RECENTLY REDISCOVERED BARYONYCHINE TEETH (DINOSAURIA: THEROPODA): NEW MORPHOLOGIC DATA, RANGE EXTENSION & SIMILARITY TO *CERATOSAURUS*

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ABSTRACT

Newly identified baryonychine teeth from the UK Wealden illustrate the morphologic variability and stratigraphic range of this taxon. Whilst common in the formations in which they occur, their distinctive fluted and finely serrated teeth are often misidentified as crocodilian, which are superficially similar in appearance. Fourteen teeth from mainland Weald collections of the British Museum of Natural History (some collected over 150 years ago, all stored with goniopholid specimens) demonstrate the presence of baryonychines in the Hauterivian and possibly Valanginian stages of the Early Cretaceous: the oldest record of this group. An unusual laterally compressed, posteriorly recurved, and fluted tooth from the Purbeck Limestone (Late Jurassic – earliest Cretaceous) may extend the range of baryonychines even further. Some specimens from the Barremian Wessex Fm (Isle of Wight, UK) and older mainland deposits show both lingual and labial fluting, previously seen only in teeth from Spain. Spanish specimens can no longer be considered phylogenetically distinct based on this character.

The fluted premaxillary and anterior dentary teeth of *Ceratosaurus* (and to a lesser extent, some other ceratosaurs e.g. *Masiakasaurus*) bear remarkable similarity to the fluted teeth of baryonychines. Whether this represents convergence or a real phylogenetic signal requires further analysis. However, isolated teeth identified as *Ceratosaurus sp.* from the Late Jurassic of Tendaguru, Tanzania, can no longer be assigned with confidence to this taxon and should be reassessed, especially as ceratosaur lateral teeth are unknown from these strata.

The observed phylogenetic trend towards reduced denticle size in baryonychines through to spinosaurines suggests that the hypothetical ancestral condition possessed larger denticles, similar to typical theropods and what is seen in the Tendaguru teeth. A ceratosaur origin for baryonychines has been previously suggested and subsequently rejected by recent workers. However, this relationship should be critically reassessed considering the similarity between these taxa, and recent phylogenetic analyses placing *Ceratosaurus* closer to the Tetanurae.

Introduction

Known from a partial associated skeleton from the Early Cretaceous (Barremian) of Surrey, UK, the theropod dinosaur Baryonyx was hailed as an enigmatic new taxon upon its initial description (Charig & Milner, 1986). So unusual was its crocodile-like morphology, unlike any other theropod known at the time, it was placed into its own family: the Baryonychidae. Subsequent new discoveries, and reanalysis of old specimens, have shown that *Baryonyx* is closely related to the similarly enigmatic *Spinosaurus* (Stromer, 1915) from the Early Cretaceous (Cenomanian; Smith et al, 2006) of Bahariya, Egypt. A modern consensus has family Spinosauridae comprising Baryonychinae (*Baryonyx*, *Cristatusaurus*, *Suchomimus*) and Spinosaurinae (*Spinosaurus*, *Angaturama*, *Irritator*). Baryonychines are all older and less derived than spinosaurines (although see Sanchez-Hernandez et al, 2007); as such, it is likely that their morphology is closer to the ancestral state. Not having much experience with spinosaurine material, I will concentrate on baryonychines.

The highly specialized morphology of the Spinosauridae has always made their origins and relationships something of an enigma, with many branches of the theropod tree suggested as possible sistergroups. Currently, Spinosaurids are thought to be allied with the Torvosaurids forming the Spinosauroidea: a basal clade in the Tetanurae (e.g. Sereno et al, 1998; Rauhut, 2003). However, their specialized nature, and the generally poor phylogenetic resolution for basal theropods leaves this diagnosis as tentative. The origins of Spinosaurids would be better resolved if we had more material, especially from the Earliest Cretaceous and Late Jurassic. The skeletal record of all dinosaurs is notable patchy, but teeth are far more common and often diagnostic to family level. The distinctive teeth of baryonychines might therefore help in tracing back the history of the group.

PART 1- Identifying baryonychine teeth

The teeth of baryonychines are often mistaken for those of contemporaneous crocodylomorphs (typically goniopholids, Fig. 2). The similarities are superficial; baryonychine teeth have a number of attributes that make them easily discernable.

Characteristic morphology & variation in Wessex Fm baryonychine teeth:
Based on observation of dozens of specimens (see figs) from the Wessex Fm (Barremian) of the Isle of Wight, UK, it is clear that not all teeth exhibit each attribute equally. Although it is possible that more than one baryonychid species is present in the Wessex Fm, the short time period spanned by the unit, and especially the beds from which specimens have been collected, makes it more parsimonious to assume that slight morphological differences are the result of tooth position, individual, or ontogenetic variation. This is reinforced by variability seen in the type specimen (especially the premaxilla and maxilla), showing that *Baryonyx* has considerable variation in dental morphology within even a single animal.

