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The Cretaceous (Cenomanian) continental record of the Laje do Coringa flagstone (Alcântara Formation), northeastern South America

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The fossil taxa of the Cenomanian continental flora and fauna of São Luís Basin are observed primarily in the bone bed of the Laje do Coringa, Alcântara Formation. Many of the disarticulated fish and tetrapod skeletal and dental elements are remarkably similar to the chronocorrelate fauna of Northern Africa. In this study, we present a summary of the continental flora and fauna of the Laje do Coringa bone-bed. The record emphasizes the existence of a trans-oceanic typical fauna, at least until the early Cenomanian, which may be interpreted as minor evolutionary changes after a major vicariant event or as a result of a land bridge across the equatorial Atlantic Ocean, thereby allowing interchanges between South America and Africa. The paleoenvironmental conditions in the northern Maranhão State coast during that time were inferred as forested humid areas surrounded by an arid to semi-arid landscape.

1. Introduction

The record of Mesozoic continental faunas in the northern region of South America is extremely poor. In Maranhão State of northern-northeastern Brazil (Fig. 1 A), this lack of records is in contrast to the extensive distribution of Cretaceous sedimentary rocks. The Alcântara Formation have yielded the primary records of the Cenomanian continental fauna in this region.

Price (1947) first reported the presence of dinosaur remains in the sedimentary facies of the northern Maranhão State and proposed the interpretation that the sequence of outcropping in the beaches of Alcântara was deposited during the Cretaceous. Klein and Ferreira (1979) described an estuarine assemblage in the deposits of the eastern border of São Marcos Bay, identifying this sequence as Cenomanian in age; this dating was confirmed by the presence of palynomorph biozones (Pedrão et al., 1993a). Several dinosaur track sites were described on both sides of the bay (Carvalho and Gonçalves, 1994; Carvalho, 1995; Carvalho and Pedrão, 1998; Carvalho, 2001), even before a significant number of vertebrate fossils were found.

The Laje do Coringa bone bed (Fig. 1 B), Alcântara Formation, early Cenomanian, is the most important Cretaceous outcrop of the northern coastal area (Corrêa Martins, 1997). Although most of the skeletal remains collected therein are fractured and eroded, important information has been recovered from it.

Medeiros and Schultz (2001, 2002) recognized remarkable similarities between the continental faunas of northeastern Brazil and northern Africa during the mid-Cretaceous, most notably with the material from southeast Morocco (Lapparent, 1960; Cavin et al., 2010). A striking similarity has been noticed between the northern Brazilian fish record and that of Kem Kem in Morocco (Cavin and Dutheil, 1999; see also Cavin et al., 2010). This similarity is evident when we compare the Moroccan taxa with those of the Alcântara Formation. The present study analyses the data from the fossil record of the Alcântara Formation and the aspects concerning paleoenvironmental inferences and its distribution in the Gondwana context during the mid-Cretaceous.

2. The fossil record of the Laje do Coringa bone bed

Located on a sandy and muddy beach on the eastern side of Cajual Island (Fig. 1), the Laje do Coringa outcrop is the richest fossiliferous site of the Alcântara Formation. Holz (2003) considered it a transgressive lag. Conifers are common amongst the

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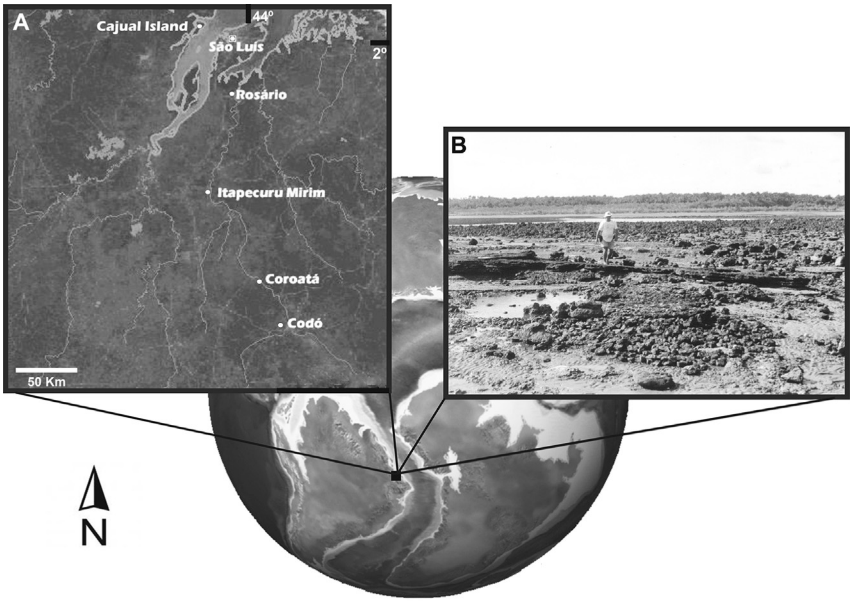

Fig. 1. Area of occurrence of Cretaceous rocks in northern Maranhão state, northeastern Brazil, as originally located during Gondwana pull apart. A – Cajual Island and Itapecuru River Valley; B – Photo of Laje do Coringa site.

petrified plants (Fig. 2 A). Araújo et al. (2011) referred most of a sample of logs to Araucariaceae.

