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Cretaceous sauropod diversity and taxonomic succession in South America

Caio César de Jesus Faria [a, b, *], Bernardo González Riga [c], Carlos Roberto dos Anjos Candeiro [b, 1], Thiago da Silva Marinho [d, e], Leonardo Ortiz David [c], Felipe Medeiros Simbras [f], Roberto Barboza Castanho [g], Fellipe Pereira Muniz [b, 1], Paulo Victor Luiz Gomes da Costa Pereira [a]

[a] Universidade Federal do Rio de Janeiro, Programa de Pós-Graduação em Geologia, Instituto de Geociências, CCMN, Cidade Universitária, Ilha do Fundão, Av. Athos da Silveira Ramos, 274, Bloco G, 21941-916 Rio de Janeiro, RJ, Brazil
[b] Universidade Federal de Uberlândia, Laboratório de Geologia, Avenida 20, 1.600 Bairro Tupã, Ituiutaba, Minas Gerais, Brazil
[c] Laboratorio de Dinosaurios, Facultad de Ciencias de Exactas y Naturales, Universidad Nacional de Cuyo, Avda. Padre Contreras 1300, (5500) Mendoza, Argentina/CONICET, IANIGLA, CCT-Mendoza, Argentina
[d] Instituto de Ciências Exatas, Naturais e Educação (ICENE), Universidade Federal do Triângulo Mineiro (UFTM), Av. Dr. Randolfo Borges Jr. 1700, Univerdecidade, 38064-200 Uberaba, Minas Gerais, Brazil
[e] Centro de Pesquisas Paleontológicas L. I. Price, Complexo Cultural e Científico de Peirópolis (CCCP/UFTM), Bairro Peirópolis, Uberaba, Minas Gerais, Brazil
[f] Petróleo Brasileiro S. A. (PETROBRAS), Avenida República do Chile, 330, Centro, Rio de Janeiro, RJ, Brazil
[g] Laboratório de Geotecnologias, Curso de Geografia, Campus Pontal, Universidade Federal de Uberlândia, Uberlândia, Minas Gerais, Brazil

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ABSTRACT

The South American sauropod dinosaurs fossil record is one of the world's most relevant for their abundance (51 taxa) and biogeographical implications. Their historical biogeography was influenced by the continental fragmentation of Gondwana. The scenery of biogeographic and stratigraphic distributions can provide new insight into the causes of the evolution of the sauropods in South America. One of the most important events of the sauropods evolution is the progressive replacement of Diplodocimorpha by the Titanosauriformes during the early Late Cretaceous. The fluctuation of the sea levels is frequently related to the diversity of sauropods, but it is necessary to take into account the geological context in each continent. During the Maastrichthian, a global sea level drop has been described; in contrast, in South America there was a significant rise in sea level (named 'Atlantic transgression') which is confirmed by sedimentary sequences and the fossil record of marine vertebrates. This process occurred during the Maastrichtian, when the hadrosaurs arrived from North America. The titanosaurs were amazingly diverse during the Late Cretaceous, both in size and morphology, but they declined prior to their final extinction in the Cretaceous/Paleocene boundary (65.5Yrs).

1. Introduction

The dinosaurs fossil records comprises diverse findings dating back to the nineteenth century, by pioneers such as Ameghino, Lydekker, Woodward, and von Huene (Lydekker, 1893; Ameghino, 1898; Colbert, 1984; Novas, 2009; Martinelli et al., 2010; Bittencourt and Langer, 2011; Calvo et al., 2011).

In South America, the most representative group of dinosaurs is Sauropoda, a clade of huge herbivores that exhibits an amazing diversity both in size and morphology. To date, 40 sauropod taxa have been found in Argentina, 10 in Brazil and one in Chile (see Appendix). In Argentina, the sauropods are represented mainly by

* Corresponding author. Universidade Federal do Rio de Janeiro, Programa de Pós-Graduação em Geologia, Instituto de Geociências, CCMN, Cidade Universitária, Ilha do Fundão, Av. Athos da Silveira Ramos, 274, Bloco G, 21941-916 Rio de Janeiro, RJ, Brazil. Tel.: +55 21 25989464, +55 34 32715249.

E-mail addresses: 321caioster@gmail.com (C.C. de Jesus Faria), bgonriga@yahoo.com.ar (B.G. Riga), candeiro@pontal.ufu.br (C.R. dos Anjos Candeiro), tsmarinho@gmail.com (T. da Silva Marinho), felipe.simbras@gmail.com (F.M. Simbras), robertocastanho@pontal.ufu.br (R.B. Castanho).

[1] Tel.: +55 34 32715249.

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Titanosauriformes, Dicraeosauridae, and Rebbachisauridae. They have been recovered from Angostura Colorada, Bajo Barreal, Allen, Anacleto, Lohan Cura, Candeleros, Portezuelo, La Amarga, Rio Neuquen, Cerro Barcino and Huincul formations (Martinelli et al., 2010; Navarrete et al., 2011; Ibiricu et al., 2012).

In Brazil, they are recorded mostly from rocks of the Adamantina, Presidente Prudente, and Marília formations of the Bauru Group (e.g., Santucci and Bertini, 2001), and their evolution during the breakup of Gondwana has considerable biogeographic relevance (Novas, 2009). Other occurrences of sauropods have been reported in Alcântara Formation, Itapecuru Formation (both São Luís-Grajaú Basin), Parecis Group (Paraná Basin), Açu Formation (Potiguar Basin), and Quiricó Formation (Sanfranciscana Basin) (Langer et al., 2010; Martinelli et al., 2010). Outside Argentina and Brazil, sauropods in South America have only been reported in Chile with a single species named *Atacamatitan chilensis* Kellner et al., 2011 (see Appendix).

Although there are numerous papers on South American sauropods, few studies analize and synthesize the available information. Therefore, the aim of this work is to achieve a synthesis of these dinosaurs, with special focus on distribution between northern and southern South American taxa, including aspects of age and paleoenvironment context.

