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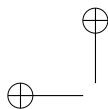
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Mesozoic dinosaurs from Brazil and their biogeographic implications

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ABSTRACT

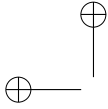
The record of dinosaur body-fossils in the Brazilian Mesozoic is restricted to the Triassic of Rio Grande do Sul and the Cretaceous of various parts of the country. This includes 21 named species, two of which were regarded as *nomen dubium*, and 19 consensually assigned to Dinosauria. Additional eight supraspecific taxa have been identified based on fragmentary specimens and numerous dinosaur footprints known in Brazil. In fact, most Brazilian specimens related to dinosaurs are composed of isolated teeth and vertebrae. Despite the increase of fieldwork during the last decade, there are still no dinosaur body-fossils of Jurassic age and the evidence of ornithischians in Brazil is very limited. Dinosaur faunas from this country are generally correlated with those from other parts of Gondwana throughout the Mesozoic. During the Late Triassic, there is a close correspondence to Argentina and other south-Pangaea areas. Mid-Cretaceous faunas of northeastern Brazil resemble those of coeval deposits of North Africa and Argentina. Southern hemisphere spinosaurids are restricted to Africa and Brazil, whereas abelisaurids are still unknown in the Early Cretaceous of the latter. Late Cretaceous dinosaur assemblages of south-central Brazil are endemic only to genus or, more conspicuously, to species level, sharing closely related taxa with Argentina, Madagascar, Indo-Pakistan and, to a lesser degree, continental Africa.

Key words: Brazil, Dinosauria, Triassic, Jurassic, Cretaceous, paleobiogeography.

INTRODUCTION

The sesquicentennial history of dinosaur research in Brazil (e.g., Allport 1860, Marsh 1869, Mawson and Woodward 1907, Huene 1942, Price 1960, 1961, Colbert 1970, Arid and Vizotto 1971, Bertini and Campos 1987, Frey and Martill 1995, Kellner and Campos 1996) is experiencing, since the last decade, its more prolific period. Taxa from a variety of dinosaur clades have been recorded in the Triassic strata of the Santa Maria and Caturrita formations (Langer et al. 2007a), the mid-Cretaceous of the Araripe and São Luís-Grajaú basins (Frey and Martill 1995, Kellner 1996a, b, 1999, Medeiros et al. 2007), and the Late Cretaceous of Baur

and Parecis groups (Franco-Rosas et al. 2004, Langer et al. 2004). Although still limited for some geological periods and taxa (Kellner and Campos 2000), Brazilian dinosaur records have yielded significant data for studies of the phylogeny and evolution of the group throughout the Mesozoic. Among several aspects of dinosaur research that are drawing attention in the last years, biogeography is particularly noticeable (Forster 1999, Moreno 1999a, Upchurch et al. 2002, Butler et al. 2004, Smith et al. 2008, Nesbitt et al. 2009). Indeed, biogeography is growing as a science (Lomolino et al. 2006, Morrone and Guerrero 2008), and much of its conceptual framework is well set. Nonetheless, as empha-



endemic range, upon which all paleobiogeographic hypotheses are erected. In this paper, we provide a reevaluation of the Brazilian dinosaur record from Triassic to Cretaceous ages based primarily on body-fossils, and discuss their relevance in the light of recent hypotheses dealing with dinosaur biogeography in the Mesozoic (Upchurch et al. 2002, Sereno et al. 2004, Krause et al. 2006, Nesbitt et al. 2009).

DINOSAUR RECORD IN THE BRAZILIAN MESOZOIC

GONDWANA II SUPERSEQUENCE (PARANÁ BASIN)

Triassic dinosaurs in Brazil were exclusively collected from rocks of the Santa Maria and the overlying Caturrita formations, in central Rio Grande do Sul (Fig. 1, Table I, II, Langer et al. 2007a). These units belong to the Rosário do Sul Group (Andreis et al. 1980), which corresponds to the Gondwana Supersequence II of the Paraná Basin (Milani 2004). Recent studies explain the origin of this Supersequence as the infilling of tectonically restricted half-graben depocenters (Milani 2001, 2004, Zerfass et al. 2003). The Santa Maria Formation is composed predominantly of red mudstones (Andreis et al. 1980, Scherer et al. 2000, Silva et al. 2003) and encompasses two distinct faunal associations of Ladinian and Carnian age (Barberena 1977, Langer et al. 2007a), as also suggested by stratigraphic studies (Zerfass et al. 2003). The Ladinian sequence represents a more humid phase within a generally seasonal and semi-arid climate. Fossil tetrapods were preserved either in lacustrine environments or in flood plains of an anastomosed fluvial system (Scherer et al. 2000, Zerfass et al. 2003). The Carnian sequence was formed in a similar environment, but the presence of aeolian deposits suggests an increased aridity (Zerfass et al. 2003). The coarser-grained, red sandstones of the Caturrita Formation represent the establishment of a perennial braided fluvial system, hinting at the return of more humid conditions (Holz and Scherer 2000, Zerfass et al. 2003). The age of this unit has been generally accepted as Norian (Rubert and Schultz 2004, Bonaparte et al. 2007, Langer et al. 2007a).

The only possible dinosaur recovered from the

(Huene 1942, Langer 2004) to *Pseudosuchia* (Galton 2000), or even *Silesauridae* (Dzik 2003). However, the specimens referred to this taxon, which include isolated vertebrae, teeth, elements of the pectoral member and pelvic girdle (Galton 2000), are too incomplete to allow their unequivocal identification as a dinosaur (Langer et al. 2010). No osteological remains from other parts of Pangaea suggest the presence of dinosaurs in the Ladinian, but possible footprints from Europe and Argentina (Haubold and Klein 2002, Marsicano and Barredo 2004, Diedrich 2009) may represent earliest dinosaurs in the fossil record. Although the attribution of several of these Triassic footprints has been disputed (King and Benton 1996), the issue is still unresolved (Melchor and de Valais 2006, Marsicano et al. 2007, Silva et al. 2008).

The Carnian witnessed the beginning of the dinosaur radiation, although taxa attributed to this clade are still rare (Langer et al. 2010, Nesbitt et al. 2009). This radiation has been studied in the light of the climatic changes registered in the end of the Triassic (Tucker and Benton 1982, Golonka and Ford 2000). In the Late Triassic strata of Rio Grande do Sul, these events are represented by an aridity increase during the Carnian (Zerfass et al. 2003), leading to the establishment of a mesoxerophytic flora dominated by the gymnosperm *Dicroidium* and concomitant faunal changing (Azevedo et al. 1990).

