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Large-sized theropod *Spinosaurus*: an important component of the carnivorous dinosaur fauna in southern continents during the Cretaceous

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Abstract – The Early Cretaceous of North Africa has Spinosaurinae dinosaur remains such as *Spinosaurus* recorded in Algeria (Guir Basin, Kem Kem beds), Egypt (Bahariya Formation), Morocco (Kem Kem beds), and Tunisia (Ain El Guettar Formation). Until now, three possible *Spinosaurus* species were identified: *Spinosaurus aegyptiacus*, *Spinosaurus* sp. and *Spinosaurus* "B". The occurrence of this genus in the Albian-Cenomanian rocks of Africa suggests that the temporal and geographic distribution of these spinosaurines is the largest one among all genera and species of megapredators from the middle Cretaceous of Africa. The fossil record of *Spinosaurus* from the Albian to the Cenomanian shows a 20 million year persistence of this genus in Gondwanan ecosystems.

Keywords: theropod dinosaur / distribution / Early Cretaceous / Africa

Résumé – *Spinosaurus* (théropode de grande taille) : une composante importante de la faune de dinosaures carnivores des continents méridionaux au cours du Crétacé. Le Crétacé inférieur d'Afrique du Nord renferme des restes de dinosaures spinosaurinés, tels que *Spinosaurus* répertorié en Algérie (Bassin du Guir, *Kem Kem beds*), en Égypte (Formation Bahariya), au Maroc (*Kem Kem beds*) et en Tunisie (Formation Ain El Guettar). Jusqu'à ce jour, trois espèces de spinosaure sont reconnues : *Spinosaurus aegyptiacus*, *Spinosaurus* sp. et *Spinosaurus* "B". La présence de ce genre dans les terrains albo-cénomaniens d'Afrique suggère que la répartition temporelle et géographique de ces spinosaurinés est la plus étendue de tous les genres et espèces de méga-prédateurs du Crétacé moyen d'Afrique. Le registre fossile de *Spinosaurus*, depuis l'Albien jusqu'au Cénomanien, indique une présence de 20 millions d'années pour ce genre dans les écosystèmes gondwaniens.

Mots clés : théropode dinosaure / distribution / Crétacé inférieur / Afrique

1 Introduction

Spinosaurus (Stromer, 1915) is the better known spinosaurid genus from the mid-Cretaceous of northern Gondwana. Its fossil remains have been reported to several localities in North Africa. In the literature, the paleogeographic distribution of this taxon is usually described to the Albian-Cenomanian of Algeria, Egypt, Morocco, and Tunisia (Bouaziz *et al.*, 1988; Buffetaut, 1989; Russell, 1996; Taquet and Russell, 1998; Buffetaut and Ouaja, 2002; Dal Sasso *et al.*, 2005; Bertin, 2010; Benyoucef *et al.*, 2015).

Since Stromer's (1915) first publication on *Spinosaurus aegyptiacus*, many anatomical, taxonomic, phylogenetic, biogeographic and paleobiological papers about this genus have been published (*e.g.*, Milner, 2003; Buffetaut *et al.*, 2004; Dal Sasso *et al.*, 2005; Rayfield *et al.*, 2007; Benyoucef *et al.*, 2015; Hendrickx *et al.*, 2016). Nevertheless, there are few studies that detail the fossil record distribution of *Spinosaurus*. The aim of the present paper is to document and analyze the distribution of the *Spinosaurus* genus in northern Gondwana and to elucidate the coastal habitats occupied by the group during the mid-Cretaceous.

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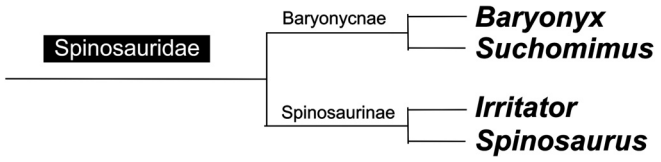

Fig. 1. Phylogenetic relationships of the middle Cretaceous species of the Spinosauridae family (modified from Hendrickx *et al.*, 2016).

2 Taxon rank

Spinosaurus gives name to the family which includes two subfamilies: Baryonychinae and Spinosaurinae (Fig. 1). Baryonychinae includes the genus *Baryonyx* (Charig and Milner, 1986), reported from England, Spain, Portugal (Buffetaut, 2007; Bertin, 2010), and possibly Morocco (Buffetaut, 1989). This genus is closely related to *Suchomimus* (Sereno *et al.*, 1998) which is recorded in Niger. The subfamily Spinosaurinae comprises the genera *Spinosaurus* (Martill and Hutt, 1996), from North Africa, and *Irritator* from northern Brazil (Hendrickx *et al.*, 2016). The synapomorphies of Spinosaurinae include: non-curved tooth crown, absence of serrations in the tooth crown, alveoli relatively spaced apart, the first premaxillary tooth is much smaller than the second and third premaxillary teeth, large diastema within the premaxillary rosette (Sereno *et al.*, 1998), a smooth lateral surface of the dorsal quadratojugal contact, presence of anterior and posterior margins delimiting the dorsal quadratojugal contact, quadrate foramen ventrally positioned (Hendrickx *et al.*, 2016).