Pteridophyta are also common, represented by *Paradoxopteris sanctiluigi* Mussa et al., 2000 (Fig. 2 B). Hundreds of prints and some rare 3D preserved specimens of an undetermined Equisetales were also found (Fig. 2 C).

Medeiros and Schultz (2002, 2004) identified many of the vertebrate remains collected at the Laje do Coringa site. Ganoid

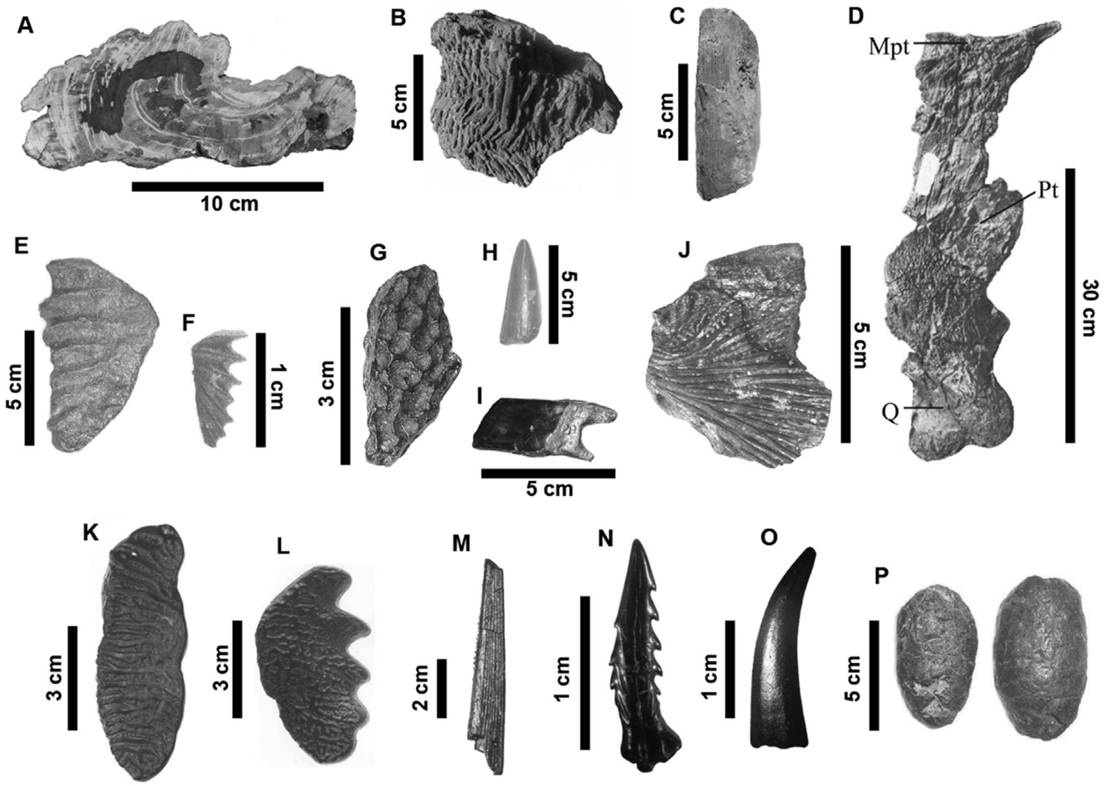

Fig. 2. Fossils from Laje do Coringa site: A – Conifer log; B – Stem of *Paradoxopteris sanctiluigi* (Pteridophyta); C – Stem of Equisetales indet.; D – Palato-quadrate of *Mawsonia gigas* (Mpt – metapterygoid, Pt – pterygoid, Q – quadrate); E – *Ceratodus brasiliensis* tooth plate; F – *Arganodus tiguidiensis* tooth plate; G – Crocodile osteoderm; H – Crocodile tooth; I – Scale of *Lepidotes* sp.; J – Post-parietal of *Mawsonia gigas*; K – Tooth plate of *Equinoxiodus alcantarensis* (Dipnoi); L – Tooth plate of *Equinoxiodus* sp.; M – *Tribodus cf. limae* (hybodont shark) dorsal spine; N – Rostral tooth of *Atlanticopristis equatorialis* (Elasmobranchii, Sclerorhynchidae); O – Tooth of Ornithocheiroid pterosaur; P – Coprolites of reptiles indet.

