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Spinosaurid Dinosaurs from the Early Cretaceous of North Africa and Europe: Fossil Record, Biogeography and Extinction

Dinossauros Espinossaurídeos do Cretáceo Inicial do Norte da África e Europa: Registro Fossilífero, Biogeografia e Extinção.

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Abstract

We review the fossil records of spinosaurid dinosaurs in order to discuss this group’s evolution and distribution in Europe and North Africa during the Early Cretaceous. Along with their eastern Laurasian distribution during the Cretaceous, these theropods have been found in coastal deposits of Europe and North Africa dated from the Barremian to the Cenomanian. The main occurrences of spinosaurid remains are in the deposits of northern Gondwana and western Laurasia, which suggests that these regions were very important in spinosaurid evolution prior to the Cenomanian. Later, spinosaurids were seemingly replaced in northern Gondwana by other top predator groups, including the abelisauroids.
Keywords: theropod spinosaurids; “middle” Cretaceous; biogeography

Resumo

Aqui nos revisamos os registros de dinossauros de spinosaurídeos e discutimos a evolução e distribuição deste grupo na Europa e no Norte da África durante o Cretáceo Inferior. Juntamente com sua distribuição Laurasiana oriental durante o Cretáceo, esses terópodes foram encontrados em depósitos costeiros da Europa e do Norte da África datados do Barremiano ao Cenomaniano. As principais ocorrências de restos de espinossáuridos estão nos depósitos do norte de Gondwana e Laurasia ocidental, o que sugere que estas regiões foram importante de sua evolução antes do Cenomaniano. Posteriormente, os espinossáuridos foram aparentemente substituídos no norte de Gondwana por outros grupos predadores de topo, incluindo abelissauroideos.
Palavras-chave: espinossaurídeos terópodes; Cretáceo “médio”; biogeografia

1 Introduction

Spinosaurids – the group of long-snouted and possibly semiaquatic theropods – are one of the most distinctive dinosaur groups. Fossil remains of these predators are known from many localities from the Lower Cretaceous of Africa (Algeria, Egypt, Niger, Sudan, Tanzania, Tunisia), Europe (England, Portugal, Spain), South America (Brazil), Asia (China, Laos, Thailand), and Australia (e.g., Kellner & Campos, 1996; Sereno *et al*., 1998; Benton *et al*., 2000; Buffetaut & Ouaja, 2002; Sues *et al*., 2002; Medeiros, 2006; Buffetaut, 2008, 2012; Buffetaut *et al*., 2008; Hone *et al*., 2010; Barrett *et al*., 2011; Kellner *et al*., 2011; Allain *et al*., 2012; Medeiros *et al*., 2014; Hendrickx *et al*., 2016; Sales *et al*., 2017). Knowledge about spinosaurids has increased significantly in the last few decades as new fossil remains, including various new species, have been found in several new Gondwanan and Laurasian localities (Buffetaut & Ingavat, 1986; Sereno *et al*., 1998; Benson *et al*., 2009; Buffetaut, 2012; Allain *et al*., 2012; Hendrickx *et al*., 2016). The most diverse and best preserved records of these dinosaurs are from the Early-mid Cretaceous strata of North Africa and Europe. Spinosaurids and two other groups of large theropods, the abelisauroids and carcharodontosaurids, comprise the most important members of the large-bodied terrestrial predator fauna of these regions. Among these large theropods, spinosaurids have the most diverse and abundant fossil record in the Early Cretaceous deposits of northern Brazil, northern Africa, and Europe (England, Portugal, and Spain). Therefore, it is now possible and desirable to place these specimens in a biogeographic context in order to understand their turnover prior to the Cenomanian. As such, the focus of this review is on the best-known spinosaurids of North Africa and Europe.