Hone and Holtz (2017) recently presented a summary of the synapomorphies of Spinosauridae. These synapomorphies are well-defined by: the presence of a premaxillary rosette; external nares positioned posteriorly to the premaxillary tooth row (Sereno *et al.*, 1998); highly elongated maxillae; tooth crowns with subcircular cross-sections; a large elongation of the dorsal neural spines, being more than twice as high as the vertebral centra (Benson, 2010); presence of vertical grooves in tooth crowns; anterior carina placed at the base of the crown of maxillary teeth and dentary bones; presence of a ventral keel in the anterior and posterior dorsal and cervical vertebrae; and presence of pneumatic cavities at the center of the base of the neural spines, tilting towards the posterior dorsal region of the vertebra (Evers *et al.*, 2015).

3 Paleogeography and tectonic events of the mid-Cretaceous: a brief review

During most part of the Mesozoic, the continental masses were divided into two main continents: Laurasia, in the Northern Hemisphere, and Gondwana, in the Southern Hemisphere (Pitman *et al.*, 1993; Hay *et al.*, 1999). By the end of the Cretaceous, these land masses had started to break-up, leading to the modern continental arrangement (Hay *et al.*, 1999).

The split of Gondwana started in the Early Jurassic as a consequence of the rifting along the continental borders of what is today South America and Africa (including the northern border close to Europe). The rift continued during the Cretaceous when the South Atlantic ocean began to form, splitting Gondwana into eastern and western land masses (Pitman *et al.*, 1993; Arai, 2015; Melo *et al.*, 2016; Strozyk *et al.*, 2017; Charton *et al.*, 2018). Eastern Gondwana comprised of Africa and India-Madagascar, while western Gondwana was made up of South America, Antarctica, and Oceania. By the end of the Cretaceous, India separated from Madagascar and moved northwest until its eventual collision with Eurasia. The land masses of eastern Gondwana – represented today by Africa – remained connected to South America and, during some periods, Europe until Albian (Hay *et al.*, 1999; Canudo *et al.*, 2009).

Two main paleogeographic features allowed spinosaurids to inhabit northern Gondwana and part of Laurasia (North Africa + northern Brazil + western Europe) during the middle Cretaceous: the "Western Gondwana bridge", present during the period where Africa was still connected to South America (Arai, 2015; Melo *et al.*, 2016; Strozyk *et al.*, 2017), and the sporadic pre-Cenomanian connection between Africa and Europe *via* the Iberian and Italian peninsulas (Canudo *et al.*, 2009). Thus, these (possibly transitional) geographic connections between the north of the African plate and other land masses present at the end of the Early Cretaceous enabled faunal interchanges that affected directly the faunal composition of the terrestrial ecosystems of what today is Africa and influenced the evolution of the genus *Spinosaurus*.

Lastly, Africa was once an isolated area, separated from the Gondwana and Laurasia land masses, especially during the Cenomanian, but with some possible connection with southern Laurasia *via* Apulia and Iberian microplates (Pletsch *et al.*, 2001; Zarconea *et al.*, 2010; Torices *et al.*, 2012). As a result, this continent did not share the same evolutionary history of its terrestrial animals with other areas of Gondwana and even Laurasia. Furthermore, Africa was affected by marine transgressions during the middle Cretaceous, that separated the African, European, and American marginal basins (*e.g.*, São Luís, Tataouine, Humar, Shushan) (Candeiro, 2015; Candeiro *et al.*, 2011, 2017). This isolation probably leads to a faunal differentiation from other areas.

4 *Spinosaurus* records

In the following, we present a brief description of the known records, localities, materials, and comments of *Spinosaurus* specimens from the Albian-Cenomanian of North Africa (Fig. 2, Tab. 1).

Albian – Tunisia

Spinosaurus cf. aegyptiacus Stromer, 1915

Geological unity and age: Chenini Member (Ain El Guettar formation), late Albian, Tunisia.

Material: BM231 – rostral part of the left dentary with two teeth.

Comments: Buffetaut and Ouaja (2002) described an incomplete dentary from the Chenini member (late Albian) in the region of Jebel Miteurda, province of Tataouine, Southern Tunisia. According to the authors, this material is similar to the species' holotype, yet it is smaller than the *Spinosaurus aegyptiacus* described by Stromer (1915).

Cenomanian – Egypt

Spinosaurus aegyptiacus

Geological unity and age: Bahariya formation, Cenomanian, Egypt.