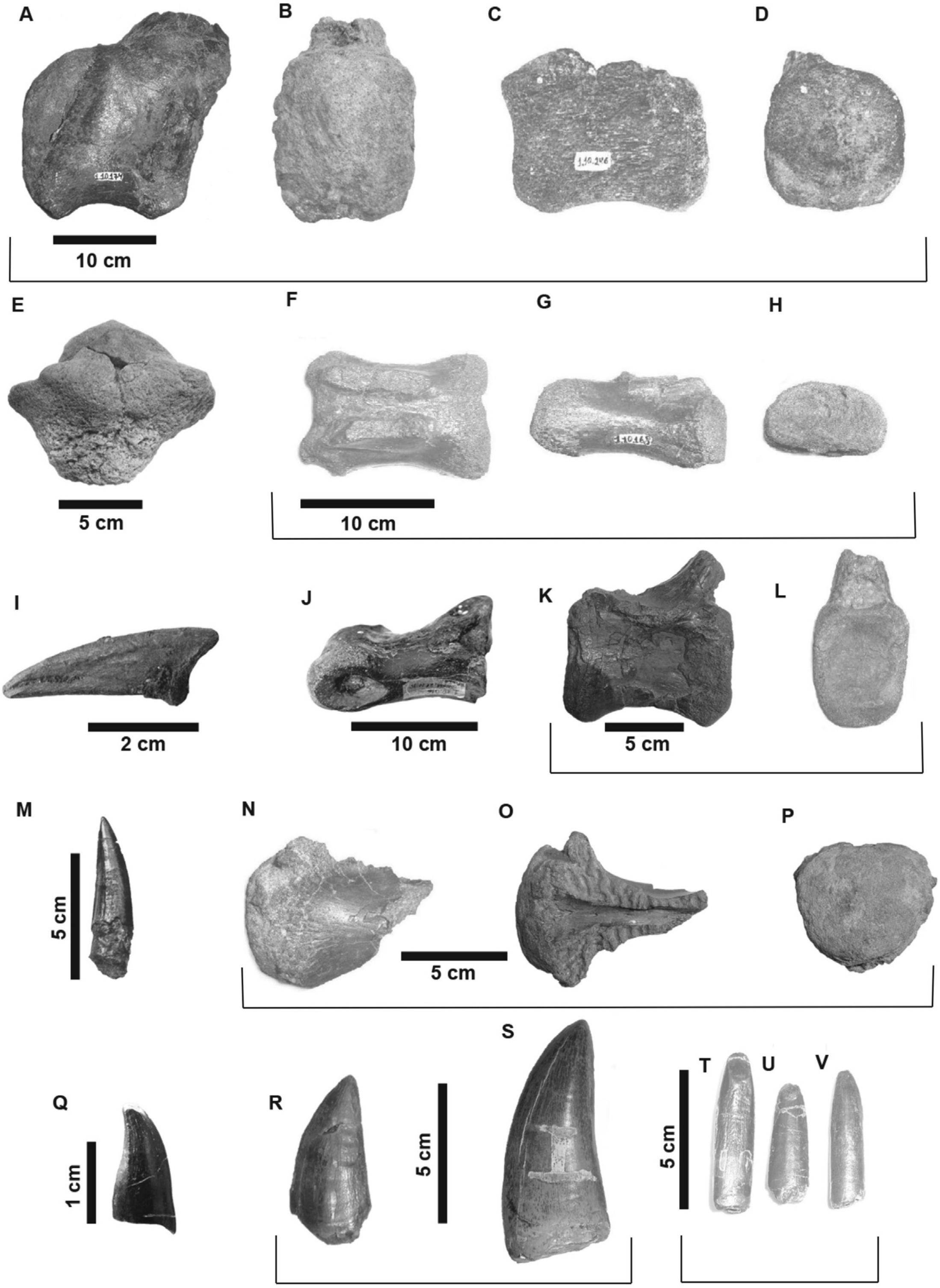

Fig. 3. Titanosauridae caudal centrum in lateral (A) and posterior (B) views; Andersauridae caudal centrum in lateral (C) and posterior (D) views; E – Titanosaur osteoderm; Rebbachisauridae caudal distal centrum in dorsal (F), lateral (G) and posterior (H) views; I – Claw of a reptile indet.; J – Theropod phalange; *Sigilmassasaurus brevicollis* caudal vertebra in lateral (K) and posterior (L) views; M – Tooth of *Spinosaurus* sp.; Dorsal centrum of *Spinosaurus* sp. In lateral (N), dorsal (O) and anterior (P) views; Q – *Masiakasaurus*-like tooth; Teeth of *Carcharodontosaurus* sp. from Laje do Coringa (R) and Itapecuru valley (S); T – *Malawisaurus*-like tooth in lingual view; U and V – Sauropod teeth in lingual view.

mineralized scales are the most common fish remains (Fig. 2 I). In Brazilian Cretaceous deposits, these scales have been interpreted as indicating the presence of *Lepidotes*. Nonetheless, Gallo and Brito (2004) remark the possibility of misidentification when only the scales are found. Lungfishes, such as *Ceratodus brasiliensis* (Fig. 2 E), *Arganodus tiguidiensis* (Fig. 2 F) (Castro et al., 2004) and *Ceratodus humei* (Toledo et al., 2005), are well represented by their dental plates. The South American taxon *Equinoxiodus alcantarensis* Toledo et al., 2011 (Fig. 2 K) was also a dipnoan species living in the Cenomanian of northeastern Brazil and is recorded in the Alcântara

Formation. An unnamed species of this genus, provisionally referred as *Equinoxiodus* sp. (Fig. 2 L), is to be described in a forthcoming article.