Herbivorous dicynodonts were the dominant primary consumers in pre-Carnian stages of the Santa Maria Formation paleoenvironment. In the Carnian-Norian, this dominance decreased with the diversification of rhynchosaurs, with a maxillomandibular apparatus specialized in crushing hard plant material (Benton 1983b), and the arising of small herbivorous/omnivorous dinosauriforms as *Saturnalia tupiniquim* Langer et al. 1999, and *Sacisaurus agudoensis* Ferigolo and Langer 2007. In addition, recent fieldwork in the Santa Maria Formation suggests the presence of larger-bodied sauropodomorphs anatomically similar to *Saturnalia* (Da Rosa et al. 2006). Secondary consumers, predominantly composed by rauisuchian taxa in the Ladinian, became more diversified in the Carnian with the arising of small-bodied

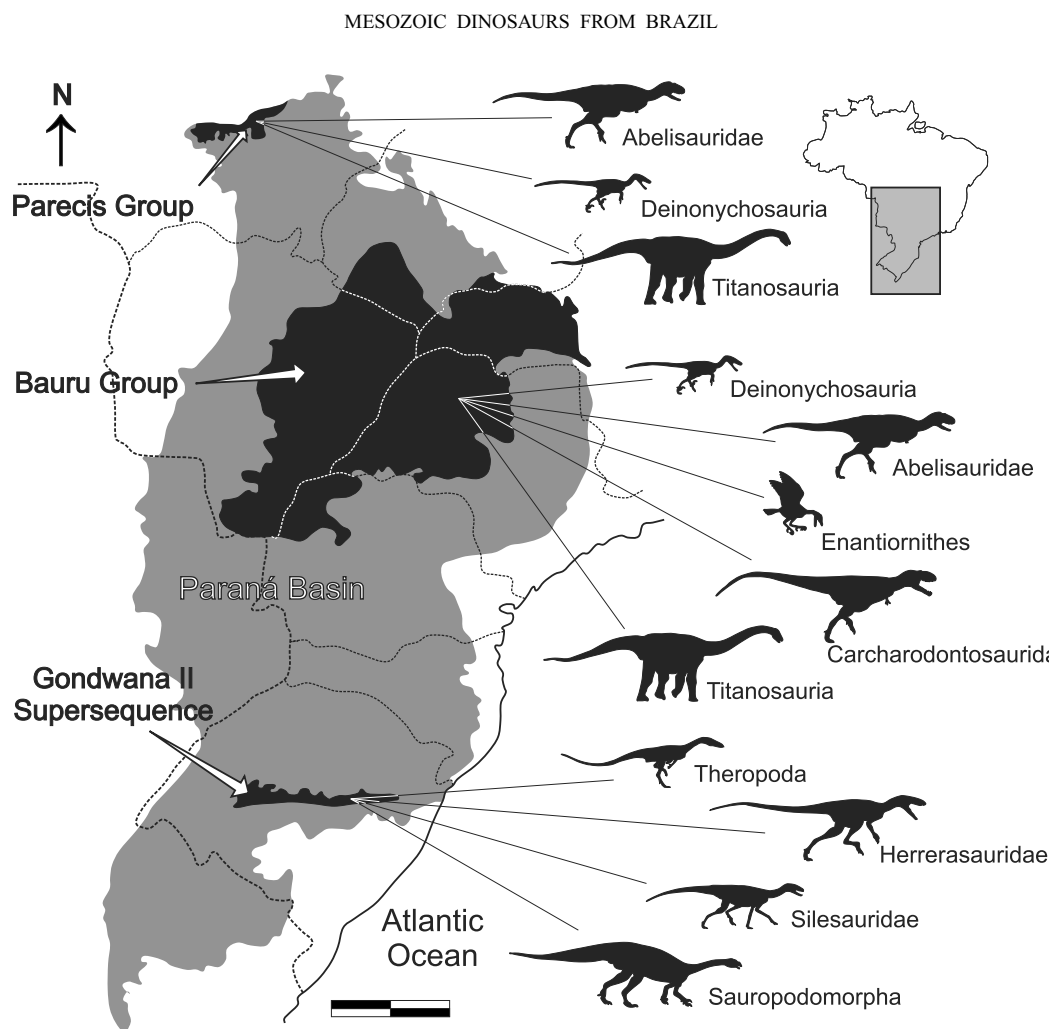
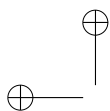
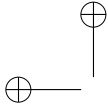


Fig. 1 – Map of south-central Brazil depicting the Paraná Basin (grey), and Gondwana II Supersequence, Bauru and Parecis groups. The dinosaur record follows Tables I-II. Modified from Silva et al. (2003) and Milani (2004). Scale = 200 km.

Novas 1992, Novas 1997, Langer 2004, Bittencourt and Kellner 2009, Alcober and Martinez 2010, Langer et al. 2010). Norian records from the Chinle Formation (Long and Murry 1995, Nesbitt et al. 2007) and Dockum Group (Nesbitt and Chatterjee 2008) have been recurrently mentioned (Irmis et al. 2007a, Nesbitt et al. 2009, 2010), but these are based on less complete material. Herrerasaurids have been preliminary reported in India (Novas et al. 2009a), but additional data is needed to fully evaluate these occurrences. Basal members of the sauropodomorph lineage are represented by *Saturnalia*

Argentina, and a possible occurrence in southern (Raath 1996, Langer et al. 1999). Some authors proposed a close relationship between these wide taxa/specimens (Ezcurra and Novas 2009, Ezcurra). If this hypothesis is confirmed, the saturnalian would represent the first sauropodomorph-related in the southern hemisphere.

From a global perspective, dinosaur diversification becomes more evident in the Norian, when sauropodomorphs and theropods are variably registered in Argentina, North America, Europe, and South Africa



sis probably represents a theropod (Fig. 2) (Bonaparte et al. 1999, Langer et al. 2007b, Bittencourt 2008), although this classification has been disputed in favor of a sauropodomorph affinity (Bonaparte et al. 2007, Ezcurra 2010), while the plateosaurid *Unaysaurus tolentinoi*, described by Leal et al. (2004), represents a South American branch of the worldwide prosauropod diversification (Fig. 2) (Buffetaut et al. 1995, Galton and Upchurch 2004a, Yates 2007a). Additional saurischian specimens recovered from the Caturrita Formation require further inquiry to allow a robust classification within any dinosaurian clade (Kischlat and Barberena 1999, Lyrio et al. 2004).

