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REVIEW ARTICLE

Late Cretaceous mosasaurids of northeastern Brazil: a summary of their record and a paleobiogeographical survey

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ABSTRACT. The coastal region of northeastern Brazil holds one of the most important records of mosasaurids from the Late Cretaceous of South America. Analysis of these discoveries allowed us to create a picture of the composition of the fauna, as well as the diversity and paleobiogeography of these clades. In the region, the mosasaurid fossils are contained in Cenomanian to Maastrichtian geological units of epicontinental marine origin, in the Cotinguiba (Sergipe-Alagoas Basin), Alcântara (São Luís Basin), Itamaracá (Paraíba Basin), Calumbi (Sergipe-Alagoas Basin), and Gramame (Paraíba Basin) formations. Paleogeographic data corroborate that these deposits represent low-latitude equatorial environments. The Brazilian fauna is represented by fourteen taxa from one family (Mosasauridae), two subfamilies (Mosasaurinae: Prognathodontini, Globidensini and Mosasaurini; Plioplatecarpinae: Plioplatecarpini), and some indeterminate mosasaurid specimens. Mosasaurids from the northeastern region of Brazil resemble Late Cretaceous marine reptiles from western Africa (Angola, Congo, and Morocco), suggesting faunal continuity in the seaway that bridged these areas. The study of this marine fauna is crucial to understanding the evolutionary and paleobiogeographic history of the group during the opening of the South Atlantic Ocean.

Keywords: Marine reptiles, Distribution, Late Cretaceous, Northeastern Brazil.

RESUMEN. Mosasaurios del cretácico superior del noreste de brasil: un resumen de su registro y paleobiogeografía. La región costera del noreste de Brasil presenta uno de los más importantes registros de mosasaurios del Cretácico Superior de Sudamérica. Un exhaustivo análisis de estos registros se presenta en esta contribución para proveer una nueva perspectiva sobre la composición faunal y la diversidad y paleobiogeografía de estos clados. Los fósiles de mosasaurios en la región se encuentran en unidades geológicas de edad cenomaniana a maastrichtiana de origen marino epicontinental. Particularmente en las formaciones Cotinguiba (cuenca Sergipe-Alagoas), Alcântara (cuenca São Luís) , Itamaracá (cuenca Paraíba), Calumbi (cuenca Sergipe-Alagoas) y Gramame (cuenca Paraíba). La evidencia paleogeográfica confirma que estos depósitos representan ambientes ecuatoriales de baja latitud. El registro fósil estudiado incluye catorce tazones de una familia (Mosasauridae), dos subfamilias (Mosasaurinae: Prognathodontini, Globidensini y Mosasaurini; Plioplatecarpinae: Plioplatecarpini), y especímenes indeterminados de mosasaurios. El registro fósil estudiado presenta similitudes con aquél del Cretático Superior del oeste de África (Angola, Congo y Marruecos), lo cual sugiere continuidad faunal a través de la vía marítima que conectó estas regiones. El estudio de esta fauna fósil marina se considera crucial para entender la historia evolutiva y paleobiogeográfica del grupo durante la apertura del océano Atilántico sur.

Palabras clave: Repitles marinos, Distribución, Cretácico Superior, Noreste de Brasil.

1. Introduction

Our knowledge about the marine reptiles that inhabited Mesozoic seas, particularly during the Cretaceous, plays a key role in the study of the paleobiogeography and the marine habitat of this period of great global change. Several studies have helped to clarify the geographical distribution of these reptiles and their paleoenvironmental preferences, presenting us with good fossil records from the coastal margins of Gondwana and Laurasia (*e.g*., Massare, 1994; Benson *et al*., 2010; Bardet *et al*., 2014; Polcyn *et al*., 2010, 2014).