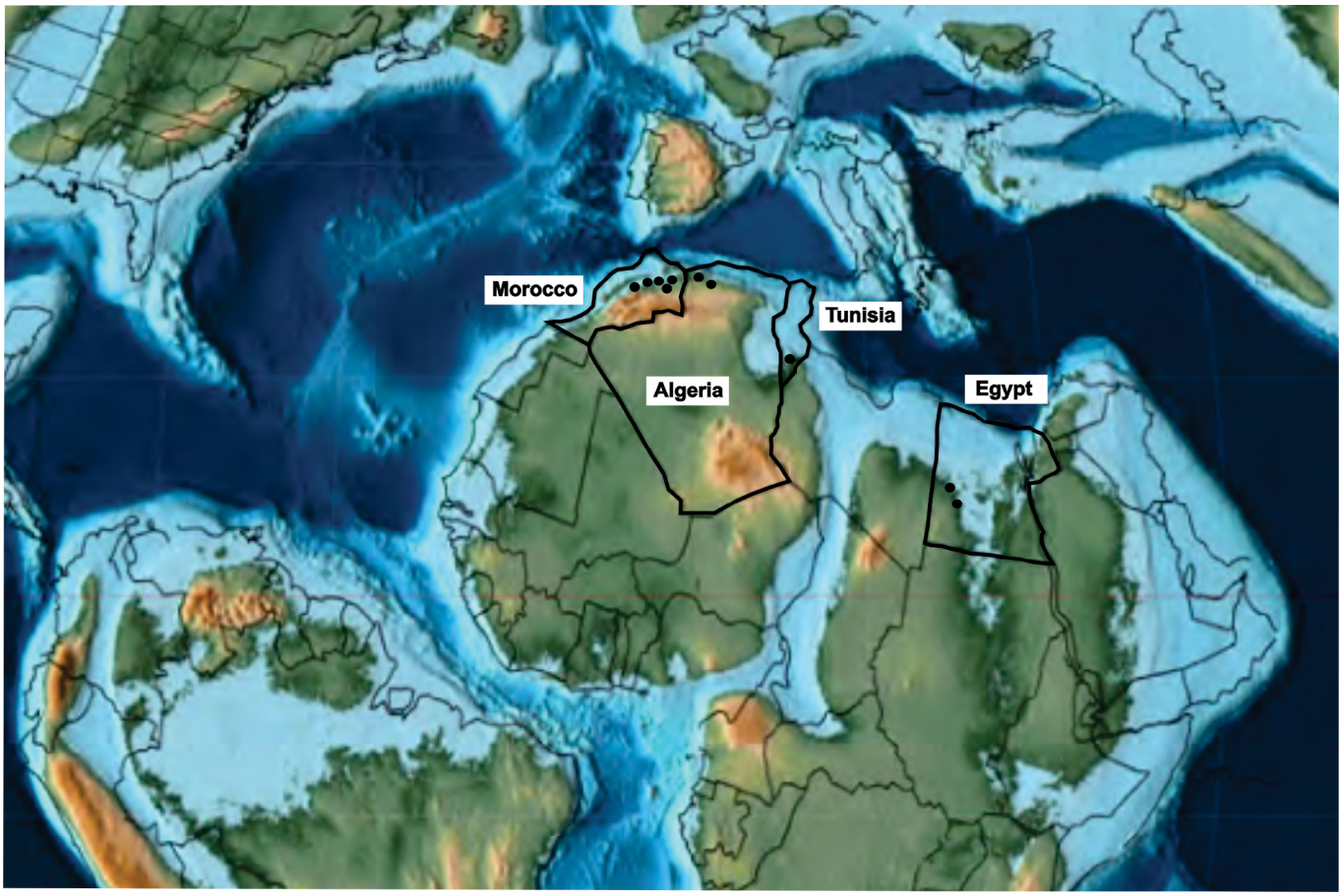

Fig. 2. Gondwanan early Late Cretaceous *Spinosaurus* species distribution (black points).

Material: BSP 1912 VIII 19 – partially complete skeleton with cranial and postcranial elements.
Comments: *Spinosaurus aegeptiacus* was described by Stromer (1915) after materials found in the rocks of the Bahariya formation, in Central Egypt (Fig. 3). According to Sereno *et al.* (1998), the layers of this deposit are dated from the Cenomanian. The materials consisted of a small fragment of maxilla, a fragment of jaw, nineteen teeth, two cervical vertebrae, seven dorsal vertebrae, three sacral vertebrae, one caudal vertebrae, some ribs, and elements of the gastralia. The holotype was destroyed during the World War II (Taquet, 1984; Sereno *et al.*, 1999).

Spinosaurus "B"
Geological unity and age: Bahariya formation, Cenomanian, Egypt.
Material: BSP 1912 VIII 19 – vertebrae and hindlimb bones.
Comments: *Spinosaurus* "B" was described by Stromer (1915) and it was found in a locality close to where the aforementioned *S. aegyptiacus* was collected. The material was quite fragmented and Stromer (1934) assigned it as "*Spinosaurus* B", considering it to be sufficiently different to belong to another species. This material was also destroyed during the World War II.

Early Cenomanian – Algeria/Morocco
Spinosaurus cf. aegyptiacus
Geological unity and age: Kem Kem beds, Algeria, (MNHN SAM 124, MNHN SAM 125-128); Kem Kem beds, early Cenomanian, Morocco (NMC 50791).
Material: NMC 50791 – a mid-cervical vertebra (Russell, 1996); MNHN SAM 124 is from the Gara Samani region, northwestern edge of Tademait (Taquet and Russell, 1998) – a fragment of the rostrum with part of the premaxilla, a fragment of dentary, and vomers; MNHN SAM 125 – a premaxillary fragment; MNHN SAM 126 – a cervical centrum; MNHN SAM 127 – a cervical centrum; MNHN SAM 128 – a dorsal neural arch.
Comments: NMC 50791 was originally described by Russell (1996) as *Spinosaurus maroccanus*, and other materials were assigned to this species by Taquet and Russell (1998). Later, some authors (*e.g.*, Sereno *et al.*, 1998; Bertin, 2010) confirmed that all specimens assigned to *S. maroccanus* belong to this type species. Taquet and Russell (1998) described other materials that were also from Gara Sami and assigned them to *Spinosaurus cf. aegyptiacus* (Bertin, 2010).

