

**ABELISAUROIDEA AND CARCHARDONTOSAURIDAE
(THEROPODA, DINOSAURIA) IN THE CRETACEOUS OF SOUTH AMERICA.
PALEOGEOGRAPHICAL AND GEOCRONOLOGICAL IMPLICATIONS**

**Abelisauroidea e Carcharodontosauridae (Theropoda, Dinosauria) na
América do Sul durante do Cretáceo. Implicações paleogeograficas e geocronologicas**

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ABSTRACT: *In this contribution an up-to-date list of abelisauroid ceratosaurians and carcharodontosaurid allosaurians recognized in South America is presented. Abelisauroids and carcharodontosaurids in South America show rich species diversity and a wide range of temporal and geographical distribution. At least eight formally described species of Abelisauroidea are recognized in Argentina and only one in Brazil; in contrast, only one species of Carcharodontosauridae is known for all South America. The fossil record of abelisauroids and carcharodontosaurids in South America shows a dominance of abelisauroids in the upper late Cretaceous, while the dominance of carcharodontosaurids as large predators was during the Cenomanian-Turonian. Although knowledge of the evolution of Abelisauroidea and Carcharodontosauridae in South America, as well as in the rest of Gondwana is still far from being complete, intensive explorations in recent years have provided greater insight into the composition of theropod faunas in the Cretaceous of Gondwana.*

Keywords: Abelisauroidea; Carcharodontosauridae; Cretaceous; South America.

RESUMO: *Na presente contribuição é apresentada uma lista atualizada dos ceratossaurios abelissauroides e dos alossaurios carcarodontossaurídeos sul-americanos. Os abelissauródeos e carcarodontossaurídeos possuem uma grande diversidade específica e com uma grande distribuição temporal e geográfica. São reconhecidas oito espécies de Abelisauroidea na Argentina e somente uma no Brasil, em contraste, só é conhecida uma espécie de Carcharodontosauridae na América do Sul. O registro fóssil denota uma importância dos abelissauroides no Cretáceo mais tardio, contudo o predomínio dos carcarodontossaurídeos como os grandes predadores somente ocorreram durante o Cenomaniano-Turoniano. Apesar da escassez do conhecimento da evolução dos Abelisauroidea e Carcharodontosauridae na América do Sul como o resto do Gondwana, a intensiva exploração nos últimos anos tem produzido um grande incremento de dados e brindado*

com novas luzes para a melhor compreensão da composição faunística desses terópodes do Cretáceo do Gondwana.

Palavras-chave: Abelisauroida; Carcharodontosauridae; Cretáceo; América do Sul.

1 – INTRODUCTION

The abelisauroid ceratosaurians and carcharodontosaurid allosaurians are the best-known large predatory theropod dinosaurs of the Cretaceous of Gondwana. Abelisauroids have been recognized in several localities of Argentina (BONAPARTE, 1991A, 1996; BONAPARTE; NOVAS, 1985; BONAPARTE; POWELL, 1980; BONAPARTE; NOVAS; CORIA, 1990; CORIA; CHIAPPE; DINGUS, 2002; LAMANNA; MARTINEZ; SMITH, 2002; MARTINEZ ET AL. 1986; RAUHUT ET AL. 2003), Brazil (BERTINI, 1996; BITTENCOURT; KELLNER, 2002; CANDEIRO ET. 2004A,B; KELLNER; CAMPOS, 2002;), India (CHATTERJEE, 1978; HUENE; MATLEY, 1933; WILSON ET AL. 2003; NOVAS; AGNOLIN; BANDYOPADYAY, 2004), and Madagascar (LAVOCAT, 1955; CARRANO; SAMPSON; FORSTER, 2002; SAMPSON; CARRANO; FORSTER, 2001; SAMPSON ET AL. 1998;). Beside Gondwanan regions, abelisauroids are also documented in France (BUFFETAUT ET AL. 1988) and Spain (ASTIBIA ET AL. 1990).

The record of carcharodontosaurids is less abundant and mainly restricted to Argentina (CORIA; SALGADO, 2000; VICKERS-RICH ET AL. 1999) and Continental Africa (Morocco; SERENO ET AL. 1996; STROMER, 1915); nevertheless, a few isolated tooth remains were also collected in the upper Cretaceous beds of Brazil (CANDEIRO ET AL., 2002, 2004A,B).

The fossil record of abelisauroids and carcharodontosaurids in South America shows rich species diversity and a wide range of temporal and geographical distribution. Thus, remains attributed to both

groups were unearthed with increasing frequency in recent decades.

2 – OBJECTIVES AND METHODOLOGY

In this contribution, we present an up-to-date list of Abelisauroida and Carcharodontosauridae taxa recognized in the Cretaceous of South America. Furthermore, we evaluate the paleogeographical and chronostratigraphical distribution of both groups in South America during the Cretaceous as the result of Gondwanan plate tectonics.

The data on abelisauroid and carcharodontosaurid species for the present review are mostly based in literature sources as well as in the direct observation of the specimens. The term Abelisauroida is used *sensu* Bonaparte (1991b), Novas (1992), Carrano, Sampson, Forster (2002), and Wilson et al. (2003), as the clade of ceratosaurians that includes Abelisauridae plus Noosauridae. The term Carcharodontosauridae follows the definition of Coria and Currie (2003) as a family of Allosauroida that comprises all descendants of the most recent common ancestor of *Giganotosaurus* and *Carcharodontosaurus*.

For the stratigraphic units in the Neuquén Basin we follow the arrangement proposed by Leanza (1999), and Leanza and Hugo (2001). For other stratigraphic units we follow: Southern Basins, Page et al. (1999); Salta Basin, Salfity and Marquilla (1999); San Luis Basin, Medeiros and Schultz (2002), and Bauru Basin, Fernandes and Coimbra (1996).

3 – PALEO GEOGRAPHY AND UPPER CRETACEOUS TECTONIC EVENTS: A BRIEF REVIEW

During most of the Mesozoic the continental masses were principally arranged in two separated continents: Laurasia in the north and Gondwana in the south (BONAPARTE, 1986; FORSTER, 1999; HAY ET AL, 1999; PITMAN ET AL, 1993). By the end of the Mesozoic these masses started to separate into their modern conformation.

The separation of Gondwana started in the late Jurassic as a product of rifting along the present South America and Africa borders. This separation continued, by the Cretaceous times the South Atlantic Ocean started to form, and Gondwana split into the Eastern and Western landmasses (PITMAN ET AL., 1993). Eastern Gondwana comprised of Africa, India-Madagascar; whereas Western Gondwana included South America, Antarctica, and Oceania. By the late Cretaceous India separated from Madagascar and started the northwest movements that lead to a collision with Eurasia. Western Gondwanan landmasses were still connected by the beginning of the Tertiary (HAY ET AL., 1999; PASCUAL; ORTIZ JAUREGUIZAR; PRADO, 1996; SAMPSON ET AL. 1998).

