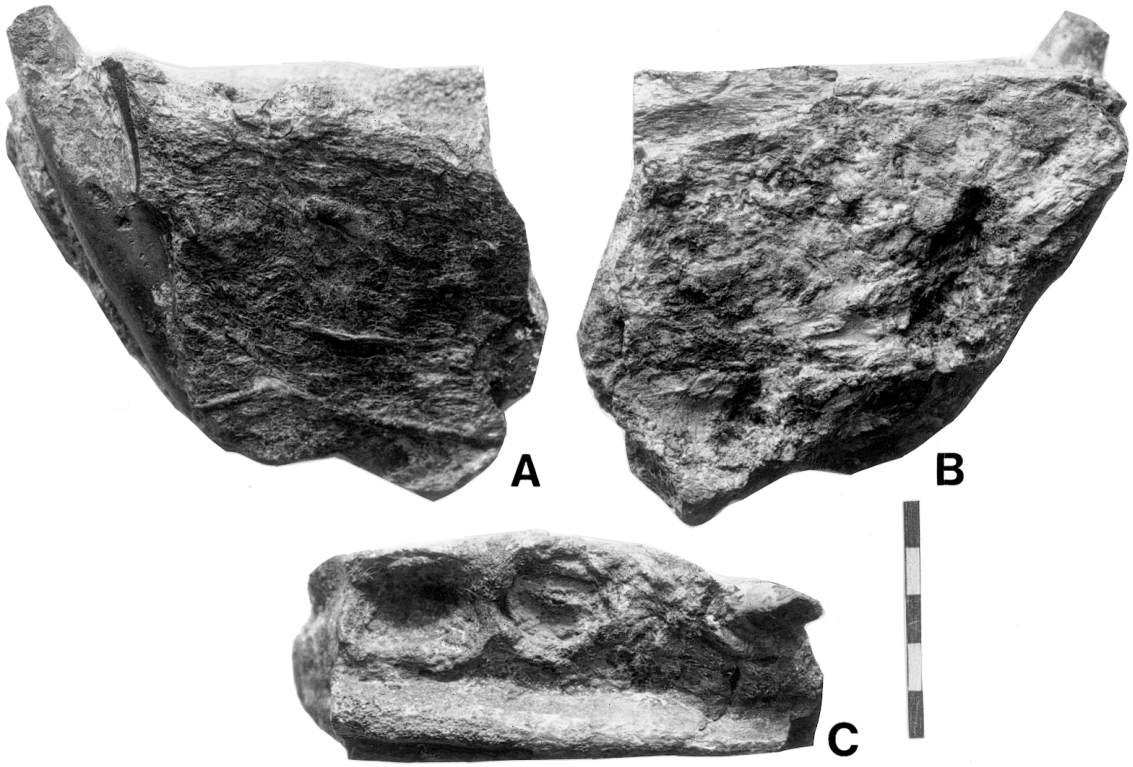

FIG. 2. – Rostral part of left dentary of *Spinosaurus* cf. *aegyptiacus* from the Albian Chenini Formation of Jebel Miteur, southern Tunisia (palaeontological collection of the Office National des Mines, Tunis, n°BM231), in lateral (A), medial (B) and dorsal (C) views. Scale bar : 50 mm.
FIG. 2. – *Partie antérieure d'un dentaire gauche de* Spinosaurus *cf.* aegyptiacus *de la formation Chenini (Albien) du Jebel Miteur, Sud tunisien (collection paléontologique de l'Office National des Mines, Tunis, n°BM231), en vues latérale* (A), *médiale* (B) *et dorsale* (C). *Barre d'échelle : 50 mm.*

similar, with rugosities only in the rostralmost part of the lingual surface of the bone [Stromer, 1915]. As already noted by Stromer [1915], this does not suggest a firmly fused symphysis. Apparently, in *Spinosaurus*, as in *Baryonyx* [Charig and Milner, 1997], the symphysis was effected mainly by connective tissue, and some mobility may have been possible between the mandibular rami.