Early Cenomanian – Morocco
Spinosaurus cf. aegyptiacus
Geological unity and age: Kem Kem beds, early Cenomanian, Morocco.

Table 1. *Spinosaurus* record from North Africa.

Taxa	Locality	Geological unit	Age	Materials	Selected authors
Spinosaurus aegyptiacus					
Spinosaurus cf. aegyptiacus	Jebel Miteur, Tataouine, Tunisia	Chenini Formatio	Early Albian	Left dentary	Buffetaut and Ouaja (2002)
Spinosaurus cf. aegyptiacus	Taouz municipality, Morocco	Kem Kem beds	Early Cenomanian	Premaxillae, maxillae, external nares, nasals	Dal Sasso *et al.* (2005)
Spinosaurus cf. aegyptiacus	Taouz municipality, Morocco	"Hammada du Guir" beds	Cenomanina	An isolated tooth, two jaw fragments	Buffetaut (1989)
Spinosaurus aegyptiacus	Erfound, Morocco	Kem Kem beds	Cenomanian	Partial skeleton	Ibrahim *et al.* (2014)
Spinosaurus "B"					Stromer (1934)
Spinosaurus sp.	Tafilalt, Morocco				Buffetaut (1989)
Spinosaurus aegyptiacus (*marrocanus*)	Gara Samani, Algeria	Ifezounae Formation	Early Cenomanian	Two median cervical vertebra, dentary fragments, dorsal neural arch,	Russell (1996)
Spinosaurus aegyptiacus (*marrocanus*)	Gara Samani, Algeria		Early Cenomanian	Isolated rostrum, a premaxilary and neural arch of dorsal vertebra	Taquet and Russell (1998)
Spinosaurus aegyptiacus	Béchar municipality, Western Algeria UTL.25-MN1 UTL.25-KDI	"Grès rouges" Formation, Guir Basin	Cenomanian	Teeth	Benyoucef *et al.* (2015)
Spinosaurus marrocanus	Gadoufaoua, Aïr Massif, north Niger; Gara Samani, Algeria MNHN SAM	Gadoufaoua, Gara Samani	Albian	Both premaxillae, maxillae, vomers, fragmente of premaxilla, centra of two cervical vertebrae, neural arch of dorsal vertebra	Russell (1996)

Material: MSNM V4047 – a large snout with premaxillae and maxillae and the rostral part of the nasal bones; UCPC-2 – caudal part of a pair of nasal bones and a small fragment of a left maxilla.
Comments: MSNM V4047 and UCPC-2 were assigned to *Spinosaurus cf. aegyptiacus* based on rostral specimens that revealed important information about the paleoecology and body size of this species and positioned it as the largest known species of superpredators from the Cretaceous (Dal Sasso *et al.*, 2005).

Spinosaurus aegyptiacus
Geological unity and age: Kem Kem beds, early Cenomanian, Morocco.
Material: FSAC-KK 11888 – a partial skeleton of a subadult.
Comments: Ibrahim *et al.* (2014) described the material of a subadult individual assigning it to *S. aegyptiacus* and characterizing it as a neotypic specimen. However, according to Evers *et al.* (2015), this material can not be considered a neotype due its subadult characteristics.

Spinosaurus cf. aegyptiacus
Geological unity and age: Kem Kem beds, early Cenomanian, Morocco.
Material: NHM R16420 – a premaxilla and a fragment of maxilla; NHM R16420 – a dentary.
Comments: Milner (2003) describes jaws of *S. cf. Aegyptiacus*. Although brief, the descriptions are significantly informative.

Spinosaurus sp.
Geological unity and age: Kem Kem formation, early Cenomanian, Morocco.
Material: IMGP 969/1 – a fragment of right maxilla; IMGP 969-2 – a fragment of jaw; IMGP 969-3 – one tooth.
Comments: Buffetaut (1989, 1992) assigned these specimens to *Spinosaurus* sp. The material was collected in the municipality of Taouz, Hammada du Guir, Southeastern Morocco.

Spinosaurus aegyptiacus
Geological unity and age: Kem Kem beds, early Cenomanian, Morocco.
Material: MHNM.KK374 a.KK375 e.KK377 a.KK378; MSNM V6896 – Five quadrates.
Comments: Hendrickx *et al.* (2016) recently described five cranial specimens assigned to *S. aegyptiacus* and classified as "Morphotype 1". The material belongs to different individuals and presents distinct ontogenetic stages. These new specimens allowed the authors to infer that these dinosaurs had feeding habits that were not necessarily exclusively piscivorous – a hypothesis that had already been proposed by other authors (*e.g.*, Charig and Milner, 1997; Buffetaut *et al.*, 2004).