Several anatomical, taxonomic and systematic studies of Spinosauridae have been published over the last few decades (e.g., Buffetaut & Ingavat, 1986; Sereno *et al*., 1998; Benton *et al*., 2000; Buffetaut, 2008, 2012; Benson *et al*., 2009; Allain *et al*., 2012; Hendrickx *et al*., 2016). Nevertheless, the biogeographic distribution of this group in Africa and Europe has received much less attention. Accordingly, the aim of this paper is to document and analyze the fossil record, biogeography and extinction of spinosaurids in western Europe and North Africa during Cretaceous Period.

2 The Spinosaurids of Western Laurasia and Northern Gondwana

Spinosaurids may have been a globally distributed group (Barret *et al*., 2011). However, their best fossils come from the Early-mid Cretaceous of Northern Africa and Europe. Many records of spinosaurid dinosaurs have been reported from different locations in Algeria, Egypt, Morocco, Niger, Portugal, Spain, Tunisia and the United Kingdom (Figure 2). The geological units bearing these specimens range in age from the Barremian to the Cenomanian. For many decades, and particularly over the last 20 years, fossils of basal and derived spinosaurids have been found in these strata.

All known spinosaurid species have large body sizes, elongated and laterally compressed skulls (some specimens also have cranial crests), and large claws on the manus, and some species also possess elongated neural spines on the vertebrae that supported some type of sail or hump, which was probably used for some combination of display, thermoregulation, and perhaps even swimming behaviors (Bailey, 1997).

Currently, there are 11 known species of possible spinosaurid dinosaurs, whose records come from northern Gondwana and Laurasia. Unlike other top predators that also inhabited Gondwana (Carcharodontosauridae and Abelisauroidea), the spinosaurids show a more restricted distribution in northern and western Gondwana, from the Barremian to the Cenomanian (Table 1). Spinosauridae includes two subfamily-level subclades, Spinosaurinae and Baryonychinae (*sensu* Hendrickx *et al*., 2016) (Figure 1). Their evolutionary history dates from the Early Cretaceous, and they were mainly distribution in northern Gondwana and western Laurasia. The absence of spinosaurids after the Cenomanian is an interesting observation, with evolution and biogeographic implications, which is discussed below.

2.1 Europe

The only spinosaurid species thus far described from England is *Baryonyx walkeri* from the Barremian Weald Clay Formation (Charig & Milner, 1997). The associated material by Charig & Milner (1986) contains a premaxilla, vomers, an anterior portion of the left maxilla, some skull bones,

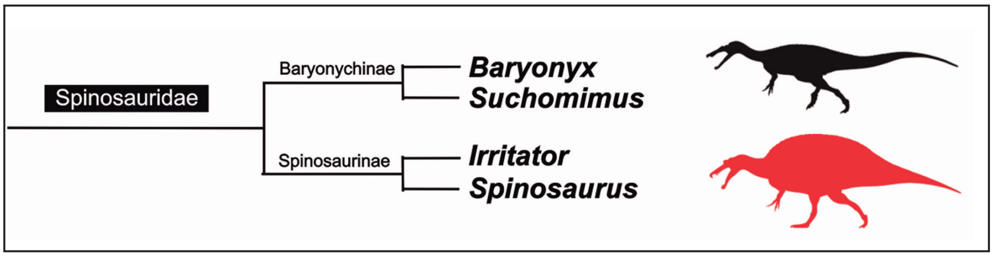

Figure 1 Phylogenetic relationships of the species of Spinosauridae family from middle Cretaceous (modified from Hendrickx *et al*., 2016).