Two main paleogeographic features allowed abelosaurids and carcharodontosaurids to attain a widespread distribution during Cretaceous times. These were the “Gondwanan Bridge” that linked India-Madagascar and the South America-Oceania platforms, and the “North bridge,” connecting north Africa and Europe (e.g. HAY ET AL. 1999). In addition, South America and North America were sporadically connected through Central America at the end of the Cretaceous (BONAPARTE, 1986; BONAPARTE ET AL. 1984). Thus, these transient geographic connections between West Gondwana and other landmasses during the late Cretaceous permitted faunal interchanges that directly influenced the faunal composition of the terrestrial ecosystems (BONAPARTE, 1991B; SAMPSON ET AL. 1998).

Finally, it is worth mentioning that during the late Cretaceous South American areas shared the same paleogeographical history; however during the Maastrichtian the southern-most part of South America was affected by the Maastrichtian-Danian marine transgression, which separated the Argentinean and Brazilian basins (Salta and Neuquén Basins in Argentina and Bauru Basin in Brazil) (PASCUAL; ORTIZ JAUREGUIZAR; PRADO, 1996; ZAMBRANO, 1987). This disconnection could have caused same faunal differentiation between the northern and southern parts of South America.

4 – ABELISAUROIDEA AND CARCHARODONTOSAURIDAE BACKGROUND

Abelisauroidea is a ceratosaurian clade that includes small to large-sized predators that evolved during the Cretaceous in Gondwanan landmasses. The group is composed of two families, Abelisauridae and Noasauridae, which are widely distributed in both temporal and geographical rank. Abelisauridae was created by Bonaparte and Novas (1985) to accommodate *Abelisaurus comahuensis*. After this first discovery, knowledge of the group was increased considerably by new discoveries, and by the reinterpretation of fragmentary and isolated remains; which permitted the recognition of an important radiation on Gondwanan landmasses during the Cretaceous including several adaptative morphotypes (BONAPARTE, 1991B).

Noasauridae was erected by Bonaparte and Powell (1980) to include a single species, *Noasaurus leali* from Lecho Formation (Salta Province). Subsequently this family was related to abelosaurids (BONAPARTE, 1991B; BONAPARTE; NOVAS; CORIA, 1990).

Beside South America (Table 1), abelisaurid species were also recognized in India: *Indosuchus raptorius* Huene and Matley, *Indosaurus matleyi* Huene (BONAPARTE, 1986, 1991B; BONAPARTE; NOVAS; CORIA, 1990; CHATTERJEE,

1978; CHATTERJEE; RUDRA, 1996; NOVAS; AGNOLIN; BANDYOPADYAY, 2004), *Lametasaurus indicus* Matley (WILSON ET AL. 2003), and *Rajasaurus narmadensis* Wilson, Sereno, Srivastava, Bhatt, Khosla, and Sahni (WILSON ET AL. 2003); Madagascar: *Majungatholus atopus* Lavocat (SAMPSON ET AL. 1998); Niger: *Rugosaurus primus* and *Spinostropeus gautieri* Sereno, Wilson, Conrad (SERENO, WILSON; CONRAD, 2004); Sereno, Duthiel, Larochene, Larsson, Lyon, Magwene, Sidor, Varicchio and Wilson: *Deltadromeus agilis* (SERENO ET AL. 1996); and France: *Tarascosaurus salluvicus* Le Loeuff and Buffetaut (LE LOEUFF; BUFFETAUT, 1990). Noosaurids discovered in India include *Laevisuchus indicus* Huene (CARRANO; SAMPSON; FORSTER, 2002; NOVAS; AGNOLIN; BANDYOPADYAY, 2004); and from Madagascar *Masiakasaurus knopfleri* Sampson, Carrano and Forster (CARRANO; SAMPSON; FORSTER, 2002; SAMPSON; CARRANO; FORSTER, 2001).

Other non-South American abelisauroids of uncertain affinities are *Jubbulpuria tenuis* Huene and Matley, *Ornithomimoides mobilis* Huene and Matley, *O.? barasimlensis* Huene and Matley, *Coeluroides largus* Huene and Matley, and *Dryptosauroides grandis* Huene and Matley, from India — *nomen nudum* (NOVAS; AGNOLIN; BANDYOPADYAY, 2004); *Elaphrosaurus bambergi* Janensch from Tanzania (CARRANO; SAMPSON; FORSTER, 2002; WILSON ET AL. 2003); and *Genusaurus sisteronis* Accarie, Beau-doin, Dejoux, Friès, Michard and Taquet from France (ACCARIE ET AL. 1995).

Carcharodontosauridae is a family of allosauroid theropods, which is composed of the largest theropod species (CORIA; SALGADO, 2000; Table 2). The first recognized member of this family was *Carcharodontosaurus saharicus* Stromer from Continental Africa (Algeria, Niger, Tunisia, Sudan and Morocco; SERENO ET AL. 1996; STROMER, 1915; 1931); then later followed *Acrocanthosaurus atokensis* Stoval and Langston from United States (HOLTZ, 2000; SERENO ET AL., 1996),

and *Giganotosaurus carolinii* Coria and Salgado from Argentina (CORIA; SALGADO, 1995; SERENO ET AL. 1996) were included. Most recent research supports the hypothesis that the Carcharodontosauridae are allosaurians; nevertheless, it is noteworthy that Novas (1997) found several derived features shared between carcharodontosaurids and abelisauroids suggesting a close phylogenetic affinity with the latter.

5 – ABELISAUROIDEA AND CARCHARODONTOSAURIDAE SPECIES

The following is a brief, annotated list of abelisauroid and carcharodontosaurid taxa from the Late Cretaceous of South America (Tables 1 and 2). The Argentinean and Brazilian species and records are in chronological order (from early to late forms).

5.1 – Abelisauroidea

5.1.1 – Argentina

Ligabueino andensi Bonaparte, 1996. *Ligabueino andensi* comes from the La Amarga Formation (Hauterivian-Barremian), La Amarga locality, southern Neuquén Province (BONAPARTE, 1996). *Ligabueino* is a very small theropod that is based on; a cervical and two dorsal vertebral neural arches, right ilium, two incomplete pubis, a left femur, and two pedal phalanges. This species is considered to be a basal abelisauroid (BONAPARTE, 1996) with possible noosaurid affinities (CARRANO; SAMPSON; FORSTER, 2002).