Mosasaurids and plesiosauroids inhabited oceans and seas worldwide millions of years ago, especially during the Cretaceous period (*e.g*., Motani, 2009; Madzia and Cau, 2020). These groups may be considered as cosmopolitans because their fossil remains are found all over the world (Bardet *et al*., 2014). During the Late Cretaceous, the Laurasian margins (Europe and North America) were transformed into several island areas (Baraboshkin *et al*., 2003; Csiki-Sava *et al*., 2016), while the separation of the African plate from the South American plate resulted in not as many regions and was linked to phosphate and carbonate sedimentation in some areas (*e.g*., Gramame Formation) (El Gadi and Brookfield, 1999). Both former Gondwanan margins bear remains of continental and marine fossil vertebrates (Lingham-Soliar, 1994; Jacobs *et al*., 2006, 2009; Schulp *et al*., 2006; Bardet, 2012).

The records of mosasaurid reptiles from the Brazilian and African margins have been known since the 20th Century but few studies focused on the Brazilian occurrences only (Bardet *et al*., 2008, 2015; Bardet, 2012; Mulder *et al*., 2013).

William Chandless (1829-1896) found the first "mosasaurid" fossil in Brazil in 1865, from Rio Acre, south of the mouth of the Purus river, Amazonas (8º45' S-67º23' W) (Chandless, 1866). Louis Agassiz and Elizabeth Agassiz identified these remains as two vertebrae of *Mosasaurus* (Agassiz and Agassiz, 1868: p. 409; Branner, 1890). Riff *et al*. (2010), however, reported that the material was apparently lost and considered unlikely the attribution to *Mosasaurus* to be correct.

Knowledge of Brazilian Cretaceous mosasaurids stagnated over the second half of the 20th Century, where the pioneering studies of Price (1957) and Carvalho (1996) stood out. Cranial and postcranial mosasaurid remains have been found in the northeastern region (Maranhão, Paraíba, Sergipe, Alagoas, Pernambuco, and possibly in the Acre states), and are of Cenomanian to Maastrichtian age (Carvalho and Azevedo, 1998a, b; Gallo *et al*., 2001; Medeiros, 2001). The geographical distribution of the mosasaurid record of Brazil delimits a great paleogeographic domain encompassing the eastern margin of South America and the western margin of Africa and is thus important to understand the overall distribution of the group in the Southern Hemisphere. The objectives of this study are, therefore: 1) to provide an overview of the mosasaurid records of the Brazilian coast with particular emphasis on the little-known northeastern margin; and 2) to review their space-time distribution.

2. Methods

Information about the mosasaurids of northeastern Brazil was mostly collected from the literature (abstracts, articles, and books). Geological and chronological data on these occurrences were obtained from literature for the Sergipe-Alagoas (Souza-Lima, 2008), Paraíba (Barbosa and Lima-Filho, 2006), and São Luís (Rossetti and Trucknebrod, 1997; Rossetti, 2004) basins (Fig. 1). Fourteen mosasaurid taxa have been reported so far, represented by one mosasaurid family (Mosasauridae) and two mosasaurid subfamilies (Mosasaurinae and Plioplatecarpinae), and some indeterminate mosasaurid remains. Teeth and vertebrae are the most common mosasaurid fossils. Examples of mosasaurid teeth are shown in figure 2.

3. Late Cretaceous Brazilian mosasaurid-bearing basins

São Luís Basin

The São Luís Basin (Fig. 1) is a rift-type, coastal basin located in northern Maranhão State. Its main geological outcrops occur along the São Marcos Bay and comprise the late Albian-early Cenomanian Alcântara Formation (Rossetti and Trucknebrodt, 1997; Rossetti, 2004). The Alcântara Formation consists of a succession of sandstones, mudstones, and limestones deposited in a shallow to transitional marine environment (Rossetti, 2003; Santos and Carvalho, 2009), and its fossil record yields diverse vertebrates, including teeth of indeterminate mosasaurids (Carvalho and Vilas-Bôas, 1999; Vilas-Bôas and Carvalho, 2001; Lindoso *et al*., 2012).

