An early spinosaurid dinosaur from the Late Jurassic of Tendaguru (Tanzania) and the evolution of the spinosaurid dentition

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Abstract - An isolated theropod tooth from the terminal Jurassic of the Tendaguru (Tanzania), originally referred to *Labrosaurus (?) stechowi*, is described as the type specimen of a new genus and species of spinosaurid theropod. It shows an enamel ornamentation reminiscent of *Baryonyx* and allied forms, but differs from all other known spinosaurids by the large size of the denticles borne by the carinae. The new taxon is the earliest currently known spinosaurid. It sheds some light on aspects of dental evolution in spinosaurids, which seems to have been characterised by reduction of the denticles.

Keywords: Dinosauria, Theropoda, Spinosauridae, teeth, Late Jurassic, Tendaguru, Tanzania.

Un dinosaure spinosauridé primitif du Jurassique supérieur du Tendaguru (Tanzanie) et l'évolution de la denture des spinosauridés - Une dent de théropode isolée du Jurassique terminal du Tendaguru (Tanzanie), rapportée à l'origine à *Labrosaurus* (?) *stechowi*, est décrite comme spécimen type d'un nouveau genre et d'une nouvelle espèce de théropode spinosauridé. Elle montre une ornementation de l'émail rappelant *Baryonyx* et des formes apparentées, mais diffère de tous les autres spinosauridés connus par la grande taille des denticules portés par les carènes. Ce nouveau taxon est le plus ancien spinosauridé connu. Il éclaire certains aspects de l'évolution des dents chez les spinosauridés, qui semble avoir été caractérisée par la réduction des denticules.

Mots-clés: Dinosauria, Theropoda, Spinosauridae, dents, Jurassique supérieur, Tendaguru, Tanzanie.

INTRODUCTION

Among the many fossils collected by the German expeditions of 1909-1912 from the Late Jurassic dinosaur-bearing beds of what was then the south-eastern part of Deutsch-Ostafrika (today Tanzania) were numerous isolated theropod teeth (230 according to Janensch, 1925), which were described by Janensch, first in a short preliminary paper (Janensch, 1920) and then in a large monograph (Janensch, 1925) on the "coelurosaurs and theropods" from the Tendaguru Beds. The precise identification of isolated theropod teeth is fraught with difficulties, and Janensch attempted both to provide identifications for as much as possible of the Tendaguru material and to describe distinct morphotypes in great detail. Besides teeth of various sizes showing the "usual" smooth, blade-like theropod pattern, for which Janensch provided tentative identifications, the Berlin collection includes a few specimens which show more unusual characters, including a more or less marked enamel ornamentation. Among these are teeth which show considerable similarities with those of some spinosaurid theropods (Fowler, 2007; Buffetaut, 2008). The present paper describes a new spinosaurid taxon on the basis of a re-examination of that material at the Museum für Naturkunde in Berlin, carried out in 2007.

Institutional abbreviations

DMR: Department of Mineral Resources, Thailand. MB: Museum für Naturkunde der Humboldt-Universität, Berlin, Germany. NHMUK: Natural History Museum, London, UK. UT: Geology Department, University Al Fateh, Tripoli, Libya.

HISTORY OF PREVIOUS RESEARCH

The theropod teeth from Tendaguru bearing an ornamentation of ridges and grooves on the lingual face (and sometimes the labial face as well) were tentatively referred by Janensch (1920, 1925) to the poorly known genus *Labrosaurus* Marsh, 1879, as *Labrosaurus* (?) *stechowi*. Janensch further distinguished several morphological "types" among this material. Janensch's referral of these Tendaguru teeth to *Labrosaurus* was based on similarities, notably in enamel ornamentation, with a tooth from the Morrison Formation described by Marsh (1896) as *Labrosaurus sulcatus*. The genus *Labrosaurus*, originally erected on postcranial elements, has had an intricate taxonomic history, as Marsh applied it, under various specific names, to other specimens from North America, including the above-mentioned tooth (see Madsen & Welles, 2000, for a review). Madsen and Welles (2000) considered that the North American material attributed to *Labrosaurus* in fact belongs either to *Allosaurus* or to *Ceratosaurus*, the "*Labrosaurus sulcatus*" tooth being in fact an anterior tooth of *Ceratosaurus*.

