

中国河南晚白垩世地层一枚可能属于重爪龙亚科(兽脚亚目:棘龙科)的牙齿化石¹⁾

洪大卫¹ 徐星¹ 王德友²

(1 中国科学院古脊椎动物与古人类研究所 北京 100044)

(2 河南省国土资源研究院 郑州 450000)

摘要:中国河南晚白垩世中段地层马家村组发现了一枚大型兽脚龙类牙齿。该牙牙体长,呈圆锥状,横断面卵圆形,沿长轴微向后缘弯曲,前后缘均有大量锯齿状突起,这些特征显示其很可能是重爪龙类牙齿。这可能代表了重爪龙类在亚洲地区的首次发现,也是该类恐龙在晚白垩世地层中的首现,由此表明重爪龙类在时间和地域分布上较之前研究观点更为广泛。综合棘龙科的化石形态学以及推知的生态学证据看,较之其他兽脚类,棘龙类化石记录很少,很可能意味该类动物数量确实稀少,造成这种现象的原因可能是其过分特化的身体形态。

关键词:亚洲,兽脚类,恐龙,棘龙类,生态

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A PROBABLE BARYONYCHINE (THEROPODA: SPINOSAURIDAE) TOOTH FROM THE UPPER CRETACEOUS OF HENAN PROVINCE, CHINA

David W. E. HONE¹ XU Xing¹ WANG De-You²

(1 *Institute of Vertebrate Palaeontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044 dhone@ivpp.ac.cn*)

(2 *Scientific Academy of Land and Resources of Henan Zhengzhou 450000*)

Abstract A single large theropod tooth was recovered from the middle Upper Cretaceous Majiacun Formation, Henan Province, China. The morphology of the tooth strongly suggests that it belongs to a baryonychine spinosaurid theropod based on the following features: long, conical tooth with a sub-circular cross-section, slight recurvature along the length of the tooth and numerous fine denticles on both anterior and posterior carinae. This tooth therefore may represent the first record of the baryonychines in Asia, and the first in the Late Cretaceous. This suggests that the baryonychines were more widely distributed both geographically and temporally than previously thought. Based on the gross morphology and inferred ecology of spinosaurids as a whole, we note that these animals are surprisingly rare in the fossil record compared to other theropod clades. This suggests that in life they may have been genuinely rare animals, perhaps as a result of their extreme morphological specialisation.

Key words Asia, theropod, dinosaur, spinosaurid, ecology

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1 Introduction

Spinosaurid theropods are an interesting and highly specialised clade of non-avian dinosaurs. Despite their large size and wide temporal and geographic distribution they are known only from isolated teeth and a few skeletal remains (Holtz et al., 2004; Dal Sasso et al., 2005). Accurate identification of isolated spinosaurid teeth has proven difficult given their varied morphology (Medeiros, 2006) and similarity to the teeth of other Mesozoic reptiles, most notably crocodiles (e. g. see Holtz et al., 2004; Buffetaut et al., 2008), yet they remain an interesting and unusual case of extreme specialisation in theropod evolution (Holtz et al., 2004; Rayfield et al., 2007).

The Spinosauridae is a clade of basal tetanuran theropods consisting of two closely related groups, the Spinosaurinae and Baryonychinae (Holtz et al., 2004). Both are large bodied with elongate jaws and (for theropods) unusually long, straight and sub-cylindrical teeth (Holtz, 1998). Spinosaurids are interpreted as active predators of both other dinosaurs and fish based on their morphology (Holtz et al., 2004; Rayfield et al., 2007 and references therein) and stomach contents (Charig and Milner, 1997), and are thought to have lived primarily in and around freshwater (Holtz, 1998; Milner, 2003; Amiot et al., 2009).

Currently there are only two confirmed records of spinosaurids from Asia, an Early Cretaceous spinosaurine from Thailand (*Siamosaurus*—Buffetaut and Ingavat, 1986) and spinosaurine teeth from southern China that may belong to the same or a similar genus (Buffetaut et al., 2008). Here we report the first spinosaurid from the Late Cretaceous of Asia based on an isolated tooth. The tooth is referred to the Baryonychinae and represents the first record of this clade in Asia and the first in the Late Cretaceous. This significantly extends the geographic and temporal range of this clade.