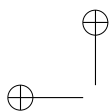
The recent discovery of two new dinosaur-related forms from the Santa Maria beds provides significant biogeographic data on the origin and early evolution of dinosaurs. Cabreira et al. (2007) announced an alleged primitive neotheropod with coelophysoid affinities from the Carnian of Santa Maria Formation based on cranial and postcranial remains. However, this specimen bears similarities with some basal sauropodomorphs (e.g., Langer et al. 1999, Martinez and Alcober 2009). The dinosauriform *Sacisaurus agudoensis* from the Caturrita Formation (Frigolo and Langer 2007) is allied with *Silesaurus opolensis* from the Carnian of Poland (Dzik 2003), in the Silesauridae. This clade encompasses other species from North America, Africa, and South America (Irmis et al. 2007a, Bittencourt and Langer 2009, Nesbitt et al. 2009, 2010, Langer et al. 2010), ranging from Anisian to Norian times. In this context, *S. agudoensis* is a late representative of the silesaurids. The phylogenetic position of this group as basal dinosauriforms is better supported by cladistic analyses (Langer 2004, Ezcurra 2006, Langer and Benton 2006, Yates 2007a, b, Irmis et al. 2007a, Nesbitt et al. 2009, 2010), although an ornithischian affinity has been suggested by many authors (Dzik and Sulej 2007, Frigolo and Langer 2007, Langer et al. 2007a, Niedzwiedzki et al. 2009). The biogeographic and biochronological implication of this conundrum is evident. If silesaurids are treated as ornithischians, the occurrence of silesaurids in Anisian strata of the African Manda Formation (Nesbitt et al. 2010) re-

tively, if silesaurids are not ornithischians, the low diversity of the latter group in comparison with saurischians in Late Triassic vertebrate assemblages remains to be satisfactorily explained. This is especially intriguing for the Carnian-Norian of south Brazil, as ornithischian taxa are known from correlated deposits of both Argentina and South Africa (Casamiquela 1967, Báez and Marsicano 2001, Irmis et al. 2007b, Butler et al. 2007).

ARARIPE BASIN

Dinosaurs from the Araripe Basin (Fig. 3, Table I, II) are restricted to the Santana Formation, which was deposited in the context of post-rift tectonic events that led to the fragmentation of Gondwana and opening of the South Atlantic Ocean (Ponte and Appi 1990, Ponte 1996, Ponte and Ponte Filho 1996). This includes the Rio da Batateira Formation, which initiates a regressive-transgressive sedimentary cycle with the deposition of fluviolacustrine sediments into the depressions formed during rifting (Ponte and Ponte Filho 1996). The overlying Santana Formation is associated with the subsequent development of an extensive lacustrine system and an eventually massive marine incursion (Maisey 1991, Arai and Coimbra 1990). This sequence ends with the regressive phase of the cycle, represented by the fluvial sandstones of the Exu Formation (Beurlen 1971, Assine 1992). The main fossil bearing localities of the Santana Formation, in the northeastern region of Brazil, are widespread along the borders of the Araripe Plateau (Kellner and Campos 1999, 2000, Kellner 2002a, Kellner et al. 2002, Viana and Neumann 2002, Martill 2007a). Several authors divide the Santana Formation into Crato, Ipubi, and Romualdo members (Beurlen 1971, Ponte and Ponte Filho 1996, Kellner and Campos 1999, 2000, Fara et al. 2005). This proposal will be followed here, although the treatment of these subunits as individual formations has also gained support in the literature (Assine 1992, Martill 1993, Martill and Wilby 1993, Neumann and Cabrera 1999, Maisey 2000, Martill 2007a, Martill and Heimhofer 2007).

The geology of the Crato Member has been recently reviewed (see Martill et al. 2007a) and only a



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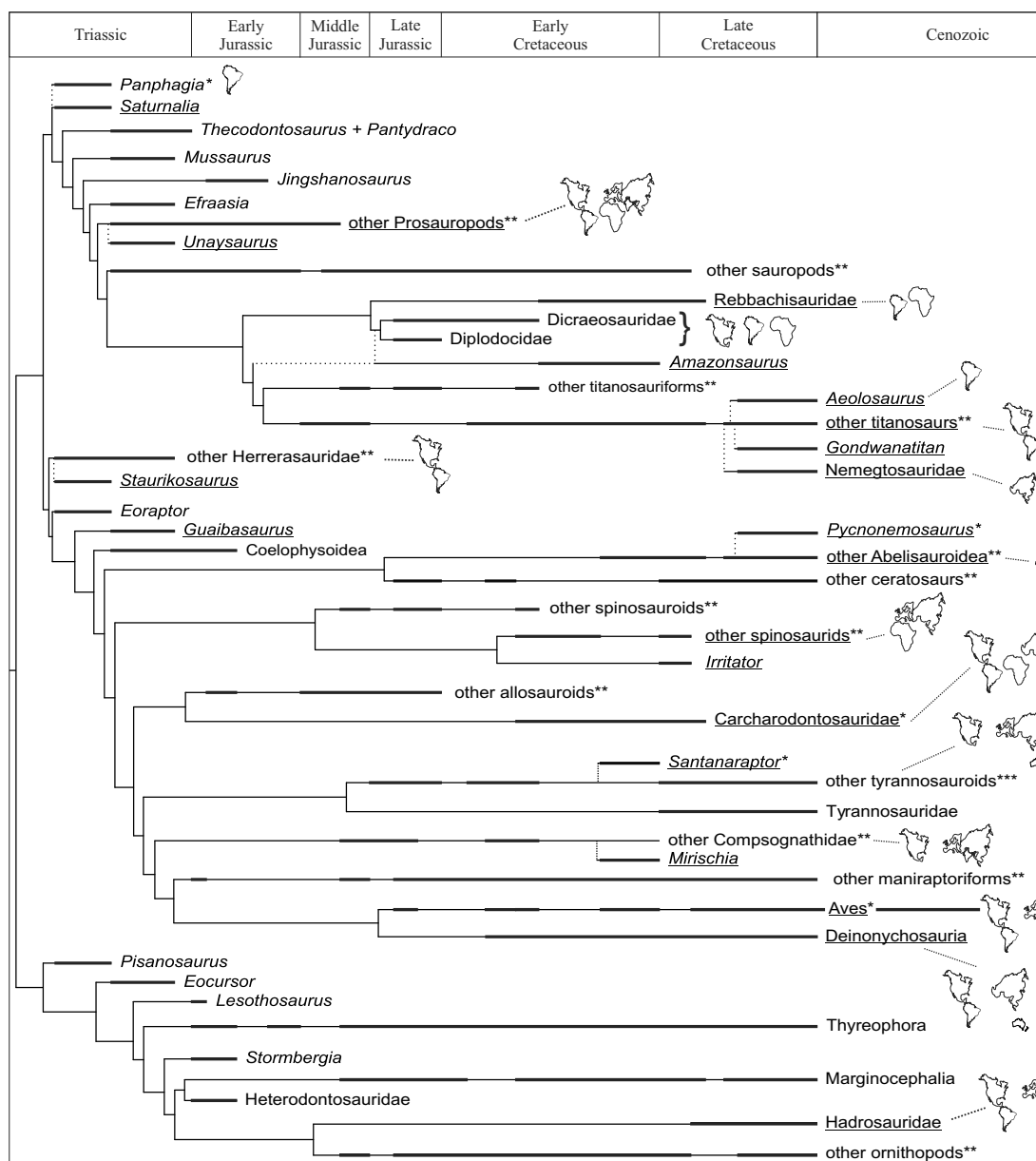