In dorsal view, the rostral part of the alveolar row is clearly visible. The rostralmost alveolus is only partially preserved because of the incomplete preservation of the rostral end of the bone. However, the broken tip of a relatively small tooth is visible rostrolingually to the much larger second tooth. The first tooth of the dentary was thus small by comparison with the following ones, as in *Spinosaurus aegyptiacus* [Stromer, 1915], and unlike the condition in *Baryonyx walkeri*, in which the first alveolus is relatively large [Charig and Milner, 1997]. Only the lingual and caudal rims of the oval-shaped second alveolus are preserved, a large tooth is still present inside this alveolus. Between the second and third alveoli, there is an 18 mm long interalveolar space ; this long space is reminiscent of *Spinosaurus aegyptiacus* rather than of *Baryonyx walkeri*, in which the rostral alveoli are close-set. The space between the large, oval-shaped third and fourth alveoli is much shorter. The bone is broken just caudal to the fourth alveolus.

Rostrocaudal diameters of the alveoli :
1st alveolus : ?
2nd alveolus : 27 mm
3rd alveolus : 24 mm
4th alveolus : 30 mm

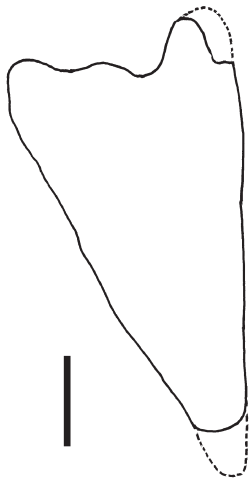

FIG. 3. – Outline of cross-section of left dentary of *Spinosaurus* cf. *aegyptiacus* (Office National des Mines, Tunis, n°BM231), at the level of the bony wall between the third and fourth alveoli, showing the medial ridge (right). Scale bar : 20 mm.
FIG. 3. – *Section transversale du dentaire gauche de* Spinosaurus *cf.* aegyptiacus *(Office National des Mines, Tunis, n°BM231), au niveau de la cloison osseuse entre les troisième et quatrième alvéoles, montrant la crête médiale (à droite). Echelle : 20 mm.*

Contrary to the condition in *Baryonyx walkeri* [Charig and Milner, 1997], no evidence of interdental plates can be seen lingual to the alveoli ; this is reminiscent of the type of *Spinosaurus aegyptiacus* as figured by Stromer [1915]. A longitudinal groove [the paradental groove of Charig and

Milner, 1997] runs along the lingual side of the alveolar row, as in *Baryonyx* and *Spinosaurus*. Lingual to this groove is a prominent well-marked longitudinal ridge, which merges with the lingual side of the jaw. This ridge is rounded in cross-section and its height gradually increases caudally.. In lingual view, it has a straight dorsal edge, and completely hides the alveoli from view. This tall ridge is not present in *Baryonyx walkeri* [see the description and figures in Charig and Milner, 1997], but was a prominent feature of the dentary of the type of *Spinosaurus aegyptiacus* [Stromer, 1915]. A more caudal spinosaurid dentary fragment from the Cenomanian of Morocco in the collections of the Esperaza Dinosaur Museum also shows a distinct lingual ridge. This ridge thus seems to be a distinctive feature of *Spinosaurus* (or spinosaurines : see below).

Only two teeth are preserved in the alveoli of this fragment. The first tooth is very poorly preserved, only its broken tip being apparent. Although its tip is missing, the second tooth is better preserved, and clearly visible because of the destruction of the rostrolateral wall of the alveolus. The enamel, however, has largely been destroyed, but seems to be partly preserved on the lingual side, where it can be seen only in cross-section. What is visible is in fact mostly the limonitised dentine core of the tooth, which gives a fairly good idea of its original shape. It is straight, with no noticeable separation between the crown and the root, which is long and tapers ventrally. The crown also tapers distally and apparently was only slightly compressed laterally. Nothing can be said about the carinae. The general shape of the tooth is very similar to that of the teeth figured and described by Stromer [1915], and to that of isolated teeth from the Chenini Sandstones [see Bouaziz *et al.*, 1988].

Length of tooth (as preserved) : 94 mm.

The longitudinal axis of the tooth is at an angle of about 120° relative to the lingual ridge of the dentary.

It appears from the above comparative description that the spinosaurid jaw fragment from Jebel Miteur does not differ from *Spinosaurus aegyptiacus* in any significant way, whereas it is clearly different from *Baryonyx walkeri*. It therefore seems legitimate to refer it to the genus *Spinosaurus*. According to Sereno *et al.* [1998], with whom we agree (see discussion below), there is currently one valid species of *Spinosaurus*, *S. aegyptiacus* STROMER, 1915, and the specimen from Jebel Miteur can be referred to as *Spinosaurus* cf. *aegyptiacus*. The Tunisian specimen apparently belonged to a smaller individual than the type of *Spinosaurus aegyptiacus*, with an estimated length of the tooth row of 460 mm, compared with 520 mm in the Egyptian specimen.

