



# A CATALOGUE OF MATERIAL AND REVIEW OF THE SPINOSAURIDAE

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## ABSTRACT

Spinosaurids are a monophyletic clade of large-bodied, long-snouted theropod dinosaurs known from minimal skeletal material. In an effort to assist future research on this unusual clade, a catalogue of past spinosaurid discoveries is presented. Database information includes specimen numbers, material identification, locality information, depositional environments, stratigraphic detail, generic or subclade assignment, tooth measurements, tooth placement, and detailed notes on the nature of the finds themselves when needed. Previously reported biogeographic and faunal dispersal patterns suggest that spinosaurids may eventually be found in North American strata, potentially having migrated from western Europe in the Early Cretaceous and eastern Asia over the Beringian isthmus in the Late Cretaceous. This database may be useful for predicting future points of spinosaurid discovery.

## Introduction

Spinosaurids, a highly morphologically specialized group of tetanuran theropod dinosaurs most distinctly characterized by their laterally compressed snouts and subconical crocodile-like teeth have undergone a substantial surge of study and interest in recent years. The clade was first erected on the basis of a series of disarticulated bones and teeth uncovered in the Cenomanian dated Bahariya Oasis of north-central Egypt by an expedition funded by the

German paleontologist Ernst Freiherr Stromer von Reichenbach (1870-1952) (Stromer, 1915). Among these fossils was a group of dorsal vertebrae with markedly hypertrophied neural spines (some up to 1.65 meters in height), which Stromer referenced when naming the taxon *Spinosaurus aegyptiacus*. However, the holotype and all referred material were demolished in an Allied air raid on the city of Munich April 12/13, 1944 (Stromer, 1915; Stromer, 1934 but especially see Smith *et al.*, 2006), and for some time remained something of a paleonto-

logical mystery. Thankfully, our understanding of these remarkable animals has grown a great deal due to the many discoveries made within the last several decades.

Partial skeletons have been described from the Cenomanian of Egypt (Stromer, 1915), the Aptian of Niger (Sereno *et al.*, 1998) and the Barremian of England (Charig & Milner, 1997), as well as several remarkable cranial and axial fossils from what is likely the Albian and Cenomanian of South America (Kellner & Campos, 1996; Martill *et al.*, 1996; Sues *et al.*, 2002; Bittencourt & Kellner, 2004; Machado & Kellner, 2008). Aside from these fossils, spinosaurid material generally tends to be quite rare, most frequently consisting of isolated teeth and bone fragments (Holtz *et al.*, 2004; figure 1).

Recent phylogenetic analyses suggest that the clade can be split into two separate groups, primarily distinguishable by cranial and dental differences: the Spinosaurinae and Baryonychinae (Charig & Milner, 1986, Sereno *et al.*, 1998, Holtz *et al.*, 2004). Cranially, baryonychines are distinguished from spinosaurines by an in-

creased number of teeth in the mandible, a lesser degree of retraction of the anterior margin of the external nares (limited to the first half of the maxillary tooth row), and differing premaxillary tooth size. Specifically, the premaxillary alveolus 1 is only slightly smaller in diameter than alveoli 2 and 3, whereas in spinosaurines the premaxillary alveolus 1 is less than one half the diameter of premaxillary alveoli 2 and 3 (Sereno *et al.*, 1998; Dal Sasso *et al.*, 2005).

Though all spinosaurid teeth display a degree of conical shape (thought to be indicative of an at least partly piscivorous lifestyle – Rayfield *et al.*, 2007), baryonychine teeth are generally more laterally compressed in form than those attributed to the Spinosaurinae. Additionally, spinosaurine teeth lack serrated carinae and on average display less posterior curvature when compared to their baryonychine counterparts (*pers. obs.*) whose teeth are typically quite finely serrated (Martill & Hutt, 1996). Though ribbing or 'fluting' structures have been reported on the crowns of both subclades, the texture tends to be more distinctive in spinosaurine



Figure 1. Skeletal reconstructions of *Baryonyx walkeri*, *Suchomimus tenerensis*, and *Spinosaurus aegyptiacus*. Silhouette represents the largest known fragmentary material of *Spinosaurus*. Scale bar = 1m. Courtesy of Scott Hartman ([www.skeletaldrawing.com](http://www.skeletaldrawing.com)).

teeth, whereas baryonychine ribbing is most often light and restricted to the lingual face. However, a fair amount of morphological variation has been reported for spinosaurid teeth, and identification should be done with a degree of caution (Fowler, 2007; Hone *et al.*, 2010).

Spinosaurid fossil traces have been reported from Europe, Asia, Africa, and South America (Holtz *et al.*, 2004). As yet, no confirmed North American spinosaurid fossils have been found. They have a wide temporal distribution, with documented discoveries spanning the Late Jurassic (Buffetaut, 2008b) through the Late Cretaceous (Hone *et al.*, 2010).

Due to the scarcity of spinosaurid fossils, and the lack of character resolution in many early studies, their affinities within Neotheropoda have fluctuated throughout the years. Though long-spined allosauroids like *Acrocanthosaurus atokensis* (Stovall & Langston, 1950) were periodically included within the Spinosauridae (Walker, 1964; Romer, 1966), this classification scheme was ultimately abandoned. With the discovery of *Baryonyx walkeri* in the Barremian of England, Charig & Milner (1986) placed the taxon within a family they dubbed the Baryonychidae, suggesting that there were not enough affinities between it and *Spinosaurus* to validate placing the pair within a monophyletic clade. However, this particular designation was questioned by various authors (Paul, 1988; Buffetaut, 1989), and began to fall out of favor by the 1990s (Serenó *et al.*, 1994; Serenó *et al.*, 1998; Holtz, 2000; Holtz *et al.*, 2004). A cladistic analysis performed by Serenó *et al.* (1994) placed the spinosaurids and torvosaurids in a clade dubbed the Torvosauroidea (now known as Megalosauroidea – Benson, 2010), which was later defined as a “comprises *Spinosaurus aegyptiacus* and all taxa sharing a more recent common ancestor with it than with *Passer domesticus*, *Megalosaurus bucklandi*, or *Allosaurus fragilis*” by Holtz *et al.* (2004: 97). Recent analyses have consistently placed spinosaurids within Megalosauroidea near the base of Tetanurae (Serenó *et al.*, 1998, Holtz *et al.*, 2004, but especially see Benson, 2010).

With the rarity of described spinosaurid fossil material in mind, this paper seeks to provide a collections catalogue and review to spur future research on this curious clade. Though the group has received a material review in recent years (Holtz *et al.*, 2004), and has had a

fair amount of biogeographic work (Buffetaut, 2009), many extraordinary discoveries have been made since Holtz *et al.*'s (2004) review that bear a great deal of importance for the field of spinosaurid research. Though in many instances this catalogue overlaps with information found within the Paleobiology Database (<http://paleodb.org>), it differs in several key respects. Firstly, the information provided is intended for a specialized subset of workers, and so is arranged in such a fashion that the needed data is more instantly accessible. Secondly, detailed information on the material type is listed. Though the Paleobiology Database lists occurrences of various fossil taxa, the exact variety of fossil material within the given occurrence is often left vague (*e.g.* “MNN GD 500, a set of postcrania”, in reference to the *Suchomimus tenerensis* holotype). Finally, though the measurements themselves are derived from the publications individual teeth were described in (and so were not directly confirmed by the author), dental measurements may form an important basis for future numerical analyses, and are presently lacking for the Spinosauridae in the Paleobiology Database. For fossils requiring further discussion (*e.g.* those with issues of taxonomic validity, or those with a range of measurements nonassignable to individual teeth), notes are provided. When such information was merited, the entries are listed as such under the ‘Reference’ column in the database.

### Institutional Abbreviations

BM	Office National des Mines (La Charguia, Tunisia)
CAM	“Cameroon” (exact location unspecified)
CMP	Museo de la Valltorta (Castellón, Spain)
GMNH	Gunma Museum of Natural History (Tonmioka, Japan)
HAI	Henan Geological Museum (Zhengzhou, China)
IMGP	Institut und Museum für Geologie und Paläontologie of the Georg-August Universität (Göttingen, Germany)
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology (Beijing, China)

IWCMS	Dinosaur Isle (Isle of Wight Museum of Geology) (Sandown, UK)
J.G.	Museo Arqueológico Paleontológico (Salas de los Infantes, Spain)
LINHM	Long Island Natural History Museum (Long Island, NY)
MG	Museu Geológico (Lisbon, Portugal)
MN	Museu Nacional / UFRJ (Rio de Janeiro, Brazil)
MNHN	Muséum National d'Histoire Naturelle (Paris, France)
MNN	Musée National du Niger (Niamey, Republic of Niger)
MPG	Museo Paleontologico de la Galve (Teruel, Spain)
MPZ	Museo Paleontologico de la Universidad de Zaragoza (Zaragoza, Spain)
MUZ PIG	Geological Museum of the Polish Geological Institute (Warsaw, Poland)
MSNM	Museo di Storia Naturale di Milano (Milan, Italy)
NHM	Natural History Museum (London, England)
NMC	Canadian Museum of Nature (Ottawa, Canada)
PS	Museo de Dinosaurios (Burgos, Spain)
XMMDFEC	Xixia Museum of Dinosaur Fossil Eggs of China (Xixia, China)
SMNS	Museum für Naturkunde Stuttgart (Stuttgart, Germany)
UFMA	Universidade Federal do Maranhão (São Luis, Brazil)
UPC	University of Chicago Paleontological Collections (Chicago IL)