The palato-quadrate and the post-parietal cranial material of the giant coelacanthid *Mawsonia gigas* (Fig. 2 D, J) were found in Laje do Coringa. The size of some bones reveal that the individuals who lived in the northern Maranhão state are amongst the largest ever recorded (Medeiros and Schultz, 2002; Medeiros et al., 2011). Hybodontid shark dorsal spines, laterally compressed with lateral parallel ribs and with two rows of alternating barbs on the posterior margin, referred to as *Tribodus* cf. *limae,* have been collected (Fig. 2 M). An exclusive South American species and genus of sclerorhynchiform rays, *Atlanticopristis equatorialis* Pereira and Medeiros, 2008 (Fig. 2 N) exhibiting rostral teeth with both anterior and posterior barbed margins, and the closely related *Onchopristis* cf. *numidus* (Pereira and Medeiros, 2003) are recorded by their rostral teeth. The possible occurrences of some other types of fishes have also been recorded: hook-like pharyngeal teeth that possibly indicate the presence of *Stephanodus* and distinctive spines attributable to *Bartschichthys* (Pereira and Medeiros, 2003). Sousa et al. (2004) described a dental plate with tiny round teeth that was thought to be related to pycnodontiforms.

All of the collected dinosaurian vertebral centra are devoid of a neural complex. The procoelous anterior caudal centra (Fig. 3 A, B) have a peculiar morphology: tall and sub-rectangular in anterior and posterior views, with a posterior bulge and anterior margin of the neural canal placed beyond the anterior limit of the articular face (Salgado and Garcia, 2002, Fig. 2). They are diagnostic for the presence of titanosaurids. Massive amphiplatyan vertebral caudal elements, with high lateral faces gently concave and the suture of the neural arch placed anteriorly, were referred to as Andesauridae (Fig. 3 C, D) based on the similarities with those determined by Calvo (1999: Fig. 6) and Russell (1996: Fig. 32). One keeled osteoderm was found (Fig. 3 E), with irregular perforations and foramina at the external surface, rugose internal surface with interwoven bone pattern and foramina and the presence of a bulb and root separated by a cingulum. This osteoderm was attributable to titanosaurs by Lindoso et al. (2013) based on previously described features (D'Emic et al., 2009; Salgado, 2003). Medeiros and Schultz (2004) documented the presence of a diplodocoid dinosaur closely related to *Rayososaurus tessonei* (= *Rebbachisaurus tessonei* or *Limaysaurus tessonei*) based on several caudal centra, including those shown in Fig. 3 F, G, H. They are flattened, constricted in the dorsal view, with articular surfaces that are very concave and a neural canal that is long and anteriorly placed. These caudal distal centra are similar to those of the well-preserved specimen described by Calvo and Salgado (1996) and on display in the museum of the Universidad del Comahue, at Neuquén, Argentina. Fragments of neural spines that are cross-shaped in the dorsal view provide more evidence of a rebbachisaurid related species in the mid-Cretaceous of Brazil (Castro et al., 2007; Medeiros et al., 2007). Sauropod teeth are less common than those of theropods. A form closely related to *Malawisaurus dixeyi* (Fig. 3 T) was part of the community. The specimen is slightly expanded in the middle region, recurved lingually and texturized on the surface, with a large distal wear facet and a D-shaped cross section (Wilson and Sereno, 1998). Other specimens, which display a peg-like shape (Fig. 3 U, V), may be referred to titanosaurids or diplodocoid rebbachisaurid sauropods (Medeiros et al., 2007).

The theropods are represented in the Laje do Coringa outcrop by teeth and some isolated skeletal elements, such as phalanges (Fig. 3 J) and vertebrae. Two amphicoelic caudal centra, which are laterally compressed, sub-rectangular in the lateral view and feature a neural spine that is laterally wider than antero-posteriorly long and postero-dorsally oriented and emerges from the posterior half of the neural arch (Fig. 3 K, L), are similar to African specimens described and illustrated by Russell (1996, Fig. 12 E, F, G) and Stromer (1934: Pl. 1, Figs. 5, 6). Medeiros and Schultz (2002) referred these specimens to *Sigilmassasaurus brevicollis*, a controversial northern African taxon erected by Russell (1996) as a theropod but considered an iguanodontid by Novas (2009).