Institutional abbreviations XMDFEC, Xixia Museum of Dinosaur Fossil Eggs of China. IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

2 Locality information

The tooth was collected from the Majiacun Formation, Sanlimiao, Xixia County, Henan Province. The bed from which the fossil was recovered is in the mid-section of the formation, so although the formation spans the Late Coniacian through to the Late Santonian (Wang and Feng, 2008:103), the tooth is likely from the middle Santonian. The tooth bearing beds are a set of light purple and red muddy siltstones and fine calcareous sandstone.

The Majiacun Formation has also yielded dinosaur eggs, including *Dendroolithus* and *Paraspheroolithus*, and invertebrate traces (*Scoyenia*) (Wang and Feng, 2008:103–104). Although dinosaur skeletal remains have been recovered from this formation, they have yet to be described.

3 Description

Tooth morphology The specimen (XMDFEC V0010, casts are also housed at the IVPP as IVPP FV* 1786) is a single, well preserved tooth crown missing the very tip and with some minor breaks (see Fig. 1). The root is not preserved. Given the quality of preservation of the tooth and the lack of evidence of any form of tumbling or transport, it is likely that this was a tooth shed from the jaws of the animal during life, rather than becoming separated from the cranium after death. There is some wear on the base of the crown with missing and discoloured enamel. The maximum length of the preserved tooth is 52 mm, and probably only a few more mil-

limeters are missing from the tip. The tooth is 15 mm long anterioposteriorly and 9 mm labiolingually, measured at the base for a Crown Base Ratio (CBR) of 0.6.

The tooth is long, tapers evenly to the tip and is very slightly D-shaped in cross-section being somewhat more flat on the lingual face and bowed on the labial face (though this is overall much closer to a circular cross-section than a more normal laterally compressed theropod tooth as is common for spinosaurids). The tooth exhibits a gentle posterior recurvature along its length. In anterior and posterior view, it shows a slight sinusoidal curve labio-lingually (see Fig. 1), a feature that does not appear to be the result of breakage or distortion.



Fig. 1 Tooth XMDFEC V0010 seen in (left to right) labial, anterior, lingual and posterior views
Scale bar = 10 mm

The tooth has clearly defined carinae on both the anterior and posterior faces, and both have small, fine serrations (denticles). The denticles have suffered some wear, which makes them hard to make out along most of the length of the tooth but in places are clear and well-preserved. The denticles are similar in morphology on both faces and run from the base of the tooth to the break at the tip. There are 24 denticles per 5 mm on the anterior face of the tooth (measured at the midpoint) for a ratio of 4.8 per mm. The denticles are more worn on the posterior face and had to be measured at a point distal to the midpoint and over only 4 mm. This gave a total of 18 denticles over 4 mm and thus 22.5 over 5 mm, or 4.5 per mm (see Fig. 2). The Denticle Size Difference Index (Rauhut and Werner, 1995) is therefore 1.09, indicating that these are very similar on the anterior and posterior carinae.

The enamel surface of the tooth is largely smooth and without the strong dorso-ventral ornamentation seen in many spinosaurid teeth (see below). There are exceptionally faint anteroposterior flutes on the lateral surfaces of the tooth but these are widely spaced and shallow.

Identification Identification of this tooth as theropodan rather than from another reptilian clade is difficult as in the past spinosaurid teeth having been confused with crocodiles and pliosaurs as well as other reptiles (e. g. see Sánchez-Hernández et al., 2007; Buffetaut et al., 2008). However, the combination of characters (and especially the presence of both anterior

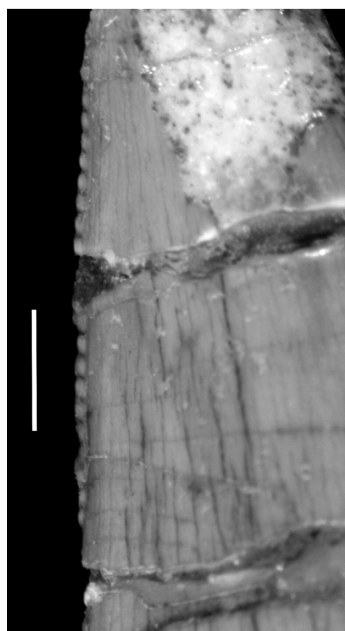


Fig. 2 Denticles on the distal posterior carina of XMDFEC V0010 seen in lingual view
Scale bar = 2 mm