Width, and curvature
Width and curvature can be the easiest initial means to pick out baryonychid teeth from those of crocodilians. Baryonychine teeth vary in cross section from conical and crocodile-like (Fig. 3), to moderately laterally compressed (Fig. 4). They have weak to moderate lingual curvature, and moderate posterior curvature. Crocodilians tend to have moderate to strong lingual curvature, but no posterior curvature. The posterior curvature of baryonychine teeth is not as pronounced as seen in more typical theropods (Fig. 1), which tend to show very little or no lingual curvature.

Denticles
Baryonychines are characterized as possessing very fine denticles (~7 per mm, Charig & Milner, 1997) running from the apex to the base of the crown on both mesial and distal carinae. By comparison, denticles are absent from crocodylomorphs, other than in a few aberrant marine taxa, and some basal forms with easily recognizable morphology. The typical theropod condition is to have overall lower denticle density, with carinae on only the upper 30-50% of the mesial side, and the full length of the distal side (with some exceptions, e.g. Tyrannosauridae). On occasion, wrinkles may be seen curving up towards the denticles (Fig. 5) also seen in spinosaurines (Medeiros, 2006). These are very similar in appearance to what is described in *Carcharodontosaurus* (Sereno et al, 1996), and thought peculiar to this clade.

Possession and distribution of fine denticles is a consistent character seen in all observed baryonychine teeth. However, denticles may be nearly or completely (cont…)

Fig. 1: *Neovenator*: two 'typical' theropod teeth, Isle of Wight (lateral view)

Fig. 2: a 'typical' *Goniopholis* tooth from the Isle of Wight (lingual, posterior)

Fig. 3: typical baryonychine teeth, stout, lingual flutes, finely serrated (lingual, labial / labial, lingual)

Fig. 4: laterally compressed, weakly faceted baryonychine (lingual, posterior, labial, anterior)

Fig. 5: weakly faceted baryonychine, with wrinkles on anterior carina (lingual labial)

Fig. 6a: baryonychine teeth with fluting on both lingual and labial sides, Isle of Wight

Fig. 7. (above): baryonychine tooth with labial & lingual faceting, no fluting.

Fig. 6b (right): baryonychine tooth with weak fluting on both lingual and labial sides

obliterated by long wear facets down the mesial and distal carinae (e.g. Milner & Kirkland, 2007), perhaps explaining the unexpected "spinosaurine" teeth of Sanchez-Hernandez et al (2007).

Surface texture
Granular/wrinkled enamel
The surface texture of baryonychine teeth is described as "finely granular" (Charig & Milner, 1997), and was not seen to vary amongst observed specimens. The texture is unlike other theropod dinosaurs and crocodylomorphs, but not unlike that seen in sauropods.

Longitudinal fluting and/or faceting
A 'typical' baryonychine tooth possesses 6-7 ridges and flutes ("ribs" of Buffetaut, 2007) concentrated towards the centre of the lingual side of the crown, with the enamel smoothening out towards the carinae. Ridges are sometimes present on both lingual and labial sides (Fig. 6). In specimens observed that show this character, the crowns have always been conical, with poor lateral compression. Conversely, sometimes fluting is absent from both sides of the crown (Fig.s 5). When ridges are not present, they are instead replaced by a flat faceted surface (Fig. 7), or just a typically theropodan smooth surface (Fig.s 4 & 5). Teeth lacking fluting tend to be more laterally compressed. This is unlike the condition in goniopholid teeth, where ridges are much finer and extend almost to the unserrated carinae.

New specimens

Dorset County Museum G95a, a baryonychine?
DCM-G95a (Fig. 8) resides in the collections of Dorset County Museum, Dorchester, UK. It is stored alongside a goniophold tooth (DCM-G95b), and labeled as "saurian", both teeth were labeled as having been collected from the "Purbeck?" (Lowermost Cretaceous) of Swanage. DCM-G95a exhibits granular enamel, baryonychine-like fluting on the lingual side only, a smooth labial side, slight lateral compression, moderate lingual curvature and moderate posterior curvature: characters indicating a baryonychine affinity. However, it shares some similarities with pliosaur teeth, which could certainly also be found from the Swanage area. The specimen does not show any denticles, weakening support for a baryonychine identity, but these could have been worn off the carinae.