Ilokelesia aguadagrandensis Coria and Salgado, 2000. *Ilokelesia aguadagrandensis* is from the Huincul Formation (Cenomanian-Turonian; Río Limay Subgroup) in the Aguada Grande locality, eastern Neuquén Province. *Ilokelesia* is based on some skull bones, two cervical, one dorsal, and five articulated vertebrae, fragmentary ribs, some haemal arches, and some pedal phalanges (CORIA; SALGADO, 2000). This species is considered to be a

basal abelosaurid (CORIA; SALGADO, 2000).

Xenotarsosaurus bonapartei Martínez, Giménes, Rodríguez, and Bochaty, 1986. *Xenotarsosaurus bonapartei* comes from the Bajo Barreal Formation (middle Cenomanian-late Turonian) in the Sarmiento Department, in the southern part of the Chubut Province. *Xenotarsosaurus* is a medium-sized abelosaurid based on two incomplete cervico-dorsal vertebrae, a right femur, tibia and fibula, and a fused astragalus-calcaneus (MARTÍNEZ ET AL. 1986).

Velocisaurus unicus Bonaparte, 1991a. *Velocisaurus unicus* comes from the Bajo de la Carpa Formation (Santonian; Río Colorado Subgroup) of Neuquén city, Neuquén Province. This species is a small theropod, which is only known from the right tibia and almost complete right foot. *Velocisaurus* was tentatively interpreted as a Ceratosauria (BONAPARTE, 1991A); in addition some authors have found a few features in common with noosaurids (CARRANO; SAMPSON; FORSTER, 2002). Nevertheless, new materials should confirm the taxonomic status of this taxon.

Abelisaurus comahuensis Bonaparte and Novas, 1985. *Abelisaurus comahuensis* comes from the Anacleto Formation (Santonian-Early Campanian; Río Colorado Subgroup; HEREDIA; SALGADO, 1999) in the Río Negro Province. *Abelisaurus* is a medium to large (6 to 7 m long) theropod that is only known from a partial skull of about 0.85 meters (Figs. 1 and 2). Since the discovery of this species, the diversity and phylogenetic relationships of abelisauroids have begun to be more understood, it has also provided new insights on the biogeographic distribution of this gondwanic lineage of theropods (BONAPARTE, 1986, 1991B).

Aucasaurus garridoi Coria, Chiappe, and Dinges, 2002. *Aucasaurus garridoi* was recently described from an almost complete skeleton from the Anacleto Formation (early Campanian; Río Colorado Subgroup) from Auca Mahuevo, eastern Neuquén Province (CORIA; CHIAPPE; DINGUS, 2002). *Auca-*

saurus was unearthed from the same mudstone and siltstone strata that has produced several remains of fossilized nests, eggs, and embryos of still undetermined but possible titanosaur neosauro pods (CHIAPPE; CORIA, 2000). *Aucasaurus* and *Carnotaurus* (see below) were nested together in the Tribe Carnotaurini as the most derived members of the family Abelisauridae (CORIA; CHIAPPE; DINGUS, 2002).

Carnotaurus sastrei Bonaparte, 1985. *Carnotaurus sastrei* from La Colonia Formation (Maastrichtian) of Chubut Province is, without a doubt, the best-known abelosaurid. The skeleton is almost complete (with exception of the distal portion of the tibiae, both fibulae, the hind feet, and the medial and distal end of the tail), and exceptionally well preserved including the skin impressions (BONAPARTE; NOVAS; CORIA, 1990). After the original taxonomic designation of *Carnotaurus* (BONAPARTE, 1985), a complete description of the whole skeleton was performed by Bonaparte, Novas, Coria (1990); revealing a lightly-built theropod about 7 meters long, with the skull high and short bearing two prominent frontal horns (Fig. 3).

Noasaurus leali Bonaparte and Powell, 1980. *Noasaurus leali* comes from the Lecho Formation (Maastrichtian), southern Salta Province. *Noasaurus* is a small theropod based on; a complete left maxilla, a right quadrate, a cervical neural arch, a dorsal vertebral body, cervical ribs, the right metatarsal II, a pedal phalanx, and an ungual phalanx of the foot. Because of derived features found in the maxilla and in the cervical neural arch, Bonaparte and Powell (1980) erected the family Noosauridae, which previously was regarded as part of the gondwanan radiation of abelisauroids (BONAPARTE, 1991B; NOVAS, 1997). In addition, closely related forms to *Noasaurus* were reported from the Maastrichtian of Madagascar (CARRANO; SAMPSON; FORSTER, 2002; SAMPSON; CARRANO; FORSTER, 2001).

Other abelisauroid remains. In the Cerro Barcino Formation (Hauterivian-Barremian) at Cerro Chivo,

northern Chubut Province, two isolated caudal vertebrae of a medium sized abelisaurid were reported (RAUHUT ET AL. 2003). Furthermore, an isolated but nearly complete left maxilla with some teeth was discovered in the Bajo Barreal Formation (middle Cenomanian-late Turonian) in the Sierra de San Bernardo, Chubut Province, and subsequently was assigned to the subfamily Carnotaurinae (LAMANNA; MARTINEZ; SMITH, 2002).

5.1.2 – Brazil

Pycnonemosaurus nevesi Kellner and Campos, 2002. *Pycnonemosaurus nevesi* comes from the Adamantina Formation (Turonian-Santonian) of the Cambebe area, Mato Grosso State, and represents the first Brazilian abelisaurid formally described (KELLNER; CAMPOS, 2002). This species is based on five teeth (BITTENCOURT; KELLNER, 2002), parts of seven caudal vertebrae, fragments of ribs, and an incomplete right tibia and

fibula. *Pycnonemosaurus* is a medium to large-sized theropod of approximately 6 to 7 meters in length, regarded as an abelisaurid because it share several derived features with other well known member of the group, such as *Ilokelesia*, *Carnotaurus*, and *Aucasaurus* (KELLNER; CAMPOS, 2002).

Abelisaurid remains. The first abelisaurid from Brazil was discovered by Bertini (1996). This material consists of a partial premaxilla with a tooth. The specimen was discovered in Adamantina Formation sediments (Bauru Group, Turonian-Santonian) in São Paulo (Santo Anastácio area) and Minas Gerais (Prata area) States. Furthermore, Candeiro (2002) and Candeiro et al. (2002, 2004a,b) reported abelisaurid teeth from the states of Minas Gerais (Peirópolis area) and São Paulo (Alfredo Marondes, Flórida Paulista, Santo Anastácio) in the Adamantina and Marília Formations (Late Maastrichtian) of the Bauru Group. These remains are very fragmentary, making an accurate identification difficult.