A NOTE ON SPINOSAURID SYSTEMATICS

The classification of spinosaurs has been the subject of extensive discussion. The idea that *Baryonyx* (and similar forms) and *Spinosaurus* are closely related forms, first defended by Paul [1988] and Buffetaut [1989, 1992], is now generally accepted [Kellner and Campos, 1996 ; Charig and Milner, 1997 ; Taquet and Russell, 1998 ; Sereno *et al.*, 1998]. Charig and Milner [1997] place *Spinosaurus* and *Baryonyx* in two distinct families, the Spinosauridae and Baryonychidae, respectively, and include both families in the superfamily Spinosauroidea, a systematic arrangement followed by Naish *et al.* [2001]. Sereno *et al.* [1998] give those taxa lower ranks, with two subfamilies, Spinosaurinae and Baryonychinae, within a single family Spinosauridae. The phylogenetic meaning of both arrangements is basically the same. Because *Baryonyx* and *Spinosaurus* have many apomorphies in common, we prefer to follow the opinion of Sereno *et al.* [1998].

The contents of both subfamilies are worth discussing. The Spinosaurinae comprise, of course, *Spinosaurus* itself. Besides the type species, *Spinosaurus aegyptiacus* STROMER, 1915, from the Cenomanian of Egypt, a second species, *Spinosaurus maroccanus*, was erected by Russell [1996], on the basis of differences in the proportions of a cervical centrum from Morocco, as compared with *S. aegyptiacus*. This seems a flimsy basis for the erection of a distinct species, all the more so that Stromer's original material (which, according to Stromer [1915] was somewhat crushed) is no longer available for direct comparison, and that the exact position in the cervical section of the vertebral column of the isolated vertebra used by Russell in his definition is somewhat uncertain. We therefore follow the opinion of Sereno *et al.* [1998] and consider *Spinosaurus maroccanus* as a *nomen dubium*. The material from the Albian of Gara Samani (Algeria) referred to *Spinosaurus maroccanus* by Taquet and Russell [1998], which includes a well preserved upper jaw, can hardly be compared with the type specimen of *Spinosaurus aegyptiacus*, which included only a tiny fragment of the maxilla. As mentioned above, we agree with Sereno *et al.* [1998] and consider that there is currently no convincing evidence for the occurrence of more than one species of *Spinosaurus* in the Albian and Cenomanian of North Africa (well preserved jaw material from Morocco currently being studied by A.C. Milner, London, may confirm or contradict this).

Sereno *et al.* [1998] also place *Irritator challengeri*, from the Albian of Brazil [Martill *et al.*, 1996] in the subfamily Spinosaurinae. *Angaturama limai*, from the same formation in Brazil [Kellner and Campos, 1996], may for the time being be considered as a junior synonym of *Irritator challengeri* [Charig and Milner, 1997] – the types of *Irritator challengeri* and *Angaturama limai*, which anatomically complement each other, may even belong to the same specimen [Sereno *et al.*, 1998]. Some characters, such as unserrated teeth, do suggest that *Irritator* is more closely related to *Spinosaurus* than to *Baryonyx*, and we therefore agree with its placement in the Spinosaurinae, as advocated by Sereno *et al.* [1998].

The Baryonychinae include *Baryonyx walkeri*, from the Barremian and possibly Hauterivian of England [see Charig and Milner, 1997, and Martill and Hutt, 1996, for discussions of British finds] and Spain [Vierra and Torres, 1995]. As noted by Charig and Milner [1986, 1990, 1997], spinosaurid premaxillae with serrated teeth from the supposedly Aptian Elrhaz Formation of Niger, originally described by Taquet [1984] as dentaries, and redescribed by Kellner and Campos [1996] and Taquet and Russell [1998], are extremely similar to the premaxilla of *Baryonyx*. Taquet and Russell [1998] have described them as a new spinosaurid taxon, *Cristatusaurus lapparenti*, supposedly differing from *Baryonyx* by a "brevirostrine condition of premaxilla". However, what is meant by this is unclear, and there appears to be no significant difference between the pre-

maxillae from Niger and that of *Baryonyx*. Therefore, as noted by Naish *et al.* [2001, p. 246], "it is arguable as to whether *Cristatusaurus* can be distinguished from *Baryonyx*", Sereno *et al.* [1998] consider *Cristatusaurus* as a *nomen dubium*, and the material referred to it by Taquet and Russell as belonging to an indeterminate species of baryonychine. We agree with Charig and Milner [1997] that this material can be referred to as *Baryonyx* sp., so that *Cristatusaurus* should be considered as a junior synonym of *Baryonyx*.