Fig. 2 – Cladogram depicting the phylogenetic relationships within dinosaurs, with emphasis on the Mesozoic record from Brazil. from Lloyd et al. (2008). Thicker lines over branches represent temporal range of the clade. Underlined names refer to taxa recorded in Brazil and maps denote the records in areas other than Brazil. (*) Taxa not present or with distinct composition in comparison with the original. (**) Paraphyletic groups. Some taxa from the original cladogram were omitted. Assemblage of supraespecific taxa followed the clade definition from TaxonSearch (Serenio et al. 2005). Maps redrawn from Turner (2004).

te and Ponte Filho 1996, Maisey 2000, Neumann et al. 2000, either fresh, brackish, or hypersaline waters.

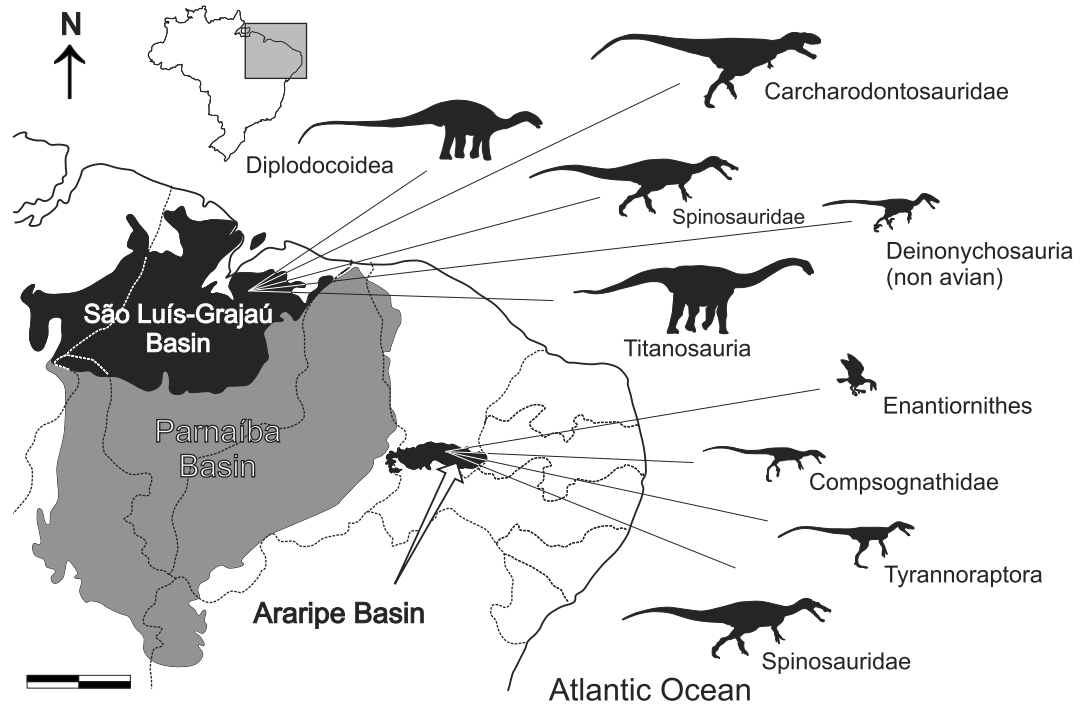
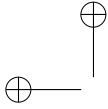
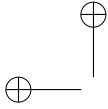


Fig. 3 – Map of northeastern Brazil depicting the Parnaíba Basin (grey), and São Luís-Grajaú and Araripe basins (black). The dinosaur record follows Tables I-II. Modified from Martill (1993), Rossetti (2001) and Santos and Carvalho (2004). Scale = 200 km.

rine environment (Maisey 1990, 1991, 2000). Due to the exquisite fossil preservation, the Crato Member is the first of two *Lagerstätten* of the Santana Formation (Kellner and Campos 1999). The Ipubi Member represents a transitional evaporitic phase (Beurlen 1971, Ponte and Ponte Filho 1996, Martill and Wilby 1993), and its fossil content, which does not include dinosaurs, is insignificant if compared to the other stratigraphic units of the Santana Formation (Kellner 1999). The Romualdo Member is mainly composed of shale and marls whose fossils are three-dimensionally preserved in calcareous nodules (Kellner and Campos 1999, 2000). Due to the high diversity, abundance and excellent preservation of the specimens, this member represents the second *Lagerstätte* of the Santana Formation (Kellner and Campos 1999, Fara et al. 2005). The sediments of this unit are Albian in age (Pons et al. 1990, but see Martill 2007b) and were deposited in a shallow brackish environment, which was formed during an episodic

event, which formed an epicontinental sea over a significant portion of north-northeastern Brazil (but see Martill 2007a). Whichever scenario is better supported by available data, the dinosaurs are land-dwelling, and can be regarded as allocthonous components of the Romualdo Member thanatocenoses (Naish et al. 2004).