In their revision of the genus *Ceratosaurus*, Madsen and Welles (2000) discussed material from Tendaguru, including the cranial and post-cranial elements described by Janensch (1925) as *Ceratosaurus* (?) *roechlingi* and the teeth designated as *Labrosaurus* (?) *stechowi*. On the basis mainly of a quadrate, they concluded that a large species of *Ceratosaurus* was probably present at Tendaguru, and that the *Labrosaurus* (?) *stechowi* teeth, showing an ornamentation similar to that of anterior teeth of *Ceratosaurus*, could be referred to it. In their review of the Ceratosauria, Carrano and Sampson (2008) discussed *Ceratosaurus* (?) *roechlingi* and concluded that a basal ceratosaur was indeed present at Tendaguru, but they did not mention the teeth identified as *Labrosaurus* (?) *stechowi*.

On the basis of Janensch's work, Fowler (2007) suggested that the ornamented theropod teeth from Tendaguru should be reassessed by comparison with baryonychine teeth, and that they may support a ceratosaurian origin for baryonychines. Independently, after revising Janensch's material at the Museum für Naturkunde in Berlin, Buffetaut (2008) concluded that while some of these teeth probably belonged to ceratosaurs, others could be referred to an early spinosaurid. The present paper formalises this identification by erecting a new taxon for the spinosaurid teeth from Tendaguru. Although isolated theropod teeth have often been considered as having little systematic value, various studies (e.g. Currie *et al.*, 1990 ; Baszio, 1997 ; Sankey, 2001 ; Sankey *et al.*, 2002 ; Smith *et al.,* 2005 ; Longrich, 2008 ; Sankey, 2008 ; Cillari, 2010) have shown that they can be diagnostic when sufficient attention is paid to morphology and enamel ornamentation. Spinosaurids have especially distinctive teeth that generally differ significantly from those of other theropods, and among the group, differences in morphology and ornamentation allow to distinguish taxa (Medeiros, 2006 ; Buffetaut *et al.*, 2008). It therefore seems legitimate to erect a new taxon of early spinosaurid dinosaur on the basis of its distinctive teeth.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The specimens mentioned in the present paper were collected on or in the vicinity of Tendaguru hill, in southeastern Tanzania (see Bussert *et al.,* 2009 for a recent detailed map of the area).

The type specimen of the new spinosaurid taxon described below (MB.R.1084) comes from what was called the "Obere Sauriermergel" by Janensch and other members of the German Tendaguru expeditions. In their recent revision of the local stratigraphy, Bussert *et al.* (2009) consider these "Upper Saurian Marls" as a member of the Tendaguru Formation and designate them as the Upper Dinosaur Member. The Upper Dinosaur Member is unconformably overlain by the *Rutitrigonia bornhardti-schwarzi* Member, which contains Early Cretaceous marine fossils, and it overlies the marine *Indotrigonia africana* Member, which is probably Tithonian in age (Bussert *et al.,* 2009). The Upper Dinosaur Member has been variously considered as latest Jurassic or earliest Cretaceous in age (see review in Bussert *et al.,* 2009). Bussert et al. (2009, p. 165) consider that "more work is needed to decide unambiguously whether the Upper Dinosaur Member is wholly Late Jurassic or, in part, Early Cretaceous" ; in their correlation chart, they consider it as Tithonian.

Other ornamented theropod teeth from Tendaguru referred by Janensch (1920, 1925) to *Labrosaurus* (?) *stechowi* come from what he called the "Mittlere Sauriermergel", referred to as the Middle Dinosaur Member of the Tendaguru Formation by Bussert *et al.* (2009). This member underlies the Tithonian *Indotrigonia africana* Member, and overlies the Oxfordian to Kimmeridgian *Nerinella* Member. Bussert *et al.* (2009) consider it as late Kimmeridgian in age.

SYSTEMATIC DESCRIPTION

Dinosauria Owen, 1842
Theropoda Marsh, 1881
Spinosauridae Stromer, 1915
***Ostafrikasaurus*, n.g.**
***Ostafrikasaurus crassiserratus*, n. sp.**

Diagnosis : A spinosaurid dinosaur with teeth which are moderately compressed labiolingually. The enamel is finely wrinkled and bears ridges which are more numerous and more pronounced on the lingual face than on the labial face. The anterior and posterior carinae are serrated. Differs from all other spinosaurids in the relatively large size of the denticles (2 to 4 denticles per mm).