Teeth having a nearly straight crown and rounded basal section with non-serrated carinae and both faces (labial and lingual) exhibiting longitudinal sub-facets or flutes (Fig. 3 M) are very common in the Brazilian fossiliferous site. A vertebral fragment that is very constricted in its median portion with a rounded articular face (Fig. 3 N, O, P) recalls the anterior half of the dorsal centra of *Spinosaurus aegyptiacus* (Stromer, 1915; Pl.2, Figs. 3 and 4, 5, 6). These teeth and vertebrae suggest the taxon represented in the Laje do Coringa site to be congeneric with that of the northern African genus (Medeiros and Schultz, 2001, 2002). Nevertheless, Kellner et al. (2011) erected the taxa *Oxalaia quilombensis* based on the anteriormost portion of a maxilla. The variation observed in a very representative sample of isolated teeth (275 specimens), including teeth with no longitudinal enamel flutes, indicates that more than one spinosaurid lived in the Cenomanian of northeastern Brazil (Medeiros, 2006), exactly as also observed in the Kem Kem deposits (Richter et al., 2013). Easily identifiable large teeth (Fig. 3 R, S) were referred to *Carcharodontosaurus* sp. (Vilas Bôas et al., 1999) because of their size, shape and distinctive transversal enamel wrinkles (see Sereno et al., 1996). The teeth of *Carcharodontosaurus* (Fig. 3 R, S) and spinosaurid (with unserrated carinae) were collected in the

Fig. 4. On land: sauropod titanosaurids (left) and andesaurids (right); theropod spinosaurid (center) and noasaurid (right); sawfish *Atlanticopristis equatorialis*. Flying: Anhangueridae. In the water: left – *Mawsonia gigas* (close to the surface), Pycnodontiform (middle) *Myliobatis* sp. (botton); right – *Tribodus* sp. (sharks), *Lepidotes* sp. (up), ceratodontid (middle), and the sawfish *Onchopristis* sp. (background).

Laje do Coringa site (early Cenomanian) and are also common in the Albian deposits of the Itapecuru Formation that occur inland along the valley of the Itapecuru river (Medeiros and Schultz, 2002).

Teeth with peculiar morphology, i.e. very compressed laterally with the tips of the large denticles of the posterior carina oriented apically, suggest that dromaeosaurid (possibly velociraptorine) dinosaurs were part of the Alcântara Formation vertebrate community (Vilas Bôas, 1999; Elias et al., 2004). A reptile claw (Fig. 3 I) is possibly related to a small-sized theropod.

The teeth of a noasaurid form (Fig. 3 Q) closely related to and larger than *Masiakasaurus knopfleri* were recently identified (Lindoso et al., 2012). The teeth are distally curved, exhibiting an apex that is more rounded than pointed, with the mesial carina deflected to a lingual position and the distal one deflected labially.

Crocodile teeth and osteoderms (Fig. 2 G, H) are the more easily identifiable elements in the Laje do Coringa bone-bed. Some teeth indicate that the crocodiles could reach more than 6 m in length, comparable to the extant species *Crocodylus niloticus*. Notosuchid crocodiles are represented by two species: *Coringasuchus anisodontis* Kellner et al., 2009 and *Candidodon itapecuruense* (Santos et al., 2011).

Some snake vertebrae (Hsiou et al., in press) that were possibly closely related to Madtsoiidae were identified. Pterosaurs referred to as ornithocheiroids (Fig. 2 O), including Anhangueridae, were identified (Elias et al., 2007) based on the long and slender isolated teeth that are recurved or twisted at the distalmost portion, with moderate to strong labio-lingually compressed crowns, without carinae and smooth enamel surfaces. Some fragments of flat dermal bones may possibly pertain to turtles, but they are not sufficiently complete to allow confident identification. The only chelonian specimen thus far described is an incomplete carapace of an undetermined species referred to Pelomedusoides collected in the city of Alcântara (Moraes-Santos et al., 2001), about 10 km far from the Laje do Coringa site.

Coprolites (Fig. 2 P), which are represented by forms of different sizes and shapes, are common at the Laje do Coringa site. These ovoid or conical forms were evacuated by herbivorous/omnivorous animals, whereas the spiral forms were most likely formed by chondrichthyans (e.g. hybodont sharks), dipnoans or other sarcopterygians. Cylindrical coprolites also occur, some containing ganoid scales, which were produced by undetermined predatory reptiles (Souto and Medeiros, 2012).

Based on the palynological biozones and invertebrates, the sequences along the northernmost portion of the Itapecuru river valley were dated as Albian (Pedrão et al., 1993b), and those of the Alcântara Formation along the coast line were defined as being deposited in the early Cenomanian (Klein and Ferreira, 1979; Pedrão et al., 1993a). Theropod taxa (*Carcharodontosaurus* sp. and spinosaurids) and fish, such as *Mawsonia gigas* and *Ceratodus brasiliensis*, are amongst the most common fossils recovered in these two regions, indicating that the paleocommunity to which these species belonged lived throughout the Albian and early Cenomanian in northeastern Brazil (Medeiros and Schultz, 2002; Medeiros et al., 2007).