Paraíba Basin

The outcrops of the Paraíba Basin (Fig. 1) occupy a narrow, nearly 8-km long coastal strip along the states of Paraíba and Pernambuco, and extend over an area of ~130 km^2 between the Mamanguape Fault, in the north, and the Pernambuco lineament, in the south (Barbosa and Lima-Filho, 2006). The Paraíba Basin comprises the Beberibe, Itamaracá, Gramame, Maria Farinha, and Barreiras formations (Beurlen, 1967; Barbosa *et al*., 2003).

The deposition of the Itamaracá Formation occurred between the middle Campanian and the early Maastrichtian (Barbosa *et al*., 2003). These strata consist of recrystallized silicic limestones and calcareous sandstones, the latter previously considered as part of the Gramame Formation. Many mosasaurid teeth are known from the Itamaracá Formation and are referred to the following taxa: *Carinodens* (previously *Globidens*) *belgicus*, *Globidens* sp., *Mosasaurus anceps*, *Mosasaurus beaugei*, *Eremiasaurus* cf. *heterodontus*, *Platecarpus* sp., and *Prognathodon* sp. (Carvalho, 1996; Azevedo and Carvalho, 1997; Carvalho *et al*., 1997; Carvalho and Azevedo, 1998a, b). Furthermore, there are vertebral remains referred to *Plioplatecarpus* sp. (Souza-Lima, 2001; Bertini, 2002).

The Maastrichtian Gramame Formation has alternating sucessions of marls and mudstones rich in planktonic foraminifera. It was deposited

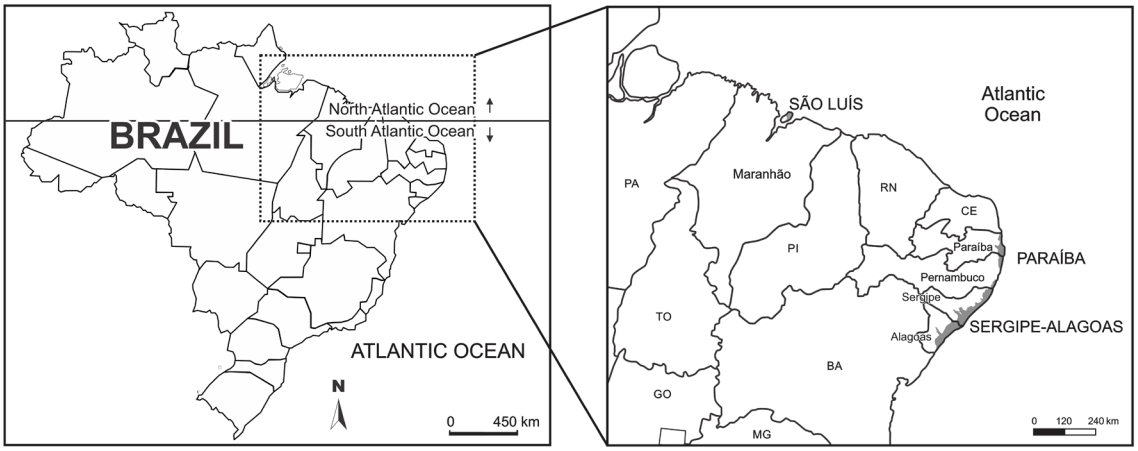

FIG. 1. Brazilian mosasaurid-bearing basins from northeastern Brazil.