Taxa	Formation	Age	Country	Selected References
Europe				
Baryonyx walker	Weald Clay Formation	Barremian	England	Charig & Milner (1986)
Baryonyx walker	Enciso Group	Barremian	Spain	Charig & Milner (1997), Vieira & Torres (1995)
Baryonychinae indet.	Wessex Formation	Barremian	England	Martill & Hutt (1996)
	Papo Seco Formation		Portugal	
Africa				
Spinosaurus aegyptiacus	Bahariya Formation	Cenomanian	Egypt	Stromer (1915)
Spinosaurus maroccanus	Kem Kem Beds	early Cenomanian	Morocco	Russel (1996), Sereno et al. (1998)
Spinosaurus maroccanus	Kem Kem Beds	Albian	Algeria	Taquet & Russel (1998), Sereno et al. (1998)
Cristatusaurus lapparenti nomen nudum	Elrhaz Formation	Aptian	Niger	Taquet & Russel (1998), Sereno et al. (1998)
Suchomimus tenerensis	Elrhaz Formation	Aptian	Niger	Sereno et al. (1998), Hendrickx et al. (2016)
Spinosaurus cf. aegyptiacus	Kem Kem Beds	Early Cenomanian	Morocco	Buffetaut & Ouaja (2002)
Spinosauridae indet.	Kem Kem Beds	early Cenomanian	Algeria, Morocco, Tunisia	Buffetaut (1998), Buffetaut (1989), Russell (1996), Kellner (1996), Kellner & Mader (1997)
Spinosaurinae indet.	Kem Kem Beds	earl Cenomanian	Morocco	Hendrickx et al. (2016)
Spinosauridade indet.	Chenini Member (El Guettar Formation)	Aptian	Tunisia	Benton et al. (2000)

Table 1 Barremian-Cenomanian spinosaurid records from Europe and Africa.

both dentaries, teeth, an axis, most of the cervical vertebrae, some dorsal vertebrae, one caudal vertebra, a cervical rib, dorsal ribs, gastralia, chevrons, both scapulae, a coracoid, both humeri, manual phalanges (including the ungual phalanges), an incomplete ilium, a pubis, an ischium, the proximal end of the left femur and the distal end of the right femur, an incomplete left fibula, the right calcaneum, the distal ends of the metatarsals, and the pedal phalanges of both feet (including the ungual ones).

At first, Charig & Milner (1986) did not consider *B. walkeri* as belonging to Spinosauridae, and it was Paul (1988) and Buffetaut (1989a,b) who were the first authors to associate this species with *Spinosaurus aegyptiacus* Stromer, 1915. It is now widely accepted that *Baryonyx* is an exemplary taxon of spinosaurid. Many authors (e.g., Sereno *et al*., 1998; Hendrickx *et al*., 2016) have considered *Baryonyx* as belonging to a spinosaurid subclade, called Baryonychinae, which also includes *Suchomimus tenerensis*.

There is also additional material of *Baryonyx*, in addition to the type specimen from England. Charig & Milner (1986) reported a fragment of left maxilla from Spain that was collected in the Enciso Group (Barremian) deposits. This material was referred by Vieira & Torres (1995) to *Baryonyx walkeri*. Ruiz-Omeñaca *et al*. (2005) reported additional Baryonychine teeth from same geological unit.

Martill & Hutt (1996) reported teeth of Baryonychinae from the Barremian Wessex Formation of the Isle of Wight. This material was assigned to this subfamily because it possessed finely serrated carinae, along with sharing a general morphological form and a number of denticles similar to *B. walkeri*. More recently, Mateus *et al*. (2011) described a series of spinosaurid bones from the Barremian Papo Seco Formation of Portugal.

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This includes a partial dentary, isolated teeth, a pedal ungual, two calcanea, presacral and caudal vertebrae, a fragmentary pubis, a scapula, and rib fragments. They assigned this material to *Baryonyx walkeri*. They also reassessed several historic specimens from Europe that were previously referred to *Suchosaurus*, which they considered to be a *nomen dubium*; they reassigned these teeth to Baryonychinae indet.