3. The mid-Cretaceous community of the Alcântara Formation

Fossil specimens collected in Laje do Coringa are very similar to African forms. Confident identification revealed the presence of *Mawsonia gigas*, *Ceratodus brasiliensis*, *Ceratodus humei*, *Arganodus tiguidiensis*, *Onchopristis* cf. *numidus*, *Tribodus* cf. *limae*, *Carcharodontosaurus* sp., Diplodocoidea, Titanosauridae, Spinosauridae and a noasaurid with *Masiakasaurus*-like teeth. Other specimens are evidently of the same genus or family and possibly of the same species as those present in the African deposits (see Medeiros et al., 2007), but the fragmentary nature of the record and the uncertainties in the identification also present in the African forms make it difficult to establish their real taxonomic affinities.

Several northern African assemblages can be compared with the Laje do Coringa assemblage (e.g. Stromer, 1915, 1931, 1934; Lapparent, 1960; Tabaste, 1963; Benton et al., 2000; Cavin et al., 2010; Richter et al., 2013; Läng et al., 2013) and particularly the record from the Cenomanian of the Kem Kem region, Morocco (Table 1). This similarity indicates that most of the collected taxa from the bone bed represent a continental paleocommunity rather than just a gathering of ecologically unrelated fossil elements. Some marine items (see Vilas Bôas and Carvalho, 2001) may have been intermixed with the continental material as a consequence of the side-by-side deposition of marine and fluvial sediments in an estuarine environment. This deposition would facilitate their mixture during reworking. Most of the identified taxa are congruent with several northern African communities, indicating that the process of transport and re-deposition involved ecologically integrated taxa. Holz (2003) discussed a detailed sequence of the reworking and formation of the Laje do Coringa.

Some new species and genera have been identified to include new forms that are, to the best of our knowledge, restricted to the Alcântara Formation: *Atlanticopristis equatorialis* Pereira and Medeiros, 2008, *Equinoxiodus alcantarensis* Toledo et al., 2011, *Coringasuchus anisodontis* Kellner et al., 2009 and *Oxalaia quilombensis* Kellner et al., 2011.

The assemblage of fish recorded in Laje do Coringa is dominantly continental, and the presence of *Mawsonia*, *Onchopristis*, *Arganodus*, *Tribodus*, *Ceratodus brasiliensis* (=*africanus*) and *C. humei* establishes a close relationship with the northern African fish community. This transoceanic occurrence has already been described (Maisey, 2000; Cavin and Dutheil, 1999; Dutra and Malabarba, 2001; Cavin et al., 2010) and distinguishes this fauna from the South American austral occurrences. Although a Cenomanian age has been suggested for the Santana Formation in northeastern

Table 1
Comparison of the vertebrate faunas from Laje do Coringa and from the Kem Kem beds (as listed by Cavin et al., 2010). Other taxa from North Africa and Madagascar are recorded in the Brazilian site (see text).

Laje do Coringa, Brazil	Kem Kem beds, Morocco
Mawsoniidae	*Mawsonia lavocati*
Mawsonia gigas	
Sclerorhynchidae	*Onchopristis numidus*
Onchopristis cf. *numidus*	
Atlanticopristis equatorialis	
Hybodontidae	*Tribodus* sp.
Tribodus cf. limae	
Dipnoi	*Ceratodus humei*
Ceratodus humei	*Ceratodus* (=*Neoceratodus*) *africanus*
Ceratodus brasiliensis	
Arganodus tiguidiensis	
Equinoxiodus alcantarensis	
Equinoxiodus sp.	
Pycnodontiformes	indet
indet.	
Rebbachisauridae	*Rebbachisaurus garasbae*
cf. Limaysaurus	
Spinosauridae	*Spinosaurus* cf. *aegyptiacus*
Spinosaurus sp.	
Oxalaia quilombensis	
Carcharodontosauridae	*Carcharodontosaurus saharicus*
Carcharodontosaurus sp.	
Dromaeosauridae	Indet.
indet.	
Dinosauria incertae sedis	*Sigilmassasaurus brevicollis*
Sigilmassasaurus brevicollis	

Brazil (Sues et al., 2002), most authors assume an older deposition (Aptian-Albian) for its fossiliferous levels. Microfossils indicate the younger age of its upper sequence, the Romualdo member, as middle Albian (Coimbra et al., 2002), some six to nine millions of years older than the Alcântara Formation. No other assemblage including continental tetrapods is recorded in the mid-Cretaceous of northern South America. The tetrapod assemblage of Santana Formation is strongly biased with a dominance of theropods amongst the dinosaurs. This would be a consequence of ecologic or taphonomic factors (Naish et al., 2004). Most tetrapod osteologic materials collected at the Santana Formation are not coincident with those from Alcântara Formation what precludes a detailed comparison. The occurrence of the spinosauroid *Irritator challengeri* and its possible junior synonym *Angaturama limai* (Martill et al., 1996; Kellner and Campos, 1996) establishes a link, although weak, between this Early Cretaceous assemblage and the Cenomanian fauna of Laje do Coringa. Nonetheless, the fish fauna from the Santana Formation is closely related to that of the Alcântara Formation and to the African faunas of the same age (Cavin and Dutheil, 1999; Maisey, 2000).