2. Sauropod background

Sauropods were a successful group of quadrupedal, long-necked herbivore dinosaurs from the Late Triassic to the Cretaceous/Paleogene boundary, and, included the largest terrestrial animals that ever existed (Martin, 2006; Martinelli et al., 2010). Wilson and Sereno (1998) defined this clade as a stem group of 'sauropodomorphs more closely related to *Saltasaurus* than to *Plateosaurus*' with a set of unique synapomorphies such as: large nares, distal part of the tibia covered by an ascending process of the astragalus, short hind limbs in comparison with the tarsal length, and at least three sacral vertebrae. The Cretaceous record of gondwana sauropod dinosaurs is remarkably more abundant and diverse than the Triassic and Jurassic ones (Powell, 1986; Salgado et al., 1997).

Among the Cretaceous sauropods, the clade Titanosauria is one of the largest recorded in the world as well as in South America, but other groups of sauropods also occurred during the Cretaceous of Argentina, like Dicraeosauridae and Rebbachisauridae (Fig. 1). In Brazil, the titanosaurian taxa are relatively abundant and represented by *Maxakalisaurus topai* (Kellner et al., 2006); *Adamantisaurus mezzalirai* (Santucci and Bertini, 2006); *Aeolosaurus maximus* (Santucci and Arruda-Campos, 2011); *Baurutitan britoi* (Kellner et al., 2005); *Gondwanatitan faustoi* (Kellner and Azevedo, 1999), among others.

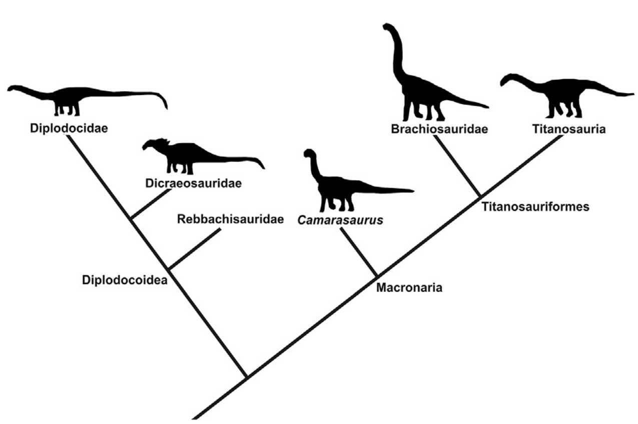

Fig. 1. Simplified sauropod cladogram (modified from Mannion et al., 2011).

3. Results

This overview was made with information acquired from publications and some unpublished data of materials under study by the authors. The synthesis of data in Appendix and figures is a necessary step to discuss the topic.

3.1. Notes on Cretaceous South American sauropods

Most information on the Cretaceous sauropod faunas of South America is from Argentina (Neuquén and Austral basins), Brazil (Paraná, São Luís-Grajaú and Sanfranciscana basins), and Chile (Tolar Formation) (Fig. 2). It provides roughly 70% of the total records of the Cretaceous sauropods in Gondwana. These basins include some exceptional outcrops and well-developed stratigraphic sequences. In South America, knowledge of Cretaceous sauropods has increased in the last decade (e.g., Salgado et al., 1997; De la Fuente et al., 2007; Novas, 2009; Martinelli et al., 2010; González Riga, 2010) with papers published on sauropod records from the Neuquén Basin and Bauru Group of Early-Late Cretaceous. To date, 51 valid species have been described (see Appendix). The sauropod fauna of Argentina, Brazil, and Chile come from stratigraphic levels of continental sequences of rocks assigned to the interval between the Berriasian to Maastrichtian.

3.2. Lower Cretaceous

The fossil record of South American sauropods from the Lower Cretaceous is relatively reduced, including 10 species (Appendix). In Argentina sauropod species from strata of the Neuquén and San Jorge Basins; in Brazil these dinosaurs were found in São Luís-Grajaú and Sanfranciscana basins (Carvalho et al., 2003; Zaher et al., 2011).

The San Jorge Basin (Archangelsky et al., 1994; Bridge et al., 2000) is exposed in central Patagonia (Chubut Province, Argentina) and composed of thick sedimentary sequences from the Early to Late Cretaceous that constitute the Chubut Group and sauropod-bearing Aptian-Albian Cerro Barcino Formation. In this basin was found and reported the somphospondylian titanosauriform *Chubutisaurus insignis* (Del Corro, 1975), as well as theropods (abelisaurids and carcharodontosaurids), crocodyliforms, and titanosaurs.

The Lower Cretaceous of the Neuquén Basin (Garrido, 2010) is a terrestrial dinosaur-bearing sequence known by La Amarga and Lohan Cura formations. The youngest member (Barremian) of La Amarga Formation is the Piedra Parada Member where the dicraeosaurid *Amargasaurus cazaui* (Salgado and Bonaparte, 1991), rebbachisaurids *Zapalasaurus bonapartei* (Salgado et al., 2006), *Amargatitanis macni* (Apesteguía, 2007) were reported. From the Aptian-Albian Rayoso Formation have been reported the rebbachisaurid *Rayososaurus agrioencis* (Bonaparte, 1996) have been reported. La Amarga Formation, recognized as Late Aptian-Albian age, sauropod record consists of somphospondylian titanosauriform *Agustinia ligabuei* (Bonaparte, 1999), rebbachisaurid *Limaysaurus tessonei* (Salgado et al., 2004), *Comahuesaurus windhauseni* (Carballido et al., 2012), and the somphospondylan *Ligabuesaurus leanzai* (D'Emic, 2012). Recently, the diplodocid *Leinkupal laticauda* was reported from the Bajada Colorada Formation with an estimated age from late Berriasian-Valanginian (Gallina et al., 2014).

The Early Cretaceous fauna from Brazil is lesser known than its Late Cretaceous and also sparse when compared with localities of Argentina. This rarity is due to its restricted geographic distribution