and posterior carinae with fine denticles in combination with the curvature of the tooth—Sánchez-Hernández et al., 2007) can be used to separate the tooth from other non-spinosaurid reptiles, notably pliosaurs. Although several clades of crocodiles (e. g. sebecosuchians and pristichampsids) have ‘ziphodont’ teeth—that is those with carinae and denticles (Riff and Kellner, 2001; Turner and Calvo, 2005) and some of which are laterally compressed, these can still be distinguished from theropod teeth. In this case the tooth is more strongly recurved and more laterally compressed than those of ziphodont crocodiles and the denticles are finer. This suggests that this is indeed a theropod tooth.

Further complexity is however added by the distribution of characters seen in spinosaurine and baryonychine teeth (e. g. see Medeiros, 2006; Canudo et al., 2008) and the fact that many teeth assigned to either clade were not associated with diagnostic skeletal material. With the loss of the holotype *Spinosaurus* material (see Buffetaut, 1989), and the absence of a detailed description of *Suchomimus* (Serenó et al., 1998; Holtz et al., 2004) we are left to rely on the holotype of *Baryonyx* (Charig and Milner, 1997) alone for the baryonychines and the holotype of *Irritator* (Sues et al., 2002) for the spinosaurines, with only partial jaws or skulls available for some other specimens (e. g. see Taquet and Russell, 1998). Descriptions of isolated teeth are therefore typically based around a few key characters that clearly vary within the two clades

(they can be strongly present through to reduced or even absent) and can appear in either.

Spinosaurine tooth crowns are typically straight, circular in cross-section, with strong enamel ornamentation (vertically orientated ridges) and have carinae lacking denticles (Sues et al., 2002; Holtz et al., 2004; Medeiros, 2006; Sánchez-Hernández et al., 2007; Buffetaut et al., 2008). In contrast, baryonychine tooth crowns are generally slightly curved posteriorly along their length, have a slightly compressed and oval cross-section, show reduced ornamentation (often present on only the lingual face) and have fine, densely packed denticles on their carinae (Charig and Milner, 1997; Sereno et al., 1998; Taquet and Russell, 1998; Ruiz-Omeñaca et al., 2005; Sánchez-Hernández et al., 2007).

However, there are significant degrees of variation seen in the two clades, with for example some spinosaurine teeth being described with reduced ornamentation (Medeiros, 2006; Sánchez-Hernández et al., 2007) and with some degree of lateral compression (Medeiros, 2006) or some serrations on the carinae (Canudo et al., 2008). There are also teeth ascribed to Baryonychinae with missing carinae (Sánchez-Hernández et al., 2007) and with strong or even absent ornamentation (Ruiz-Omeñaca et al., 2005; Sánchez-Hernández et al., 2007). While not commented on in the literature to any great extent, spinosaurine teeth are typically larger than those of the baryonychines, as the former were absolutely larger animals on average (Dal Sasso et al., 2005; Hone et al., 2005) and the baryonychines also had approximately twice as many teeth in the dentary as the spinosaurines (Buffetaut, 1989), though perhaps a similar number in the maxilla (Dal Sasso et al., 2005).

The presence of close to five denticles per mm on the carinae of the tooth is quite close to that of previously reported counts for other baryonychine teeth. These have been recorded as approximately 7 per mm for a *Baryonyx*-like tooth from Portugal (Buffetaut, 2007) and a range of

6–13 per mm for baryonychines reported by Ruiz-Omeñaca et al. (2005)—though it is not always clear where these were measured and in the case of the latter, counts were higher in smaller teeth. However, the values for XMDFEC V 0010 are also close to (though higher than) the count of 2–4 denticles per mm made on a spinosaurine tooth from Tendaguru by Buffetaut (2008). The count for the present tooth is therefore a little lower than may be expected for a baryonychine but higher than for spinosaurines, but close to published figures for both clades. The denticles are a little larger closer to the distal part of the tooth which may explain the slightly lower count on the posterior face and at the tip, there are as few as 2–3 per mm. This has not been recorded in spinosaurids before, but this may be an absence in the literature as opposed to a novel feature of this tooth.