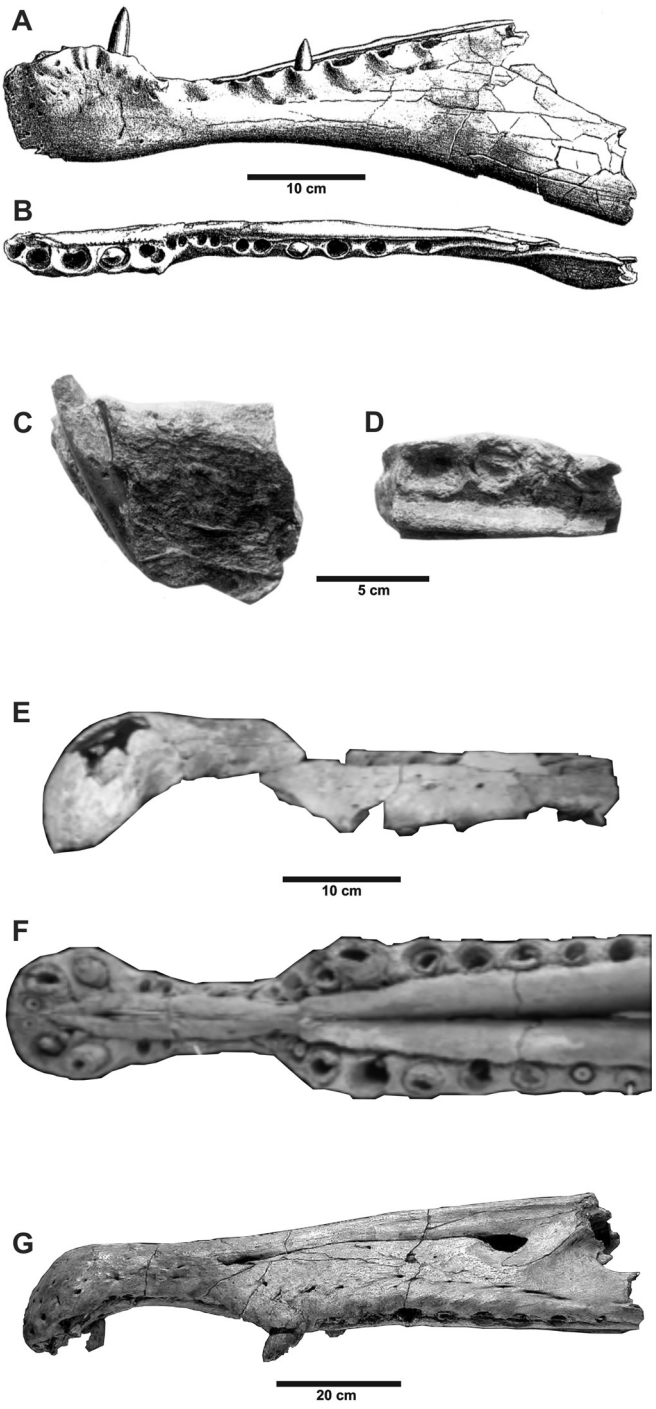

Fig. 3. Most complete *Spinosaurus* species skulls from early Late Cretaceous formations from Northern Africa. *Spinosaurus aegyptiacus* (from Stromer, 1915), BSP 1912 – dentary, A in lateral and B in dorsal views. *Spinosaurus cf. aegyptiacus* (from Buffetaut and Ouaja, 2002), BM231 – rostral part of left dentary, C, in lateral and in D dorsal views. *Spinosaurus marrocanus* (*nomen dubium*) (Taquet and Russell, 1998) MNHM SAM 124 – left maxilary, E in lateral and F dorsal views. *Spinosaurus cf. S. aegyptiacus* (from Dal Sasso *et al.*, 2005) MSNM V4047 – left maxilary, G in lateral in dorsal view.

Early Cenomanian – Algeria
Spinosaurus aegyptiacus
Geological unity and age: Guir basin, early Cenomanian, Algeria.
Material: UTL25-MN1-12 79 – teeth; UTL25-KD1-1 – two teeth.
Comments: The material was recently described by Benyoucef *et al.* (2015) and it only comprises teeth. These fossil remains were found in the areas of Kénasda and Nenaguir which are part of a larger region known as Continental Intercalaire where rocks of the Kem Kem beds and of the Guir Basin are exposed between Algeria and Morocco. This region has been prolific in fossils, showing a large and diverse terrestrial and marine vertebrate fauna (Cavin *et al.*, 2010).

5 Results

5.1 Distribution of records

Classically, *Spinosaurus* is known from incomplete skeletons from Egypt, where the first described material was found. Since the second half of the last century, a significant number of *Spinosaurus* specimens from Algeria, Morocco, and Tunisia have been formally described (Buffetaut, 1989, 1992; Taquet and Russell, 1998; Benton *et al.*, 2000; Buffetaut and Ouaja, 2002; Milner, 2003; Dal Sasso *et al.*, 2005; Ibrahim *et al.*, 2014; Benyoucef *et al.*, 2015; Hendrickx *et al.*, 2016). Although most material is referable to isolated specimens, some are very well preserved and have been exclusively found in Albian and Cenomanian rocks, suggesting this genus inhabited a large geographic area in North Africa during the middle Cretaceous. Currently, the Cenomanian material is the most representative and abundant fossil record found in Morocco, with a total of six records. Buffetaut (2007) widely discussed the Trans-African similarities between the Cenomanian phases and the spinosaurines from Morocco, Tunisia, and Egypt, pointing out the presence of *Spinosaurus* along an extensive African Gondwana coast during the mid-Cretaceous. Curiously, despite the fact that the African plate was connected to Europe during some periods and permanently connected to South America at that time, there are no records of *Spinosaurus* outside Africa, even during the Albian. By the end of the Albian period, a biogeographic barrier appeared with the Atlantic opening, when the depth of this ocean definitely increased (Fig. 4) and its waters became quite cold (Maisey, 2000), preventing the crossing of these large terrestrial predators to South America.