2.2 Africa

Spinosaurus aegyptiacus (Stromer, 1915) was the first spinosaurid discovered. The first specimens of this taxon were found in the Cenomanian-aged Bahariya Formation, which outcrops within the Bahariya depression in Central Egypt. The material comprises a small fragment of maxilla, a part of the dentary, nineteen teeth, two cervical vertebrae, seven dorsal vertebrae, three sacral vertebrae, one caudal vertebra, some ribs, and parts of the gastralia (Stromer, 1915). The most conspicuous characteristics of this taxon are the presence of very elongated neural spines on the dorsal vertebrae and the elongated and laterally compressed dentary, with teeth having a conical transverse section but lacking serrations. Unfortunately, the holotype was destroyed during World War II (Taquet, 1984; Sereno *et al*., 1998). However, the monograph published by Stromer (1915) is well illustrated, so on the basis of the figures alone it is possible to observe the many diagnostic features of *S. aegyptiacus*. More recently, several new specimens of *S. aegyptiacus* have been reported from Northern Africa, which confirm many of Stromer's observations and provide a more complete picture of what this strange animal would have looked like (e.g., Dal Sasso *et al*., 2005; Ibrahim *et al*., 2014). However, a complete or near-complete skeleton of *S. aegyptiacus* has yet to be found, meaning that many ideas about the body size, posture, locomotion, and behaviors of this famous dinosaur are still uncertain, despite much attention surrounding recent discoveries (see discussion in Evers *et al*., 2015).

Buffetaut (1989b) described a fragment of maxilla with circular alveoli from the Kem Kem Formation. Spinosauridae indet. specimens were described by Buffetaut (1989b) and Russell (1996) from Morocco, the Albian Ain El Guettar Formation of Tunisia (Bouaziz *et al*., 1988; Buffetaut & Ouaja, 2002) and the Kem Kem Formation of Algeria (Taquet & Russell, 1998). Recently, Hendrickx *et al*. (2016) described six isolated and well-preserved quadrates that they assigned to two Spinosaurinae morphotypes, which add additional records of this group from the early Cenomanian Kem Kem Formation of Morocco. There are also indeterminate isolated teeth from the same unit in Morocco that were described by Kellner (1996) and Kellner & Mader (1997). Benton *et al*. (2000) additionally report some teeth from the Aptian Chenini Member (El Guettar Formation) deposits of southern Tunisia, which they assigned to Spinosauridae.

A second species of *Spinosaurus*, *S. maroccanus*, was described from the early Cenomanian Kem Kem Formation of Morocco by Russell (1996). The material comprises fragments of the dentaries, two middle cervical vertebrae, and one dorsal neural arch. Later, Taquet & Russell (1998) assigned other material found in Algeria to *S. maroccanus*: a rostrum with both premaxillae, maxillae, vomers, fragments of a right dentary, a fragment of premaxilla, two vertebral centra from cervical vertebrae, and a neural arch of a dorsal vertebra. Sereno *et al*. (1998) considered this species a *nomen dubium* due the lack of diagnostic features that confirm the occurrence of more than one *Spinosaurus* species in the Albian and Cenomanian strata of North Africa. This idea has been followed by some later authors, who considered *S. maroccanus* to be the same species as the earlier named *S. aegyptiacus* (e.g., Ibrahim *et al*., 2014), but other workers have recently argued that *S. maroccanus* may indeed be valid (e.g., Evers *et al*., 2015).

Cristatusaurus lapparenti Taquet & Russell, 1998, from the Elrhaz Formation (Aptian) of Niger, was described based on two separate premaxillae, a fragment of the right maxilla and dentary, and teeth. The description was also based on other material assigned to this species: a fused premaxilla and dorsal vertebrae. Charig & Milner (1997) recognized these specimens as *Baryonyx* sp., Sereno *et al*. (1998) considered *C. lapparenti* as *nomen dubium*, and Buffetaut & Ouaja (2002) reinforced the idea that *Cristatusaurus* should be considered as a junior synonym of *Baryonyx,* which extends the occurrence of this genus to northern Africa.

Le Loeuff *et al*. (2010) described isolated Baryonychinae teeth from the Hauterivian-

Barremian of the Cabao Formation of Libya, which are the earliest Spinosauridae record from North Africa and Europe.