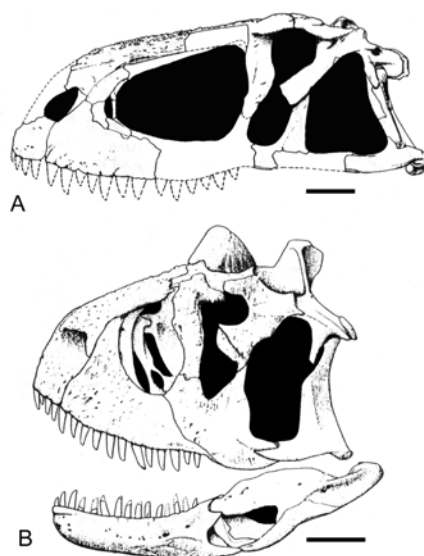


Figure 1 – Skulls of Abelisauridae. A, *Abelisaurus comahuensis* Bonaparte and Novas (modified from BONAPARTE AND NOVAS, 1985); B, *Carnotaurus sastrei* Bonaparte (modified from BONAPARTE, NOVAS, CORIA, 1990). Scale bar represents 10 cm.

Table 1 – Abelisauroidea records from South America.

Abelisauroidea	Country	Stratigraphy	Reference Selected
<i>Ligabueino andensi</i>	Argentina	La Amarga, Barremian	Bonaparte (1996)
<i>Llokelesia aguadagrandensis</i>	Argentina	Huincul Fm., Cenomanian-Turonian	Coria and Salgado (2000)
<i>Xenotarsosaurus bonapartei</i>	Argentina	Bajo Barreal Fm., middle Cenomanian-Late Turonian	Martinez et al. (1986)
<i>Velocisaurus unicus</i>	Argentina	Bajo de La Carpa, Turonian	Bonaparte (1991a)
<i>Pycnonemosaurus nevéis</i>	Brazil	Adamantina Fm., Turonian-Santonian	Campos and Kellner (2002)
<i>Abelisaurus comahuensis</i>	Argentina	Anacleto Fm., Santonian-Early Campanian	Bonaparte (1991b)
<i>Aucasaurus garridoi</i>	Argentina	Anacleto Fm., Santonian-Early Campanian	Coria, Chiappe and Dingus (2002)
<i>Carnotaurus sastrei</i>	Argentina	La Colonia Fm., Maastrichtian	Bonaparte, Novas and Coria. (1990)
<i>Noasaurus leali</i>	Argentina	Lecho Fm., Maastrichtian	Carrano, Sampson, Forster (2002)
Carnosaurinae	Argentina	Bajo Barreal Fm., middle Cenomanian-Late Turonian	Lamanna, Martinez and Smith (2002)
Abelisauridae	Argentina	Cerro Barcino Fm., Hauterivian-Barremian	Rauhut et al. (2003)
Abelisauridae	Brazil	Adamantina Fm., Turonian-Santonian; Marília Fm., Late Maastrichtian	Candeiro et al. (2004a,b)

5.2 – CARCHARODONTOSAURIDAE

5.2.1 – Argentina

Giganotosaurus carolinii Coria and Salgado, 1995. *Giganotosaurus carolinii* comes from the Candeleros Formation (Cenomanian, Río Limay Subgroup) of the El Chocón locality, Neuquén Province. This species is considered to be the largest theropod in the world with a skull length of about 1.7 meters (CALVO; CORIA, 2000; CORIA; SALGADO, 1995) (Figs. 3 and 4). *Giganotosaurus* is based on approximately 70% of the skeleton, including several skull bones, teeth, and most of the postcranial elements (CORIA; CURRIE, 2003; CORIA; SALGADO, 1995;). In addition, isolated teeth and a fragment of a left dentary from the same stratigraphic horizons of the holotype of *Giganotosaurus* were described and assigned to the genus (CALVO, 1999; DE VALAIS; APESTEGUÍA, 2001).

Quilmesaurus curriei Coria, 2001. *Quilmesaurus curriei* comes from the Allen Formation (Campa-

nian-Maastrichtian) of the Salitral Ojo de Agua locality, Río Negro Province. This species consists of only a distal portion of a right femur and a complete right tibia. *Quilmesaurus* was originally regarded as a non-ceratosaur theropod possibly related to *Giganotosaurus* (CORIA, 2001). Later, *Quilmesaurus* was considered an abelisauroid (Kellner and Campos, 2002), but recently Juárez Valieri, Fiorelli and Cruz (2004) regarded it as *nomen dubium* due to the lack of derived features needed to construct a robust taxon.

Carcharodontosaurid remains. Isolated teeth and skeletal remains are recognized from the Cerro Barcino (Hauterivian-Barremian; Chubut Province; NOVAS; DE VALAIS, 2001; VICKERS-RICH ET AL. 1999;), Mata Amarilla (Turonian; Chubut Province; NOVAS ET AL. 1999), Anacleto (Santonian; Neuquén Province; ALCOBER ET AL. 1998), Los Alamitos (Late Campanian; Río Negro Province; APESTEGUÍA ET AL., in press.), and Allen (Campanian-Maastrichtian; Río Negro Province; MARTINELLI; FORASIEPI, in press) Formations.

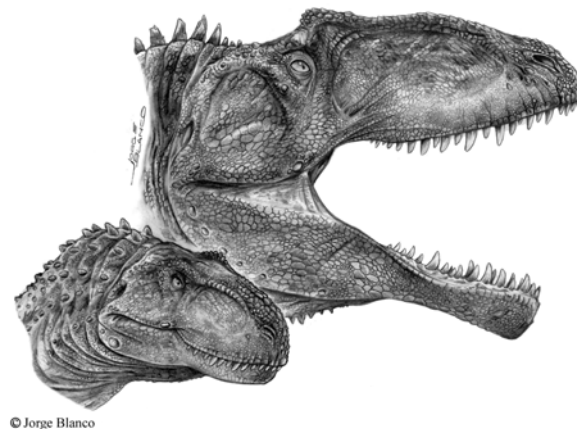


Figure 2 – Life reconstruction of *Abelisaurus comahuensis* Bonaparte and Novas (left) and *Giganotosaurus carolinii* Coria and Salgado (right) performed by the paleoartist Jorge Blanco. Both species are in scale.

5.2.2 – Brazil

Carcharodontosaurid remains. Recently carcharodontosaurid remains were reported in the Adamantina (Turonian-Santonian, Bauru Group; CANDEIRO ET AL. 2002, 2004A), and Marília Formations (Maastrichtian, Bauru Group; CANDEIRO, 2002; CANDEIRO ET AL., 2004B). Many carcharo-

dontosaurid teeth have been found in the Cenomanian-Turonian beds of Maranhão State in recent years. Medeiros and Shultz (2002) attributed these teeth coming from the São Luis Basin (VILASBOAS ET AL., 1999) as being of *Carcharodontosaurus saharicus*; nevertheless, we prefer to consider as carcharodontosaurid indet. due to the lack of diagnostic features.