The current records regarding the paleogeographic and stratigraphic distribution of *Spinosaurus* in northern Gondwana show that these theropods occupied areas represented today by Algeria, Egypt, Morocco, and Tunisia. *Spinosaurus aegyptiacus*, *Spinosaurus cf. aegyptiacus*, *Spinosaurus* "B", and *Spinosaurus sp.* were discovered in North Africa. *Spinosaurus cf. aegyptiacus* is recorded from the Albian of both Tunisia and Algeria, while *Spinosaurus aegyptiacus* is recorded in the early Cenomanian of the latter. In Egypt, the records of *Spinosaurus aegyptiacus* and *Spinosaurus* "B" are

from the early Cenomanian. Finally, the Moroccan record of *Spinosaurus aegyptiacus,* as well as of three other different specimens of *Spinosaurus cf. aegyptiacus* and *Spinosaurus* sp., are all from the early Cenomanian (Fig. 2, Tab. 1).

The genus *Spinosaurus* is reported from 11 localities from the mid-Cretaceous of North Africa. On the other hand, there are no records of *Spinosaurus* in other areas of Gondwana or even Laurasia, where other spinosaurids (*e.g.*, *Baryonyx*, *Irritator*, *Oxalaia*, *Siamosaurus*, *Suchomimus*) have been recorded (western Europe, southeastern Asia, and northern Brazil) (Bertin, 2010; Candeiro *et al.*, 2017). Therefore, it seems that the paleogeographic distribution of *Spinosaurus* is the result of a unique faunal interchange that occurred between the Albian and the Cenomanian only in North Africa. The observed distribution of *Spinosaurus* in this region could be the product of its evolution, dispersion or selective preservation which occurred exclusively in the coastal areas of Africa. Until now, spacial and temporal differences in the composition of the northern Gondwanan species of *Spinosaurus* are unknown. It is possible that this scenario was induced by this taxonomic "stability" caused by paleoecological trends suitable to the evolution of this taxon. *Spinosaurus* is the most common theropod reported from North Africa in comparison to other carnivorous dinosaurs. As a consequence, this taxon could have been more numerous than other northern Gondwanan theropods (*e.g.*, Carcharodontosauridae: *Carcharodontosaurus saharicus* Depéret and Savornin, 1925; *Eocarcharia dinops* Sereno and Brusatte, 2008; Abelisauridae: *Rugops primus* Sereno *et al.*, 2004; Spinosauridae/Baryonychinae: *Sigilmassasaurus brevicollis* Russell, 1996). It is still an enigma why *Spinosaurus* was not yet found in nearby regions (western Laurasia and eastern Gondwana).

The oldest record of *Spinosaurus* is from the Ain El Guettar formation, in Tunisia (Buffetaut and Ouaja, 2002), and from the Albian Kem Kem beds in Algeria (Russell, 1996; Taquet and Russell, 1998). The presence of the genus in these formations as well as in the early Cenomanian of the Bahariya formation and Kem Kem beds shows that the derivation of this taxon occurred in northern Gondwana during the first stage of the Late Cretaceous.

The fossil record of *Spinosaurus* from Cenomanian formations of North Africa is important for many reasons. The 11 records of this genus directly correlates these predators with the abelisaurs and carcharodontosaurs from areas of the same age in Algeria, Egypt, and Morocco (Novas *et al.*, 2013; Candeiro, 2015) – today these areas are in the northern east-west edge of Africa. Hence, this also correlates the *Spinosaurus* record with the chronostratigraphic time scale of the Gondwanan pattern of northern Gondwana. These correlations indicate that this group became top predators in a large area of occurrence where other megacarnivorous were also present.

This study shows that the geographic distribution of the genus *Spinosaurus* was generalized during the mid-Cretaceous. The fossil record of this spinosaurinae suggests the existence of faunal connections in the beginning of the Late Cretaceous that occurred only among the areas of North Africa. These theropods were terrestrial animals that lived nearby coastal environments (Cavin *et al.*, 2010; Candeiro *et al.*, 2011) and, thus, it depended of land bridges as migration routes. By the end of the Albian period, these land bridges that