Suchomimus tenerensis was described by Sereno *et al*. (1998) and comes from the Albian Elrhaz Formation of the Ténéré desert, in Niger. The described material comprises an articulated premaxilla and maxilla, a right quadrate, partial dentaries, an axis, a posterior cervical vertebra, a posterior dorsal vertebra, two caudal vertebrae, and several isolated teeth and bones. In a recent paper Hendrickx *et al*. (2016) described the quadrates of *Suchomimus*, *Baryonyx*, "*Cristatusaurus*", and *Spinosaurus*, which reaffirmed that *S. tenerensis* is indeed a diagnostic taxon compared to other spinosaurids. There has been some debate in the literature as to whether *Suchomimus* should be considered a genus separate from *Baryonyx*, which we consider to be more in the realm of semantics than science, as it is widely regarded that these two dinosaurs are separate species and closely related.

There is also a wealth of other spinosaurid fossils from Northern Africa. Buffetaut & Ouaja (2002) reported the anterior part of a left dentary, bearing two teeth, from the early Cenomanian Kem Kem Formation of Morocco. They identified this specimen as *Spinosaurus* cf. *S. aegyptiacus*.

3 Remarks

3.1 Biogeographical importance

The biogeographic distribution of spinosaurids from the Early-mid Cretaceous of North Africa and Europe has been discussed in some studies that considered all the known records of this group (e.g., Buffetaut & Ouaja, 2002; Milner, 2003; Candeiro, 2015). As mentioned above, there is no doubt about the presence of spinosaurids in the Early Cretaceous of England, Portugal and Spain. At least two subfamilies are known and, apparently, one is more common than others in different areas (Spinosaurinae in northern South America and northern Africa; and Baryonychinae in Europe and some regions of Africa). However, a great amount of unidentified material still needs to be formally described, and some of these fossils may show that these two subfamilies were more widespread. Here, we simply evaluate what is currently known about the occurrences and distribution of Spinosauridae in the fossil record of Europe and Africa, based on the published literature (Figure 2). The presence of spinosaurids in these areas can be explained by faunal interchange between Europe and Africa during the Early-mid Cretaceous (Sereno *et al*., 1998; Canudo *et al*., 2009). During that time, Africa and Europe were connected by land in the region of the former western Atlantic Ocean as a result of local orogenic activity (Canudo *et al*., 2009; Fanti, 2012).

The discovery of numerous records of *Spinosaurus* and *Baryonyx* is evidence of the extensive distribution of large spinosaurids in North Africa in the Albian and afterwards. The phylogenetic relationships of spinosaurids indicate that they originated much earlier, however. They are sister taxon to Megalosauridae, a diverse clade of Laurasian and Gondwanan species that originated by the Middle Jurassic (e.g., Benson, 2010; Carrano *et al*., 2012). This indicates that the spinosaurid lineage extends back to this time as well, and was certainly present by the beginning of the Early Cretaceous, when the African continent was still connected to Europe.

There is one further phylogenetic relationship that deserves comment. Within Spinosauridae, Baryonychinae and Spinosaurinae are sister taxa. This relationship implies that derived spinosaurids may have appeared in Africa before the Albian, based on the earlier age of the European baryonychines.

Therefore, two distinct spinosaurid lineages (pre-Cenomanian Baryonychinae in Africa, Europe and Asia; and Albian-Cenomanian Spinosaurinae in Africa and South America) were dominant at different times in the separated areas of northern Gondwana and western Laurasia. The latter group includes a variety of spinosaurines of medium to large body sizes that are recorded in several African localities. The large fossil record and great diversity of this subfamily on this continent shows that this group was dominant among the terrestrial fauna until the Cenomanian.