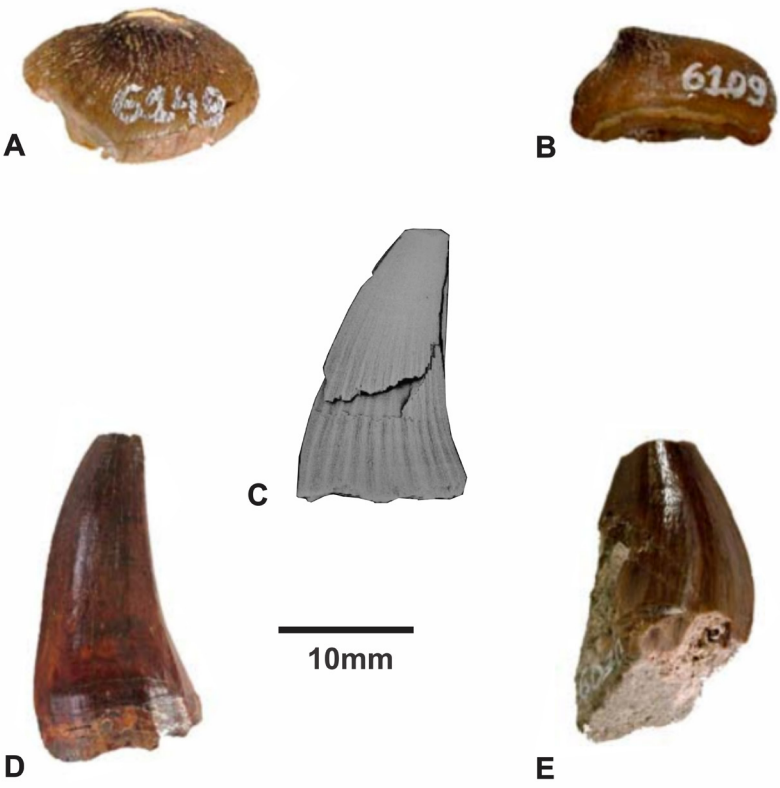

FIG. 2. Examples of mosasaurid teeth from the Late Cretaceous of northeastern Brazil. **A.** *Globidens belgicus* (Gramame Formation). **B.** *Globidens* sp. (Gramame Formation). **C.** *Platecarpus* sp. (Cotinguiba Formation). **D.** *Mosasaurus beaugei* (Itamaracá Formation). **E.** *Mosasaurus* (*Leiodon*) *anceps* (Calumbi Formation). A, B, and D from Carvalho (1996). C from Bengtson and Lindgren (2005).

on a shallow marine platform, in a low to medium energy environment (Barbosa and Lima-Filho, 2006). The mosasaurid teeth found in this formation are very diverse and refer to *Globidens belgicus*, *Globidens phosphaticus, Globidens* sp., *Mosasaurus* cf. *anceps*, *Mosasaurus* cf. *beaugei*, *Mosasaurus beaugei*, *Eremiasaurus* cf. *heterodontus*, *Platecarpus* sp., and *Prognathodon* sp. (Price, 1957; Carvalho, 1996; Azevedo and Carvalho, 1997; Carvalho *et al*., 1997; Carvalho and Azevedo, 1998a, b; Bardet *et al*., 2008, 2013).

Sergipe-Alagoas Basin

The Sergipe-Alagoas Basin (Fig. 1) occupies a narrow coastal strip in the states of Pernambuco, Alagoas, and Sergipe, and has a submerged portion that extends beyond the limits of the narrow continental shelf of Brazil. The basin is internally differentiated into four sub-basins: Cabo, Alagoas, Sergipe, and Jacuípe (Souza-Lima, 2008). The Sergipe-Alagoas Basin has one of the most extensive and complete sedimentary successions among the basins of the eastern continental margin of Brazil, including deposits from the Paleozoic, the Jurassic pre-rift phase, the Early Cretaceous rift phase, and from later sedimentary successions related to the drift phase (Souza-Lima, 2008). In terms of mosasaurid fossiliferous content, the Continguiba and Calumbi formations are briefly described below.

The Cotinguiba Formation consists of shales deposited during a marine transgression, in a neritic to upper bathyal paleoenvironment, from the early Cenomanian to the middle Coniacian (Souza-Lima *et al*., 2002). So far, only *Platecarpus* sp. and *Angolasaurus* sp. teeth have been identified in this geological unit (Bengtson and Lindgren, 2005).