### Database Notes (see Appendices)

#### *Spinosaurid Tooth Identification*

Because of their specialized nature, the identification of spinosaurid dentition can be complex. Many clades have convergently evolved conical teeth throughout their evolutionary history, though due to their shared geographic and temporal range spinosaurid teeth are most likely to be mistaken for the teeth of crocodylian taxa and vice versa (Holtz, 1998). This difficulty arises in that though spinosaurid teeth are distinctive in

morphology, they have several characters (longitudinal ridges, conical form, etc.) that are also found in those of non-spinosaurid taxa (Fowler, 2007). Baryonychine teeth are characterized by fine, uniform serrations (which differ from the more bulky serrations found on the teeth of many ziphodont crocodylians, Riff & Kellner, 2001), a slight degree of posterior curvature (differing from the lingual curvature common to most crocodylians, though posterior curvature has been reported for some taxa, Norell *et al.*, 1994), and distinctive ridges generally found on the lingual face (Charig & Milner, 1997). The ridges tend to be more prominent in spinosaurine teeth (which lack serrations, Buffetaut *et al.*, 2008), though ridge morphology has been shown to vary between spinosaurid teeth (Martill & Hutt, 1996; Charig & Milner, 1997; Torcida *et al.*, 1997; Buffetaut, 2007; Fowler, 2007), and should not be used as a primary basis of identification. Crocodylian taxa have been reported with similar longitudinal ridges (*e.g.* *Brachychampsa*, *Goniopholis*, Holland, 1905; Norell *et al.*, 1994), and may be mistaken for spinosaurid teeth. Though spinosaurid teeth are typically quite conical in form, their crown base ratio (see Smith *et al.*, 2005) can vary. Adding further complication, crocodylian teeth with labial/lingual compression have been described (Norell *et al.*, 1994; Sereno & Larsson, 2009). Granular textures can be found on the crowns of some spinosaurid teeth, though a somewhat similar morphology has been reported on a mosasaur tooth (Charig & Milner, 1997; Hasegawa *et al.*, 2010 and references therein). Because of the morphological variation seen in spinosaurid teeth, a detailed study on their dentition seems merited, though such a thing is beyond the scope of this publication.

#### *Buffetaut & Ingavat (1986): Siamosaurus suteethorni Teeth*

Uncovered in the Early Cretaceous Sao Khua Formation of Northeastern Thailand (initially thought to be Late Jurassic, see Buffetaut & Suteethorn, 1998), these teeth represent the first known spinosaurid material from Asia (Buffetaut & Ingavat, 1986). As reported in other spinosaurid teeth, the collection displays a certain amount of morphological variability, with cross sections ranging from ovular to near circular. Marked ribbing is displayed on both the

labial and lingual faces, with roughly 15 ribs per side. Interestingly, the mesial and distal carinae were reported to lack serrations, a characteristic associated with teeth assigned to the Spinosaurinae. However, pending cranial material from the taxon bearing these teeth, their affinities within the Spinosauridae are currently tentative, and are listed in the database as 'indeterminate subclade.'

*Siamosaurus suteethorni* was erected based upon the then-novel morphology of the teeth, using specimen TF 2043a as the holotype (Buffetaut & Ingavat, 1986, figure 2). However, because much has been learned about the nature of spinosaurid dentition since their publication, a redescription dealing with their generic validity is currently being prepared (Buffetaut pers. comm.).

#### *Congleton (1990): Cameroon Teeth*

These teeth, collected in a series of expeditions in the Koum Basin of Northern Cameroon (Congleton, 1990) bear a fair resemblance to those commonly assigned to the Baryonychinae, with distinctive labial/lingual ridges and fine denticulation. However, the teeth differ from standard



Figure 2. Spinosaurid teeth. A) *Siamosaurus suteethorni* holotype, Thailand (Sao Khua Formation – Pre-Aptian); B) Indeterminate spinosaurid, Thailand (Khok Kruat Formation – Aptian). Images not to scale. Courtesy of Eric Buffetaut.

baryonychine teeth in that the serrations are entirely restricted to the distal margin (Charig & Milner, 1986; Charig & Milner, 1997; Martill & Hutt, 1996; Fowler, 2007). A similar serration pattern has been reported by several authors, though the Cameroon fossils represent the only spinosaurid teeth with this sort of denticulation described outside of Spain (Ruiz-Omeñaca *et al.*, 1997; Infante *et al.*, 2005; Ruiz-Omeñaca *et al.*, 2005; Sánchez-Hernández *et al.*, 2007; Canudo *et al.*, 2008; Gasca *et al.*, 2008).

Most of the teeth bearing this serration pattern are quite small (those reported by Infante *et al.*, 2005; Ruiz-Omeñaca *et al.*, 2005; Sánchez-Hernández *et al.*, 2007 and Congleton, 1990 display mesio-distal basal lengths ranging from 2 to 7.51 mm). However, teeth discussed by Ruiz-Omeñaca *et al.*, 1997 and Canudo *et al.*, 2008 fall outside this size range (ranging from 7.4 to as much as 19.48 mm). Whether this kind of denticle morphology is a byproduct of ontogenetic, interspecific, or intraspecific variation has yet to be determined.

#### *Martill & Hutt (1996): Isle of Wight Tooth Measurements*

Mesio-distal lengths range from 8 to 23 mm. Medial lateral widths not provided. Maximum preserved crown heights range from 18 to 44 mm. Serrations are found on both the mesial and distal carinae, with 7 to 8 denticles per mm.

#### *Kellner & Campos (1996): Angaturama limai Taxonomic Assignment*

*Angaturama limai*, named on the basis of a rostral cranial fragment from the Romualdo Member of the Santana Formation of Brazil, is now considered by most authors to be a junior synonym of the spinosaurine *Irritator challengeri* (Charig *et al.*, 1997; Sereno *et al.*, 1998; Buffetaut & Ouaja, 2002; Sues *et al.*, 2002; Dal Sasso *et al.*, 2005), an assertion maintained here. Because they both come from the same stratigraphic area, and their remains evidently compliment each other so well, it has been postulated that both cranial fragments may belong to the same specimen (Sereno *et al.*, 1998).

#### *Russell (1996)/Taquet & Russell (1998): Spinosaurus moroccanus and Cristatusaurus lapparenti Taxonomic Assignments*

A group of bones uncovered in the Albian of Morocco were used by Russell (1996) to es-

establish a second species of *Spinosaurus*, based upon the “relatively greater central and neural arch length” of a cervical vertebra (*Ibidem*: 360). However, this distinction is fairly dubious and very well may be a byproduct of a differential placement in the cervical series (Rahaut, 2003; Dal Sasso *et al.*, 2005). Therefore, the species *Spinosaurus moraccanus* is here considered nomen dubium (as per Sereno *et al.*, 1998) and all referred material (including a rostral cranial fragment described by Taquet & Russell, 1998 whose features share no particular distinction from that described by Dal Sasso *et al.*, 2005) is instead referred to *Spinosaurus cf. aegyptiacus* in the database.

Similarly, cranial and vertebral material were assigned to a species of baryonychine spinosaurid dubbed *Cristatusaurus lapparenti* by Taquet & Russell (1998), a taxon said to be generically separated from *Baryonyx walkeri* by the ‘brevirostrine condition’ of the premaxilla. Though not elaborated upon by the authors, this was likely in reference to the characteristic spinosaurid terminal rosette. Based upon inspection of previously published photographs and line drawings (Charig & Milner, 1997; Sereno *et al.*, 1998; Taquet & Russell, 1998), I find no particular distinction between the holotypic remains of *Cristatusaurus lapparenti* and the fossil material of other baryonychine spinosaurids, a conclusion also made by several previous authors (Charig & Milner, 1997; Sereno *et al.*, 1998; Sues *et al.*, 2002). Though it may likely belong to *Suchomimus tenerensis*, the specimen is instead listed as ‘baryonychine indet.’ in the database because of the fragmentary nature of the material.

#### *Medeiros (2006): Cajual Island (Brazil) Teeth*

Tooth length measurements given likely reflect the length of the crown in addition to root length (though not specifically stated by the author). Of superlot UFMA 1.2.444, 273 teeth were collected, with tooth lengths ranging between 13 and 98 mm, though he suggested that some tooth fragments may belong to teeth exceeding the 100 mm mark.

#### *Sánchez-Hernández et al. (2007): Spanish Spinosaurine Report*

A series of six teeth were attributed to the Spinosaurinae by Sánchez-Hernández *et al.* (2007), based upon their lack of serrated carinae

and semi-conical to conical shape. Fowler (2007) suggested that though they are in all likelihood spinosaurid teeth, the lack of serrated carinae may be instead due to a variety of wear facet in which much of the mesial and distal carinae are drastically worn away or outright obliterated (*e.g.* Milner & Kirkland, 2007). However, pending restudy of the specimens, they are listed in the database as ‘questionable spinosaurine.’

#### *Buffetaut et al. (2005): Thailand Skeletal Material*

Buffetaut *et al.* (2005) briefly reported on a partial spinosaurid skeleton from the fluvial deposits of the Aptian dated Khok Kruat Formation of northeastern Thailand. Remains included several dorsal and cervical vertebrae as well as various pelvic elements with baryonychine characters. Interestingly, they also reported on an elongate neural spine of a morphology somewhat reminiscent of that of *Spinosaurus aegyptiacus* (Stromer, 1915), though not quite as tall in stature (using the provided figure, length of the spine is roughly 60 cm). These represent the first reported skeletal remains of an Asian spinosaurid.