The second phase of the African evolution of spinosaurids occurred close to the Cenomanian-Turonian boundary, when the spinosaurid-rich theropod fauna was replaced by the Abelisauridae (Novas *et al*., 2013). There are no unequivocal spinosaurids known from Africa, or anywhere else,

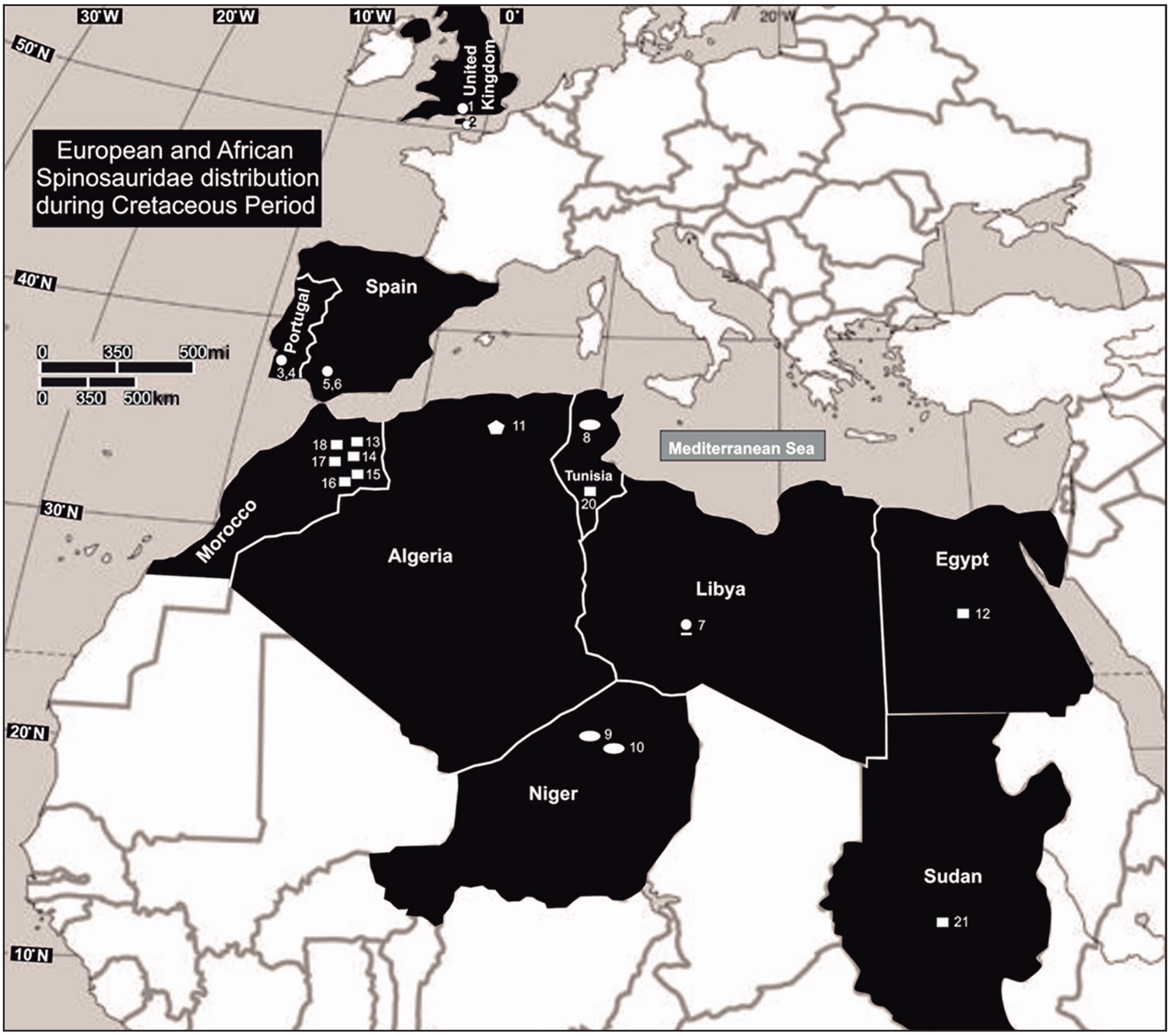

Figure 2 Baryonychinae and Spinosaurinae records distribution in Europe and North Africa during middle Cretaceous. 1, Barremian *Baryonyx walker*i; 2, Baryonychinae; 3, 5, 6; 4, *Baryonyx*; 7, 8; 9, *Suchomimus*; 10-14, *Spinosaurus aegyptiacus*; 15-17, 19-21, Spinosauridae indet.; 18, Spinosaurinae.

after the Cenomanian (although see Hone *et al*., 2010, for a possibly Santonian record from China).

3.2 Spinosaurid Extinction

Apparently, the spinosaurid extinction in Africa and Europe (Canudo *et al*., 2009) occurred in the mid Cretaceous (Aptian-Cenomanian). According to Russell & Paesler (2003), it is possible to hypothesize that the following series of events were responsible for the faunal change during this period: (1) the equatorial climates of the mid Cretaceous were unstable and non-seasonal; (2) there were severe convective storms. In addition, it seems that the atmospheric dynamics during the Cretaceous was significantly different from nowadays, as the evidence suggests that: (1) increased levels of atmospheric carbon dioxide probably triggered the emission of other gases that contributed to the greenhouse effect; and (2) increased humidity levels reduced the daytime temperature variations but affected their mechanisms of evaporative thermoregulation. While the hypothesis that these events caused the mid Cretaceous faunal turnover cannot be easily tested, they do present a possible mechanism.