The Calumbi Formation is formed by shales, sandstones, and siltstones. The unit includes some

Santonian rocks but only late Campanian layers are exposed (Souza-Lima *et al*., 2002). Mosasaurid teeth from these latter layers are referred to the following taxa: *Globidens Belgicus, Mosasaurus* (*Leiodon*) *anceps*, *Mosasaurus beaugei*, *Platecarpus* sp., *Prognathodon* sp., *Plioplatecarpus* sp., and *Angolasaurus* sp. (Bertini, 2002; Polcyn *et al*., 2007).

4. Discussion

4.1. Summary of the Late Cretaceous Brazilian mosasaurid fossil record

The Late Cretaceous Brazilian fossil record of mosasaurids comprises fourteen taxa (*Carinodens belgicus*, *Globidens belgicus*, *Globidens phosphaticus*, *Globidens* sp., *Mosasaurus* cf. *anceps*, *Mosasaurus anceps*, *Mosasaurus* (*Leiodon*) *anceps*, *Mosasaurus* cf. *beaugei*, *Mosasaurus beaugei*, *Eremiasaurus* cf. *heterodontus*, *Platecarpus* sp., *Prognathodon* sp., *Plioplatecarpus* sp., and *Angolasaurus* sp.) representing one family (Mosasauridae), two subfamilies (Mosasaurinae: Prognathodontini, Globidensini and Mosasaurini; Plioplatecarpinae: Plioplatecarpini) and some indeterminate mosasaurid specimens. Although few taxa have been assigned to more inclusive taxonomic levels, their geographic and age distribution is llustrative in providing general trends in the composition of the local fauna over geological time (Table 1). For example, *Globidens*, *Mosasaurus*, and *Prognathodon* are abundant in Maastrichtian deposits and show high taxonomic diversity in the Itamaracá and Gramame formations.

The largest number of mosasaurid records is observed in the Gramame Formation, summing a total of nine records (*Globidens belgicus, G. phosphaticus, G. sp.*, *Mosasaurus* cf. *anceps*, *Mosasaurus* cf. *beaugei*, *Mosasaurus beaugei*, *Eremiasaurus* cf. *heterodontus*, *Platecarpus* sp., and *Prognathodon* sp.), followed by the Itamaracá Formation with eight taxa (*Carinodens belgicus*, *Globidens* sp., *Mosasaurus anceps*, *Mosasaurus beaugei*, *Eremiasaurus* cf. *heterodontus, Platecarpus* sp., *Prognathodon* sp., and *Plioplatecarpus* sp.). These formations are similar both in age and faunal composition to the Moroccan Phosphate beds (Lingham-Soliar, 1994; Jacobs *et al*., 2006, 2009; Schulp *et al*., 2006; Bardet, 2012).

Late Cretaceous mosasaurids of Brazil are known exclusively from three basins in the Cretaceous of the Maranhão, Sergipe, Alagoas, Paraíba, and Pernambuco states (Fig. 1). These basins are small in area but have yielded important marine herpeto- and ichthyofauna (*e.g.,* Gallo *et al*., 2010; Lindoso and Carvalho, 2021, and references therein).

4.2. Spatial and temporal taxa distribution

The geologic history of the east coast of Brazil during the Cretaceous was directly influenced by the opening of the South Atlantic Ocean (Souza-Lima *et al*., 2002; Granot and Dyment, 2015). This major event led to the formation of transtensional basins in Western Africa and a shear zone in Central Africa, contributing to the formation of the Nigeria and Sudan basins (Heine *et al*., 2013). The opening also allowed for a faunal interchange between the marine fauna that inhabited the continental platforms of South America and Africa (Jacobs *et al*., 2006; Schulp *et al*., 2006). Similarly, marine transgressions from the early Cretaceous allowed for further exchange via the connections between the Tethys Sea and the newly formed Atlantic Ocean via northern Africa (Fanti, 2012; O'leary *et al*., 2019).