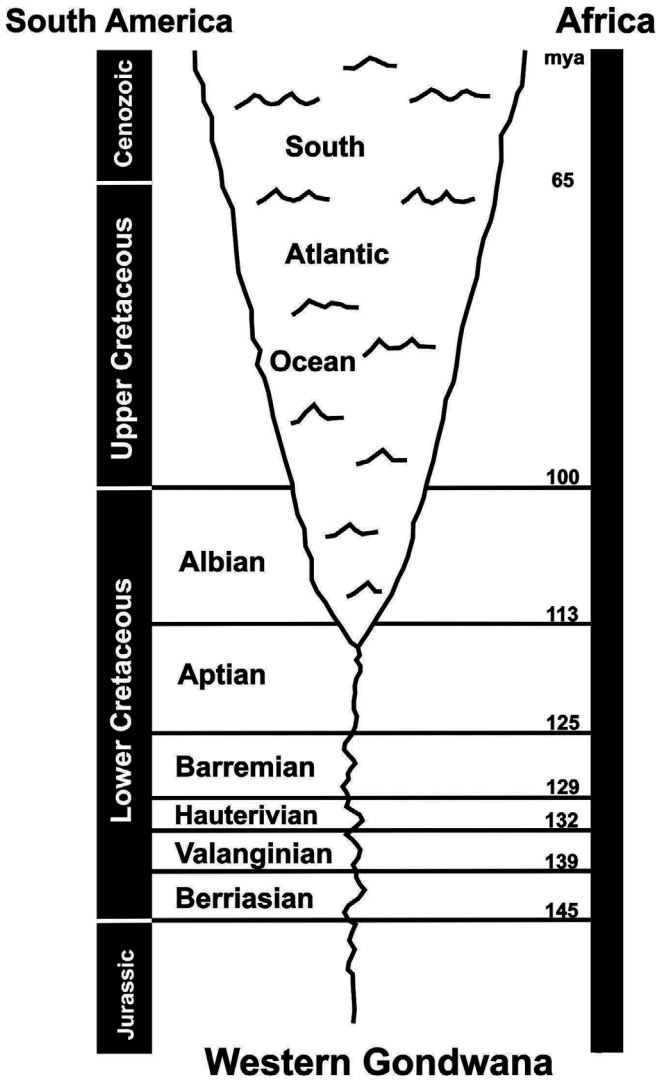

Fig. 4. Block diagram of the break up between the Africa and South America plates during the Cretaceous (modified from Maisey 2000).

connected the African plate with Europe and South America no longer existed. Today, the fossil record of *Spinosaurus* suggests that this taxon originated in certain areas of North Africa during the Albian and later dispersed to other northern areas of this continent. Their records from the mid-Cretaceous of northern Gondwana are unique because the paleogeographic reconstructions during the Albian-Cenomanian of Africa actually reflects a restricted distribution in middle latitudes from east to west. During the Late Albian and the Cenomanian, the northern part of Gondwana suffered with marine ingressions (Maisey, 2000). As a consequence, no faunal interchange among terrestrial dinosaurs occurred between Africa and Northern Brazil, since the marine waters possibly became a physical barrier to their dispersal.

5.2 Macrohabitat niche

In the literature, the mid-Cretaceous occurrence and preference of *Spinosaurus* for coastal regions and brackish waters of northern Gondwana is documented (Russell, 1996;