We can reasonably suppose that these hypothetical events involved environmental changes, including faunal changes, and that its immediate effects influenced the spinosaurid fauna and other reptile groups widespread in Gondwana (e.g., Pelomedusidae, Araripemydidae, Notoshuchidae, Araripesuchidae, Dicraeosauridae, Titanosauria, Carcharodontosauria, Abelisauria). Unfortunately, the specific causes of the faunal shift recorded at the beginning of the Late Cretaceous, as well as the origin of the environmental changes, are far from being understood, partly because there are few data, especially from North Africa. In this region, the records show that the maximum sea level transgression occurred during the Cenomanian right before the final break-up between Africa and South America, concomitant with the main rise of sea level (Eaton *et al*., 1997; Benton *et al*., 2000; Russell & Paesler, 2003). The theropod fauna from the Cenomanian of North Africa and Brazil comprises the same groups of carcharodontosaurids and spinosaurids (Vilas-Bôas *et al*., 1999; Medeiros, 2006; Candeiro *et al*., 2011; Medeiros *et al*., 2014), indicating that the spinosaurid turnover in these regions occurred no earlier than the end of the Cenomanian.

According Jacobs *et al*. (1993) and Sereno *et al*. (1998, 1999) the northern part of Gondwana seems to have been the critical region for the extinction of some theropod lineages (e.g. carcharodontosaurids and spinosaurids) during the Cenomanian (Figure 3). With the absence of spinosaurids in northern Gondwana, there was a significant increase in the number and diversity of abelisauroids. Indeed, the post-Cenomanian abelisauroid fauna became the dominant group in Gondwana and later reached western Laurasia.