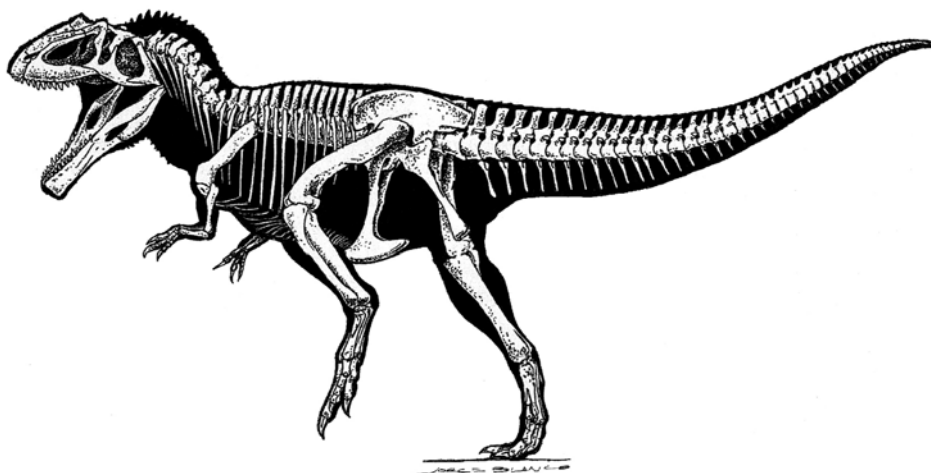


Figure 3 – Reconstruction of the skeleton of the carcharodontosaurid *Giganotosaurus carolinii* Coria and Salgado performed by the paleoartist Jorge Blanco. Estimated length is of about 14 meters.

Table 2 – Carcharodontosauridae records from South America

Carcharodontosauridae	Country	Stratigraphy	ReferenceSelected
<i>Giganotosaurus carolinii</i>	Argentina	Candeleros Fm., Cenomanian	Coria and Currie (2003)
<i>Quilmesaurus curriei</i>	Argentina	Allen Fm., Campanian-Maastrichtian	Coria (2001)
Carcharodontosauridae	Argentina	Cerro Barcino Fm., Hauterivian-Barremian; Mata Amarilla Fm., Turonian; Anacleto Fm., Santonian-Early Campanian; Allen Fm., Campanian-Maastrichtian; Los Alamos Fm, Campanian	Martinelli and Forasiepi (2004)
Carcharodontosauridae	Brazil	São Luis Basin, Albian-Cenomanian; Adamantina Fm., Turonian-Santonian; Marília Fm., Late Maastrichtian	Medeiros and Schultz (2002), Candeiro et al. (2004a,b)



Figure 4 – Solid square, Abelisauroidea. Brazil: 1, *Pycnomosaurus*; Abelisauridae, 2, Peirópolis; 3, Prata; 4, Santo Anastácio; 6, Flórida Paulista; Argentina; 7, *Noasaurus*; 8, *Abelisaurus*; 9, *Aucasaurus*; 10, *Ilokelesia*; 11, *Ligabueino*; 12, *Velocisaurus*; 13, *Xenotarsosaurus*; 14, Carnotaurinae; 15, Abelisauridae. Solid circle, Carcharodontosauridae. Brazil: A, Carcharodontosauridae; B, Peirópolis; C, Prata; D, Alfredo Marcondes; Argentina: E, *Giganotosaurus*; F, *Quilmesaurus*; Carcharodontosauridae, G, Plaza Huincul area; H, Los Alamos area; I, Bajo Santa Rosa; J, Cerro Barcino; K, Mata Amarilla, Chubut Province.

6 – DISCUSSION AND CONCLUSIONS

The paleogeographical distribution of Abelisauroidea and Carcharodontosauridae remains is the product of the long, isolated evolution of both groups on Gondwanan landmasses (BONAPARTE, 1986).

The early occurrence of Abelisauridae comes from the Hauterivian-Barremian Cerro Barcino Formation (Chubut Province; RAUHUT ET AL. 2003); suggesting that the abelisauroids split into the two recognized families (Abelisauridae and Noosauridae) at least in the early Lower Cretaceous. From these times, *Ligabueino andensi* is also known from the La Amarga Formation (Neuquén Province; BONAPARTE, 1996), and is regarded as a basal abelisauroid (BONAPARTE, 1996; CARRANO; SAMPSON; FORSTER, 2002); however further studies and materials should clarify its affinities within this group. Both Neuquén and Chubut discoveries represent the oldest Cretaceous records of theropods in South America (BONAPARTE, 1996; RAUHUT ET AL. 2003).

In the early Lower Cretaceous, carcharodontosaurid remains are also found at Cerro Barcino (Chubut Province, NOVAS; DE VALAIS, 2001; VICKERS-RICH ET AL., 1999); indicating that both groups of large theropods (abelisauroids and carcharodontosaurids) appeared together in the fossil record as two distinctive gondwanic clades. During the Cenomanian-Turonian, the occurrence of carcharodontosaurids is high in South America (CORIA; SALGADO, 1995; DE VALAIS; APESTEGUÍA, 2001; NOVAS ET AL. 1999) as well as in Continental Africa (e.g. Sereno et al., 1996), and comprises the largest theropod forms. Some authors postulated that carcharodontosaurids became extinct in the Turonian (APESTEGUÍA, 2002); nevertheless, some isolated teeth and postcranial remains suggest the presence of a member of this family in the Santonian Anacleto Formation (Neuquén Province; ALCOBER ET AL., 1998), Late Campanian Los Alamitos (Río Negro Province; Apesteguía et al. in press), Campanian-Maastrichtian Allen Formation (Río Negro Province; MARTINELLI;

FORASIEPI, in press), Turonian-Santonian Adamantina Formation (Brazil; CANDEIRO ET AL. 2002), and in the Maastrichtian Marília Formation (Brazil; CANDEIRO, 2002; CANDEIRO ET AL., 2003, 2004B). Therefore, if the taxonomic identification of these records is correct and the features used for recognizing carcharodontosaurid affinities are unequivocal (e.g. wrinkles in the crown tooth), the group persisted into the latest Upper Cretaceous. Moreover, it is worthy to mention that presumably Campanian-Maastrichtian carcharodontosaurids are small to medium-sized, contrasting with older taxa characterized by their large size.

When the carcharodontosaurid record is more abundant (in the Cenomanian-Turonian), medium to large size abelisaurids are also known (CORIA AND SALGADO, 2000; MARTÍNEZ ET AL., 1986). The most derived abelisaurids appear well documented in the Late Cretaceous with extremely specialized forms such as *Carnotaurus sastrei* (BONAPARTE; NOVAS; CORIA, 1990). Carnotaurins are known in the Santonian-Campanian (CORIA; CHIAPPE; DINGUS, 2002) and in the Maastrichtian (BONAPARTE; NOVAS; CORIA, 1990; PASCUAL ET AL. 2000); nevertheless, Lamanna, Martinez and Smith (2002) described a carnotaurin maxilla from the Bajo Barreal Formation (late Cenomanian-early Turonian) and suggested that the origin of this subfamily took place before the middle Cretaceous. We believe that more material is required to confirm this suggestion.