Overall the tooth presented here is clearly a much closer match to the baryonychine morphology than the spinosaurine one. The tooth lacks any ornamentation (more common in baryonychines), and has clearly defined carinae with very fine denticles (denticles are more commonly present in baryonychines, though the denticles counts themselves are somewhat ambivalent given the diversity seen in spinosaurid teeth). It is laterally compressed to a degree seen in other baryonychines (e. g. c. f. Sánchez-Hernández et al., 2007), is curved posteriorly along its length, and is relatively small (being similar in size to the smaller teeth of both *Suchomimus* (based on photographs provided by S. Brusatte) and *Baryonyx*—Charig and Milner, 1997). The slight sinusoidal curvature of the tooth when seen in anterior view has not previously been reported in spinosaurids, although teeth of *Suchomimus* show some lingual curvature (based on photographs provided by S. Brusatte). The asymmetrically compressed cross-section is similar to the teeth illustrated by Buffetaut (2008) and has also been noted in some other cases (e. g. see Canudo et al., 2008).

The possibility remains therefore that this is either a highly unusual spinosaurine tooth with a large number of baryonychines-like features, or less likely, belongs to a ziphodont crocodile. However, the weight of the evidence suggests that our interpretation is correct. We therefore refer this tooth to the Baryonychinae.

4 Discussion

The assignment of this tooth to the baryonychine branch of the spinosaurids significantly extends their known range both biogeographically and temporally. While spinosaurids as a whole are known from four continents and from the Late Jurassic to the Late Cretaceous (see Table 1), the baryonychines were formerly unknown either in the Late Cretaceous or in Asia. While spinosaurid teeth are certainly common in at least some formations (e. g. Medeiros, 2006) they are on the whole rather rare as fossils. Combined with the difficulty of distinguishing them from

Table 1 Temporal and geographic distribution of spinosaurid remains

| | Continent | Late Jurassic | Early Cretaceous | Late Cretaceous |
|--------------|---------------|---------------|-----------------------------|-----------------------------|
| Spinosaurine | Asia | — | Skeletal material and teeth | — |
| | Europe | — | Teeth | — |
| | Africa | — | Skeletal material and teeth | Skeletal material and teeth |
| | South America | — | Skeletal material and teeth | Teeth |
| Baryonychine | Asia | — | — | Tooth—reported here |
| | Europe | — | Skeletal material and teeth | — |
| | Africa | Teeth | Skeletal material and teeth | — |
| | South America | — | — | — |

Note: Possible spinosaurid teeth have also been reported from the Upper Cretaceous of Uzbekistan (Holtz et al., 2004), but this has yet to be verified. Data taken from: Buffetaut, 1989, 2008; Buffetaut et al., 2008; Holtz et al., 2004; Medeiros 2006; Sánchez-Hernández et al., 2007.

the teeth of other reptiles, this makes even isolated cases without the support of associated skeletal material, worthy of note.

It is interesting to note just how rare spinosaurids as a whole are. Although there are records of teeth from numerous formations (and in some cases the teeth themselves are numerous, though this is common for theropods in general), skeletal material is conspicuous by its absence. Apart from the partial skeletal material on which names have been erected (i. e. *Spinosaurus*, *Baryonyx*, *Suchomimus*, *Irritator*, *Cristatusaurus*, *Angaturama*; see Holtz et al., 2004 and references therein) very little else has been reported (e. g. see Buffetaut, 1989, 2007; Dal Sasso et al., 2005) and these additional specimens are primarily jaw fragments containing teeth. Even the name-bearing specimens are incomplete and several comprise only partial skulls. Based on the large number of both cranial and postcranial characters that are diagnostic for spinosaurids (e. g. see Sereno et al., 1998; Holtz et al., 2004), and the interest which the clade attracts, it is unlikely that isolated material has remained misdiagnosed or unreported in the literature. Spinosaurid skeletal material can therefore be considered rare.