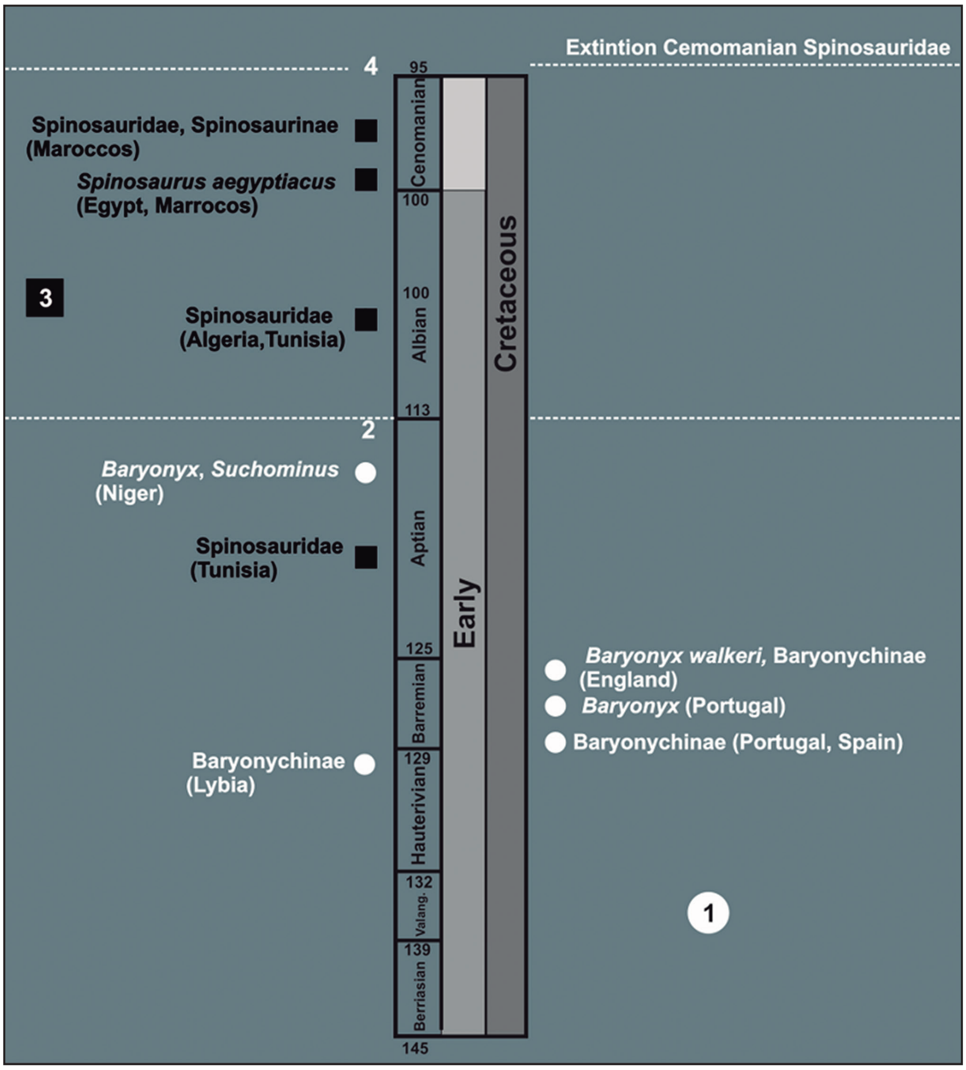

Figure 3
Western Europe and North Africa spinosaurid geochronological distribution. Circles, Baryonychinae and Squares, Spinosaurinae; 1 - Baryonychinae high diversity, 2 - Spinosaurinae high diversity, 3 – Baryonychinae possible extinction, 4 – Spinosauridae Cenomanian extinction.

4 Final Remarks

We have learned a great deal about the fossil record of Early-mid Cretaceous dinosaurs from northern Africa and Europe over the past few decades. This gives great insight into the evolution and distribution of the spinosaurids, one of the strangest groups of dinosaurs to ever live. However, there is still much to be discovered. Better correlation with other areas, particularly eastern Gondwana and eastern Laurasia, is crucial, because some spinosaurid records are known from these other regions and clearly have bearing on the evolution of the species of northern Africa and Europe. Better geochronology can calibrate the timing of evolutionary changes in this group. Furthermore, it can also permit better comprehension of the ecosystems in which these carnivores lived, including faunal shifts and environmental conditions of their habitats. Clearly, we have much to learn about the evolution of the strange crocodile-skulled spinosaurids.

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