All dinosaurs from the Santana Formation are theropods (Table I, II), and at least four different clades have been identified. The only mention of ornithischians (Leonardi and Borgomanero 1981) was based on a bone fragment interpreted as part of an ischium, later reidentified as a rib and tentatively assigned to a spinosaurid due to its size (Machado and Kellner 2007). Several types of feathers from the Crato Member (Martins Neto and Kellner 1988, Kellner 2002b, Kellner et al. 1994, Martill and Figueira 1994, Martill and Frey 1995) initially hint at the presence of avian taxa in the Aptian-Albian of northeastern Brazil. However, this hypothesis has been challenged by the occurrence of asymmetrical feathers



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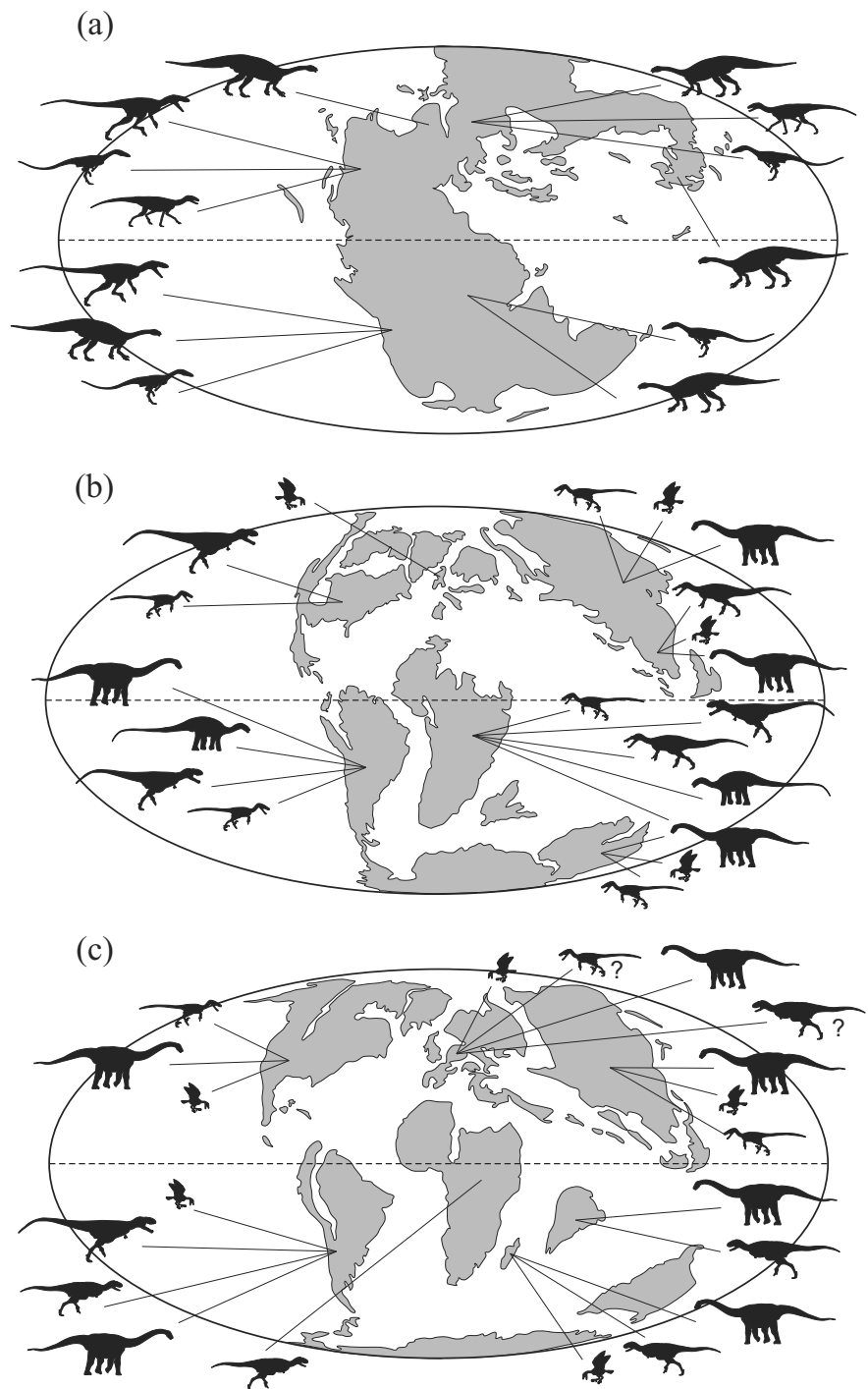
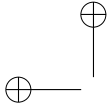
Member. One of the specimens is quite incomplete and housed in Frankfurt; the other is more complete and held in a private collection in Japan. The authors did not provide further data on the provenance of the specimens, as occur with most materials from the Santana Formation often collected without any stratigraphical control (Fara et al. 2005). Among the relevant features described by Naish et al. (2007, plates 25-26), the Frankfurt specimen bears evidence of asymmetrical feathers, while the Japan individual shows a reversed hallux. The occurrence of Aves in the Crato Formation is expected both chronostratigraphically and biogeographically, as this clade is known since the Late Jurassic and widespread in the Early Cretaceous (Fig. 2, 4b) (Padian 2004).

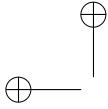
The most common theropods from the Santana Formation are the spinosaurids, with two described species and additional postcranial remains (Martill et al. 1996, Kellner and Campos 1996, Kellner 1996b, Sues et al. 2002, Bittencourt and Kellner 2004, Machado and Kellner 2005). This clade (Fig. 2) has been recorded in the Barremian of Europe (Charig and Milner 1997, Buffetaut 2007) and Early Cretaceous of Thailand and China (Buffetaut and Ingavat 1986, Buffetaut et al. 2008), but reached its greatest diversity in the Aptian-Cenomanian of northern Africa (Fig. 4b, Stromer 1915, Taquet and Russell 1998, Sereno et al. 1998, Buffetaut and Ouaja 2002, Dal Sasso et al. 2005, Smith et al. 2006), when faunistic similarities with northeastern Brazil are evident. Typical Laurasian theropod clades have been tentatively reported in the Romualdo Member of the Santana Formation. Frey and Martill (1995) referred an incomplete sacrum to *Oviraptorosauria*, a group that has also been registered in other parts of the Gondwana, as Australia (Currie et al. 1996) and Argentina (Frankfurt and Chiappe 1999). However, more recent studies contested these evidences (Makovicky and Sues 1998, Kellner 1996b, Agnolín and Martinelli 2007), and further work is needed to confirm the Gondwanan occurrence of this clade. The small-bodied *Santanaraptor placidus*, based on an incomplete postcranial skeleton not yet described in detail, was initially related to Maniraptoriformes (Kellner 1999) and later to Tyrannoraptora