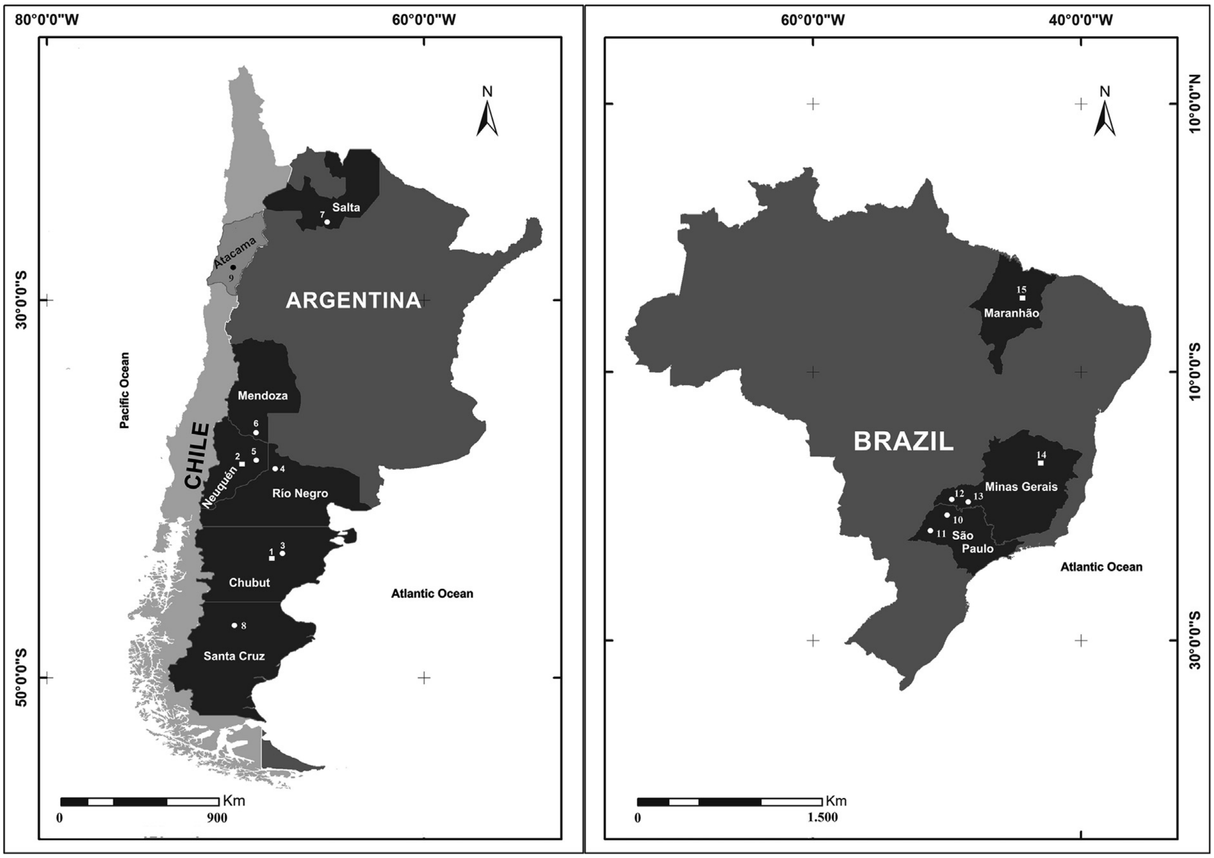

Fig. 2. Map showing the Cretaceous units and outcrop areas approximately that carried the sauropod fauna mentioned in the text. (1) Formation, Aptian-Albian Cerro Barcino Formation, (2) Albian-Aptian Lohan Cura Formation and La Amarga, (3) Bajo Barreal Formation, Campanian-Maastrichtian, (4) Allen Formation, Campanian-Maastrichtian, (5) Candeleros Formation, Cenomanian, and the Santonian Plottier Formation, (6) Rio Neuquén Formation, late Turonian-late Coniacian, (7) Pari Aike Formation, early Maastrichtian, (8) Bajo Barreal Formation, Late Cretaceous, (9) Tolar Formation, Late Cretaceous, (10) Adamantina Formation, Campanian-Maastrichtian, Aptian-Albian, (11) Adamantina Formation, Turonian-Santonian, (12) Adamantina Formation, Late Cretaceous, (13) Maastrichtian Marília Formation, (14) Aptian Quiricó Formation, (15) Itapecuru Formation.

and low sauropod diversity could be related to the low number of collections and studied localities. The nemegtosaurid titanosaur *Tapuiasaurus macedoi* (Zaher et al., 2011) was recovered from the Aptian Quiricó Formation, Areado Group (Sanfranciscana Basin). The Albian Itapecuru Group (São Luís-Grajaú Basin) is an important dinosaur-bearing unit in northern Brazil from which was found the rebbachisaurid *Amazonsaurus maranhensis* (Carvalho et al., 2003) and other indeterminate dinosaur remains.

3.3. Late Cretaceous

3.3.1. Argentina

The Argentinean sauropod record comes from the Patagonia, Neuquén, Austral, and Golfo San Jorge Basins (Santa Cruz, Chubut, Neuquén and Río Negro Provinces), central-western Argentina, Neuquén and Colorado Basins (Mendoza and La Pampa Provinces), and northwestern Argentina (Salta Province). The Late Cretaceous Brazilian sauropod species comes from Bauru Group of the Minas Gerais, Mato Grosso, and São Paulo states. The unique Chilean sauropod dinosaur species is known from Late Cretaceous Tolar Formation (Appendix).

The Neuquén Basin is located in the northwestern Patagonia (Argentina) and consists of the most important dinosaur-bearing Basin from southern continents (Leanza et al., 2004; Garrido, 2010; Calvo et al., 2011). A diverse and representative Gondwana sauropod species has been reported from all Late Cretaceous Neuquén Group units, which comprise, according to Garrido (2010), the following formations deposited between the early Cenomanian and the middle Campanian: Candeleros, Huincul, Cerro Lisandro, Portezuelo, Los Bastos, Sierra Barrosa, Plottier, Bajo de la Carpa, and Los Colorados. Allen Formation and equivalents (Loncoche, Los Alamitos, and Angostura Colorada) was deposited during the late Campanian-early Maastrichtian. It is the lower unit of the Malargue Group and unconformably overlies the Neuquén Group.

The record comprises the lithostrotian titanosaur *Quetecsaurus rusconii* (González Riga and David, 2014) (Cenomanian-early Turonian), the titanosaur *Andesaurus delgadoi* from the Candeleros Formation (early Cenomanian), and the Lithostrotian titanosaur *Argentinosaurus huinculensis* (Bonaparte and Coria, 1993) from the Huincul Formation (late Cenomanian-early Turonian).