Type specimen : an isolated tooth, MB.R.1084, "Typus a" of Janensch (1925).

Referred specimen : isolated tooth MB.R.1091, "Typus d" of Janensch (1925), from the Middle Dinosaur Member of the Tendaguru Formation.

Locus typicus : Tendaguru, southeastern Tanzania, quarry *Om* (Janensch, 1925).

Stratum typicum : "Oberer Sauriermergel" (Janensch, 1925), Upper Dinosaur Member of the Tendaguru Formation of Bussert *et al.* (2009).

Derivatio nominis : *Ostafrikasaurus*, from the name used by the Germans (*[Deutsch]-Ostafrika*) for the part of East Africa including Tendaguru at the time of the expeditions of the Berlin Museum, and *saurus*, from σαυρός, Greek for a lizard ; *crassiserratus*, from the Latin *crassus*, thick, and *serratus*, serrated, referring to the large size of the serrations on the carinae.

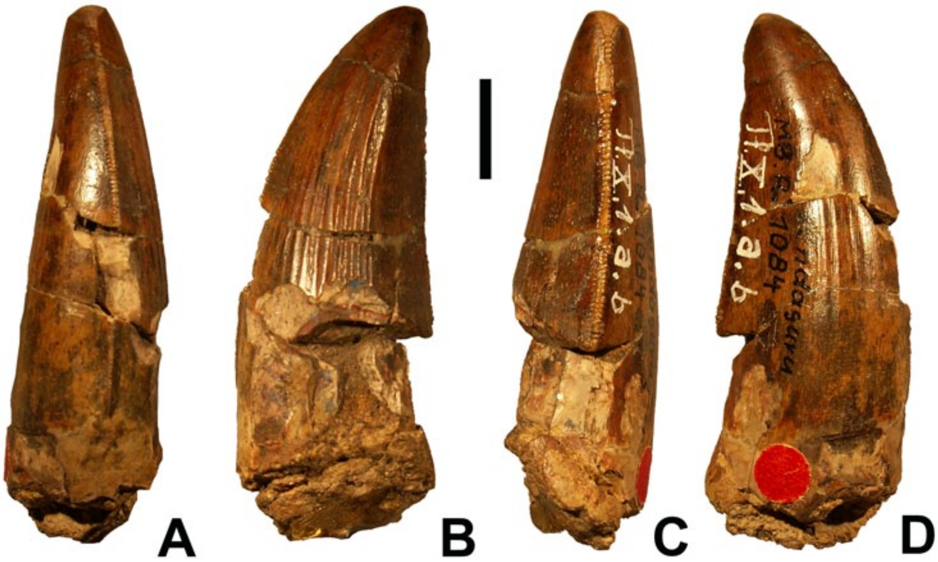

Fig. 1 - Holotype of *Ostafrikasaurus crassiserratus*, isolated tooth MB.R.1084 from the terminal Jurassic of the Tendaguru, Tanzania, in mesial (A), lingual (B), distal (C) and labial (D) views. Scale bar : 10 mm.

Description : there is little to add to Janensch's careful description of isolated tooth crown MB.R. 1084 (Fig. 1), which is 46 mm in apicobasal height. It is only moderately compressed (see cross-sections in Janensch, 1925, pl. X), with the lingual face more convex mesiodistally than the labial one. The mesial margin is convex, whereas the distal margin is almost straight, with only a very slight concavity, so that the crown is recurved mesiodistally, whereas there is no significant labiolingual curvature. The apex is rounded because of wear. Well defined mesial and distal carinae are present, both are serrated. The denticles extend from the apex to the base of the crown on the mesial carina, and probably also did on the distal carina, although its basal part is not completely preserved. The denticles are much worn at the apex, especially on the mesial carina. There are about 2 denticles per mm on the distal carina. On the mesial carina, the denticles become smaller near the base of the crown : there are 2 denticles per mm near the apex, and 3 to 4 near the base. The denticles are perpendicular to the margin of the tooth and have a rounded apex. There are no "blood grooves". Both faces bear an enamel ornamentation. The lingual face is more ornamented than the labial one ; it bears ten ridges of various lengths, orientated apicobasally, none of which reaches the apex. The ridges are about 1 mm apart at most. Mesially, there is a zone without ridges which is about 3 mm wide. Distally, a similar zone without ridges becomes narrower towards the apex (from 8 to 4 mm wide). The enamel also shows a very fine wrinkling between the ridges and on the ridge-free zones (Fig. 2). The labial face shows only 4 weakly marked ridges, which do not extend as far towards the apex as on the lingual face. The enamel bears the same fine wrinkling as on the lingual face.