are known in virtually all continents at the end of the Early Cretaceous (Rauhut 2003). Holtz (2004) related *S. placidus* to Tyrannosauroidae (Fig. 2), which is congruent with at least another Gondwanan occurrence of the group (Benson et al. 2010). The clade Comptosauridae was identified in the Santana Formation on the skeletal remains attributed to *Mirischia astutric* (Martill et al. 2000, Naish et al. 2004). Both the only Gondwanan and the youngest record of the group, otherwise known only from the Late Jurassic and Early Cretaceous of China and Europe (Zhou et al. 2003, Holtz et al. 2004, Hwang et al. 2004, et al. 2004).

SÃO LUÍS-GRAJAÚ BASIN

The São Luís-Grajaú Basin was formed by partial subsidence of the former Parnaíba Basin (Fig. 3), followed by the uplift of the Ximbioá Arc during the opening of the South Atlantic Ocean, in an area corresponding to the north of the Maranhão State (Góes and Rossetti 2004, Santos and Carvalho 2004). The dinosaurs from this region (Carvalho et al. 2003, Medeiros et al. 2007) were all recovered from rocks of the Itapecuru Group, including the lacustrine deposits of the Codó Formation and the aeolian sandstones of the Grajaú Formation, both of Aptian age (Rossetti et al. 2001a). According to Lacerda et al. (2001), but see also Rossetti and Truckenbrodt (2001) and Santos and Carvalho (2004), the Itapecuru Group is divided in three stratigraphic units: a) the Albiense, b) the “Undifferentiated Unit”, represented by several lithologies with complex and diverse lithology associated with marine, lacustrine, and floodplain environments; c) the Alcântara Formation, composed of stratified sandstones, mudstones, and limestones deposited during the Cenomanian in an estuarine environment; d) the Itapecuru Formation whose age ranges from the Late Cretaceous to Paleocene, and devoid of dinosaur records. Frey et al. (2001b) suggested a dry, warm climate during the deposition of the “Undifferentiated Unit”, while the Alcântara Formation is associated with an increasingly humid, but still seasonal semi-arid climate. The so-called “Itapecuru Formation” which crops out





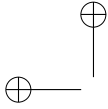
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2001a, Santos and Carvalho 2004). The most important fossil localities with dinosaur remains of the São Luís-Grajaú Basin are: Coroatá and Mata (“Undifferentiated Unit”/“Itapecuru Formation”: Carvalho et al. 2003, Ribeiro et al. 2003, Castro et al. 2007) and Ilha do Cajual and Praia da Baronesa (Alcântara Formation: Elias et al. 2007, Medeiros et al. 2007).

The Itapecuru Group dinosaur fauna (Fig. 3, Table I, II) based on skeletal remains includes specimens attributed to Sauropoda and Theropoda (Carvalho et al. 2003, Medeiros et al. 2007), and a possible ornithischian record (Avilla et al. 2003). Carvalho and Pedrão (2000) have recorded theropod and ornithischians footprints. The fossil preservation is, however, not exceptional, hampering their identification. Among theropods, several genera from North Africa as *Carcharodontosaurus*, *Sigilmassasaurus* (Serenó et al. 1996, Novas et al. 2005a, 2006, Brusatte and Sereno 2007), and *Spinosaurus* have been reported based on isolated vertebrae and teeth (Vilas Bôas et al. 1999, Medeiros 2006, Medeiros and Schultz 2001, 2002, Medeiros et al. 2007, Ribeiro et al. 2003). Yet, the diagnoses of these taxa include anatomical details not available in the Itapecuru Group material, and they are here treated only as indeterminate Carcharodontosauridae and Spinosauridae (Table I, II). Additionally, the record (Medeiros and Schultz 2002, p. 156) of “*Baharijasaurus*” [sic] (= *Bahariasaurus* Stromer 1934), a possible carcharodontosaurid from North Africa (Rauhut 1995, Holtz et al. 2004), is also uncertain and here referred to as an indeterminate theropod. Carcharodontosauridae and Spinosauridae specimens are known from both the “Undifferentiated Unit” and the Alcântara Formation, the latter also yielding a new spinosaurid (see Kellner et al. 2011), increasing to 19 the number of dinosauriform species from Brazil consensually assigned to Dinosauria. These records are congruent with the already mentioned abundance of spinosaurids in the Cenomanian of North Africa (Fig. 2, 4b) (Russell 1996, Sereno et al. 1998, Dal Sasso et al. 2005, Smith et al. 2006). Carcharodontosaurids are also common in the Aptian to Cenomanian of Africa and South America (Holtz et al. 2004, Sereno et al. 2004,

Further isolated teeth from the Itapecuru were referred to Velociraptorinae (Elias et al. 2007), a maniraptoran group of disputed taxonomic value within Dromaeosauridae (Makovicky et al. 2006) recorded in the Early Cretaceous of North America and Late Cretaceous of Eurasia (Norell and Makovicky 2004). In this work, we consider all Brazilian records of Velociraptorinae (see below: Bauru Supersequence as indeterminate Deinonychosauria (Table I, II), plus new findings that would allow a more accurate identification of these specimens. In Gondwana, dromaeosaurid deinonychosaurs are known based on several specimens from the Cenomanian-Maastrichtian of Argentina (Novas and Puerta 1997, Novas and Pol 2005, Calvo 2004, Makovicky et al. 2005, Novas et al. 2009b) and possible records in the Cenomanian of central Argentina (Rauhut and Werner 1995) and Albian of Argentina (Fig. 4b) (Currie et al. 1996).