#### *Salgado et al. (2009)/Canudo et al. (2004): Argentine Tooth Report*

Uncovered in the Cerro Lisandro Formation of south central Argentina, this tooth is somewhat questionably identified as spinosaurid by the authors. Though the conical shape and labial/lingual ridges are generally indicative of a spinosaurid identification, the tooth exhibits uncharacteristically large serrations (inclined towards the apex) for members of the clade. The serration size is relatively similar to those of ziphodont crocodiles (Riff & Kellner, 2001; Turner & Calvo, 2005; Larrson & Sues, 2007). However, its identification is tentative and is therefore listed as a questionable indeterminate spinosaurid in the database.

## Spinosaurid Review

### *Spinosaurid Ecology*

With their wide geographic distribution and specialized morphology, spinosaurids were a remarkable component of Mesozoic ecosystems. However, compared to other large bodied theropod clades (for example, tyrannosaurids, Currie *et al.*, 2003; Carr & Williamson, 2004), their preserved skeletal material is quite sparse. As a

consequence, we can only make minimal (and still sometimes speculative) inferences about their ecological dynamics. Combining their distinctive morphological features with the little dietary evidence we do have (including remnants of fish, juvenile dinosaurs, and pterosaurs, Charig & Milner, 1997; Buffetaut *et al.*, 2004), it would seem that spinosaurids had a very broadly based diet (figure 3). It has been suggested that they would have made superb scavengers (*e.g.* Kitchener, 1987) and it seems likely that, as with most extant carnivores, this would certainly be something spinosaurids would have pursued when given the opportunity. The degree to which the clade supplemented their diet with fish (as suggested by the acid etched scales found with the holotypic specimen of *Baryonyx walkeri*, as well as the crocodylian-like morphology of the clade) requires further testing, though finite element analysis performed by Rayfield *et al.* (2007) strongly supports the hypothesis of a piscivorous lifestyle. In the study, the torsional and bending stresses of the rostrum of *Baryonyx walkeri* were compared to those of a 'generic theropod' model, the extant American alligator (*Alligator mississippiensis*), and the extant Indian gharial (*Gavialis gangeticus*). It was found that the response of the rostrum to stress loads varied between taxa, and that the stress loading capabilities of the *Baronyx walkeri*

rostrum much more closely matched that of the gharial than that of the American alligator or the generic theropod model, being especially well suited for resisting bending stresses. Given that the diet of the Indian gharial is primarily composed of fish (Whitaker & Basu, 1982), it seems likely that the skull of *Baryonyx walkeri* would have functioned in a similar manner. However, as mentioned by Rayfield *et al.* (2007), much work remains to be done on the issue, especially focusing on how the skull functions as a component of the craniocervical complex.

Furthermore, a detailed intra-generic analysis of spinosaurid cranial biomechanics has yet to be performed. Specifically, the rostral material known for *Spinosaurus aegyptiacus* (Dal Sasso *et al.*, 2005) and that of baryonchine spinosaurids (Charig & Milner, 1997; Sereno *et al.*, 1998; Taquet & Russell, 1998) differs to a noticeable degree in the width of the anterior premaxillary region and its relationship to the width of the more posterior portions of the rostrum (figure 4). In *Spinosaurus aegyptiacus*, the 'terminal rosette' (the hook-like structure of the rostrum) is markedly expanded into a somewhat circular profile in dorsal view, which begins to thin posteriorly at the 3rd premaxillary alveolus. This rostral thinning ceases at the 4th premaxillary alveolus, where the rostrum maintains a subparallel profile until it expands once



Figure 3. Life restoration of *Spinosaurus aegyptiacus*. Fauna based upon the Kem Kem region of Morocco (Cavin *et al.*, In press). Courtesy of Brian Engh (<http://dontmesswithdinosaurs.com/>)

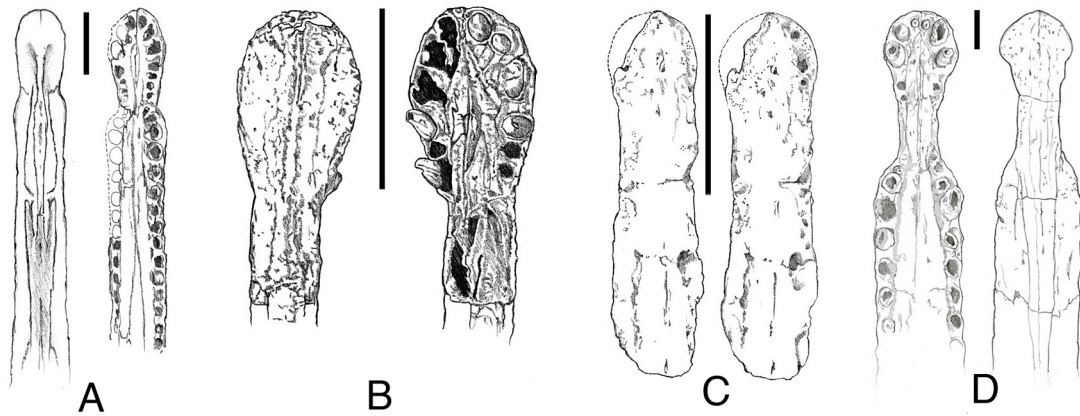


Figure 4. Preserved rostral material for the Spinosauridae in dorsal and ventral views. A) *Suchomimus tenerensis* (Sereno *et al.*, 1998); B) *Baryonyx walkeri* (Charig & Milner, 1997); C) *Irritator challengeri* (Kellner & Campos, 1996); D) *Spinosaurus aegyptiacus* (Dal Sasso *et al.*, 2005). Scale bar = 10 cm. Courtesy of Matt von Rooijen ([www.optimisticpainter.wordpress.com](http://www.optimisticpainter.wordpress.com)).

again at the 1st maxillary alveolus. This expansion then reaches a width subequal to that of the maximum diameter reached by the terminal rosette at the 3rd maxillary alveolus, a form maintained for the rest of the preserved rostrum. In baryonchines, there is little difference in the width of the terminal rosette (which has a more ovular profile) relative to the rest of the rostrum. In *Irritator challengeri*, this subparallel arrangement of the premaxillae and maxillae is even more prominent than that seen in baryonchines (Kellner & Campos, 1996). It should be investigated whether the arrangement of the premaxillae and maxillae in *Spinosaurus* is related to the downturned nature of its terminal rosette (relative to the more upwardly oriented rosette of most other known spinosaurid cranial material). Though a similarly circular profile was briefly reported in a Brazilian spinosaurine (Machado *et al.*, 2009), the rosetta's orientation was not discussed. How the difference in serration density may have related to the ecological dynamics of spinosaurid taxa should also be subjected to inquiry.

Of possible ecological importance, the dentition of *Spinosaurus aegyptiacus* bears a similarity to the teeth of the Nile crocodile (*Crocodylus niloticus*). In *C. niloticus*, the 4th premaxillary tooth and the 1st and 4th dentary teeth are enlarged to assist in prey seizure (Brazaitis, 1973; Iordansky, 1973). Likewise, the 5th maxillary tooth is similarly expanded, often used to crush small bones and compress food items prior to swallowing (Njau & Blumenschine, 2006). In *Spinosaurus*, the 2nd and 3rd premaxillary teeth are distinctively larger than the surrounding teeth (Dal Sasso *et al.*, 2005: figures 1 and 5).

So too are the 3rd and 4th maxillary teeth. However, the dentition of the two taxa differs in that dentary teeth 10 and 11 of the Nile crocodile are enlarged, while in *Spinosaurus*, the mid to posterior dentary teeth (6-15) are comparatively small (Stromer, 1915; Smith *et al.*, 2006), though dentary teeth 2-4 are relatively large. Previous work (Hone & Rauhut, 2010) suggests that osteophagy may not have been a particularly common practice by theropod predators, and as such it seems unlikely that the large maxillary teeth of *Spinosaurus* were preferentially used for bone crushing (though as they stated in the review, the evidence is presently equivocal). This is not to say that bones were immune to damage during feeding, but any marked or broken bones would likely be a passive product of the feeding process, and not an active goal (this idea is exemplified by a broken spinosaurid tooth embedded in an azhdarchid cervical vertebra, a relatively lightly built bone, Buffetaut *et al.*, 2004). More direct feeding evidence is needed to test this hypothesis. Given their anteroventral inclination and relative proximity to the terminal rosette, the maxillary teeth 3 and 4 of *Spinosaurus aegyptiacus* may have had a function in stabilizing struggling prey.

Biomechanical analysis of the spinosaurid quadrate articulation (Hendrickx & Buffetaut, 2008) suggested an interesting variety of prey acquisition: as the animal's upper jaw moved downward, the posterior regions of the mandible would have diverged laterally, likely to ease the passage of otherwise excessively large prey items into the digestive system (including, by inference, fish). Furthermore, they suggested that as the jaws opened, the anterior



mandibular rami would have diverged due to the weak and short symphyseal region, allowing the mouth and pharynx to widen. Similar cranial morphologies are found in extant semipiscivorous avian taxa (pelicanids) and ornithocheiroid pterosaurs (Bennet, 2001). However, whether the present evidence suggests that cranial kinesis is possible within non-avian dinosaur taxa has been questioned (Holliday & Witmer, 2008). With the absence of any kind of extant biomechanical analogue, rigorous computer simulations or physical reconstructions might be used to investigate potential uses for the massive hand claws characteristic of various members of the clade, taking the orientation and the degree of movement allowed for the arms and wrists into account.