Fig. 2 - Close-up of lingual face of holotype of *Ostafrikasaurus crassiserratus*, MB.R. 1084, showing large serrations, finely wrinkled enamel and ribbing. Scale bar : 10 mm.

Comparisons: as noted above, Janensch (1920, 1925) ascribed to *Labrosaurus* (?) *stechowi* several teeth with an ornamented enamel, from the Middle Dinosaur Member of the Tendaguru Formation, which he described as distinct types. *Ostafrikasaurus crassiserratus* is based on the single tooth (BM.R. 1084) placed by Janensch in his type a. Among Janensch's other types, only type d shows significant similarities with type a. It is represented by tooth BM.R. 1091, which resembles BM.R. 1084 in being curved mesiolingually but not labiolingually and in having a similar cross-section, although it is somewhat thicker mesially. The main difference lies in the enamel ornamentation, with only 5 ridges on the lingual face, which stop well below the apex. Enamel wrinkling cannot be clearly seen because the tooth has been coated with varnish, but seems to have been weak. Serrations are present on both carinae, there are about 3 denticles per mm. The differences between this tooth and the type specimen of *Ostafrikasaurus crassiserratus* may be within the range of variation of a single taxon, but it should be remembered that they come from different members of the Tendaguru Formation.

The other morphological types distinguished by Janensch show greater differences with the type of *Ostafrikasaurus crassiserratus*. In particular, the holotype of *Labrosaurus* (?) *stechowi*, BM.R. 1083, assigned to type b by Janensch (1925), is an isolated tooth with poorly preserved enamel which is curved both mesiodistally and labiolingually and D-shaped in cross-section at the base. Both carinae are serrated, but the mesial one is much worn so that the denticles are hardly visible. They are better visible on the distal carina (2 denticles per mm). The ornamentation consists of only three short ridges on the lingual face. Janensch's type b is also represented by BM.R. 1087, which is very similar to BM.R. 1083.

Janensch's type c, represented by BM.R. 1090, differs even more from the type of *Ostafrikasaurus crassiserratus*, in being curved labiolingually, but not mesiodistally, and by lacking a mesial carina, the mesial margin being simply rounded, so that the tooth is D-shaped in cross-section, without labiolingual constriction. The ornamentation consists of 5 strong ridges on the lingual face, whereas the labial surface is smooth.

Finally, Janensch's type e, represented by BM.R. 1092, does not differ much from the "normal" theropod type. The crown shows a mesiodistal curvature, and labiolingual compression is more marked that in the other types. The mesial carina does not reach the base of the crown. There are 3 denticles per mm. The ornamentation is limited to 2 extremely weak short ridges on the lingual face. The enamel is otherwise smooth, with only some weak "ripples", transversal to the apicobasal axis of the tooth, which are somewhat reminiscent of what is seen on *Carcharodontosaurus* teeth (Depéret & Savornin, 1927).

Because of the above-mentioned morphological differences, there seems to be no compelling reason to place all the types recognised by Janensch in the same taxon. Type c is very distinctive in lacking a mesial carina, and its peculiar cross-section suggests that BM.R. 1090 is a premaxillary tooth. As noted by Buffetaut (2008), Janensch's types b and c can presumably be identified as anterior teeth of ceratosaurids. In *Ceratosaurus*, both the premaxillary teeth and the anterior dentary teeth are grooved lingually (Madsen & Welles, 2000), a condition very similar to that seen in types b and c. If the present interpretation is correct, both a ceratosaurid and a spinosaurid are present at Tendaguru, and purported similarities between their ornamented teeth cannot be used to support a close phylogenetic relationship between these two families, contrary to the opinion of Fowler (2007).