The lithostrotian titanosaur *Petrobrasaurus puestohernandezi* (Filippi et al., 2011a) and rinconsaurian titanosaur *Rinconsaurus caudamirus* (Calvo and González Riga, 2003) were discovered in the Plottier Formation (Coniacian-early Santonian), the lognkosaurian titanosaur *Mendozasaurus neguyelap* (González Riga, 2003) and rinconsaurian titanosaur *Muyelensaurus pecheni* (Calvo et al., 2007a) were discovered in the middle-late Coniacian strata of the Sierra Barrosa Formation, the lognkosaurian titanosaur *Futalognkosaurus dukei* (Calvo et al., 2007b) was discovered in the late Turonian-early Coniacian strata of the Portezuelo Formation, and the somphospondylian titanosauriform (or basal titanosaur after phylogenetic criteria) *Malarguesaurus florenciae* (González-Riga et al., 2009) was found in the early-middle Coniacian strata of the Los Bastos Formation.

Bonitasaura salgadoi (Apesteguía, 2004), *Traukutitan eocaudata* Juaréz-Valieri and (Calvo et al., 2011), and *Elaltitan lilloi* (Mannion and Otero, 2012) are lithostrotian titanosaurs discovered in the Santonian strata of the Bajo de la Carpa Formation.

The lithostrotian titanosaurs *Antarctosaurus wichmannianus* (Huene, 1929), *Barrosasaurus casamiquelai* (Salgado and Coria, 2009), *Narambuenatitan palomoi* (Filippi et al., 2011b), *Overosaurus paradasorum* (Coria et al., 2013), *Pitekunsaurus macayai* (Filippi and Garrido, 2008), and the saltasaurinae titanosaur *Neuquensaurus australis* (Powell, 1986) were found in the early-middle Campanian strata of the Anacleto Formation.

Some sauropods are known from the Bajo Barreal Formation (Cenomanian-Turonian of the Chubut Group): the aeolosaurini titanosaur *Aeolosaurus colhuehuapiensis* (Casal et al. 2007), lithostrotian titanosaurs *Epachthosaurus sciuttoi* (Powell, 1990), *Drusilasaura deseadensis* (Navarrete et al., 2011) and *Argyrosaurus superbus* (Lydekker, 1893), and the rebbachisaurid *Katepensaurus goicoecheai* (Ibiricu et al., 2013).

From Angostura Colorada Formation, the aeolosaurini titanosaur *Aeolosaurus rionegrinus* (Powell, 1987) has been reported. The sauropod fauna from the Allen Formation (late Campanian-early Maastrichtian) was represented by lithostrotian titanosaurs *Bonatitan reigi* (Martinelli and Forasiepi, 2004), *Panamericansaurus schroederi* (Porfiri and Calvo, 2010), and *Pellegrinisaurus powelli* (Salgado, 1996), and the saltasaurinae titanosaur *Rocasaurus muniosi* (Salgado and Azpilicueta, 2000).

Sauropod species dinosaurs known from Salta Group (Salfity and Zambrano, 1990; Marquillas et al., 2005) were recovered in Lecho Formation (Campanian-early Maastrichtian) and comprise the saltasaurinae titanosaur *Saltasaurus loricatus* (Bonaparte and Powell, 1980). New and detailed studies of *Neuquensaurus* improve our taxonomic and phylogenetic knowledge (D'Emic and Wilson, 2011).

Finally, in the Austral Basin of Santa Cruz Province, lithostrotian titanosaur *Puertasaurus reuilli* (Novas et al., 2005) was discovered in the Pari Aike Formation (early Maastrichtian).

3.3.2. Brazil

The Late Cretaceous sauropods from Brazil are represented by species assigned to the Titanosauria group. All of them have been recovered from the upper interval of the Bauru Group (Turonian-Maastrichtian), Paraná Basin, and they have been found in São Paulo and Minas Gerais states. The Aeolosaurini group is represented by *G. faustoi* (Kellner and Azevedo, 1999) and *Aeolosaurus maximus* (Santucci and Arruda-Campos, 2011), both from São Paulo state, which also provides the Titanosauria *A. mezzalirai* (Santucci and Bertini, 2006) and *Brasilotitan nemophagus* (Machado et al., 2013), all from Campanian-Maastrichtian.

In Minas Gerais state, the main region that has provided sauropod species is the Triângulo Mineiro, where crops out the Adamantina, Uberaba, and Marília formations. The district of Peirópolis is the most prolific location for sauropod species, where the Titanosauria group is represented by *B. britoi* (Kellner et al., 2005), *Trigonosaurus pricei* (Campos et al., 2005), and *Uberabatitan ribeiroi* (Salgado and Carvalho, 2008). From Prata municipality, in the uppermost levels of the Adamantina Formation (Late Campanian – Early Maastrichtian), was recovered the skeleton of the *M. topai* (Kellner et al., 2006), another Titanosauria.

Other localities have already provided sauropod material and their geology is poorly known, as the Mato Grosso state and the Rio Grande do Norte state. From Mato Grosso, were recovered materials of an indeterminate Aeolosaurini (Franco-Rosas et al., 2004).

3.3.3. Chile

From Late Cretaceous Tolar Formation of the Atacama Desert (Antofagasta Region), northern Chile, has been recorded the first titanosaur species *A. chilensis* (Kellner et al., 2011). Chilean sauropod record demonstrated that this area has potential for new findings.

4. South American sauropod diversity analysis

4.1. Introduction

One of the most relevant aspects of the historical biogeography is the influence of continental fragmentation and the fluctuation of sea levels in the evolution of terrestrial vertebrate faunas. Sauropods are a model because they achieved a nearly Pangaean distribution by the Middle Jurassic and persisted until the peak of continental isolation at the end of the Cretaceous (Wilson and Sereno, 1998). The history of South American sauropod is a complex topic. Herein, we outline some aspects as a preliminary study. Fifty one sauropod species have been discovered in South America and most of them are titanosaurs. During the Late Cretaceous, titanosaurs were the dominant megaherviborous of the faunas. In contrast, in North America for most of the Late Cretaceous the ornithischian dinosaurs were the most abundant herbivorous vertebrates during the Late Cretaceous (Benton and Harper, 2009; Coria et al., 2012).

Among the important evolutionary events of sauropods history one of the most remarkable is the progressive replacement of Diplodocimorpha by the Titanosauriformes (see citations in De la Fuente et al., 2007). This aspect can be confirmed by a graphic that shows curves based on the number of genera through time (Fig. 3). In the record of the Lower and Early-Late Cretaceous, rebbachisaurids are present in Northern Patagonia (e.g. *Amargasaurus*, *Rayososaurus*) and confirm the biogeographic connection with Africa, before the formation of the Atlantic Ocean. The extinction of some Diplodocimorpha has been reported by some authors in southern continents (e.g., Salgado et al., 2004; Coria and Salgado, 2005; Gallina and Apesteguía, 2005; Calvo et al., 2006; Ibiricu et al., 2012), and these studies show the record of this group only until Turonian, after that only titanosaurs survived (Fig. 4).