Molecular analysis performed by Amiot *et al.* (2010) found that spinosaurids generally have an isotopic  $^{18}\text{O}$  signature more closely matched to that of aquatic taxa than that of terrestrial theropods (though the pattern was less noticeable in *Spinosaurus aegyptiacus*). This may be a byproduct of their specialized morphology, and seems to imply a semi-aquatic lifestyle. Beyond a niche partitioning strategy, the authors suggest that spending time in water might have also served a thermoregulatory function. With this in mind, Dal Sasso *et al.* (2005; 2009) briefly reported on a unique neurovascular cavity in the anteriormost portion of the rostrum of *Spinosaurus aegyptiacus* that may have functioned in a similar manner to the dome pressure receptors of extant crocodylians, aiding in underwater prey capture without relying strictly on sight (Soares, 2002). It has yet to be determined if this anatomical feature is found in other spinosaurids.

Though a causal link is questionable, it's interesting to note that the large neural spines characteristic of *Spinosaurus aegyptiacus* and the as yet unnamed spinosaurid from Thailand appear at a period of heightened global warming (likely sparked by a marked change in mantle circulation, see Wignall, 2001; Russell & Paesler, 2003), starting at the Barremian/Aptian boundary and continuing until the Santonian/Campanian. Similar vertebral morphologies independently evolved in at least four different dinosaurian groups during this time (spinosaurids, dicraeosaurids, rebbachisaurids, and iguanadontids, Lavocat, 1954; Taquet, 1976; McIntosh, 1990; Salgado & Bonaparte, 1991;

Russell, 1996). Though its phylogenetic affinities are presently unsettled, the South American sauropod *Agustinia ligabuei* also exhibits similarly elongate neural spines (Bonaparte, 1999). Although these 'sail' structures (but see Bailey, 1997) likely held multiple purposes (including display), an increase in surface area may have also helped the animals regulate their body temperature (Philips & Heath, 1992).

#### *Spinosaurid Paleogeographic and Temporal Distribution*

The traditional interpretation of spinosaurid paleogeographic dispersion suggested a vicariant model, in which the two subclades were split by the opening of the Tethys Seaway. The baryonychines were thought to have evolved in Laurasia while the spinosaurines evolved in Gondwana (Serenó *et al.*, 1998). The occurrence of *Suchomimus tenerensis* in the Aptian of Niger was explained by a single dispersal event in the Early Cretaceous, possibly over the Iberian plate (Milner, 2003; Buffetaut, 2007). However, recent research has suggested that theropod distribution was far more cosmopolitan in nature than previously supposed (figure 5; Benson *et al.*, 2010b). Tyrannosauroids, once thought to be a clade endemic to Laurasia, have been reported in late Early Cretaceous deposits of Australia (Benson *et al.*, 2010a). Similarly, derived carcharodontosaurids been reported from the Late Cretaceous of Asia (Brusatte *et al.*, 2009; Brusatte *et al.*, 2010). Because baryonychines and spinosaurines have been consistently classified as sister taxa, a vicariant model with minimal dispersal between Laurasia and Gondwana seems unlikely.

Though likely influenced by various preservational and sampling biases, most baryonichine fossil traces are known from Barremian and Aptian deposits of Europe (figure 6; Charig & Milner, 1997; Ruiz-Omeñaca *et al.*, 1997; Infante *et al.*, 2005; Ruiz-Omeñaca *et al.*, 2005; Buffetaut, 2007; Sánchez-Hernández *et al.*, 2007; Canudo *et al.*, 2008; Gasca *et al.*, 2008). The earliest known confirmed spinosaurines are found in strata dating to the Albian (*e.g.* Russell, 1996), though it's probable that this temporal discrepancy is only a sampling artifact. Although Sánchez-Hernández *et al.* (2007) reported on six teeth referred to the Spinosaurinae in early Barremian deposits of eastern Spain, their exact identification is

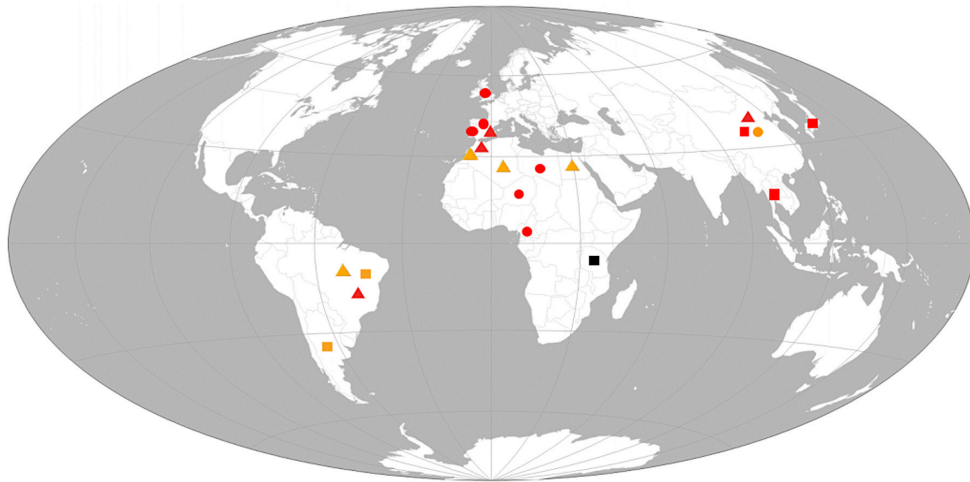


Figure 5. Countries with reported spinosaurid bearing deposits. Triangles represent the presence of spinosaurines, circles represent the presence of baryonychines, and squares represent the presence of spinosaurids of indeterminate affiliation. Black: Late Jurassic; Red: Early Cretaceous (Pre-Cenomanian); Orange: Late Cretaceous (Cenomanian and younger). Map accessed through the public domain: <http://commons.wikimedia.org/wiki/File:BlankMap-World6.svg>.

debatable. Many undescribed teeth not listed in the database have been uncovered in fossil deposits throughout Morocco and Tunisia (Benton *et al.*, 2000; McGowan & Dyke, 2009; Amiot *et al.*, 2010). Though its description was brief, a baryonchine tooth was also reported from the Early Cretaceous of Libya (Le Loeuff & Métais, 2009).

A probable baryonchine tooth from the Santonian of China (Hone *et al.*, 2010) drastically increases the subclade's temporal range (the prior youngest baryonchine reports were from the Aptian, Sereno *et al.*, 1998; Canudo *et al.*, 2008), and further emphasizes the need for more material to better understand spinosaurid dispersal history. It, along with a possible spinosaurine tooth from the Cenomanian of China (Lü *et al.*, 2009), raises some very intriguing implications about the possibility of finding spinosaurid fossils in North American strata. Starting in the Aptian/Albian, a land connection over the Beringian isthmus allowed for active faunal dispersal between Asia and western North America throughout much of the Late Cretaceous (Russell, 1993). Given that dispersal likely continued through the Campanian/Maastrichtian, and that many of the Asian dinosaur groups have closely related North American representatives (including tyrannosaurids, troodontids, ankylosaurids, dromaeosaurids, and hadrosaurids, Russell, 1993; Currie, 1995; Norell *et al.*, 2000; Godefroit *et al.*, 2004; Hurum & Sabath, 2003; Carpenter, 2004), baryonychines very well may have also migrated between continents. Though the Early

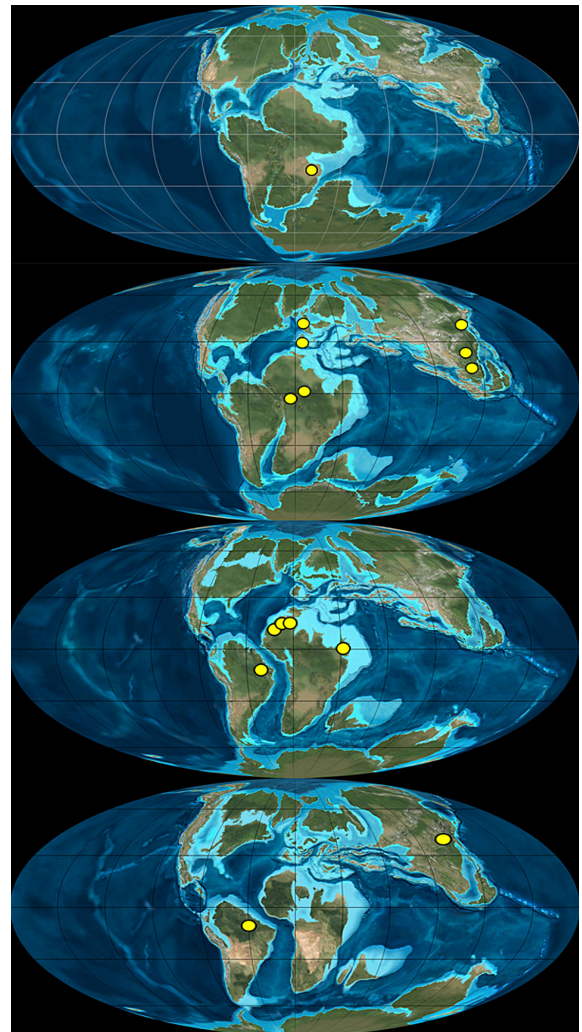


Figure 6. Generalized paleogeographic locations of spinosaurids in the Tithonian, Barremian/Aptian, Albian/Cenomanian, and Turonian/Santonian. Courtesy of Ron Blakey (<http://jan.ucc.nau.edu/~rcb7/mollglobe.html>).

to Mid Cretaceous fossil record in North America is at present quite patchy, evidence suggests that from the Barremian to the Early Aptian, floral and faunal dispersal occurred between western Europe and North America (Yong-fu, 1995; Chinnery *et al.*, 1998 and all references therein). This may have provided an additional, older dispersal route.