From the same formation in Niger, Sereno *et al.* [1998] have described a partial skeleton of a baryonychine, which they have called *Suchomimus tenerensis*. As mentioned by Sereno *et al.*, this animal is obviously closely related to *Baryonyx*. Further comparisons between these two taxa may lead to synonymise them at the generic level (A.C. Milner, pers.com.).

Siamosaurus suteethorni from the early Cretaceous Sao Khua Formation of Thailand, was tentatively referred to the Spinosauridae by Buffetaut and Ingavat [1986]. It is known only from isolated teeth which somewhat resemble those of *Spinosaurus*, but more complete material is needed to properly assess its relationships.

To sum up, it appears that spinosaurs can be divided into two groups, one including *Baryonyx* from England and Spain and similar forms from Niger, and the other including *Spinosaurus aegyptiacus*, from Egypt, Tunisia, Algeria and Morocco, and *Irritator* (including *Angaturama*) from Brazil. This is in agreement with the views put forward by Charig and Milner [1997], and Sereno *et al.* [1998]. Following the suggestion of Sereno *et al.*, these groups can be given subfamily rank within the Spinosauridae, as the subfamilies Baryonychinae and Spinosaurinae. Taquet and Russell [1998] favour a different subdivision based on supposed differences between "longirostrine" and "brevirostrine" forms, the former including "*Spinosaurus maroccanus*", *Baryonyx* and *Irritator*, and the latter comprising "*Cristatusaurus lapparenti*" and *Angaturama.* However, in view of the complete resemblance between the premaxillae of *Baryonyx walkeri* and "*Cristatusaurus lapparenti*", and of the fact that *Irritator* and *Angaturama* are in all likelihood the same animal, this interpretation appears highly unlikely.

THE DISTRIBUTION OF SPINOSAURID TAXA IN TIME AND SPACE

The stratigraphic distribution of the Spinosauridae can be summarised as follows.

The earliest known possible evidence of spinosaurids is the *Baryonyx*-like tooth crown from the Hauterivian Ashdown Sand of Sussex reported by Charig and Milner [1997]. *Baryonyx*-like teeth have also been reported from the Hauterivian of Burgos Province, in Spain [Torcida *et al.*, 1997]. Baryonychines are well represented in the Barremian of Europe (England and Spain) by the genus *Baryonyx* [Charig and Milner, 1986, 1990, 1997 ; Naish *et al.*, 2001; Vierra and Torres, 1995]. Isolated teeth from the Aptian of Spain have been referred to cf. *Baryonyx* [Torcida *et al.*, 1997]. As mentioned above, baryonychines closely resembling *Baryonyx* are known from the Elrhaz Formation of Niger [Taquet, 1984 ; Taquet and Russell, 1998 ; Sereno *et al.*, 1998], which is supposed to be Aptian in age [Taquet, 1976], although it should be admitted that uncertainties remain about its exact dating. Spinosaurines first appear in the African fossil record, with representatives of *Spinosaurus*, in the Albian of Tunisia [Bouaziz *et al.*, 1988 ; this paper] and Algeria [Djoua : Stromer, 1915 ; Gara Samani : Taquet and Russell, 1998]. *Spinosaurus* also occurs in the Cenomanian of Egypt [Stromer, 1915, 1936] and Morocco [Buffetaut, 1989 ; Russell, 1996]. The South American spinosaurines, from the Santana Formation of Brazil, are considered as Albian in age. The still enigmatic *Siamosaurus* from Thailand is known from both the Sao Khua Formation (possibly Hauterivian to Barremian in age) and the Khok Kruat Formation (Aptian-Albian).