Carballido et al. (2012) carried out a detailed analysis of rebbachisaurids based on process of dispersal, extinction, and cladogenesis and retrieved a South American origin for this lineage, and a fast dispersion to Africa and Europe during the Hauterivian–Barremian. The close connection between South America and Africa and between Africa and Europe during the Barremian–Aptian (e.g., the Apulian route; Canudo et al., 2009) lends support to this dispersion event and explains the presence of rebbachisaurids in the Barremian of Europe (Carballido et al., 2012).

4.2. Tectonic events in South America and base level flutuactions

Detailed studies like the contributions of Upchurch and Barrett (2005), Barret et al. (2009), and mainly the analysis of Mannion

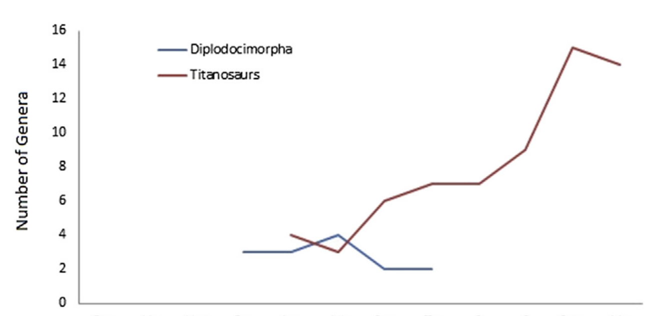

Fig. 3. Number of genera during the Cretaceous of Diplodocimorpha (Dicraeosaurids and Rebbachisaurids) and Titanosaurs (Titanosaurs and Somphospondylian titanosauriforms).

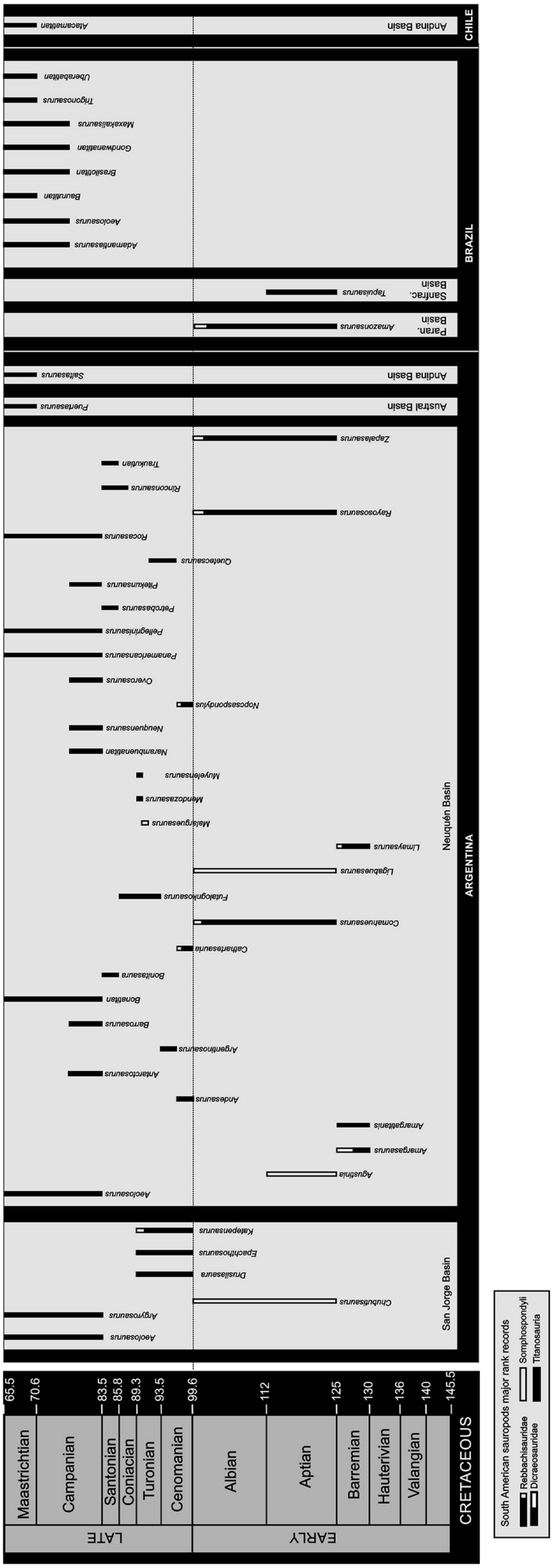

Fig. 4. Cretaceous geochronological sauropod species from South America.

et al. (2011) used several proxies and methods to analyze the diversity of sauropods through time. Mannion et al. (2011) suggested that some diversity peaks are probably related to rises and falls in sea level. However, this general hypothesis must be analyzed in each continent, including local subsidence produced by tectonic or sedimentary processes. For example, during the Maastrichthian, a global sea level drop is described by Haq et al. (1987). In contrast, in the some basins of South America, a relevant rise of sea level is confirmed by the sedimentary geology and described as an 'Atlantic transgression' (Wichmann, 1927; Andresi et al., 1974; Legarreta et al., 1989; Parras and Griffin, 2013). In Northern Patagonia, an Atlantic epicontinental sea is recorded in facies of the Malargue Group (late Campanian-Danian) and reaches a peak in the Jaguel Formation (late Maastricthian). In the top of this event, limestones of the regressive and diachronous Roca Formation from the Late Maastricthian-early Danian are recorded (Parras et al., 1998).