How regional extinctions or continental vicariance affected the clade's early evolution and dispersal is currently unknown. However, given the faunal and temporal similarity noted in the Late Jurassic faunas of the Tendaguru beds of Tanzania (where the earliest known spinosaurid tooth was located; Buffetaut, 2008b), the Morrison Formation of the United States, and the Lourinhã and Alcobaça Formations of Portugal, it is possible that spinosaurid traces may be found within them as well (Schuchert, 1918; Turner & Peterson, 2004; Mateus, 2006). At present there are no known North American spinosaurid fossils to confirm any of these hypotheses, though the presence of the basal megalosauroid *Torvosaurus tanneri* in the Late Jurassic may be telling (Mateus, 2006). A watchful eye should be kept out for potential spinosaurid traces in both museum collections (as with other rediscovered spinosaurid remains which were mislabeled as crocodylian, Fowler, 2007) and field expeditions to North American strata, especially those with predominantly fluvial, lagoonal, or lacustrine deposits. Early Cretaceous formations of special interest include the Cedar Mountain Formation of Utah (Kirkland, 2005) and the Lakota Formation of South Dakota (Dahlstrom & Fox, 1995).

## Conclusions

Although the last several decades have seen great advances, spinosaurids still remain one of the most enigmatic clades in dinosaurian paleontology. A vast amount of information about these remarkable creatures remains to be discovered. Although spinosaurids were previously thought to be more temporally limited, recent discoveries extend their known temporal range to roughly 70 million years (and with a postulated divergence in the Middle Jurassic, it would be pushed back further yet). Many studies of their biomechanical properties, ecological dynamics, morphology, geographic distribution, and evolution await.

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Appendix 1. Skeletal material. \* Denotes 'same as previous entry'. In cells left blank, data was not provided.

Taxonomic Identification	Material Type	Stratigraphic Information	Locality	Depositional Environment	Time Period	Specimen Number	Reference
Baryonychine indet.	Paired premaxillae, portion of the right maxilla and dentary	Elrabaz Formation-Tegama Series	Central Niger-Ténééré Desert-Gadoufaoua-GAD 5 quarry Niveau des Innocents	Fluvial	Aptian	MNHIN GDF 365	Taquet & Russell, 1998 See notes for taxonomic information.
*	Fused premaxillae, dorsal vertebrae	*	*	*	*	MNHIN GDF 365	*
Baryonychine indet.	Posterior cervical vertebra	Arcillas de Morella Formation	Eastern Spain-Castellón Province-near Morella city-Mas de la Parreta quarry.	Unspecified	Aptian	Unavailable	Gasulla <i>et al.</i> , 2009
<i>Baryonyx</i> sp.	Fragment of the right dentary	Papo Seco Formation	Southeastern Portugal-Losboia e Setubal Province-Boco do Chapim locality	Lagoonal	Barremian	MG 29A	L'apparent & Zbyszewski, 1957 Buffetaut, 2007
*	Fragment of the right dentary, likely from a posterior portion of the jaw	*	*	*	*	MG 29B	*
*	Fragment of the left dentary (possibly from the same animal as specimen 29A)	*	*	*	*	MG 29C	*
<i>Baryonyx</i> sp.	Left postorbital	Urbión Group	Northern Spain-Burgos province-Salas de los Infantes municipality Cameros Basin	Lagoonal	Upper Hauterivian or Lower Barremian	J.G. 6	Fuentes Vidarte <i>et al.</i> , 2001. Represents a subadult specimen
*	Left squamosal	*	*	*	*	J.G. 5	*
*	Cervical vertebra	*	*	*	*	J.G. 9	*
*	Proximal cervical rib	*	*	*	*	J.G. 2	*
*	Proximal cervical rib	*	*	*	*	J.G. 3	*
*	Proximal cervical rib	*	*	*	*	J.G. 4	*
*	Fragment of the 4th sacral fused to the 5th sacral vertebra	*	*	*	*	J.G. 8	*

Taxonomic Identification	Material Type	Stratigraphic Information	Locality	Depositional Environment	Time Period	Specimen Number	Reference
*	Caudal vertebra	*	*	*	*	J.G. 7	*
*	Chevron	*	*	*	*	J.G. 1	*
*	Left metacarpal I	*	*	*	*	J.G. 10	*
*	Left metacarpal II	*	*	*	*	J.G. 12	*
*	Left metacarpal III	*	*	*	*	J.G. 18	*
*	Left phalanx I-1	*	*	*	*	J.G. 21	*
<i>Baronyx walkeri</i>	Type specimen-partial skull, axis, 4 cervical vertebrae, 12 dorsal vertebrae, 6-7 caudal vertebrae, 1 axial rib, 3 non-axial cervical ribs, dorsal ribs, gastralia, 5 haemapophyses, both scapulae, coracoids, both humeri, left radius, left ulna, left pollex with a large ungual, left digit II or III, isolated left and right phalanges, right ilium, both pubes, left ischium, proximal portion of the left femur and distal end of the right, right fibula, right calcaneum, metatarsal fragments, and 1 pedal ungual	Upper Weald Clay Formation-Weald Clay Group	Southeastern England-Smokejack's Brickworks (Ockley Buildings Products Limited)-Wallis Wood, Ockley-near Dorking, Surrey	Fluvial mudplain	Barremian	NHM R9951	Charig & Milner, 1986; 1997
<i>Baronyx walkeri</i>	Left maxillary fragment	Enciso Group	Northern Spain-La Rioja province-near Igea	Unknown	Barremian to Late Aptian	GA-2065	Viera & Torres, 1995
<i>Irritator cf. challengerii</i>	Rostral fragment of the skull	Santana Formation-Romualdo Member	Northeastern Brazil-Southern Ceará state-Ataripe Basin	Likely lagoonal	Albian	GP/2T-5	Kellner & Campos, 1996 See notes for taxonomic information

Taxonomic Identification	Material Type	Stratigraphic Information	Locality	Depositional Environment	Time Period	Specimen Number	Reference
<i>Irritator challengeri</i>	Type specimen-partial skull, missing the rostral portion	Santana Formation-Romualdo Member	Northeastern Brazil-Ceará State-found near the farming community of Buxexé, close to Santana do Cariri city (5 km south). Because the specimen was first uncovered by a local collector, the exact locality is currently unknown	Likely lagoonal	Albian	SMNS 58	Martill <i>et al.</i> , 1996; Sues <i>et al.</i> , 2002
Spinosauridae indet.	Nine articulated vertebrae, consisting of three posterior sacrals and six anterior caudals	Santana Formation-Romualdo Member	Northeastern Brazil-southern Ceará State-possibly collected in the surroundings of Santana do Cariri City	Lagoonal/Marine(?)	Albian	MN 4743-V	Bittencourt & Kellner, 2004
Spinosauridae indet.	Premaxilla	Alcântara Formation	Northeastern Brazil-Maranhão State-Cajual Island-Laje do Coringa locality.	Estuarine	Cenomanian	MN 6117-V	Machado <i>et al.</i> , 2009
<i>Spinosaurus aegyptiacus</i>	Type specimen-Maxillary fragment, rostral dentary fragment, splenial, angular, nineteen teeth, axial neural arch, middle cervical vertebra, four dorsal vertebrae, three dorsal neural arches, anterior dorsal rib, two middle dorsal ribs, posterior dorsal rib, gastrilium, six gastrilia fragments, partial sacral vertebra, second sacral centrum, partial third sacral centrum, proximal caudal vertebra	Bahariya Formation	Western Egypt-Bahariya Oasis-relatively near the town of Bawiti By Gebel el Dist	Intertidal mangrove deposit (Palustrine)	Cenomanian	BSP 1912 VIII 19 (destroyed)	Stromer, 1915; Smith <i>et al.</i> , 2006
<i>Spinosaurus cf. aegyptiacus</i>	Mid series cervical	Kem Kem Beds	Morocco-Tafilalet region, near Er Rachidia	Fluvial	Albian/Cenomanian	NMC 50791	Russell, 1996 See notes for taxonomic information
*	Dentary fragment	*	*	*	*	NMC 50832	*