Noosauridae is still poorly known in South America but its importance as a derived, endemic group of theropods in Gondwana is remarkable (BONAPARTE, 1991B). Moreover, a new taxon from the Maastrichtian of Madagascar provides a wide knowledge of this bizarre family (CARRANO; SAMPSON; FORSTER, 2002; SAMPSON; CARRANO; FORSTER, 2001).

In summary, the fossil record of abelisauroids and carcharodontosaurids in South America shows a dominance of abelisauroids in the upper Late Cretaceous, while the dominance of large,

carcharodontosaurid predators was during the Cenomanian-Turonian. At least eight formally described species of Abelisauroidea are recognized in Argentina and only one in Brazil. In contrast, only one species of Carcharodontosauridae is known for all South America.

Although the knowledge of the evolution of Abelisauroidea and Carcharodontosauridae in South America, as well as in the rest of Gondwana, is still far from being complete, intensive explorations in recent years have provided greater insight into the composition of theropod faunas in the Cretaceous of Gondwana.

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REFERENCES

- ACCARIE, H., B.; BEUDOIN, J.; DEJAX, G.; FRIÈS, J.-G.; MICHARD, A.; TAQUET, A. Découverte d'un dinosaure théropode nouveau (*Genusaurus sisteronis* n. g., n. sp.) dans l'Albien marin de Sisteron (Alpes de Haute-Provence, France) et extension au Crétacé inférieur de la lignée cératosaurienne. **Comptes Rendus d'Académie des Sciences**. Paris. v. 320. p. 327-334, set. 1995.
- ALCOBER, O. et al. A Late Cretaceous carcharodontosaurid (Theropoda: Allosauroidae) from Argentina. **Journal of Vertebrate Paleontology**. Northbrook, v. 18, suppl. 3, p. 23A, 1998.
- APESTEGUÍA, S. Successional structure in continental tetrapod faunas from Argentina along the Cretaceous. In: SIMPÓSIO SOBRE O CRETÁCEO DO BRASIL E II SIMPÓSIO SOBRE EL CRETÁCICO DE AMÉRICA DEL SUR, 6, 2002, São Pedro. **Boletim...** São Pedro: UNESP/Rio Claro, 2002. p. 135-141.
- APESTEGUÍA, S.; CANDEIRO, R.; AGNOLIN, F. L. Late Cretaceous dwarf carcharodontosaurid in Patagônia. **Ameghiniana**. Buenos Aires, Supplement, in press.
- ASTIBIA, H.; BUFFETAUT, E.; BUSCALIONI, A. D.; CAPPETTA, H. The fossil vertebrates from Laño (Bosque Country, Spain); new evidence on the composition and affinities of the Late Cretaceous continental faunas of Europe. **Terra Nova**. Paris, v. 2, p. 460-466, mar. 1990.
- BERTINI, R. J. Evidências de Abelisauridae (Carnosauria: Saurischia) do Neocretáceo da Bacia do Paraná. In: SIMPÓSIO CRETÁCEO DO BRASIL, 6, 1996. Rio Claro. **Boletim...** São Paulo, 1996. p. 267-271.
- BITTENCOURT, J. S., KELLNER, A. W. A. Abelisauria (Theropoda, Dinosauria) teeth from Brazil. **Boletim do Museu Nacional Série Geologia**. Rio de Janeiro, v. 62, p. 1-8, mar. 2002.

BONAPARTE, J. F. A horned Cretaceous carnosaur from Patagonia. **National Geographic Research**. Washington, v. 1, p. 140-151, out. 1985.

BONAPARTE, J. F. History of the terrestrial Cretaceous vertebrate of Gondwana. In: Congreso Argentino de Paleontología y Bioestratigrafía, 4, 1986. Mendoza. **Actas...** Mendoza, 1986. p. 63-95.

BONAPARTE, J. F. Los vertebrados fósiles de la Formación Río Colorado, de la Ciudad de Neuquén y cercanías, Cretácico Superior, Argentina. **Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"**. Buenos Aires, v. 4, p. 17-123, nov. 1991a.

BONAPARTE, J.F. The gondwanian theropod families Abelisauridae and Noasauridae. **Historical Biology**. London, v. 5, p. 1-25, jan. 1991b.

BONAPARTE, J. F. Cretaceous tetrapods of Argentina. Contribution of southern South America to Vertebrate Paleontology. **Münchner Geowissenschaftliche Abhandlungen**. München, v. 30, p. 73-130, mar. 1996.

BONAPARTE, J. F.; POWELL, J. E. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda, Coelurosauria, Carnosauria, Aves). **Mémoires de la Société Géologique de France**. Paris. v. 139, p. 19-28, mar. 1980.

BONAPARTE, J. F.; NOVAS, F. E. *Abelisaurus comahuensis*, n. g., n.sp., Carnosauria del Cretácico Tardío de Patagonia. **Ameghiniana**. Buenos Aires, v. 21, p. 259-265, jul. 1985.

BONAPARTE, J. F. Et al. La Formación Los Alamitos (Campaniano-Maastrichtiano) del sudeste de Río Negro, con descripción de *Kritosaurus australis* nov. sp. (Hadrosauridae). Significado paleogeográfico de los vertebrados. **Revista de la Asociación Geológica Argentina**. Buenos Aires, v. 39, p. 284-299, may 1984.

BONAPARTE, J. F.; NOVAS, F. E.; CORIA, R. A. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. **Contribution in Science, Natural History Museum of Los Angeles Country**. Los Angeles, v. 416, p. 1-42, mar. 1990.

BUFFETAUT, E.; MECHIN, P.; MECHIN-SALESSY, A. Un dinosaure théropode d'affinités gondwaniennes dans le Crétacé supérieur de Provence. **Comptes Rendus d'Académie des Sciences**. Paris, v. 306 (S. II), p. 153-158, jan. 1988.

CALVO, J. O. Dinosaurs and other vertebrates of the Lake Ezequiel Ramos Mexia Area, Neuquén — Patagonia, Argentina. **National Science Museum Monographs**. Tokyo, v. 15, p. 13-45, jul. 1999.

CALVO, J. O.; CORIA, R. New specimen of *Giganotosaurus carolinii* (Coria and Salgado, 1995), supports it as the largest theropod ever found. **GAIA**. Lisbon, v. 1, p. 117-122, jul. 2000.