Otherwise, different from the eustatic fluctuations observed in Argentina, in the interior Brazilian basins of Paraná and Sanfranciscana or even near the coastline of the São Luís-Grajaú in the north and Potiguar in the northeast, the fluvial channelized conglomerates and sandstones lithofacies, which provided most of the Brazilian sauropod species from the latest Lower to Upper Cretaceous, are associated with the drop of the base level with different frequencies and controlled by allogenetic factors. These factors are, most of times, local tectonic movements on the buffer zone and source area or also climatic changes (Catuneanu et al., 2011), which produced sometimes subaerial unconformities or even self paleoenvironment architectural adjustments. In the case of the Brazilian basins, for example, the continental and coastal areas were progressively uplifted in an isostatic compensation response to the clockwise rotation of the Southamerican continent relative to the African continent during the Neocomian and the drift of the marginal basins of the Atlantic Ocean, as observed in Ponta Grossa Arch, Paraná Basin, and also in Ferrer-Urbano Santos Arch and Rio Parnaíba-Xambioa Lineament, São Luís-Grajaú Basin (Rezende and Pamplona, 1970; Asmus and Guazelli, 1981; Zanotto and Szatmari, 1987; Macedo, 1991; Vignol-Lelarge et al., 1994; Almeida and Carneiro, 1998; Lima and Rossetti, 1999; Strugale et al., 2007). These episodes were responsible for the creation of subaerial unconformities and incised valley that posteriorly was filled by channel deposits in the Lowstand System Tracts in interior basins.

This complex tectonic and sedimentary history is responsible to the local accumulation and preservation of sauropod fossils, displaying the stratigraphic record not calibrated to eustatic fluctuations on the continental margin of South America, different from that observed by Mannion et al. (2011) and by us in Argentina. Furthermore, the peaks of diversity of sauropods through the geological time related to low frequency eustatic fluctuations by Mannion et al. (2011) could be an artifact of the better condition for the accumulation and preservation in sedimentary basins. For example, in Bauru Group, Paraná Basin, the presence of diverse titanosaurian sauropod species in low temporal range is unknown, although, higher frequence sauropod diversity peaks are not sampled sufficiently to improve the possible effect of smaller and local scale controllers on the sedimentation and accumulation of bone bearing layers.

4.3. Depositional settings, taphonomical remarks and systematic diversity

During the Late Cretaceous, titanosaur diversity increased and displayed different adaptative types. In our study (Fig. 4), we can see how titanosaur abundance increased toward the end of the Cretaceous, but it declined prior to their final extinction at the Cretaceous/Paleogene (K/Pa) boundary (65.5 Mya). This decline is, in fact, related to the fossil record and more complex studies are necessary to confirm their causes. In Patagonia this decline of the fossil record could be related to different taphonomic process. For example, the change of the fluvial facies of the Neuquén Group to lacustrine-marine marginal facies of the Malargue Group implicates changes in their associated biostratinomic and fossil-diagenetic process.

From sedimentological viewpoint, 72% of the South American sauropods have been preserved in fluvial facies, 12% in fluvial to lacustrine, 8% in lacustrine and the other 8% in marine marginal facies (e.g. tidally flats, deltas) (Fig. 5). This record indicates that titanosaur bones are more abundant in fluvial facies, and the study of some sites indicates that crevasse splay facies (González Riga and Astini, 2007) and muddy flood plain deposits (González Riga et al., 2013) were prone to the preservation of these bones. In marine marginal facies, like the Loncoche Formation from the Mendoza Province (Argentina), fossil bones are scarse but sauropod tracks are abundant and well preserved. Taphonomic aspects indicated that titanosaurs have capacity to walk effectively over very saturated substrates of tidal flats (González Riga, 2011).

Against this statistical data from Argentinean sedimentary basins, in Brazil the sauropod fossils are preserved in facies association regarded as part of the Lowstand System Tract. It could be observed in the Early Cretaceous the fluvial dominated lacustrine deltaic sandstone facies of Quiricó Formation (Aptian), Areado Group in Sanfranciscana Basin (Campos and Dardenne, 1997; Zaher et al., 2011), and in deltaic mounth bar sandstone facies of Aptian Itapecuru Group (Lima and Rossetti, 1999; Carvalho et al., 2003; Miranda and Rossetti, 2006) and deltaic conglomeratic facies of Albian-Cenomanian Alcântara Formation (Medeiros et al., 2007; Candeiro et al., 2011) in São Luís-Grajaú Basin. In the Late Cretaceous, channel filling conglomerates and sandstones facies and flash floods conglomeratic sandy facies of the Adamantina, Presidente Prudente and Marília formations (Santonian–Maastrichtian), Bauru Group, Paraná Basin (Soares et al., 1980) and in the conglomeratic sandstones of fluvial to distal alluvial fan facies of Utiariti Formation (Campanian-Maastrichtian), Parecis Group, Rio das Mortes Rift (Chapada Graben) in north Paraná Basin (Weska, 2006). Apparently, the only exception is in the marginal lagoon and transitional sandstones facies of the uppermost interval of Açu Formation (Cenomanian), Potiguar Basin in which this interval of this unit is regarded as part of a transgressive sequence (Santos et al., 2005; Pessoa-Neto et al., 2007), similar to Loncoche Formation context in Argentina.

However, theoretically, the best ecological condition for huge herbivores like sauropods must be to include paleoenvironments

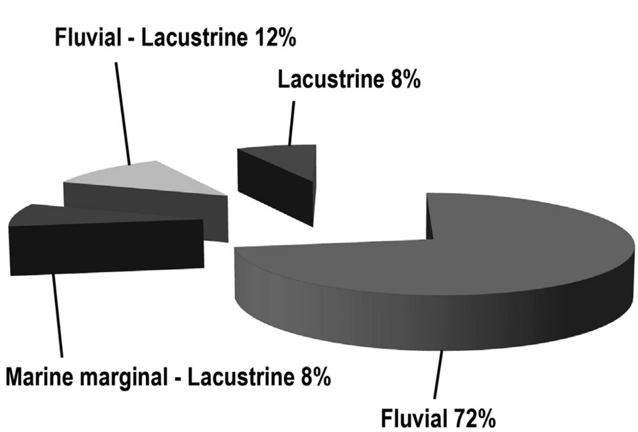

Fig. 5. Sedimentary environment of the Cretaceous sauropod record in South America.

with diverse and abundant vegetation, as it is present in fluvial and lacustrine of Neuquén Group and some lacustrine levels of the Allen Formation in Argentina (Garrido, 2010) and Bauru Group in Brazil (Soares et al., 1980). In contrast, these conditions are different in lagoons, tidal flats, and deltas influenced by the sea of the Loncoche Formation (Pramparo et al., 2008). It has not been studied in detail the behavior preferences of titanosaus, but some authors suggest that they showed a preference for inland terrestrial environments (Mannion, 2008; Mannion and Upchurch, 2010); this hypothesis is congruent with the geological context of findings described in this paper but will be confirmed by more detailed taphonomic sites.