Taxonomic Identification	Material Type	Stratigraphic Information	Locality	Depositional Environment	Time Period	Specimen Number	Reference
*	Dentary fragment	*	*	*	*	NMC 50833	*
*	Mid series cervical	*	*	*	*	NMC 41768	*
*	Mid series cervical	*	*	*	*	NMC 50790	*
*	Dorsal neural arch	*	*	*	*	NMC 50813	*
<i>Spinosaurus cf. aegyptiacus</i>	Fragment of the rostrum containing both premaxillae, maxillae, and a fragment of the median right dentary	Kem Kem Beds	Algeria-Gara Samani Northwestern edge of the Tademaït	Unspecified	Albian	MNHIN SAM 124	Taquet & Russell, 1998 See notes for taxonomic information
*	Fragment of the premaxilla	*	*	*	*	MNHIN SAM 125	*
*	Cervical centrum	*	*	*	*	MNHIN SAM 126	*
*	Cervical centrum	*	*	*	*	MNHIN SAM 127	*
*	Dorsal neural arch	*	*	*	*	MNHIN SAM 128	*
<i>Spinosaurus cf. aegyptiacus</i>	Premaxillae and partial maxillae	Kem Kem Beds	Southeastern Morocco-Hamada de Guir-near Taouz	Unspecified	Cenomanian	NHM R16420	Milner, 2003
*	Dentary	*	*	*	*	NHM R16420	*
<i>Spinosaurus cf. aegyptiacus</i>	Rostral portion of the left dentary	Chenini Formation (Ain el Guettar Group)	Southern Tunisia-a portion of the Dahar escarpment, near the town of Ghoumrassen Jebel Miteur Locality GPS coordinates (estimated from provided locality map) = 33° 7' 60.00"N / 10° 16' 60.00"E	Fluvial	Early Albian	BM 231	Buffetaut & Ouaja, 2002
<i>Spinosaurus cf. aegyptiacus</i>	Both premaxillae and maxillae, along with the rostral portion of the nasals-fused in three dimensions	? Kem Kem Beds	Southern Morocco-reportedly east of Taouz-underlying the Hammada du Guir plateau	Unknown	Early Cenomanian	MSNM V 4047	Dal Sasso <i>et al.</i> , 2005

Taxonomic Identification	Material Type	Stratigraphic Information	Locality	Depositional Environment	Time Period	Specimen Number	Reference
*	Conjoined nasals with a fragment of the left maxilla	Kem Kem Beds	Northern Morocco-near the outpost in Keneg ed Dal GPS Coordinates = 30°02' N / 5° 12' W	Fluvial	Early Cenomanian	UPC-2	*
<i>Spinosaurus</i> sp.	Fragment of the right maxilla	Kem Kem Beds (?)	Southeastern Morocco-outside Taouz, at the base of the Hammada du Guir	Fluvial (?)	Cenomanian	IMGP 969-1	Buffetaut, 1989
? <i>Spinosaurus</i> sp.	Indeterminate jaw fragment-possibly from the medial half of the right dentary	*	*	*		IMGP 969-2	*
<i>Suchomimus tenerensis</i>	Type specimen-3 cervical ribs, 12 dorsal vertebrae, 1 dorsal centrum, 1 dorsal neural spine, 10 dorsal ribs, garstria, 3-5 sacral neural spines, 1 caudal vertebra, 2-5 caudal transverse processes, 1-5 caudal neural spines, 6 caudal centra, 3 chevrons, scapula, coracoid, humerus, radius, ulna, manual ungula I, manual ungula II, metacarpal II, manual ungula III, ilium, pubis, ischium, femur, tibia, pedal phalanx	Elrhaz Formation	Central Niger-Ténéré Desert-Gadoufaoua GPS coordinates = 16°25' N / 9°7' E	Fluvial	Aptian	MNN GDF500	Sereno <i>et al.</i> , 1998
*	Articulated premaxillae and maxillae, caudal vertebra	*	*	*	*	MNN GDF501	*
*	Right quadrate	*	*	*	*	MNN GDF502	*
*	Partial dentary	*	*	*	*	MNN GDF503	*
*	Partial dentary	*	*	*	*	MNN GDF504	*
*	Partial dentary	*	*	*	*	MNN GDF505	*
*	Axis	*	*	*	*	MNN GDF506	*
*	Posterior cervical vertebra, posterior dorsal vertebra	*	*	*	*	MNN GDF507	*
*	Caudal vertebra	*	*	*	*	MNN GDF511	*

Taxonomic Identification	Material Type	Stratigraphic Information	Locality	Depositional Environment	Time Period	Specimen Number	Reference
*	Unspecified articulated presacral elements, ribs, gastralia, furcula, girdles, limbs	*	*	*	*	MNN GDF513	Lipkin <i>et al.</i> , 2007



Appendix 2a. African teeth. \* Denotes 'same as previous entry'. In cells left blank, data was not provided. All measurements in millimeters. Abbreviations: SC (subclade); B (Baryonychinae); S (Spinosaurinae); I (Indeterminate subclade); FABL (fore-aft basal length); LMW/FABL (ratio of the lateral-medial width of the tooth to its fore-aft basal length); MPH (maximum preserved height); Mesial den / mm (number of denticles on the mesial carina); Distal Den / mm (number of denticles per millimeter on the distal carina); e (estimate); p (preserved).

Locality	Stratigraphic Information	Depositional Environment	Time Period	SC	Location in jaw	FABL	LMW	LMW/FABL	MPH	Mesial den. / mm	Distal den. / mm	Specimen Number	Reference
Northern Cameroon-Koum Basin-near Mayo Djarendi-locality KB-6	Koum Formation-Grés de Gaba Member	Fluvial	Aptian	B	Unknown	7,51	5,59	0,74	8,07	0	6,98	CAM 320	Congleton, 1990 See notes for further morphology discussion
*	*	*	*	B	*	5,71	1,24	0,21	8,94	0	8,05	CAM 322	*
*	*	*	*	B	*							CAM 349	*
*	*	*	*	B	*							CAM 350	*
*	*	*	*	B	*	6,2	4,83	0,78	12,32	0	6,97	CAM 351	*
*	*	*	*	B	*							CAM 352	*
*	*	*	*	B	*							CAM 353	*
*	*	*	*	B	*	2,13	1,6	0,75	3,33	0	12,78	CAM 354	*
*	*	*	*	B	*	4,35	3,54	0,81	11,27	0	9,33	CAM 355	*
*	*	*	*	B	*							CAM 356	*
*	*	*	*	B	*							CAM 357	*
*	*	*	*	B	*	2,8	2,23	0,8	4,11			CAM 359	*
*	*	*	*	B	*	5,07	2,62	0,52	8,21	0	6,08	CAM 360	*
Northern Morocco-Khouribga-150 km SE of Casablanca (Ad-Dar al-Bajda)	? Tegana Formation	Unknown	Albian or Cenomanian	S	Unknown	34	29	0,85	126	0	0	MUZ PIG 1647.II.1	Niedzwiedzki & Gierlinski, 2002
*	*	*	*	S	*	44	30	0,68	114	0	0	MUZ PIG 1647.II.2	*
Southeastern Morocco- outside Taouz, at the base of the Hammada du Guir	Kem Kem Beds (?)	Unknown	Cenomanian	S	Fluvial (?)	-	-	-	22	0	0	IMGF 969-3	Buffetaut, 1989

Locality	Stratigraphic Information	Depositional Environment	Time Period	SC	Location in jaw	FABL	LMW	LMW/FABL	MPH	Mesial den. / mm	Distal den. / mm	Specimen Number	Reference
Morocco-Ksares Souk Province-west of the Hamada du Guir	Unknown (possibly the Kem Kem Beds)	Unknown	? Albian / Cenomanian	S	Unknown	22	17	0,77	69	0	0	LINHM 001	Kellner & Mader, 1997
*	*	*	*	S	*	17	13	0,76	60	0	0	LINHM 002	*
Tanzania	Tendaguru Group, Upper Saurian Bed Formation	Unknown	Tithonian	I	Estuarine					2 to 4	2 to 4	R1084	Buffetaut, 2008b Janesch, 1925

Appendix 2b. Asian teeth. \* Denotes 'same as previous entry'. In cells left blank, data was not provided. All measurements in millimeters. Abbreviations: SC (subclade); B (Baryonychinae); S (Spinosaurinae); I (Indeterminate subclade); FABL (fore-aft basal length); LMW (lateral-medial width); LMW/FABL (ratio of the lateral/medial width of the tooth to its fore-aft basal length); MPH (maximum preserved height); Mesial den / mm (number of denticles per millimeter on the mesial carina); Distal Den / mm (number of denticles per millimeter on the distal carina); e (estimate); p (preserved).