There are many similarities (see Table 1) between the mosasaurid assemblages of the Sergipe-Alagoas and Paraíba basins of Brazil and the Cretaceous fossil record of the central-north Atlantic coast of Africa, such as the shared presence of *Angolasaurus*, *Eremiasaurus*, *Globidens*, *Mosasaurus*, *Carinodens*, *Plioplatecarpus,* and *Prognathodon* (Carvalho, 1996; Souza-Lima and Hamsi Jr., 2003; Schulp *et al*., 2010; Arai, 2014; Jiménez-Huidobro *et al*., 2017) (Fig. 3). In northeastern Brazil, mosasaurid remains are found only in Upper Cretaceous strata, and similar faunas are found in equivalent geological units of west Africa (*i.e*., Bentiaba Formation in Angola; Dukamaje Formation in Nigeria; Phosphate beds in Morocco; Bula Zambi and Maastrichtian beds in Congo (Soliar, 1988; Lingham-Soliar, 1994; Jacobs *et al*., 2006, 2009; Schulp *et al*., 2006; Bardet, 2012). This indicates considerable faunal interchange between the Atlantic margins of Africa and South America during the Late Cretaceous.

4.3. Paleobiogeography

The Brazilian record of mosasaurids is mainly represented by Mosasaurini and Plioplatecarpini (Fig. 4) (Carvalho *et al*., 1995a, b, c; Carvalho, 1996). These groups are primarily represented by the

TABLE 1. LATE CRETACEOUS BRAZILIAN AND AFRICAN MOSAURIDS, LIMITED TO SHARED TAXA.

Taxa	Country/Geological unit							
	Brazil				Morocco	Angola	Congo	Nigeria
	Itamaracá Fm. (middle Campanian-early Maastrichtian)	Gramame Fm. (Maastrichtian)	Cotinguiba Fm. (early Cenomanian-middle Coniacian)	Calumbi Fm. (Santonian-late Campanian)	Phosphate beds (Maastrichtian)	Bentiaba Fm. (Turonian-Maastrichtian)	Gongo Basin, Bula Zambi Fm. (Maastrichtian)	Iullemmeden Basin, Dukamaje Fm. (Maastrichtian)
Carinodens (previously *Globidens) belgicu*s	X	-	-	-	X	X	-	-
*Globidens belgicu*s	-	X	-	X	X	X	X	-
Globidens phosphaticus	-	X	-	-	X	-	-	-
Globidens sp.	X	X	-	-	X	X	-	-
Mosasaurus cf. *anceps*	-	X	-	-	-	-	-	-
Mosasaurus anceps	X	-	-	-	-	-	-	-
Mosasaurus (*Leiodon*) *anceps*	-	-	-	X	X	-	-	-
Mosasaurus cf. *beaugei*	-	X	-	-	-	-	-	-
*Mosasaurus beauge*i	X	X	-	X	-	-	-	-
Eremiasaurus cf. *heterodontus*	X	X	-	-	X	-	-	-
Platecarpus sp.	X	X	X	X	-	-	-	-
Prognathodon sp.	X	X	-	X	X	X	X	X
Plioplatecarpus sp.	X	-	-	X	-	X	X	-
Angolasaurus sp.	-	-	X	X	-	X	-	-