If indeed baryonychine, the specimen is important as the Purbeck is thought to be latest Jurassic to Early Cretaceous in age, making it potentially the oldest recognized baryonychine specimen.

Various specimens in the BMNH, London: the oldest baryonychines
In an attempt to confirm the identity of DCM-G95a, I looked at the crocodilian collection in the Natural History Museum, London (BMNH), hoping to find some misidentified specimens. A selection of theropod teeth were found amongst Purbeck crocodile material (Fig. 17) but these were all very small, and I did not have time to examine them properly to ascertain if any were baryonychine, although there was one possibility.

I did find some specimens of interest: also stored amongst the goniopholids, I found 14, possibly as many as 17 typical baryonychid teeth from other UK non-Purbeck Wealden units (Table 1). Although newly recognized specimens, the presence of baryonychines in most of these units has been recognized previously (Charig & Milner, 1997). However, two specimens from the Hastings beds (R1901) are the first record of baryonychines from this unit, and are of particular interest as the Hastings beds are Valanginian and possibly Berriasian in age (Allen & Wimbledon, 1991: Fig. 9; Radley 2006a, 2006b). This would make R1901 the oldest known baryonychine teeth, slightly older than specimens described from Spain (Ruiz-Omenaca et al, 2005).

These specimens are also of historical interest as R1901 and the Purbeck theropods were part of the Samuel Beckles collection; specimens in drawer 43480 were originally part of the Mantell collection. Both collections were made over 150 years ago.

The status of *Suchosaurus cultridens* (Owen, 1841): implications for taxonomic nomenclature
Also stored in amongst the crocodilian drawers of the BMNH is a tooth (R5226, Fig. 10) labeled as *Suchosaurus cultridens*. Although somewhat worn, the morphology of R5226 is not consistent with it being a crocodilian.

Owen (1841) described some isolated teeth from the "Wealden" (Tilgate Forest, Sussex: Buffetaut, 2007) as a new crocodile: *Suchosaurus cultridens*. The name *Suchosaurus* subsequently became largely forgotten in most circles, but has prevailed amongst local collectors, particularly on the Isle of Wight, who in recent years especially, have found many of the relatively common teeth. A tooth from the Wessex Fm of the Isle of Wight, illustrated by Simpson (1993) and labeled as "*Suchosaurus*?" is clearly of baryonychine morphology: predating the identification of "*Baryonyx* sp." teeth from this formation (Martill & Hutt, 1996) by 3 years. That specimens of comparable morphology have been referred to by both names demonstrates that *Suchosaurus cultridens* teeth are clearly baryonychine and herein lies a problem.

While it is almost certainly true that *Suchosaurus* is a senior synonym of Baryonyx, the incomplete nature of *Suchosaurus* means that it is probably best to continue to use Baryonyx (Buffetaut, 2007). However, since *Suchosaurus* is the oldest recognized named genus it should take superiority over both Baryonyx and Spinosaurus with regard to hierarchal nomenclature. Thus superfamily Spinosauroidea (sensu Sereno et al 1998) becomes Suchosauroidea; family Spinosauridae (sensu: Stromer, 1915) becomes Suchosauridae, comprising Spinosaurinae (sensu Holtz et al, 2004) and Suchosaurinae (=Baryonychinae, sensu Holtz et al, 2004). Alternatively, Baryonychidae (sensu Charig & Milner, 1986) becomes Suchosauridae. These changes should occur due to ICZN rules regardless of whether *Suchosaurus* is synonymised with *Baryonyx* or not.

PART 2 – *Ceratosaurus*- convergent morphology or phylogenetic signal?

The maxillary and anterior dentary teeth of *Ceratosaurus*
The theropod dinosaur *Ceratosaurus*, from the Late Jurassic Morrison Fm, USA is unusual in that it possesses a heterodont dentition: the lateral teeth (maxilla and posterior dentary) are laterally compressed and smooth sided, as is typical for theropods, but the teeth of the premaxilla and anteriormost 3 teeth of the dentary are stout to conical (itself not so unusual), with a fluted lingual surface, and smooth labial surface (Madsen & Welles, 2000; Fig. 11). The number of flutes and their morphology is near-identical to that seen in baryonychine teeth. This has gone unnoticed in the literature thus far, possibly due to the fact that the premaxillary and anterior dentary teeth in the holotype of *Ceratosaurus* were lost prior to fossilization. Consequently this character has not been seen to be included in any phylogenetic analyses of basal theropods.

In fact, fluted teeth are seen in a number of non-tetanuran theropods including juvenile individuals of *Coelophysis* (Colbert, 1989: Fig. 12; contra Sereno et al, 1998), and *Masiakasaurus knopfleri* (Carrano et al, 2002: Fig 13), although in these taxa the fluting does not look nearly so similar to baryonychines.