The type specimen of *Ostafrikasaurus crassiserratus* resembles in many respects the teeth of relatively basal members of the family Spinosauridae, frequently placed in the subfamily Baryonychinae Charig & Milner, 1986. Comparisons (Fig. 3) have been made mainly with the teeth of the type specimen of *Baryonyx walkeri*, from the Wealden of England, and with *Baryonyx*-like teeth from the Early Cretaceous of Portugal (Buffetaut, 2007) and England, as well as with spinosaurid teeth from Asia (Buffetaut & Ingavat, 1986; Buffetaut *et al.*, 2008). The material from England includes numerous specimens from the Wealden generally identified as *Suchosaurus laevidens* Owen, 1841 (in Owen, 1840-1845), which have long been considered as belonging to crocodilians (Buffetaut, 2010), but in fact belong either to *Baryonyx* or to a related form (Milner, 2003; Buffetaut, 2007, 2010; Fowler, 2007). Characters shared by *Ostafrikasaurus crassiserratus* and baryonychine teeth include a limited labiolingual compression of the crown, a finely wrinkled enamel, and ridges (which do not reach the apex) on the lingual and labial faces. These ridges tend to be more marked and more numerous on the lingual face than on the labial face. In the type of *Baryonyx walkeri*, they are very faint or absent on the labial face (Charig & Milner, 1997), but they are more developed on other specimens, which may reflect individual variation. The *Baryonyx*-like teeth from the Early Cretaceous, ante-Aptian Cabao Formation of Libya described by Le Loeuff *et al.* (2010) are potentially important from a stratigraphic and biogeographical point of view; they resemble *Ostafrikasaurus* teeth in the shape and compression of the crown, and in their finely wrinkled enamel, but show fluting rather than ridges on the enamel and bear very small serrations. *Ostafrikasaurus crassiserratus* differs from Early Cretaceous baryonychines, however, in the larger size of the denticles borne by the carinae. In *Baryonyx walkeri*, the denticles are remarkably small by comparison with the usual condition in theropods, with about 7 denticles per mm. In *Ostafrikasaurus crassiserratus*, there are 2 to 4 denticles per mm, depending on the position on the carinae. In this respect, the Tendaguru form is similar to the majority of large theropods. As already noted by Fowler (2007) and Buffetaut (2008), this large size of the denticles can probably be considered as plesiomorphic. Later spinosaurids are characterized by significantly smaller and more numerous denticles (*Baryonyx*), or unserrated carinae (*Spinosaurus*), the Asian forms such as *Siamosaurus suteethorni* from the Early Cretaceous of Thailand (Buffetaut & Ingavat, 1986) show-