This rarity is surprising as spinosaurids have several features which might lead to a bias in favour of their being fossilised and recovered more frequently than other theropod clades. Even allowing for a misidentification of the tooth presented in this paper, they were clearly widespread (being present in Africa, Europe, South America and Asia—Holtz, 1998; Buffetaut et al., 2008) and long-lived (present from the later Late Jurassic, through to at least the early Late Cretaceous – in excess of 50 million years at least, and the date of their inferred split from the megalosaurids would increase this still further – Holtz et al., 2004). Furthermore they were large animals, comparable in size, if not bigger than other large bodied theropods (e. g. allosaurines, tyrannosaurines—Dal Sasso et al., 2005; Hone et al., 2005), and perhaps most importantly, seem to have favoured aquatic habitats (Milner, 2003; Holtz et al., 2004; Amiot et al., 2009). All of these factors imply that, for a given population of spinosaurids and of other theropods, one might expect spinosaurids to be relatively common in the fossil record. If they favoured aquatic environments then they would be more likely to die in, or close to, water and thus be more prone to burial, and their large size would tend to favour their preservation and eventual recovery. Their extensive geographical range and temporal distribution implies that they had sufficient opportunities to enter the fossil record in numerous sites at numerous times.

Two factors complicate this issue somewhat, but do not detract from the overall assertion of rarity. One argument against this implied bias for high preservation is that fact that there are no spinosaurids known from North America which has some of the most extensive Mesozoic terrestrial fossil beds and most intense collecting seen for dinosaurs. However, there are also spinosaurids known in Asia and Europe which have been studied intensely and with extensive beds, which should therefore ameliorate this factor. Also, since spinosaurids are seen in Africa, Europe and South America, it is reasonable to speculate that they were present in North America and have simply yet to be recovered which does support the concept of genuine rarity. Secondly, a more important caveat is that spinosaurids certainly appear to have been at their peak in the Early Cretaceous (based on diversity and number of specimens)—a time that is relatively poorly represented in the rock record (Fara and Benton, 2000). As such, it is possible that the inferred rarity of spinosaurids is masked by a reduced rock record in which they could be preserved. However, while this clearly would reduce the number of specimens or taxa that might be recovered, they remain rare in both the Late Jurassic and Late Cretaceous in which they were present despite the extensive rocks available there.

While direct comparisons to other theropod clades would be difficult to quantify and qualify (and is beyond the scope of this study), there are probably less than 20 spinosaurid skeletal specimens described in the literature, and the majority of which consist of only partial jaws. This is far fewer specimens than are known from some individual theropodan genera (there are

more than 60 specimens known for *Allosaurus* alone, and more than 30 each for *Tyrannosaurus* and *Tarbosaurus*, with another three tyrannosaurs known from at least five partially complete skeletons—see Holtz et al., 2004 and Holtz, 2004), let alone comparable clades. It seems therefore a strong possibility that spinosaurids were genuinely rare animals.

Spinosaurids were clearly highly specialised animals with numerous diagnostic features in their anatomy, especially relating to their cranium and associated with prey capture and consumption (e. g. Charig and Milner, 1997; Holtz, 1998; Sereno et al., 1998; Rayfield et al., 2007). It has been noted that this extreme specialisation may have allowed them to avoid competition with other theropods by targeting fish as a substantial part of their diet (Holtz, 1998), though it is also clear that they ate a variety of other foods including dinosaurs (Charig and Milner, 1997) and pterosaurs (Buffetaut et al., 2004) either as prey or through scavenging. However, while competition with other theropods might well have been alleviated, spinosaurids would have faced competition for food from other piscivorous predators such as crocodiles and the various other aquatic reptiles of the Mesozoic. Holtz et al. (2004) noted that the increased terrestrial mobility of spinosaurids compared to, for example, a large crocodylian (and obviously greater yet compared to obligate aquatic reptiles) may have allowed them to exploit habitats at the margins of water bodies by moving from ‘pond to pond’ to find food, and to this can be added that perhaps they could therefore exploit environments that other large bodied predators could not.

This combination of factors and inferred lifestyle would correlate with their rarity. If spinosaurids were specialised for marginally productive habitats (which would fit with their range of diet, which seems broader than has been recorded for other theropod clades) and were avoiding competition both from other theropods and crocodylians, this would support the currently observed data. These factors may have led to populations (some of which may have been large) of highly specialised species (one may be specialised as well as an excellent opportunist) persisting in environments which could not support other clades, and were only occasionally present in habitats that could support other taxa.

If spinosaurids were specialised predators with unusual lifestyles (as seems likely), then whilst they were exploiting a different niche to other theropods, this niche was apparently not broad. While occurring over a wide geographic and temporal range, spinosaurids were limited in both the number of taxa and perhaps the size of the individual populations compared to more ‘terrestrially’ based and more ‘typical’ theropodan predators and thus these two factors (specialisation and niche occupation) may be closely correlated.

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