The sauropod fauna of the Itapecuru Group (Tables I, II) includes Diplodocoidea and Titanosauria as well as specimens of uncertain affinities (e.g., “*trodon*”, Medeiros and Schultz 2001, Medeiros et al. 2007). Diplodocoids are represented by *Amazonasaurus maranhensis* (Carvalho et al. 2003) and indeterminate remains (Castro et al. 2007) recovered from the “Undifferentiated Unit” (“Itapecuru Formation”). Some authors regarded *A. maranhensis* as a basal macronarian (e.g., Sereno et al. 2005, Lloyd et al. 2008), but most phylogenetic studies refer this species to as diplodocoid (Salgado et al. 2004). This taxon is both geographically and chronologically widespread, with coeval records in Argentina and North America (Figs. 2, 4b) (Upchurch et al. 2004, Wilson 2005). Several isolated specimens have been regarded as Rebbachisauridae (Medeiros and Schultz 2001, 2004, Medeiros et al. 2007), a group with an abundant record in Aptian-Coniacian deposits of Argentina and North Africa (Upchurch et al. 2000, Lina and Apesteguía, 2005), but also from older strata in Europe (Serenó and Wilson 2005, Sereno et al. 2006, Mannion 2009) and possibly South Africa (Figs. 2, 4b) (Canudo and Salgado 2003). According to Medeiros and Schultz (2004), some specimens from the



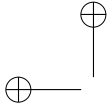
et al. 1999, Upchurch et al. 2004), and with the better known *Rayososaurus tessonei*. The latter has been referred to *Limaysaurus* by Salgado et al. (2004) and recorded in the Aptian-Cenomanian of Argentina (Calvo and Salgado 1995). Among Titanosauria, a group better discussed in the next section, indeterminate fragments were recovered from both the “Undifferentiated Unit” (Castro et al. 2007) and the Alcântara Formation, i.e., *?Aegyptosaurus*, *?Malawisaurus*, and “Titanosauridae” (Medeiros and Schultz 2001, Medeiros et al. 2007). Medeiros and Schultz (2002) also mentioned the presence of andesaurid remains in the Alcântara Formation. This poorly known and probably paraphyletic group has been described from the Cretaceous of Argentina (Bonaparte and Coria 1993, Salgado et al. 1997) with possible records in the Albion of North Africa (Russell 1996).

BAURU AND PARECIS GROUPS

The Cretaceous of the Bauru Group (*sensu* Soares et al. 1980) has so far provided the most significant record of Brazilian dinosaurs (Kellner and Campos 2000). Its strata are also referred to as Bauru Supersequence (Fig. 1, *sensu* Milani 2001) and were formed in an extensive subsidence area created by the lithostatic load of the Early Cretaceous basalts of the Serra Geral Formation, upon which the Bauru beds are discordantly deposited (Fulfaró and Perinotto 1996, Fernandes and Coimbra 2000, Milani 2004). Concentrated in the central-northern portion of the Paraná Basin, depocenter of the preceding massive basalt flood (Zalán et al. 1990), the main body of the Bauru Supersequence ranges from São Paulo and western Minas Gerais to northwestern Paraná, eastern Mato Grosso do Sul and southern Goiás (Fig. 1). Some authors consider that the Bauru beds were deposited in a differentiated tectonic context (i.e., the Bauru Basin, see Fulfaró and Perinotto 1996, Fernandes and Coimbra 2000, Fernandes 2004), but we follow the more traditional view, which includes the Bauru strata within the Paraná Basin (Baptista et al. 1984, Soares et al. 1980, Mezzalana 1981, Milani 2004).

The Bauru dinosaurs (Table I, II) are commonly found in localities of western São Paulo and Minas

stratigraphic units have been split in several smaller units (Fernandes and Coimbra 2000, Fernandes 2004), but the traditional nomenclature of Soares et al. (1980) is still largely used in paleontological studies. This occurs mainly because of the problem of referring earlier fossil findings to the new units of more elaborated stratigraphic frameworks. In an attempt to fully exploit the biogeographic data, we will again follow this traditional interpretation. The age of the Adamantina Formation as Campanian-Maastrichtian (Gobbo-Rodrigues et al. 1999, Santucci and Bertini 2001) has been challenged by Dias-Brito et al. (2001) who proposed an older (i.e., Turonian-Santonian) age for this unit. However, we agree with Gobbo-Rodrigues et al. (2003) that the concomitant occurrence of microfossils typical of Aptian-Cenomanian and Campanian-Maastrichtian intervals (Dias-Brito et al. 2001, p. 278) are not conclusive evidence for ascribing an intermediate age for the Adamantina Formation. However, it should be noted that this stratigraphical unit originated from different depositional cycles, as suggested by its division into superposed smaller units (Fernandes and Coimbra 2000). In addition, some dinosaur records that indicate a younger age for the Adamantina Formation (R.M. Santucci unpublished data) apparently comes from upper cycles (Localities L2 and L26 of Dias-Brito et al. 2001), suggesting that the Adamantina Formation congregates rocks of significantly different ages, with still poorly sampled individual biotas. The geological setting of this stratigraphic unit encompasses aeolian, lacustrine, and fluvial, i.e. braided meandering rivers, deposits (Fernandes 2004). Current data support a warm, seasonal, and arid to semi-arid climate with more humid periods (Goldberg and Garcia 2000, Dias-Brito et al. 2001). According to Goldberg and Garcia (2000), the arid conditions increased towards the top of the Bauru Group, represented by the Marília Formation. This unit is divided into the Serra da Galga, Ponte Alta, and Echapora members, composed of alluvial fans associated with braided canals and subordinated levels of aeolian sediments and calcrete (Fernandes and Coimbra 2000). The age of the Marília Formation is generally accepted as



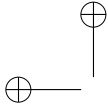
MESOZOIC DINOSAURS FROM BRAZIL

the Paraná Basin crop out in the state of Mato Grosso (Fig. 1). Their strata have been referred to the Cambambe Formation (sensu Weska et al. 1996), which was deposited in a fluviolacustrine system associated to distal parts of alluvial fans under a semi-arid to extremely arid climate (Rosa et al. 1991, Weska 2006). This unit has been traditionally referred to the Bauru Group (Franco-Rosas et al. 2004, Lacerda Filho et al. 2004), but recent work suggests that all Cretaceous rocks deposited south of the Paraguai fold belt (Almeida 1984) in Mato Grosso should be included in the Parecis Group (Weska 2006). These deposits accumulated on a crust depression formed by tectonic distension events related to the magmatic plume of Trindade (Weska 2006). The basalts of the Paredão Grande Formation, at the base of the Parecis Group, were dated 83.9 ± 0.4 Ma (Gibson et al. 1997), i.e. Late Santonian (Gradstein and Ogg 2004). This geophysical and other paleontological evidence (Franco-Rosas et al. 2004) suggest a Campanian-Maastrichtian age for the dinosaur fauna of the Parecis Group.