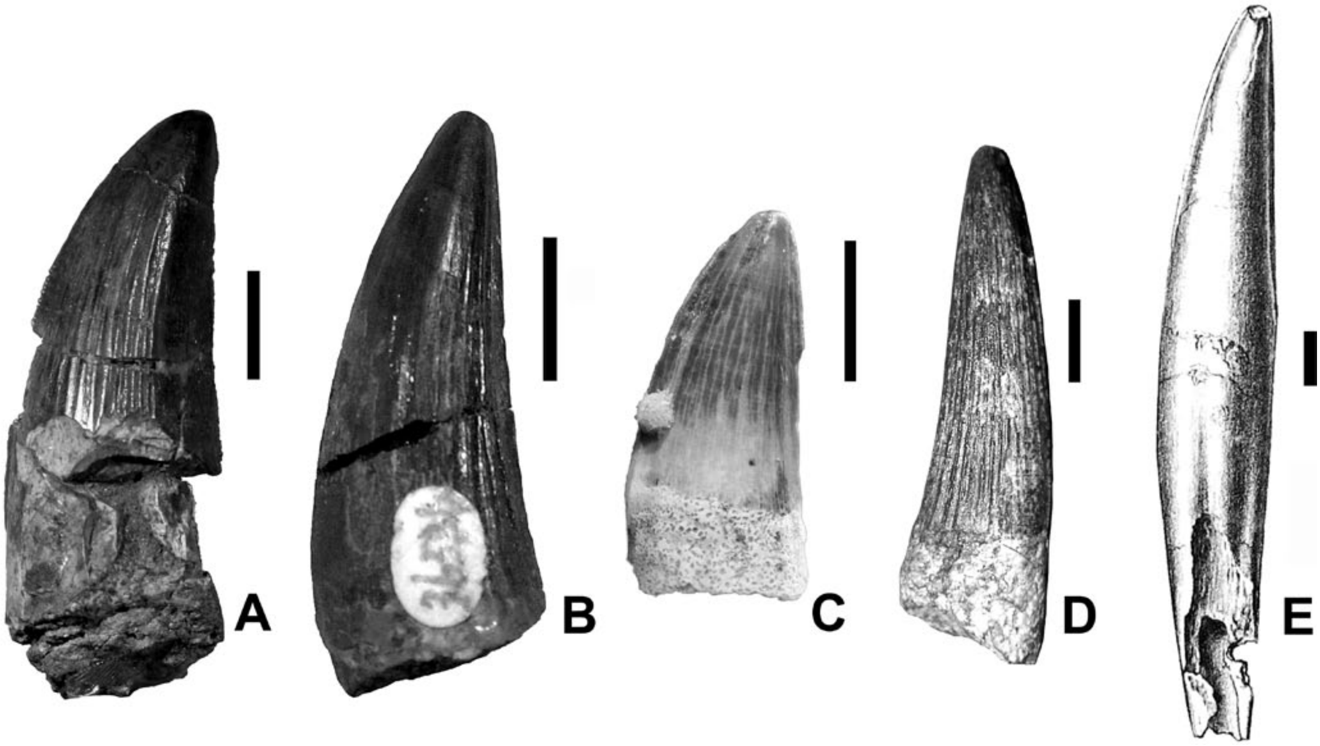

Fig. 3 - Comparison of various spinosaurid teeth. A: *Ostafrikasaurus crassiserratus*, from the terminal Jurassic of Tendaguru, Tanzania (holotype, MB. R.1084). B: cf. *Baryonyx*, from the Valanginian of England (holotype of *Suchosaurus laevidens* Owen, 1841, NHMUK 36536). C: *Baryonyx*-like tooth from the Early Cretaceous, ante-Aptian Cabao Formation of Libya (UT-JAW2). D: Holotype of *Siamosaurus suteethorni* (DMR TF-2043a) from the Sao Khua Formation (Barremian) of Thailand. E: *Spinosaurus aegyptiacus*, from the Cenomanian of Baharija, Egypt (after Stromer, 1915. Specimen destroyed in World War II). Scale bars: 10 mm.

ing an intermediate condition in which very small and indistinct serrations can still be seen, at least on unworn teeth. It should be noted that the small serrations of *Baryonyx*-like forms can easily be obliterated by wear, as seen on many "*Suchosaurus*" teeth.

Interestingly, in her comprehensive morphological study of theropod teeth, Cillari (2010) concludes that MB.R.1084 (the type of *Ostafrikasaurus crassiserratus*) is closest to *Baryonyx* and *Spinosaurus*.

DISCUSSION

One of the interesting features of the new taxon is the large size of the serrations. Reduction in the size of the serrations seems to be one of the most significant features of spinosaurid evolution, from the well developed denticles of *Ostafrikasaurus crassiserratus*, which are as large as those on the teeth of "normal" theropods of similar size, to the much smaller denticles of *Baryonyx*, the indistinct serrations of *Siamosaurus* and the unserrated carinae of *Spinosaurus*. The functional significance of this reduction remains unclear, although a link with changes in dietary adaptations appears likely. Through spinosaurid evolutionary history, reduction in serration size is apparently accompanied by changes in the shape of the crown, which becomes less compressed and less curved, this trend culminating in the straight teeth with a more or less circular cross-section of *Spinosaurus*. Convergence with crocodilians has often been mentioned (Rayfield *et al.,* 2007), and recent isotopic data suggesting a semi-aquatic mode of life for spinosaurids (Amiot *et al.,* 2010) may support the idea that the diet of spinosaurids consisted partly of fish, although direct evidence shows that it also included dinosaurs (Charig & Milner, 1997) and pterosaurs (Buffetaut *et al.,* 2004). The simplification in tooth morphology illustrated by the reduction and ultimate disappearance of serrations and the acquisition of a more or less conical crown may be a consequence of that particular diet.