Another important factor of the titanosaur diversity during the Late Cretaceous of Patagonia is the reduction of terrestrial areas caused by the Atlantic transgressions. In the Neuquén Basin a sustained subsidence allowed accommodation and preservation of a succession of rather unusual coastal lagoons, estuaries, tidal flats, and deltaic to shallow-marine facies associations with mixed tide-wave influence. Evidently, these environmental conditions reduced the land areas for the latest titanosaurs that lived in the Patagonia. The detailed study of tracksite, such as that of Titanopodus of Mendoza, suggests that titanosaurs moved through the narrow early-Andean continental bridge across the Atlantic sea-way developed in northern Patagonia (Astini et al., 2014).

Other factor during the Maastrichthian is the immigration of hadrosaurs from North America (Brett-Surman, 1979; González Riga and Casadío, 2000; Coria et al., 2012). Paleoecological studies based on the possible interaction between both groups have not been published yet.

4.4. Paleobiological considerations

The South American titanosaurs exhibits a great diversity of size (from under 7 m saltasaurids to 34 m long in *Argentinosaurus*), shapes of necks (e.g. the amazing diversity of morphology in cervical vertebrae described by González Riga (2005), presence or absence of dermal bones (ostederms), different pedal structures (see González Riga et al., 2008), and diverse skull structure and teeth (Gallina and Apesteguía, 2011; Zaher et al., 2011). Ontogenetic topics have been studied regarding embryos and osteohistology. First, the discovery of exceptionally preserved embryos, eggs, and nests in Auca Mahuevo (Neuquén Province, Patagonia) reveals new ontogenetic and phylogenetic information (Chiappe et al., 1998, 2001). Specifically, these embryos provide an opportunity to test previous hypotheses concerning neosauropod phylogeny, for instance, the correlation between different characters expressed in adult skulls (Salgado et al., 2005). Second, new osteohistological studies promise to provide new insight into the growth strategies in titanosaurs (e.g. Salgado, 2003; González Riga and Curry Rogers, 2006), as in other sauropod taxa (Curry Rogers and Ericsson, 2005). These analyses will also be important for understanding evolutionary aspects, when the sampling of thin section of most relevant sauropods species is available. It is probable that these anatomical structures are related to determinate habits and behaviors as yet unknown.

5. Conclusions

This work analyzes the fossil record of South American sauropod dinosaurs, one of the most relevant records worldwide for their abundance (51 taxa) and biogeographical implications. The historical biogeography of sauropods is clearly influenced by the continental fragmentation of Gondwana and development of the South Atlantic Ocean. For this, phylogenetic relationships are recognized between South American and African sauropod faunas until the formation of the Atlantic Ocean during the mid-Cretaceous. A fluctuation of sea levels is frequently related to the diversity of sauropods (Mannion et al., 2011), but this general correlation must be refined in each continent with the discoveries of more species and in different stratigraphical resolution to improve. In Late Cretaceous of Argentina, the sauropods are preserved in transgressive sequences, transitional to lacustrine or overbank fines facies associations, with its peak in the Maastrichtian in response to the rise of the eustatic level in South Atlantic Ocean, during its drift. In the Argentinean context, the majority of sauropods materials are preserved in channelized to flash flood or even gravity lobes associated with lowstand system tract context of the Brazilian continental sequences during Early to Late Cretaceous, in response to the progressive uplift of the South America Platform due to the drift of the South Atlantic Ocean. One of the most important evolutionary events of the sauropods marked in South America is the progressive replacement of Diplodocimorpha by the Titanosauriformes during the early Late Cretaceous.

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Appendix. South American sauropod species from Cretaceous.