Locality	Stratigraphic Information	Depositional Environment	Time Period	SC	Location in jaw	FABL	LMW	LMW/FABL	MPH	Mesial den. / mm	Distal den. / mm	Specimen Number	Reference
Northeastern Thailand-Phu Pratu Teema-On Phu Wiang Mountain, east of the city of Khon Kaen	Khorat Group-Sao Khua Formation	Fluvial	? Pre-Aptian Lower Cretaceous	I	Unknown	16,6	12,5	0,75	52.5 (47.7 crown)	0	0	TF 2043 a	Buffetaut & Ingavat, 1986 See notes for taxonomic information
*	*	*	*	I	*				24,3	0	0	TF 2043 b	*
*	*	*	*	I	*							TF 2043 c	*
*	*	*	*	I	*							TF 2043 d	*
*	*	*	*	I	*							TF 2043 e	*
*	*	*	*	I	*							TF 2043 f	*
*	*	*	*	I	*							TF 2043 g	*
*	*	*	*	I	*							TF 2043 h	*
*	*	*	*	I	*							TF 2043 i	*
Central Japan-Gunma Prefecture-Nakazato Village-near Ichinose Bridge	Sebayashi Formation-Sanchu Group	As per previous reports of the formation, likely either fluvial (deltaic) or estuarine	Upper Barremian/Aptian	I	Unknown	20	14	0,7	51	0 (?)	0 (?)	GMNH -PV - 999	Hasegawa <i>et al.</i> , 2003
Eastern China-Henan Province-Ruyang Basin-near Liudian Town-Shijiagou Quarry	Mangchuan Formation	Unknown	Cenomanian ?	S	Unknown	5			10	0	0	41HIII-00012	Lü <i>et al.</i> , 2009
Eastern China-Henan Province-Xixia County-Sanlimiao	Majiacun Formation	Likely fluvial (braided to meandering streams) per Liang <i>et al.</i> , 2009	Santonian	B	Unknown	15	9	0,6	52	4,8	4,5	XMDFEC V0010	Hone <i>et al.</i> , 2010

Locality	Stratigraphic Information	Depositional Environment	Time Period	SC	Location in jaw	FABL	LMW	LMW/FABL	MPH	Mesial den. / mm	Distal den. / mm	Specimen Number	Reference
*	*	*	*	*	*	*	*	*	*	*	*	IVPP FV* 1786 (cast)	*
Southern China- Fusui County- Guangxi Zhuan Autonomous Region	Napai Formation	Fluviolacustrine	Aptian / Albian	B	Unknown	16,5	13	0,79	69			IVPP V 4793	Buffetaut <i>et al.</i> , 2008

Appendix 2c. European teeth. \* Denotes 'same as previous entry'. In cells left blank, data was not provided. All measurements in millimeters. Abbreviations: SC (subclade); B (Baryonychinae); S (Spinosaurinae); I (Indeterminate subclade); FABL (fore-aft basal length); LMW (lateral-medial width); LMW/FABL (ratio of the lateral / medial width of the tooth to its fore-aft basal length); MPH (maximum preserved height); Mesial den / mm (number of denticles per millimeter on the mesial carina); Distal Den / mm (number of denticles per millimeter on the distal carina); e (estimate); p (preserved).

Locality	Stratigraphic Information	Depositional Environment	Time Period	SC	Location in jaw	FABL	LMW	LMW / FABL	MPH	Mesial den. / mm	Distal den. / mm	Specimen Number	Reference
Southern England-Sussex County-Tigate Forest	Wealden Units	Unknown	Unspecified-pre mid-Aptian, Early Cretaceous	B	Unknown							NHM R36536	Owen, 1841; Owen, 1878 <i>Suchosaurus cultridens</i> type specimen. See Buffetaut, 2007; 2008a
Southern England-Sussex County	Wealden Units	Unknown	Unspecified-pre mid-Aptian, Early Cretaceous	B ?	Unknown							Ji910	Seeley, 1869 Originally housed in the Woodwardian Museum of the University of Cambridge. First identified as <i>Suchosaurus</i> . See Buffetaut, 2007
Southern England-Sussex County-Crawley District-Tilgate	*	*	*	B ?	*							Ji911	*
*	*	*	*	B ?	*							Ji912	*
*	*	*	*	B ?	*							Ji913	*
Southern England-Sussex County-Cuckfield	Wealden Units	Unknown	Unspecified-pre mid-Aptian, Early Cretaceous	B ?	Unknown							NHM 3309	Lydekker, 1888 Originally referred to <i>Suchosaurus</i> . See Buffetaut, 2007

Locality	Stratigraphic Information	Depositional Environment	Time Period	SC	Location in jaw	FABL	LMW	LMW / FABL	MPH	Mesial den. / mm	Distal den. / mm	Specimen Number	Reference
*	*	*	*	B ?	*							NHM 3311	*
*	*	*	*	B ?	*							NHM 3315	*
*	*	*	*	B ?	*							NHM 3381	*
*	*	*	*	B ?	*							NHM 331121	*
*	*	*	*	B ?	*							NHM 36536	*
Southern England-Isle of Wight, Sandown	Hastings Group	*	Valangin/ Berrasian	B ?	*							NHM R635	*
Southern England-Isle of Wight	Wealden Units	*	Unspecified- pre mid- Aptian, Early Cretaceous	B ?	*							NHM R215	*
Southern England- Sussex County- Cuckfield	*	*	*	B ?	*							NHM R977	*
Southern England- more details unspecified	Wealden Units	Unknown	Unspecified- pre mid- Aptian, Early Cretaceous	B	Unknown							NHM 3316	Fowler, 2007
*	*	*	*	B	*							NHM 3279	*
*	*	*	*	B	*							NHM 3312	*
Southern England-Isle of Wight, Atherfield	*	*	*	B	*							NHM R5165	

Locality	Stratigraphic Information	Depositional Environment	Time Period	SC	Location in jaw	FABL	LMW	LMW / FABL	MPH	Mesial den. / mm	Distal den. / mm	Specimen Number	Reference
Southern England- more details unspecified	*	*	*	B	*							NHM R1901	*
*	*	*	*	B	*							NHM R5226	*
*	Hasting Group	*	Valangin/ Berrasian	B	*							NHM 26030	*
*	Wealden Units	*	Unspecified- pre mid- Aptian, Early Cretaceous	B	*							NHM 3330	*
*	*	*	*	B	*							NHM 26032	*
*	*	*	*	B	*							NHM R2312	*
*	*	*	*	B	*							NHM R2313	*
*	*	*	*	B	*							NHM 33119	*
*	*	*	*	B	*							NHM 3240	*
*	*	*	*	B	*							NHM R641	*
*	*	*	*	B	*							NHM R642	*
*	*	*	*	B	*							NHM 26031	*
*	*	*	*	B	*							NHM 10822	*

Locality	Stratigraphic Information	Depositional Environment	Time Period	SC	Location in jaw	FABL	LMW	LMW / FABL	MPH	Mesial den. / mm	Distal den. / mm	Specimen Number	Reference
Southern England-Eastern Isle of Wight-Yaverland	Wealden Group, Wessex Formation	Unknown	Barremian	B	Unknown							IWCMS 3642	Martill & Hutt, 1996 See notes for a range of measurements
Southern England-Western Isle of Wight-Hanover Point	*	*	*	B	*							IWCMS 5120	*
Southern England-Isle of Wight-Unknown Location	*	*	*	B	*							IWCMS 5122	*
*	*	*	*	B	*							IWCMS 1995,207	*
*	*	*	*	B	*							IWCMS 1995, 208	*
*	*	*	*	B	*							IWCMS 1995, 209	*
*	*	*	*	*	*							UOP97	*
Eastern Spain-Teruel Province-Castellote municipality, Aragón	Blesa Formation	Lacustrine	Upper Barremian	B	Estuarine	10	8	0,8	19	0	9,97	MPZ 98/59	Ruiz-Omeñaca et al., 1997
*	*	*	*	B	*	8	6,4	0,8	16	0	7,94	MPZ 98/59	*
*	*	*	*	B	*	7,4	6,3	0,85	17 e (10,2 p)	0	6,6	MPZ 98/59	*



Locality	Stratigraphic Information	Depositional Environment	Time Period	SC	Location in jaw	FABL	LMW	LMW / FABL	MPH	Mesial den. / mm	Distal den. / mm	Specimen Number	Reference
Northern Spain-Burgos Province-Salas de los Infantes municipality-Cameros Basin	Urbión Group	Lagoonal	Upper Hauterivian or Lower Barremian	B	Unknown					7	7	J.G. 284	Fuentes Vidarte <i>et al.</i> , 2001
Northern Spain-Burgos Province-Cabezón de la Sierra municipality-Tenada de la Rosada locality	Piedrahita de Muñó, Pedroso Group, 'Weald facies'	Unknown	Barremian to Aptian	B	Unknown				43.5	7	7	PS.C.-15,32	Torcida <i>et al.</i> , 1997
*	*	*	*	B	*							PS.C.-15,30	*
Northern Spain-Burgos Province-Salas de los Infantes municipality-Tenada de Costalomo locality	*	*	*	B	*				30	7	7	PS.CLST,2	*
Northern Spain-Burgos Province-Barbadillo del Mercado municipality-La Tejera-Valdesancho locality	*	*	*	B	*					8	7-8.	PS.TBMV, 13	*
Northern Spain-Burgos Province-Salas de los Infantes municipality-La Solana site	Castrillo de la Reina Formation	Fluvial	Late Barremian / Early Aptian	B	Unknown	14	10	0,71	27 p	6	6	PS C-1 11	Torcida Fernández <i>et al.</i> , 2003