CANDEIRO, C. R. A. **Dentes de Theropoda da Formação Marília (Santoniano-Maastrichtiano), Bacia Bauru, Região de Peirópolis, Uberaba, Minas Gerais, Brasil**. 2002, p.136. Dissertação de Mestrado, Universidade Federal do Rio de Janeiro, 2002.

CANDEIRO, C. R. A.; MARINHO, T. S.; OLIVEIRA, E. C. Distribuição geográfica dos dinossauros da Bacia Bauru (Cretáceo Superior). **Revista Sociedade & Natureza**. Uberlândia, in press, set. 2004.

CANDEIRO, R. et al.. Novos achados de Dinosauria no oeste do estado de São Paulo, na Formação Adamantina (Bacia Bauru), Cretáceo Superior. In: SIMPÓSIO SOBRE O CRETÁCEO DO BRASIL E II SIMPÓSIO SOBRE EL CRETÁCICO DE AMÉRICA DEL SUR, 6, 2002, São Pedro. **Boletim...** São Pedro: UNESP/Rio Claro, 2002. p. 409-413.

CANDEIRO, C. R. A. et al. Dinosaur remains from

- western São Paulo State, Brazil (Bauru Basin, Adamantina Formation, Upper Cretaceous). **Journal of South American Earth Science**. Columbia, in press, v. 18, 2004a.
- CANDEIRO, C. R. A.; BERGQVIST, L. P.; NOVAS, F. E.; CURRIE, P. J.; Theropod teeth from the Marília Formation (Upper Maastrichtian), Minas Gerais State, Brazil. In: ANNUAL MEETING SOCIETY OF VERTEBRATE PALEONTOLOGY, 64, 2004B, Denver, Colorado, United States of America. **Abstracts...** Denver: Denver Museum of Nature and Science and the University of Colorado Museum, 2004B. p. 204.
- CARRANO, M. T.; SAMPSON, S. D.; FORSTER, C. A. The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. **Journal of Vertebrate Paleontology**. Northbrook, v. 22, n. 3, p. 510-534, 2002.
- CHATTERJEE, S. *Indosuchus* and *Indosaurus*, Cretaceous carnosaur from India. **Journal of Paleontology**. Lawrence, v. 52, n. 3, p. 570-580, set. 1978.
- CHATTERJEE, S.; RUDRA, D. KT events in India: impact, rifting, volcanism and dinosaur extinction. **Memoir of the Queensland Museum**. Melbourne, v. 39, n. 3, p. 489-532, jul. 1996.
- CHIAPPE, L. M.; CORIA, R. A. Auca Mahuevo: Un extraordinario sitio de nidación de dinosaurios saurópodos del Cretácico Superior de Patagonia. **Ameghiniana**. Buenos Aires, (Supplement), n. 37, p. 22R, may 2000.
- CORIA, R. A. New theropod dinosaur from the Late Cretaceous of Patagonia. In: TANKE, D. H., CARPENTER, K. (EDS.), **Mesozoic Vertebrate Life**, Indiana University Press, 2001, p. 3-9.
- CORIA, R. A.; SALGADO, L. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. **Nature**. London, n. 377, p. 224-226, mar. 1995.
- CORIA, R. A. SALGADO, L. A basal Abelisauria Novas, 1992 (Theropoda-Ceratosauria) from the Cretaceous of Patagonia, Argentina. **GAIA**. Lisbon, v. 15, p. 89-102, jul. 2000.
- CORIA, R. A.; CURRIE, P. J. The braincase of *Giganotosaurus carolinii*, Dinosauria : Theropoda) from the Upper Cretaceous of Argentina. **Journal of Vertebrate Paleontology**, Northbrook, v. 22, n. 3, p. 802-811, 2003.
- CORIA, R. A., CHIAPPE, L.; DINGUS, L. A new close relative of *Carnotaurus sastrei* Bonaparte 1985 (Theropoda: Abelisauridae) from the Late Cretaceous of Patagonia. **Journal of Vertebrate Paleontology**. Northbrook, v. 22, p. 460-465, jul. 2002.
- DE VALAIS, S.; APESTEGUÍA, S. Dientes asignables a *Giganotosaurus* (Carcharodontosauria, Theropoda) provinientes de “La Buitrera”, Formación Candeleros, provincia de Río Negro. **Ameghiniana**. Buenos Aires, Supplement, n. 38, p. 6-7, may 2001.
- FERNANDES, L. A.; COIMBRA, A. M. A Bacia Bauru (Cretáceo Superior, Brasil). **Anais da Academia Brasileira de Ciências**. Rio de Janeiro, v. 68, n. 2, p. 195-205, jul. 1996.
- FORSTER, C. A. Gondwanan dinosaur evolution and biogeographic analysis. **Journal of African Earth Sciences**. Oxford, v. 28, p. 169-185, mar. 1999.
- HAY, W. W. et al. An alternative global Cretaceous paleogeography. In: BARRERA E., JOHNSON C. (EDS.), **Evolution of the Cretaceous Ocean/Climate System. Geological Society of America Special Paper**. Boulder, 1999, p. 1-47.
- HEREDIA, S.; SALGADO, L. Posición estratigráfica de los estratos supracretácicos portadores de dinosaurios en Lago Pellegrini, Patagonia septentrional, Argentina. **Ameghiniana**. v. 36, pp. 229-234, jul. 1999.