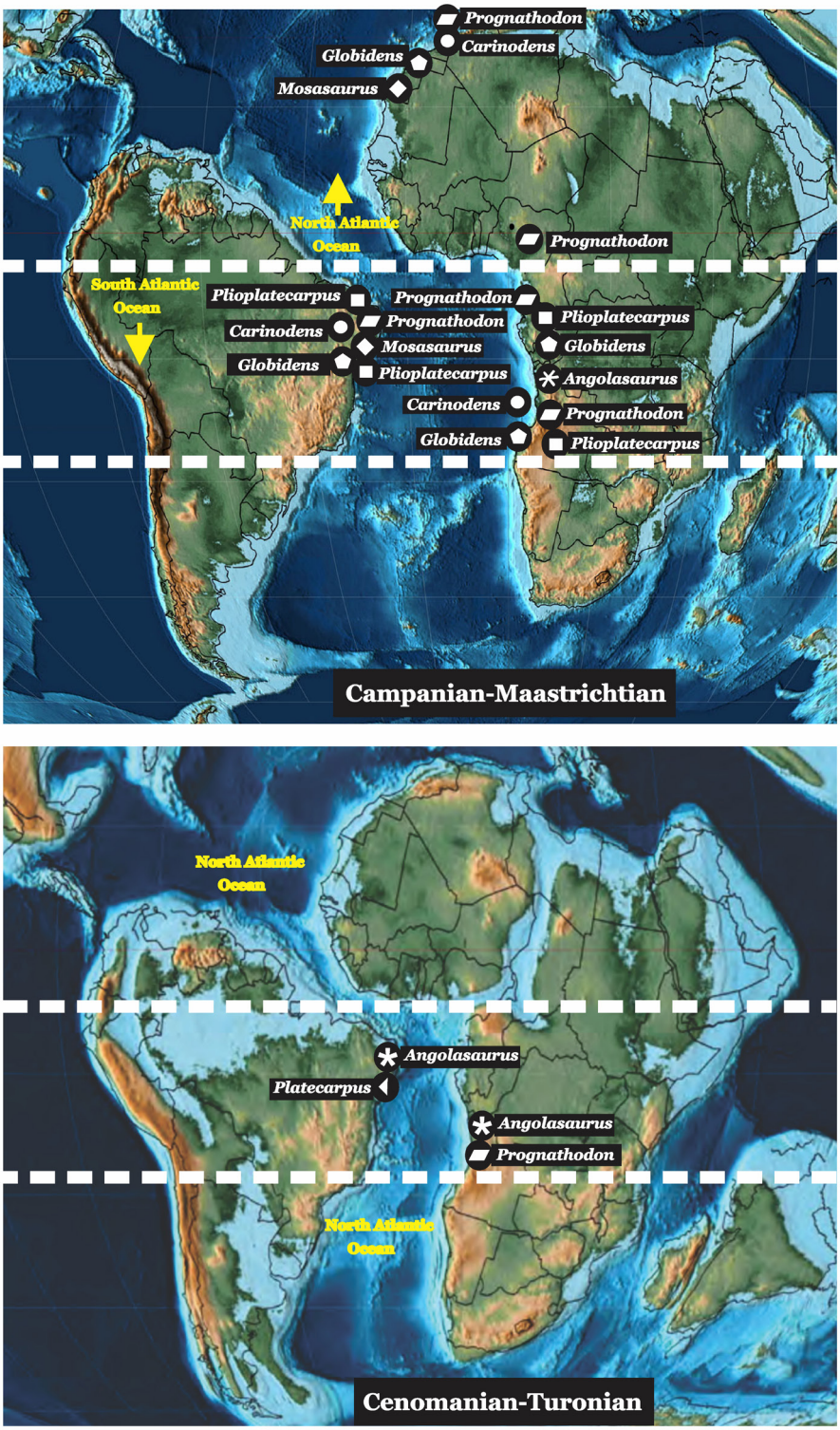

FIG. 3. Central-western Gondwanan paleobiogeographical mosasaurid genus distribution during the Late Cretaceous (modified from www.scotese.com). Segmented white lines show Equatorial areas between eastern Brazil and western Africa.