Although their subdivision of spinosaurids is unconvincing (see above), Taquet and Russell [1998] have noted that "at least two successive taxa" (by which they mean the baryonychine "*Cristatusaurus*" and the spinosaurine *Spinosaurus*) are known from the western Sahara. To be more accurate, baryonychines are known from the supposedly Aptian Elrhaz Formation of Niger, and spinosaurines are known from the Albian of Tunisia and Algeria, and from the Cenomanian of Egypt and Morocco. Thus, the currently known African record of the Spinosauridae suggests a replacement of baryonychines by spinosaurines at or near the Aptian-Albian boundary. Differences between the Albian (and Cenomanian) faunas of North Africa and the earlier ones of Niger were noted by Taquet [1976] : the theropod *Carcharodontosaurus* and the pristid fish *Onchopristis numidus* appear to be absent before the Albian. However, recent unpublished finds from the Aptian of Tunisia may suggest that *Carcharodontosaurus* is present there before the Albian, although the evidence is based on isolated teeth which can be misleading. The temporal distribution of baryonychines and spinosaurines seems to support the existence of a faunal change in northern Africa between the Aptian and Albian. The nature of the replacement of baryonychines by spinosaurines in Africa at that time is uncertain. According to Taquet and Russell [1998], their successive spinosaurid taxa "may or may not be in an ancestor-descendant relationship". An ancestor-descendant relationship is of course very difficult to demonstrate. However, the Spinosaurinae appear more derived than the Baryonychinae in several respects (contrary to the usual, and probably plesiomorphic, condition in theropods, their teeth are less compressed mediolaterally and have lost their serrations ; their premaxilla, to judge from the snout from Algeria described by Taquet and Russell, seems to be more elongated ; the neural spines of their dorsal vertebrae are much taller, at least in *Spinosaurus*), and it is not unlikely that spinosaurines were derived from baryonychine ancestors.

This possible relationship has implications for the biogeographical history of the Spinosauridae. To account for their known geographical distribution, Sereno *et al.* [1998] have put forward a biogeographical hypothesis according to which spinosaurids may originally have had a Pangaean distribution that was split by the opening of the Tethys, after which baryonychines evolved in Europe (or, more generally, in Laurasia), while spinosaurines evolved in Gondwana. This scenario involves an episode of dispersal of baryonychines from Europe to Africa during the early Cretaceous to account for their occurrence in the Aptian of Niger. One problem with this hypothesis is that no remains of spinosaurines have so

far been found on the southern continents (or elsewhere, for that matter) in rocks older than the Albian. All older spinosaurids from Africa (and from Europe as well) can clearly be referred to the Baryonychinae. Of course, negative evidence should be used with great caution, but the absence of ante-Albian spinosaurines may suggest an alternative scenario, in which the spinosaurines did appear in Gondwana, but not until the Albian. They may have evolved in Gondwana from baryonychine-like primitive spinosaurids, which themselves may have dispersed to the southern continents from Laurasia sometime during the early Cretaceous, or may have had an originally Pangaean distribution (in which case there is no need to postulate a trans-Tethyan dispersal episode). The apparent lack of ante-Aptian baryonychines on the southern continents, as compared with the occurrence of baryonychines in the Hauterivian and Barremian of Europe, may support the first hypothesis.

CONCLUSIONS

The new specimen from Jebel Miteur, although fragmentary, can be compared with the type of *Spinosaurus aegyptiacus*, and this reveals a great similarity between the Albian form from Tunisia and the Cenomanian one from Egypt, at least as far as the mandible is concerned. Previous reports of *Spinosaurus* from Tunisia were based on isolated teeth, and therefore less conclusive for identification at the generic level. The jaw fragment from Jebel Miteur thus fully confirms that *Spinosaurus* is present in the Albian of Tunisia.

A review of the currently known African spinosaurid record shows that only baryonychines are known from rocks referred to the Aptian, while only spinosaurines are reported from the Albian and Cenomanian. This may suggest replacement of one family by the other during the Aptian-Albian transition, possibly as part of a more general faunal change at that time. As spinosaurines appear to be more derived than baryonychines, an ancestor-descendant relationship between *Spinosaurus* and an earlier baryonychine cannot be excluded, and alternatives to the vicariant model of spinosaurid distribution proposed by Sereno *et al.* [1998] can be suggested.

The specimen from Jebel Miteur illustrates the potential importance of the rich early Cretaceous vertebrate localities of southern Tunisia for our understanding of theropod evolution in that part of the world.

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