Fig. 8: "Saurian" tooth from the Purbeck Fm, Dorset UK (ling, ant, lab, post)

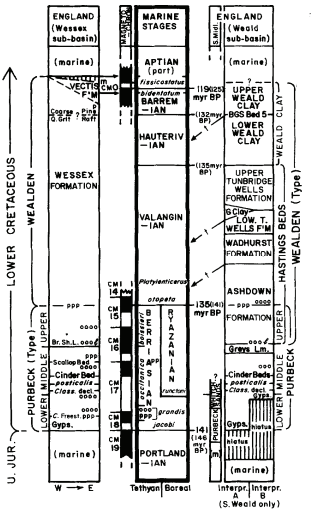
Table 1: Baryonychine teeth stored with goniopholids in the BMNH, London, UK

Draw 48340
- **Isolated teeth from Mantell coll.**
  - **3 baryonychines: 3316, 3279, & 3312**

Bottom drawer-same column
- **isolated Goniopholis teeth, Atherfield IOW UK**
  - **R5165: 1 baryonychine tooth tip with wear facets**

Hastings Beds, Beckles collection
- **R1901: 2 baryonychine teeth: 1 in matrix, 1 broken in half**

"Goniopholis sp." drawer –lots of teeth
- **26030: baryonychine**
- **36533: 1 tooth in matrix, 1 stuck on card are baryonychine**
- **3330 –appears a bit too narrow for crocodile, probable baryonychine**
- **26032 –baryonychine from the Sussex sst**
- **R213 -2 baryonychine teeth mixed in with lots of croc, Isle of Wight**
- **33119 –Tilgate forest baryonychine tooth**
- **3240 –baryonychine tooth from Sussex**
- **R642 -1 probable baryonychine tooth (med size), plus another that is fluted on both sides**
- **26031 –baryonychine in sst**
- **10822,5 –Sussex Wealden baryonychine tooth & *Lepidotes* scale**



Courtesy J. H. Madsen, Jr.

Fig. 10: (above) Isolated Isle of Wight theropod tooth attributed to *Suchosaurus cultridens*.

Fig. 9: (left) stratigraphy of baryonychine-bearing units, Wealden, UK (from Allen & Wimbledon, 1991)

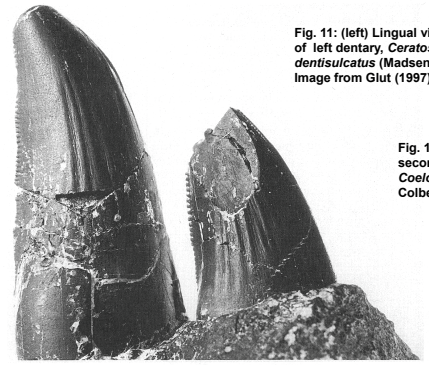


Fig. 11: (left) Lingual view, anterior teeth of left dentary, *Ceratosaurus dentisulcatus* (Madsen & Welles, 2000). Image from Glut (1997).

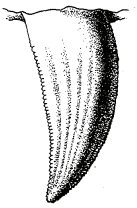


Fig. 12: (below) immature second right maxillary tooth, *Coelophysis bauri*. From Colbert (1989)

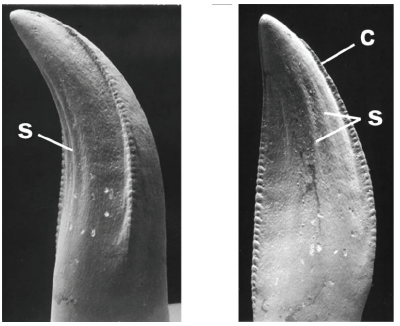


Fig. 13: Teeth of *Masiakasaurus knopfleri*. (left) anterior dentary or premaxillary tooth, posterolateral view; (right) "more posterior tooth" posterior view. Note the flutes/ridges on both teeth (marked as "s"). From Carrano et al (2002)

Isolated "*Ceratosaurus* sp." teeth, Late Jurassic, Tendaguru, Tanzania.

In his report on Late Jurassic theropods from Tendaguru, Tanzania, Janensch (1925) figured a number of fluted teeth which he assigned to *Labrosaurus*? *stechowi* (Fig. 14). Madsen & Welles (2000) ascribe these teeth to *Ceratosaurus* sp., citing their similarity to the premaxillary and anterior dentary teeth of *Ceratosaurus* (curiously enough, no lateral teeth of *Ceratosaurus* have been recovered from Tendaguru (Rauhut, 2006), although some postcrania have been attributed to ceratosaurids). Being relatively stout / laterally uncompressed, with densely packed denticles ("finely serrated": Madsen & Welles, 2000), and a fluted lingual surface, it is possible that rather than *Ceratosaurus* sp., these are teeth of a Late Jurassic baryonychine, or baryonychine ancestor. This would fit with current biogeographic models where spinosaurids evolved in Gondwana, later spreading to Europe in the Early Cretaceous.