Considering the vast South American territory, continental Cenomanian strata with vertebrate remains other than the Alcântara Formation are well represented only in Patagonia. In Argentina, dipnoans referred to Ceratodontiformes have been recorded (Ameghino, 1899, 1906; Apesteguía et al., 2007), but none of the Brazilian and African species are included. None of the other fish taxa listed in Table 1, which are shared by the Brazilian and North African faunas, have been recovered in the Cretaceous rocks of the southernmost regions of South America. The incidence of Mawsoniidae in Uruguay was dated as Late Jurassic (Soto et al., 2012) and therefore is out of the scope discussed here.

The sauropod record from Laje do Coringa is only superficially assessable because sauropod teeth are much less common than those of the theropod, and only isolated, but numerous, fragmented caudal centra have been recovered. Nevertheless, we can distinguish a much more frequent occurrence of rebbachisaurid caudal vertebrae than of Titanosauria; an aspect that is also observed in the Patagonian biota (Novas, 2009). Nonetheless a comparison of our material with those from Argentina shows a remarkable distinction regarding the theropod composition. We see that the carnivorous fauna of northeastern South America looks to have been different from the austral carnivorous composition in some aspects during the passage from the Early to Late Cretaceous. This claim is supported mainly by the differences in the proportions of teeth collected during fieldwork in northeastern Brazil and Argentinian Patagonia. Casal et al. (2009) remarked that more than 75% of the sample of theropod teeth collected from the Bajo Barreal Formation (Cenomanian – Turonian) belong to abelisauroid and that large-bodied abelisauroids coexisted with giant carcharodontosaurids during the “middle” Cretaceous in Patagonia (see also Novas, 2009). The large *Ekrixinatosaurus novasi* co-existed with *Giganotosaurus carolini*, and a dominance of the abelisauroid is evident. We have collected more than a thousand isolated theropod teeth in Laje do Coringa, northeastern Brazil. Thus, this sample is certainly representative of the carnivorous fauna. The dominance of carcharodontosaurid and spinosaurid teeth is evident and no other large sized theropod have been identified. To date, the only identified abelisauroid form is the one represented by *Masiakasaurus*-like teeth. In fact, our material looks to be very closely related to the Malagasy genus, considering that it has a specialized mandible and unique dentition (Sampson et al., 2001). Nevertheless, we call attention to the temporal distance between the two noasaurid records: Cenomanian (Brazil) and Maastrichtian (Madagascar).

In addition, a less common tooth morphotype that is very flattened and serrated on the posterior carina and has larger denticles than the anterior one and apically hooked denticles was identified as dromaeosaurid (Vilas Bôas, 1999; Elias, 2006) and is similar to the specimen from the Cenomanian of Sudan described and illustrated by Rauhut and Werner (1995) and attributed to a velociraptorine raptor.

Even when the assignment in debated, as in the case of the caudal vertebrae attributable to what Russell (1996) called *Sigilmassasaurus brevicollis* (Theropoda) but Novas (2009) considered an iguanodontid (but see McFeeters et al., 2013), the Brazilian material is related to the African fauna rather than to the Argentinian one. The dominance of Abelisauroids in the Brazilian territory is recorded only in the very Late Cretaceous of the Bauru Basin (Candeiro, 2007; Novas, 2009).

Based on the record of the Alcântara Formation, the northeastern South American mid-Cretaceous continental fauna is more similar to the northern African assemblages than to the southern South American faunas (Medeiros and Schultz, 2002; Medeiros et al., 2007). The following similarities were promptly observed when we compared the record of Laje do Coringa with that of Kem Kem, as summarized by Cavin et al. (2010):

a) The marked occurrence of Spinosauridae and *Carcharodontosaurus* and the probable existence of more than one species of the former (Medeiros, 2006; Richter et al., 2013), as well as several other shared taxa (Table 1).
b) Theropods are more diverse than sauropods, and teeth are the main dinosaurian fossil item (see also Läng et al., 2013). We treated these characteristics as consequences of a combination of ecological and taphonomic effects, although these factors are difficult to assess in a reworked deposit.
c) The presence of large bodies of water, as evidenced by the recovery of large fresh water fish, notably *Mawsonia gigas* and *Onchopristis* sp.

Despite these similarities that obviously indicate some ecological equivalence for both records, we cannot apply the ecological interpretation of Läng et al. (2013), which states that conditions were likely unfavorable for the setting of a stable terrestrial vegetation because large conifers and ferns are common in the Laje do Coringa site (Medeiros and Schultz, 2002; Araujo et al., 2011).

Because it is closely related to the Kem Kem assemblage, the Laje do Coringa assemblage also may be closely related to that of the Bahariya Formation (Egypt), which is most likely contemporaneous and has a particular combination of key taxa: *Carcharodontosaurus saharicus*, *Spinosaurus aegyptiacus* and *Onchopristis numidus* (Stromer, 1915, 1931, 1934; Le Loeuff et al., 2012).