Locality	Stratigraphic Information	Depositional Environment	Time Period	SC	Location in jaw	FABL	LMW	LMW / FABL	MPH	Mesial den. / mm	Distal den. / mm	Specimen Number	Reference
Northern Spain-Burgos Province-Salas de los Infantes municipality-Tenadas del Jabali site	*	*	*	B	*	9	7	0,78	14 p	8	6 to 8	PS-JTS 20	*
Northeastern Spain-Teruel Province-Castollote-Ladruñan	Mirambel Formation	Lacustrine	Early Barremian	B	Unknown	6,7	5,3	0,79	7,1	0	4,9	LADo-2	Infante <i>et al.</i> , 2005
Northeastern Spain-Josa Teruel Province-Cortes de Aragón-La Cantalera Quarry	Blesa Formation	Palustrine	Late Hauterivian / Early Barremian	B	Unknown	6				? 9 or 10	9,3	MPZ97   468	Ruiz-Omeñaca <i>et al.</i> , 2005
*	*	*	*	B	*	15				6 to 8	6 to 7	MPZ2001   207	*
*	*	*	*	B	*	8,1				7 to 8	6 to 7	MPZ2001   208	*
*	*	*	*	B	*	> 7,7				6 to 7	6 to 8	MPZ2005   303	*
*	*	*	*	B	*	8,7					6 to 7	MPZ2005   304	*
*	*	*	*	B	*	> 5,6						MPZ2005   305	*
*	*	*	*	B	*	6,6						MPZ2005   306	*
*	*	*	*	B	*	6,4					? 8 to 9	MPZ2005   307	*
*	*	*	*	B	*	9 e				6 to 7		MPZ2005   308	*

Locality	Stratigraphic Information	Depositional Environment	Time Period	SC	Location in jaw	FABL	LMW	LMW / FABL	MPH	Mesial den. / mm	Distal den. / mm	Specimen Number	Reference
*	*	*	*	B	*	4,7				? 10	9 to 11	MPZ2005   309	*
*	*	*	*	B	*	2,5				0	12 to 13	MPZ2005   310	*
*	*	*	*	B	*	3				0	11	MPZ2005   311	*
*	*	*	*	B	*	> 2,7					9 to 10	MPZ2005   312	*
*	*	*	*	B	*	> 4					? 9	MPZ2005   313	*
*	*	*	*	B	*	> 2,5				12	12 to 13	MPZ2005   314	*
*	*	*	*	B	*	> 2,8				? 8	9 to 10	MPZ2005   315	*
Northeastern Spain-Teruel Province-Galve area-Cerrada Roya (mina) outcrop	Camarillas Formation	Near shore fluvial deposits	Lower Barremian	B	Unknown	7	4	0,57	17	0	0	MPG CR(m)-1	Sánchez-Hernández <i>et al.</i> , 2007
*	*	*	*	B	*	6	4	0,67	12	0	0	MPG CR(m)-2	See notes for taxonomic discussion
*	*	*	*	B	*	6	6	1	18	0	0	MPG CR(m)-3	*
*	*	*	*	B	*	9	7	0,78	17	0	0	MPG CR(m)-4	*
Northeastern Spain-Teruel Province-Galve area-San Cristóbal outcrop	*	*	*	B	*	9	8	0,89	16	0	0	MPG SC-1	*
*	*	*	*	B	*	12	7	0,58	21	0	0	MPG SC-2	*

Locality	Stratigraphic Information	Depositional Environment	Time Period	SC	Location in jaw	FABL	LMW	LMW / FABL	MPH	Mesial den. / mm	Distal den. / mm	Specimen Number	Reference
Northeastern Spain-Teruel Province-Galve area-POCA outcrop	*	Mixohaline fluvial deltaic systems	*	B	*	3,9	1,9	0,49	3,9	0	? > 13	MPG POCA-6	*
*	*	*	*	B	*	3,1	1,5	0,48	3,1	0	10	MPG POCA-7	*
*	*	*	*	B	*	3	1,8	0,6	3	0	13	MPG POCA-14	*
*	*	*	*	B	*	2,8	1,5	0,53	2,8	0	10	MPG POCA-15	*
*	*	*	*	B	*	2	1	0,5	2	0	11,5	MPG POCA-18	*
Northeastern Spain-Teruel Province-Galve area-PX outcrop	El Castellar Formation	Near shore fluvial deposits	*	B	*	1,3 P	0,7 P	? Poorly pres.	1,3	0	?	MPG PX-23	*
Spain-near Morella, Castellon Province-Mas de La Parreta Quarry-locality CMP-2	Arcillas de Morella Formation	Fluvial	Early Aptian	B	Right mandibular	8,58	6,63	0,77	22,40 e	0	8	CMP2-175	Canudo <i>et al.</i> , 2008
Spain-near Morella, Castellon Province-Mas de La Parreta Quarry-locality CMP-3	*	*	*	B	Right mandibular	17,46	12,67	0,73	39,93 e	6	0	CMP3-182	*
*	*	*	*	B	Left maxillary	11,32	7,02	0,62	17,24 e	7	7	CMP3-196	*
*	*	*	*	B		17,81	11,78	0,66	38,83 e	5	6	CMP3-360	*

Locality	Stratigraphic Information	Depositional Environment	Time Period	SC	Location in jaw	FABL	LMW	LMW / FABL	MPH	Mesial den. / mm	Distal den. / mm	Specimen Number	Reference
*	*	*	*	? S	Left maxillary	16,88	13,03	0,77	32,83 e	0	0	CMP3-369	*
*	*	*	*	B		16,87	10,69	0,63	17,31	0	7	CMP3-370	*
*	*	*	*	B		9,27 e	7,02 e	0,76 e	10,82	0	5	CMP3-532	*
*	*	*	*	B	Lateral	8,78 e	6,60 e	0,75 e	15,55	8	9	CMP3-538	*
*	*	*	*	B	Lateral	19,48	12,85	0,66	40,77 e	0	6	CMP3-758	*
*	*	*	*	B		15,44	10,09	0,65	33,73 e	0	6	CMP3-759	*
*	*	*	*	B		16,85	12,99	0,77	39,35 e	7	7	CMP3-760	*
*	*	*	*			9,06	7,47	0,82	21,18	0	0	CMP3-790	*
*	*	*	*	? S		12,22	9,98	0,81	15,62	0	7	CMP3-791	*
*	*	*	*	B		8,86	6,75	0,76	20,8	9	9	CMP3-896	*
*	*	*	*	B		9,45	6,65	0,7	21,21	8	9	CMP3-897	*
*	*	*	*	B		8,08	6,46	0,8	19,82	7	7	CMP3-1012	*
*	*	*	*	B	Lateral	11,25	8,17	0,73	30,37	6	7	CMP3b-9	*
Spain-near Morella, Castellon Province-Mas de La Parreta Quarry-locality CMP-5	*	*	*	B	Lateral	14,07	10,39	0,74	24,21	6	6	CMP5b-46	*

Locality	Stratigraphic Information	Depositional Environment	Time Period	SC	Location in jaw	FABL	LMW	LMW / FABL	MPH	Mesial den. / mm	Distal den. / mm	Specimen Number	Reference
Spain-near Morella, Castellón Province-Mas de La Parreta Quarry-locality CMP-9	*	*	*	B	Left mandibular or right maxillary	17,13	11,27	0,66	36,5	8	9	CMP9-37	*
*	*	*	*	? S	Right maxillary	18,51	12,07	0,65	37,65	0	0	CMP9-49	*
Northeastern Spain-Teruel Province-Aliaga and Miravente de la Sierra	El Castellar Formation	Lacustrine	Upper Hauterivian / Lower Barremian	B		14,04	10,54	0,75	22,71	5,2	5,6	MOAL -1/1	Gasca et al., 2008
*	*	*	*	B		8,97	6,83	0,76	11,6	0	8,6	SM-2/D1	*
Eastern Spain-Castellón Province-near Portell-Mas de Curolles-I	Cantaperdius Formation	Lacustrine	Upper Hauterivian / Lower Barremian	B		14	12	0,86	35 e 30	6 to 7	6 to 7	MQ98-I-I	Falset et al., 2009

Appendix 2d. South American teeth. \* Denotes 'same as previous entry'. In cells left blank, data was not provided. All measurements in millimeters. Abbreviations: SC (subclade); B (Baryonychinae); S (Spinosaurinae); I (Indeterminate subclade); FABL (fore-aft basal length); LMW (lateral-medial width); LMW/FABL (ratio of the lateral / medial width of the tooth to its fore-aft basal length); MPH (maximum preserved height); Mesial den / mm (number of denticles per millimeter on the mesial carina); Distal Den / mm (number of denticles per millimeter on the distal carina); e (estimate); p (preserved).

Locality	Stratigraphic Information	Depositional Environment	Time Period	SC	Location in jaw	FABL	LMW	LMW/FABL	MPH	Mesial den. / mm	Distal den. / mm	Specimen Number	Reference
Southern Brazil-Sao Paulo State-Northeast of Presidente Prudente-Santo Anastácio outcrop	Adamantina Formation	Fluviolacustrine	Turonian or Santonian	I		5,97			8,6		3	UFRJ-DG 354-Rd	Candeiro <i>et al.</i> , 2004
*	*	*	*	I		10,56			18,88			UFRJ-DG 372-Rd	*
Northeastern Brazil-Cajual Island-Laje do Coringa site GPS coordinates = 28° 28' 46,6" S / 44° 28' 23,8" W	Alcântara Formation	Estuarine	Early Cenomanian	S					80	0	0	UFMA 1.20.070	Medeiros, 2006 See notes for measurement information
*	*	*	*	S					101	0	0	UFMA 1.20.443	*
*	*	*	*	S						0	0	UFMA 1.20.44 5L	*
South-Central Argentina-El Anfitatro-La Bajada Sector	Cerro Lisandro Formation	Fluvial	Late Cenomanian to Lower Turonian	I?		9	7,6	0,84	21 e	3	3,75	Endemas -PV 6	Salgado <i>et al.</i> , 2009 / Canudo <i>et al.</i> , 2004 See notes