The evolution of enamel ornamentation in spinosaur teeth shows a somewhat different pattern. The well developed ridges, especially on the lingual face, of *Ostafrikasaurus* distinguish it from most other theropods, in which the enamel is unornamented, or at most very finely wrinkled. Ridges are also present, with various degrees of development, in *Baryonyx* and allied forms, but in *Spinosaurus* the teeth tend to be smooth (Stromer, 1915), although there is considerable variation in this respect among the teeth referred to *Spinosaurus* from the Albian of Tunisia and the Cenomanian of Morocco, with some specimens as smooth as the teeth of the holotype of *Spinosaurus aegyptiacus*, while others show distinct ridges (see Bouaziz *et al.,* 1988). The Asian spinosaurids (Buffetaut & Ingavat 1986 ; Hasegawa *et al.,* 2003 ; Buffetaut *et al.,* 2008) show a different trend, namely an increase in the number of ridges.

To sum up, both reduction (leading to eventual disappearance) of the serrations and decrease of labiolingual compression of the crown seem to be general trends in the evolution of the spinosaurid dentition, leading to the conditions seen in both *Spinosaurus* and *Siamosaurus*. To the contrary, ridge development seems to be more variable, resulting in smooth crowns in *Spinosaurus aegyptiacus* and strongly ribbed crowns in *Siamosaurus suteethorni* and other Asian forms. A fine wrinkling of the enamel is widespread among spinosaurids, being found in *Ostafrikasaurus*, *Baryonyx* (including *Suchomimus* : Sereno *et al.,* 1998) and *Siamosaurus* and other Asian forms. In *Spinosaurus aegyptiacus*, the enamel is described as almost completely smooth, with only very fine wrinkles close to the base of the crown (Stromer 1915). Close examination of *Spinosaurus* teeth from Tunisia shows a fine wrinkling, similar to that observed on other spinosaurid teeth, on at least some specimens.

Ostafrikasaurus crassiserratus appears as the earliest known form showing such characters as moderate labiolingual compression of the crown, fine enamel wrinkling and ridges on the labial and lingual surfaces. Interestingly, earlier spinosauroids such as *Eustreptospondylus oxoniensis* from the Middle Jurassic of England (Sadleir *et al.,* 2008), have teeth that do not differ from the usual theropod pattern, being labiolingually compressed, with a smooth enamel. Clearly much remains poorly understood about dental evolution in spinosaurids, which apparently involved some reversals to a condition seen in non-spinosaurid theropods, as exemplified by the ribless tooth enamel of *Spinosaurus*.

The occurrence of *Ostafrikasaurus crassiserratus*, which currently appears at the most basal spinosaurid, in the latest Jurassic of Tendaguru does not imply an African origin for the Spinosauridae. In view of the still largely Pangaean palaeogeographical pattern of the Late Jurassic, it is likely that early spinosaurs had a wide geographical distribution. Many details of the palaeobiogeographical history of spinosaurids remain to be worked out, however (Buffetaut & Ouaja, 2002). The presence of a spinosaurid in the Late Jurassic of Tendaguru suggests that the family should have been present at that time in various other parts of the world, including of course the Gondwanan continents, but also North America and Europe. The case of the Asian spinosaurs is more complex, as eastern Asia seems to have been isolated from other land masses for most of the Late Jurassic and part of the Early Cretaceous. How and when spinosaurs got to eastern Asia remains unclear.

CONCLUSIONS

The probably terminal Jurassic *Ostafrikasaurus crassiserratus* appears as the earliest known spinosaurid theropod. Although it is represented only by a couple of isolated teeth, these show a combination of characters that allows both to place it among the Spinosauridae and to separate it from other spinosaurids. The new taxon sheds light on some aspects of tooth evolution in the Spinosauridae, which apparently was relatively complex, leading in some lineages (*Spinosaurus*) to a smooth enamel and in others (*Siamosaurus*) to strongly ribbed crowns. The occurrence of a basal spinosaurid in Africa in the Late Jurassic suggests that the family may have had a wide geographical distribution early in its history.

ACKNOWLEDGMENTS

Work on the material from Tendaguru at the Museum für Naturkunde in Berlin was made possible by grants from the SYNTHESYS Programme of the European Union. I thank Nicole Klein and Daniela Schwarz-Wings for access to the Berlin collections. Comparison with teeth of *Baryonyx* and other Wealden spinosaurids at the Natural History Museum (London) was made possible by Angela Milner, whom I thank for her constant support of my work on spinosaurs. Thanks to Azzurra Cillari for a copy of her unpublished Ph.D. thesis and to Gilles Cuny and Jean Le Loeuff for their useful comments.

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