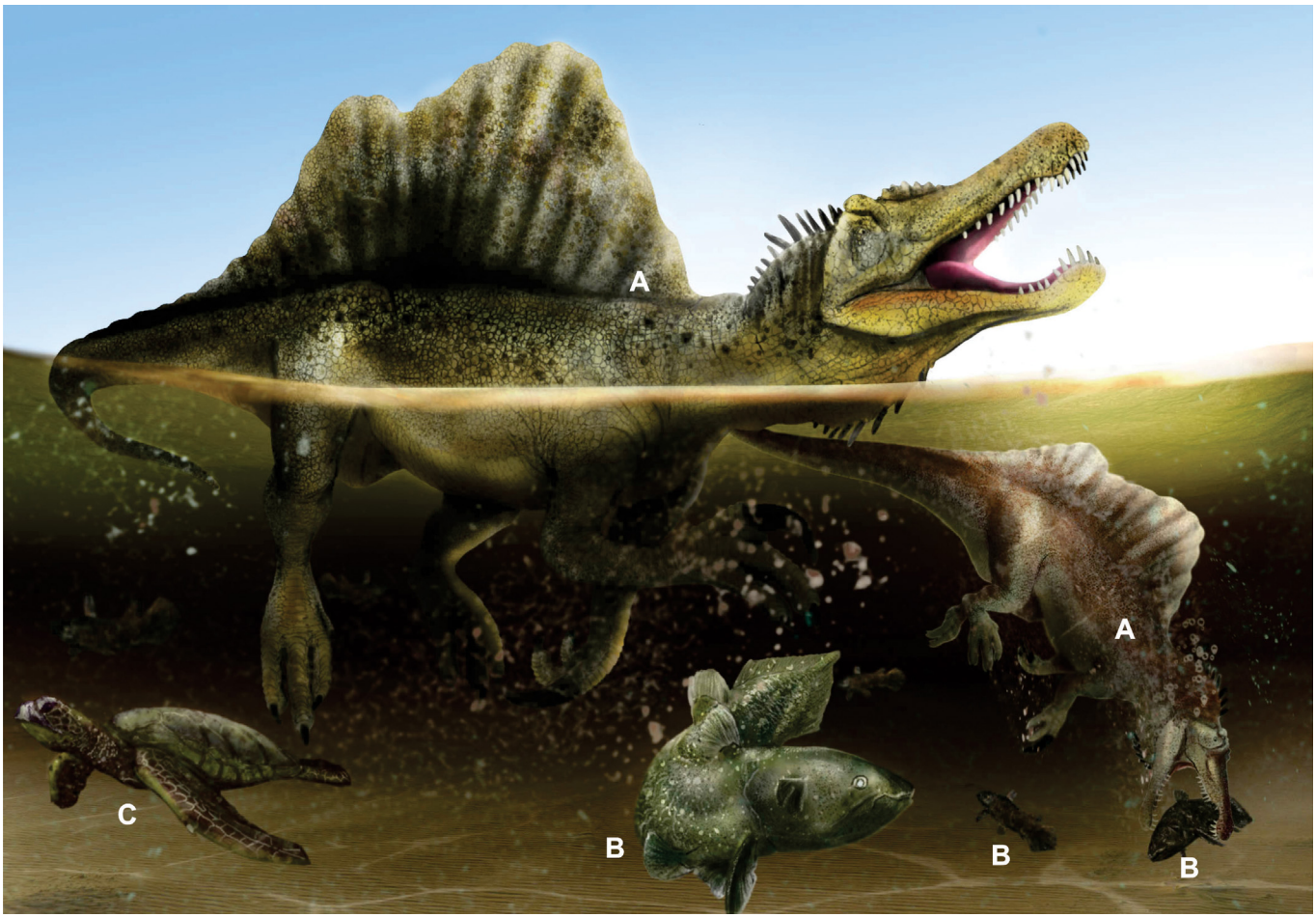

Fig. 5. Semi-aquatic paleoenvironmental reconstruction of *Spinosaurus* dinosaur during early Late Cretaceous: (A) *Spinosaurus*; (B) *Mawsonia* coelacanth fishes; (C) *Araripemys* turtle (drawing Luciano Vidal).

Russell and Paesler, 2003; Smith *et al.*, 2006). More precisely, the primary habitats used by *Spinosaurus* were flooded areas nearby deltas (Bertin, 2010). The preference of the northern Gondwanan *Spinosaurus* for mangroves and other coastal areas where brackish waters occur is probably related to the local environmental characteristics that were common to the marginal areas of Africa during the mid-Cretaceous. Naturally, these regions also had fresh water courses (see Buffetaut, 1989; Buffetaut and Ouaja, 2002; Bertin, 2010) since this large spinosaurinae was apparently absent in inland areas of the continent where other freshwater sources were present. *Spinosaurus* is also known in coastal lagoons and estuarine environments all over western Africa (Buffetaut and Ouaja, 2002; Bertin, 2010) (Fig. 5). Therefore, our regional data fully confirm the previously known information that the niches occupied by this genus were related to coastal environments.

This analysis considers a small possibility of competitive interactions between both forms (maybe different in body size) of *Spinosaurus* (*S. aegptiacus* [Stromer, 1915]), *Spinosaurus cf.* a*egyptiacus* (Dal Sasso *et al.*, 2005) and *Spinosaurus* sp. (Buffetaut, 1989) that inhabited the same areas of Morocco during the Cenomanian. We suggest that the body size difference between these taxa allowed them to coexist in the same habitat and probably produced dietary differences that minimized competition, as previously shown in other reptile taxa (see Pianka, 1973, 1986; Oliveira *et al.*, 2013). Corroborating with this, these results show that it is likely that both species differed in habitat use. However, we cannot exclude the possibility that niche differences were driven by competition (Connell, 1980; Farlow and Pianka, 2002; Oliveira *et al.*, 2013).

6 Remarks

The middle Cretaceous strata of North Africa preserved an important record of the theropod *Spinosaurus*. Although their fossil remains are usually fragmented, most specimens show diagnostic characters of the genus *Spinosaurus* that are especially present in their conical and non-serrated teeth. The fossil record of this genus in North Africa shows a restricted geographic distribution between the Albian and the Cenomanian periods. Yet, when we consider their temporal distribution, it suggests that *Spinosaurus* had a significant geological history of nearly 20 million years, a lifespan unknown for other African megapredators species (*e.g.*, *Carcharodontosaurus* – 18.5 mya [Candeiro *et al.*, 2018]). The geological evidences indicate that Africa was an island during the main period of

occurrence of this genus. The faunal composition of the spinosaurinae that inhabited the eastern coast of Africa is broadly comparable with the Cenomanian fossil records from western Africa, supporting the relative homogeneous composition of the taxon in these areas during this period. Additional studies and future field prospections in other localities could eventually reveal a wider distribution of this genus in other regions of Africa (*e.g.*, Niger, Sudan) or even in western Europe and northern South America.

Institutional abbreviations

MSNM	Museo di Storia Naturale di Milano; Milan/Italy
UCPC	University of Chicago Paleontological Collection
UTL	University of Tlemcen/Laboratory, Algeria
FSAC	Faculté des Sciences Aïn Chock, Casablanca, Morroco
IMGP	Georg-August-Universität in Göttingen, Germany

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