- HOLTZ, JR. T. R. A new phylogeny of the carnivorous dinosaurs. **Gaia**. Lisboa, v. 15, p. 5-61, jul. 2000.
- HUENE, F. V.; MATLEY, C. A. Cretaceous Saurischia and Ornithischia of the Central Provinces of India. **Palaontologica Indica**. Calcutta, n. 21, p. 1-74, 1933.
- JUÁREZ VALIERI, R. D.; FIORELLI, L. E.; CRUZ, E. *Quilmesaurus curriei* Coria, 2001. Su validez taxonómica y relaciones filogenéticas. In: Jornadas Argentinas de Paleontología de Vertebrados, 20, 2004, La Plata. **Resúmenes...** La Plata, 2004, p. 36-37.
- LAMANNA, M. C.; MARTINEZ, R. D.; SMITH, J. B. A definitive abelisaurid theropod dinosaur from the Early Late Cretaceous of Patagônia. **Journal of Vertebrate Paleontology**. Northbrook, v. 22, n. 1, p. 58-69, mar. 2002.
- LAVOCAT, R. Sur une portion de mandibule de théropode provenant du Crétacé supérieur de Madagascar. **Bulletin du Muséum National d'Histoire Naturelle**. Paris, série 2, n. 27, p. 3, mar. 1955
- LE LOEUFF, J.; BUFFETAUT, E.. *Tarascosaurus salluvicus* nov. gen., nov. sp., dinosaure théropode du Crétacé Supérieur du sud de la France. **Geobios**. Lyon, v. 25, n. 5, p. 585-594, jul. 1990.
- LEANZA, H. A. The Jurassic and Cretaceous terrestrial beds from Southern Neuquén Basin, Argentina. **Field Guide. Instituto Superior de Corrección Geológica, Serie Miscelânea**. Buenos Aires, v. 4, 3-30, 1999.
- LEANZA, H. A.; HUGO, C. A. Cretaceous red bed from the southern Neuquén Basin (Argentina): age, distribution and stratigraphic discontinuities. **Asociación Paleontológica Argentina. Publicación Especial**. Buenos Aires, n. 7, p. 117-112, jan. 2001.
- MEDEIROS, M. A.; SCHULTZ, C. L. A fauna dinosauriana da “Laje do coringa”, Cretáceo Médio do Nordeste do Brasil. **Arquivos do Museu Nacional**. Rio de Janeiro, v. 60, n. 3, p. 155-162, 2002.
- MARTINELLI, A. G.; FORASEPIA, M. Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Río Negro Province, Patagonia (Argentina) with description of a new sauropod (Titanosauridae) dinosaur. **Revista del Museo Argentino Ciencias Naturales “Bernardino Rivadavia”**. Buenos Aires, in press, 2004.
- MARTÍNEZ, R.; GIMÉNEZ, O.; RODRÍGUEZ, J.; BOCHATEY, G. *Xenotarsosaurus bonapartei* nov. gen. et sp. (Carnosauria, Abelisauridae), un nuevo Theropoda de la Formación Bajo Barreal, Chubut, Argentina. In: CONGRESO ARGENTINO DE PALEONTOLOGÍA Y BIOESTRATIGRAFÍA, 4, 1986. Mendoza. **Actas...** Mendoza, 1986. p. 23-31.
- NOVAS, F. E. La evolución de los dinosaurios carnívoros. In: SANZ, J. L., BUSCALIONI, S. (EDS.), **Los Dinosaurios y Su Entorno Biotico**. Actas del Segundo Curso de Paleontología en Cuenca. Instituto “Juan Valdez”, Cuenca, España, 1992. p. 126-163
- NOVAS, F. E. Abelisauridae. In: CURRIE, P. J., PADIAN, K., (EDS.), **Encyclopedia of Dinosaurs**, San Diego, Academic Press, p. 678-689, 1997.
- NOVAS, F. E.; DE VALAIS, S. Preliminary study of possible carcharodontosaurids (Dinosauria, Theropoda) from the Cerro Barcino Formation, Chubut Provincia. **Ameghiniana**. Buenos Aires, Supplement, n. 38, p. 14-15, may 2001.
- NOVAS, F. E.; MARTINEZ, R. D.; DE VALAIS, S.; AMBROSIO, A. Nuevos registros de Carcharodontosauridae (Dinosauria, Theropoda) en el Cretácico de Patagonia. **Ameghiniana**. Buenos Aires, Supplement, n. 36, p. 17, may 1999.

- NOVAS, F. E.; AGNOLIN, F. L.; BANDYOPADHYAY, S. Cretaceous theropods from India: A review of specimens described by Huene and Matley (1933). **Revista del Museo Argentino Ciencias Naturales**. Buenos Aires, v. 6, n. 1, p. 67-103, mar. 2004.
- PAGE, R., A. et al. Estratigrafía del Jurásico y Cretácico del Masizo de Somún-Curá, Provincias de Río Negro y Chubut. In: CAMINOS R. (ED.), **Geología Argentina**, Segemar Anales, Buenos Aires, 1999, p. 460-488.
- PASCUAL, R., ORTIZ JAUREGUIZAR, E., PRADO, J. L. Land Mammals: Paradigm for Cenozoic South American Geobiotic Evolution. **Münchener Geowissenschaftliche Abhandlungen**. München, v. 30, p. 265-319, mar. 1996.
- PASCUAL, R. et al. A highly derived docodont from the Patagonian Late Cretaceous: evolutionary implications for Gondwanan mammals. **Geodiversitas**. Paris, n. 22, p. 395-414, jul. 2000.
- PITMAN, W. C. III. et al. Fragmentation of Gondwana: The Separation of Africa from South America. In: GOLDBLATT, P. (ED.), **Biological Relationships between Africa and South America**. Yale University Press, New Haven and London, 1993, p. 15-34.
- RAUHUT, O. W. et al.. Dinosaur remains from the Lower Cretaceous of Crubut Group, Argentina. **Cretaceous Research**. London, n. 24, 487-497, mar. 2003.
- SALFITY, J. A., MARQUILLAS, R. A. La cuenca Cretácica-Terciaria del Norte Argentino. In: CAMINOS R. (ED.), **Geología Argentina**, Segemar Anales, Buenos Aires, 1999, p. 613-626.
- SAMPSON, S. D. et al. Predatory dinosaur remains from Madagascar: Implication for the Cretaceous Biogeography of Gondwana. **Science**. Washington, v. 280, 1048-1051, out. 1998.
- SAMPSON, S. D.; CARRANO, M. T.; FORSTER, C. A. A bizarre predatory dinosaur from the Late Cretaceous of Madagascar. **Nature**. London, n. 409, p. 504-506, apr. 2001.
- SERENO, P. C. et al. Predatory dinosaurs from the Sahara and the Late Cretaceous faunal differentiation. **Science**. Washington, n. 272, p. 986-991, jul. 1996.
- SERENO, P. C.; WILSON, J. A.; CONRAD, J. L. New dinosaurs link southern landmasses in the Mid-Cretaceous. **Proceedings Royal Society of London**. London, n. 88, p. 1-6, jan. 2004.
- STROMER, E. Wibeltier-Reste der Baharijestufe (unterstes Cenoman). 10. Ein Skelettrest von *Carcharodontosaurus* nov. gen. **Abhandlungen der bayerischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Abteilung**. München, n. 9, p. 1-23, 1915
- VICKERS RICH P. et al. "Big tooth" from the Early Cretaceous of Chubut province, Patagonia: a possible Carcharodontosaurid. **National Science Museum Monographs**. Tokyo, v. 15, p. 85-88, jul. 1999.
- VILAS-BOAS, I. et al. Dentes de *Carcharodontosaurus* (Dinosauria, Tyrannosauridae) do Cenomaniano, Bacia de Sao Luis (norte do Brasil). **Anais da Academia Brasileira de Ciências**. Rio de Janeiro, v. 71, n. 4, p. 846-847, nov. 1999.
- WILSON, J. A. et al. A new abelosaurid (Dinosauria, Theropoda) from the Lamata Formation (Cretaceous, Maastrichtian) of India. **Contribution from the Museum of Paleontology, University of Michigan**. Ann Arbor, v. 31, n. 1, p. 1-42, jan. 2003.