The similarity of the vertebrate taxa recorded here to those of Africa is obviously a heritage from Gondwana and may be attributed to minor evolutionary changes of the biota after the drifting apart of South America and Africa in the late Aptian or Albian. Another possibility is the putative occurrence of a land bridge that would permit genic flux and delay major morphologic differentiation of several faunal elements (Cox, 1980; Buffetaut and Rage, 1993; Calvo and Salgado, 1996). Sereno et al. (2004) also found evidence of continued faunal exchange between southern landmasses until the passage from the Early to Late Cretaceous. Although the precise localization of such a land connection is not conclusive, it possibly existed somewhere between the northeastern coast of South America and western coast of Africa, a region that most geologists and paleontologists agree was the last connection to be severed (e.g. Reyment and Dingle, 1987; Popoff, 1988; Maisey, 2000). The evidence from the Alcântara Formation reinforces this interpretation. If a connection actually existed, it would be selective. The presence of taxa exclusively from South America may indicate that species were unable to cross the equatorial Atlantic Ocean, which, by the beginning of the Cenomanian, would already have been an effective barrier to some species. The dipnoan *Equinoxiodus alcantarensis* is an example of such taxa. Another species, *Atlanticopristis equatorialis* (sclerorhynchiform), is more difficult to assess because it may be a marine form whose geographical distribution, in this case, would be influenced by other routes and barriers. Nonetheless, if *A. equatorialis* was a fresh water species, it would be another good example of isolation by the equatorial ocean.

Although we can distinguish a very consistent biogeographical signal when comparing our data with those of northern Africa, the difficulty in distinguishing the real taxonomic status of many forms recorded (e.g. *Carcharodontosarus* may or may not be *C. saharicus* and *Onchopristis* may or may not be *O. numidus*) makes it difficult to choose the more appropriate interpretation (i.e. morphological conservation after vicariance or genic flux through land connection or a combination of both). Based on geological evidence, most researchers assume that the equatorial Atlantic seaway was fully established by the end of the Albian. The effect of this vicariant event in the early Cenomanian transoceanic continental faunas cannot be easily assessed because evolutionary change cannot be precisely predicted. For instance, *Neoceratodus forsteri* has a remarkable conservative tendency, such that the dental plates of extant populations of Australia are similar to those of their Cretaceous ancestors (Kemp and Molnar, 1981). Thus, a persistent land connection, such as an island chain, would help to explain the similarity observed between the South American and African continental faunas in the early Cenomanian, but it is not an absolutely necessary assumption. In addition, the biocenosis documented here seems to have maintained a conservative tendency in northern South America throughout the Albian and early Cenomanian, as discussed above. The point to be focused on here is the obvious identity between the faunas of northeastern South America and northern Africa and the preliminary evidence of some partial isolation indicated by the endemic taxa (e.g. *Equinoxiodus alcantarensis* and possibly *Atlanticopristis equatorialis*).

The occurrence presented here is evidence against the theory known as “Africa-first”, which claims that Africa was isolated from the rest of Gondwana circa 120 m.a. (Sampson et al., 1998). The biogeographical history of Gondwanan appears to be more complex than originally believed some decades ago; this history most likely consists of a more complex network of interactions between biotas, rather than a simple branching pattern caused by vicariance; as a result, attempts to depict a single biogeographical history from each occurrence may create a distorted interpretation (Upchurch, 2008). Nonetheless, the discovered specimens presented here represent a very clear biological signal that corroborates previous observations of faunal similarity between these two trans-Atlantic regions, although it is not sufficiently complete to determine whether conservation after vicariance or genic flux by persistent land connection occurred after the continents drifted apart. These two alternatives remain the most likely interpretations of this particular evidence.

Information from the plant record, which primarily consists of the presence of conifers (Araucariaceae and possibly Taxales), Pteridophyta (*Paradoxopteris sanctiluigi*) and Equisetales (undetermined horsetails), is a good indicator of the environmental conditions. The extensive occurrence of petrified logs in Laje do Coringa and other outcrops of the Alcântara Formation in both the eastern and western edges of São Luís island (Fig. 1 A) support the interpretation that an extensive covering of conifers was distributed all over the region surrounding the São Marcos bay. The regional climate was inferred by a palynological study (Pedrão et al., 1993a) as tending to aridity. Nonetheless, the evident availability of much water in the estuarine environment and the presence of several species of dipnoans led us to interpret the local climate as being characterized by a short and stormy rainy season followed by a long dry period (Medeiros et al., 2007; Araujo et al., 2011; see Rossetti and Toledo, 1996).

4. Conclusions

The Alcântara Formation has a unique record of the South American Cenomanian continental flora and fauna, which is important for assessing the biogeographic, environmental and climatic aspects of northeastern South America soon after its separation from Africa. The floristic and faunal elements of the Laje do Coringa bone bed revealed a diverse vertebrate community that lived in the coastal forested areas of the Northern Maranhão state surrounded by a dominantly dry environment. This site indicates that the mid-Cretaceous northeastern South American continental fauna is more similar to the northern African fauna than to the austral South American one. Faunal interchanges between these two continents may have persisted until the early Cenomanian.

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