Country	Taxa	Taxonomic status	Geological unit, age	Palaeoenvironments	Reference
Argentina	*Aeolosaurus colhuehuapiensis*	Titanosauria/ Aeolosaurini	Bajo Barreal Formation, Campanian-Maastrichtian	Continental Fluvial	Casal et al. 2007.
	Aeolosaurus rionegrinus	Titanosauria/ Aeolosaurini	Angostura Colorada Formation, Campanian-Maastrichtian	Continental Fluvial	Powell, 1986, 2003.
	Agustinia ligabuei	Titanosauria	Lohan Cura Formation, Aptian	Continental Fluvial	Bonaparte, 1999.
	Amargasaurus cazaui	Dicraeosauridae	La Amarga Formation, Barremian	Continental Fluvial	Salgado and Bonaparte, 1991.
	Amargatitanis macni	Titanosauria	La Amarga Formation, Barremian	Continental Fluvial	Apesteguía, 2007.
	Andesaurus delgadoi	Titanosauria	Candeleros Formation, Cenomanian	Continental Fluvial	Calvo and Bonaparte, 1991.
	Antarctosaurus wichmannianus	Titanosauria	Anacleto Formation, Campanian-Maastrichtian	Continental Fluvial	Huene, 1929.
	Argentinosaurus huinculensis	Titanosauria	Huncuil Formation, Late Cenomanian	Continental Fluvial	Bonaparte and Coria, 1993.
	Argyrosaurus superbus	Titanosauria	Bajo Barreal Formation, Cenomanian-Turonian	Continental Fluvial	Lydekker, 1893.
	Barrosasaurus casamiquelai	Titanosauria	Anacleto Formation, Campanian	Continental Fluvial	Salgado and Coria, 2009.
	Bonatitan reigi	Titanosauria	Allen Formation, Campanian-Maastrichtian	Marine marginals – Lacustrine	Martinelli and Forasiepi, 2004.
	Bonitasaura salgadoi	Titanosauria	Bajo de la Carpa Formation, Santonian	Continental Fluvial	Apesteguía, 2004.
	Cathartesaura anaerobica	Rebbachisauridae	Huincul Formation, Cenomanian-Coniacian	Continental Fluvial	Gallina and Apesteguía, 2005.
	Chubutisaurus insignis	Somphospondyli	Cerro Barcino Formation, Albian-Aptian	Continental Fluvial	Del Corro, 1975.
	Comahuesaurus windhauseni	Rebbachisauridae	Lohan Cura Formation, Aptian-Albian	Continental Fluvial	Carballido et al. 2012.
	Drusilasaura deseadensis	Titanosauria	Bajo Barreal Formation, Cenomanian-Turonian	Continental Fluvial	Navarrete et al. 2011.
	Epachthosaurus sciuttoi	Titanosauria	Bajo Barreal Formation, Cenomanian-Turonian	Continental Fluvial	Powell, 1990.
	Futalognkosaurus dukei	Titanosauria/ Lognkosauria	Portezuelo Formation, Turonian-Coniacian	Continental Fluvial	Calvo et al., 2007a,b,c.
	Katepensaurus goicoecheai	Rebbachisauridae	Bajo Barreal Formation, Cenomanian-Turonian	Continental Fluvial	Ibiricu et al. 2013.
	Ligabuesaurus leanzai	Somphospondyli	Lohan Cura Formation, Aptian-Albian	Continental Fluvial	Bonaparte et al. 2006.
	Leinkupal laticauda	Diplodocoidea	Bajada Colorada Formation	Continental Fluvial	Gallina et al., 2014.
	Limaysaurus tessonei	Rebbachisauridae	La Amarga Formation, Barremiane – Early Aptian	Continental Fluvial	Salgado et al. 2004.
	Malarguesaurus florenciae	Somphospondyli	Portezuelo Formation, late Turonian-early Coniacian	Continental Fluvial	González Riga et al., 2009.
	Mendozasaurus neguyelap	Titanosauria/ Lognkosauria	Rio Neuquén Formation, late Turonian-late Coniacian	Continental Fluvial	González Riga, 2003.
	Muyelensaurus pecheni	Titanosauria/ Rinconsauria	Portezuelo Formation, late Turonian-early Coniacian	Continental Fluvial	Calvo et al., 2007a,b,c.
	Narambuenatitan palomoi	Titanosauria	Anacleto Formation, lower to middle Campanian	Continental Fluvial	Filippi et al., 2011b.
	Neuquensaurus australis	Titanosauria/ Saltasaurinae	Anacleto Formation, Santonian-Campanian	Continental Fluvial	Lydekker, 1893.
	Nopcsaspondylus alarcoensis	Rebbachisauridae	Candeleros Formation, Coniacian	Continental Fluvial	Apesteguía, 2007.
	Overosaurus paradasorum	Titanosauria/ Aeolosaurini	Anacleto Formation, Campanian	Continental Fluvial	Coria et al., 2013.
	Panamericansaurus schroederi	Titanosauria/ Aeolosaurini	Allen Formation, Campanian-Maastrichtian	Marine marginals – Lacustrine	Porfiri and Calvo, 2010.
	Pellegrinisaurus powelli	Titanosauria	Allen Formation, Campanian-early Maastrichtian	Marine marginals – Lacustrine	Salgado, 1996.
	Petrobrasaurus puestohernandezi	Titanosauria	Plottier Formation, Santonian	Continental Fluvial	Filippi et al., 2011a.
	Pitekunsaurus macayai	Titanosauria	Anacleto Formation, Campanian	Continental Fluvial	Filippi and Garrido, 2008.
	Puertasaurus reuilli	Titanosauria	Pari Aike Formation, early Maastrichtian	Continental Fluvial	Novas et al. 2005.
	Quetecsaurus rusconii	Titanosauria		Continental Fluvial	

(*continued*)

Country	Taxa	Taxonomic status	Geological unit, age	Palaeoenvironments	Reference
			Cerro Lisandro Formation, late Cenomanian-early Turonian		González Riga and Ortíz David, 2014.
	Rayososaurus agrioencis	Rebbachisauridae	Rayoso Formation, Aptian-Albian	Continental Fluvial	Bonaparte, 1996.
	Rinconsaurus caudamirus	Titanosauria/ Rinconsauria	Formation Portezuelo, late Turonian-Coniacian	Continental Fluvial	Calvo and González Riga, 2003.
	Rocasaurus muniosi	Titanosauria/ Saltasaurinae	Allen Formation, Campanian-Maastrichtian	Marine marginals – Lacustrine	Salgado and Azpilicueta, 2000.
	Saltasaurus loricatus	Titanosauria/ Saltasaurinae	Lecho Formation, Campanian-early Maastrichtian	Continental Fluvial	Bonaparte and Powell, 1980.
	Traukutitan eocaudata	Titanosauria	Bajo de la Carpa Formation, Senonian	Continental Fluvial	Juárez Valieri and Calvo, 2011.
	Zapalasaurus bonapartei	Rebbachisauridae	La Amarga Formation, Aptian-Albian	Continental Fluvial	Salgado et al., 2006.
Brazil	*Adamantisaurus mezzalirai*	Titanosauria	Adamantina Formation, Campanian-Maastrichtian	Continental Fluvial – Lacustrine	Santucci and Bertini, 2006.
	Aeolosaurus maximus	Titanosauria/ Aeolosaurini	Adamantina Formation, Campanian-Maastrichtian	Continental Fluvial – Lacustrine	Santucci and Arruda-Campos, 2011.
	Amazonsaurus maranhensis	Diplodocoidea	Itapecuru Formation, Aptian-Albian	Continental Fluvial – Lacustrine	Carvalho et al., 2003.
	Baurutitan britoi	Titanosauria	Marília Formation, Maastrichtian	Continental – Lacustrine	Kellner et al. 2005.
	Brasilotitan nemophagus	Titanosauria	Adamantina Formation, Turonian-Santonian	Continental Fluvial – Lacustrine	Machado et al., 2013.
	Gondwanatitan faustoi	Titanosauria/ Aeolosaurini	Adamantina Formation, Campanian-Maastrichtian	Continental Fluvial – Lacustrine	Kellner and Azevedo, 1999.
	Maxakalisaurus topai	Titanosauria/ Aeolosaurini	Adamantina Formation, late Cretaceous	Continental Fluvial – Lacustrine	Kellner et al. 2006.
	Tapuiasaurus macedoi	Titanosauria	Quiricó Formation, Aptian	Continental – Lacustrine	Zaher et al., 2011.
	Trigonosaurus pricei	Titanosauria	Marília Formation, Maastrichtian	Continental – Lacustrine	Campos et al. 2005.
	Uberabatitan ribeiroi	Titanosauria	Marília Formation, Maastrichtian	Continental – Lacustrine	Salgado and Carvalho, 2008.
Chile	*Atacamatitan chilensis*	Titanosauria	Tolar Formation, late Cretaceous	Continental – Fluvial	Kellner et al. 2011.

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