FIG. 4. Marine paleoenvironmental reconstruction of four Late Cretaceous mosasaur taxa from northeastern Brazil. **A.** *Platecarpus* (Cenomanian-Maastrichtian). **B.** *Angolasaurus* (Cenomanian-Campanian). **C.** *Prognathodon* (Santonian-Maastrichtian). **D.** *Carinodens* (Maastrichtian). Drawing made by Luciano Vidal.

genera *Carinodens*, *Plioplatecarpus*, *Prognathodon, Mosasaurus*, and *Globidens*, which have their equivalents in western and northern Africa (*e.g.*, Schulp *et al*., 2008; Bardet, 2012), and *Angolasaurus,* also found in post-Turonian sedimentary rocks in Angola (*e.g.*, Bengtson and Lindgren, 2005; Polcyn *et al*., 2007, 2010; Mulder *et al*., 2013; Bardet *et al*., 2014) (Fig. 3). The Brazilian and western African mosasaurid record supports the hypothesis that faunal interchange occurred in the low-latitude equatorial regions of western Gondwana during the opening of the South Atlantic Ocean (Jacobs *et al*., 2009; Jiménez-Huidobro *et al*., 2017).

4.4. Gondwanan correlation

The mosasaurid records from the continental margin of northeastern Brazil is indicative of a typical faunal composition from western Gondwana, similar to those of the Afro-Arabian domain, especially the records from Angola and Morocco. The mosasaurids *Globidens*, *Mosasaurus*, and *Prognathodon* are also likely characteristic of the western-southern margin of Gondwana but are present in other Laurasian coastal areas (Belgium, Netherlands, and Ukraine) as well (Lingham-Soliar and Nolf, 1989; Schulp *et al*., 2006; Jiménez-Huidobro *et al*., 2017).

Although the record of Brazilian mosasaurids is fragmentary, it shows that species like *Angolasaurus*, *Globidens*, *Mosasaurus*, *Platecarpus*, *Plioplatecarpus,* and *Prognathodon* were widely distributed in the region by the end of the Cretaceous. Bardet (2012), Bardet *et al*. (2015), and Jiménez-Huidobro *et al*. (2017) identified a transatlantic epicontinental distribution of these taxa in addition to their presence in the shallow waters of the Tethyan ocean. Bardet *et al*. (2015) and Jiménez-Huidobro *et al*. (2017), in particular, discussed the morphological similarities between the Brazilian and western African Maastrichtian mosasaurid fauna, recognizing the presence of

Prognathodontini, Globidensini, and Mosasaurini on both sides of the Atlantic. In view of these similarities, the absence of *Platecarpus* in the Central African margin was deemed intriguing, especially because this genus has a wide distribution in United States, Belgium and possibly in Africa (Lingham-Soliar and Nolf, 1989; Jacobs *et al*., 2006; Schulp *et al*., 2006; Polcyn *et al*., 2007; Mulder *et al*., 2013; Bardedt *et al*., 2015; Jiménez-Huidobro *et al*., 2017).

Even though several of the main clades of Brazilian mosasaurids recognized here are not completely endemic to Gondwana (see above), the general faunal composition is clearly reminiscent of the other Gondwanan areas. The present study indicates that all the mosasaurid records from the eastern coast of Brazil reported to date are exclusively composed by taxa that are also reported in other areas of Africa and even Europe and North America. Thus, these fossil records are a valuable source of information to aid in the understanding of the taxonomic distribution and evolution of the Late Cretaceous mosasaurids of western Gondwana.

5. Conclusions

The mosasaurid fossil record of Late Cretaceous epicontinental marine formations of the Sergipe-Alagoas, São Luís, and Paraíba basins provides one of the main and most diverse Cretaceous mosasaurid faunas of South America. Paleogeographic data corroborate that these deposits represent low-latitude equatorial Late Cretaceous environments. Brazilian records show taxonomic similarities with contemporaneous mosasaurid faunas known from Angola, Congo, and Morocco and even from the northern regions of the Atlantic Ocean. This suggests that Late Cretaceous mosasaurid faunas were, on a general scale, cosmopolitan taxa. The review presented in this study shows the potential of the Late Cretaceous formations of the northeastern coast of Brazil for understanding the mosasaurid fauna of the Southern Hemisphere and its spatial and temporal evolution.

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