Discussion & Conclusions:

It is possible that similarities in these teeth represent a remarkable convergence. Baryonychines are hypothesised to have been piscivorous, as are many crocodiles, and there is at least circumstantial evidence in support of this lifestyle in coelophysoids (Milner & Kirkland, 2007) and *Ceratosaurus* (Bakker & Bir, 2004). It is possible that independently acquired piscivorous habits caused unrelated tooth morphological convergences in these taxa. Alternatively it is possible that baryonychines may be more closely related to one of these theropod groups than previously thought. Most recent cladistic analyses of basal Theropoda have removed *Ceratosaurus* and other ceratosaurids from bring pulled into the traditional "Ceratosauria" clade (ie. inclusive of *Coelophysis* and other coelophysoids), and placed them instead as the sister-group to the Tetanurae (e.g Ezcurra & Novas, 2007; Fig. 15). Thus, it is no longer such a huge leap in character alignments to ally the spinosaurids with the ceratosaurids. A relationship between ceratosaurids and spinosaurids was originally suggested by Paul (1988) citing a number of morphological similarities, and it is perhaps time to look again at this hypothesis. An exhaustive review of basal theropod characters is beyond the scope of this poster, but an initial survey has suggested some characters used to place Spinosauridae within the Tetanurae may not be correct. This is very tentative at the present though, and requires further study.

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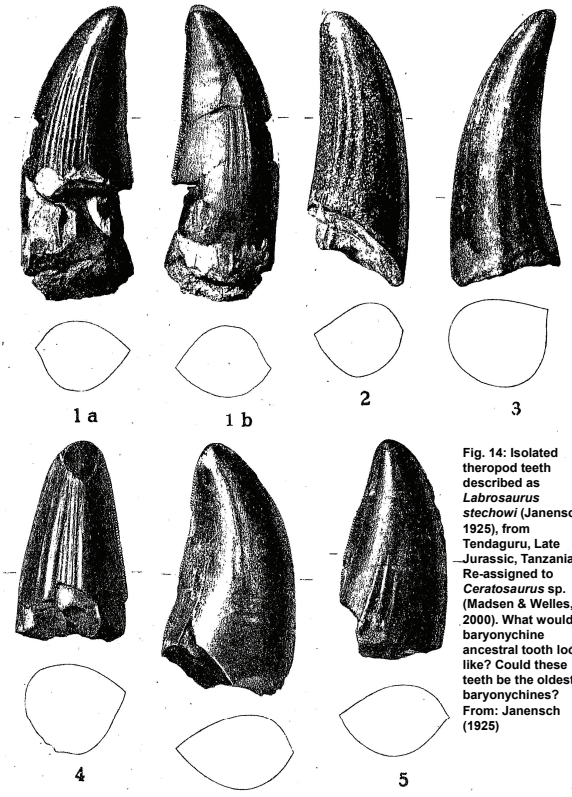

Fig. 14: Isolated theropod teeth described as *Labrosaurus stechowi* (Janensch, 1925), from Tendaguru, Late Jurassic, Tanzania. Re-assigned to *Ceratosaurus* sp. (Madsen & Welles, 2000). What would a baryonychine ancestral tooth look like? Could these teeth be the oldest baryonychines? From: Janensch (1925)

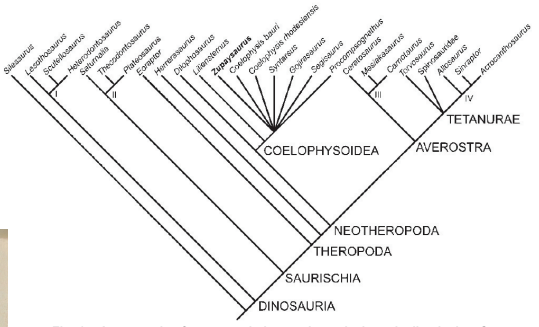

Fig. 15: An example of a recent phylogenetic analysis typically placing *Ceratosaurus* closer to Tetanurae. Note the very basal position of Spinosauridae within Tetanurae. From Ezcurra & Novas (2007)

Fig. 17: A selection of probable theropod teeth from the Purbeck, UK

Fig. 16: (right) a selection of other baryonychid teeth from the Wessex Fm, Isle of Wight