Most dinosaur specimens collected from the Cretaceous of the Paraná Basin (Table II) are isolated teeth and vertebrae (Bertini et al. 1993, Santucci and Bertini 2001, Kellner and Campos 2000, Franco-Rosas 2001, Candeiro et al. 2006a, b), while dinosaur eggs were also recorded in western Minas Gerais (‘Triângulo Mineiro’ region, Ribeiro 1999, Gobbo-Rodrigues et al. 2005). The majority of these were attributed to Titanosauria (Candeiro et al. 2006a), including those referred to the controversial group “Titanosauridae” (see Salgado et al. 1997, Wilson and Upchurch 2003, Curry Rogers 2005). In the present work, these fragmentary records are all referred to indeterminate Titanosauria. In general, titanosaur species from the Brazilian Cretaceous (Table I, II), i.e. *Adamantisaurus mezzalirai*, *Baurutitan brittoi*, *Trigonosaurus pricei*, *Gondwanatitan faustoi*, *Maxakalisaurus topai*, and *Uberabatitan ribeiroi*, have rarely been analyzed in a phylogenetic context. The most complete study is the doctorate thesis of R.M. Santucci (unpublished data), in which the former three taxa cited above are positioned in the base of a clade that also includes *Aeolosaurus*, *Gondwanatitan*, *Argentinosaurus*,

validity of this taxon was contested by Wilson and Upchurch (2003), demanding a revision of this material. A significant occurrence is that of the clade Aeolosauridae (Franco-Rosas et al. 2004). Specimens of this clade are referred to as *Aeolosaurus* and *Gondwanatitan*. They were recovered in the Adamantina Formation of São Paulo (Monte Alto and Álvares Machado areas, Bertini et al. 1999a, Kellner and Azevedo 1999) and Minas Gerais (Prata region, Candeiro et al. 2006b); in the Serra da Galga Member in western Minas Gerais (Bertini et al. 1999b); and in the Cambambe Formation of Mato Grosso (Franco-Rosas et al. 2004). These records allow the correlation with Campanian-Maastrichtian aeolosaur-bearing strata of Argentina (e.g., La Buita Colorada, Allen, Los Alamitos and Bajo formations, see Casal et al. 2007). Another record is a partial skeleton referred to Nemegtosaurus from the Adamantina Formation, in the area of Prudente (Avilla et al. 2005). This clade has been previously recorded only in the Campanian-Maastrichtian of Mongolia (Upchurch 1995, 1999) and is alternatively classified within Diplodocoidea (Upchurch 2004) or Titanosauria (Wilson 2005).

The theropod record in the Cretaceous of the Paraná Basin (Table I, II) encompasses a number of isolated teeth attributed to Abelisauridae (Bittencourt 2002, Kellner 2002, Candeiro et al. 2002, 2004, 2006), Carcharodontosauridae (Silva and Kellner 1999, Candeiro et al. 2006a), and Deinonychosauria (Bertini et al. 1997, Bertini and Franco-Rosas 2001, Franco-Rosas 2001, 2002). Among these, only the first has skeletal evidence, i.e., the partial skeleton of *Pyrocladon nevesi* (Kellner and Campos, 2002), a tibia fragment described by Bertini (1996), and a partial remains (vertebra, femur and phalanges) described by Novas et al. (2008). Other theropod skeletal remains include a scapula (Machado et al. 2008) and an ulna and phalanx (Novas et al. 2005b) attributed to Maniraptoriformes and still undescribed Enanthiornithes remains (Almeida and Nava 2005). Once proposed spinosaurid occurrences in the Bauru Group were not confirmed (Candeiro et al. 2006a). The abelisauroid fauna of the



Smith and Lamanna 2006, Malkani 2006, Krause et al. 2007, Canale et al. 2009), and alleged European records (Fig. 4c) (Le Loeuff and Buffetaut 1991, Carrano and Sampson 2002, Carrano et al. 2002). Late Cretaceous *Enanthiornithes* (Chiappe and Walker 2002) are widespread (Fig. 4c) in both Laurasia (North America, Eurasia) and Gondwana (South America and Madagascar). Campanian-Maastrichtian occurrences of carcharodontosaurids based on isolated teeth from both Argentinean and Brazilian strata (Martinelli and Forasiepi 2004, Candei-ro et al. 2006a) have been considered dubious by some authors (Canale et al. 2009). However, a preliminary report (Porfiri et al. 2008) of a post-cranial skeleton from the Late Cretaceous of Neuquén Group, Argentina, confirms the presence of post-Cenomanian carcharodontosaurids in Gondwana. Contrasting with the diversified record of Laurasian deinonychosaurs (Norell and Makovicky 2004, Makovicky and Norell 2004), South American occurrences other than isolated teeth from Brazil include a few species from the Late Cretaceous of Argentina (Novas et al. 2008).

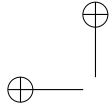
DISCUSSION

Paleogeographic reconstructions of the Middle-Late Triassic depict Pangaea as a nearly continuous supercontinent (Fig. 4a, Scalera 2001, Scotese 2002). In this scenario, dispersal would not be hampered by oceanic barriers (Shubin and Sues 1991, Langer et al. 2010), although large-scale provincialism may result from the establishment of geologic barriers (Coney 1982). Indeed, terrestrial faunal endemism is not conspicuous across Pangaea in the Late Triassic (Benton 1993, Lucas 1998, Langer 2005a), and it is widely known that the tetrapod fauna of the Gondwana II Supersequence is correlated with those from Argentina, India, and southern Africa (Bonaparte 1969, 1973, 1982, Sill 1969, Barberena et al. 1985, Scherer et al. 1995, Lucas 1998, Ray and Chinsamy 2002, Langer 2005b, Kuttu et al. 2007), sharing more inclusive but closely related taxa also with Europe and North America (Heckert and Lucas 1998, Langer 2005a).

Much has been argued on the record of the oldest

2004, Langer et al. 2010). Nesbitt et al. (2009) recently analyzed the premise of a South American protocontinent as the ancestral range for dinosaurs. Using distinct methodologies (Ronquist 1997, Ree and Smith 2008), this was the first objective study to test and corroborate the above mentioned hypothesis. The dataset of Nesbitt et al. (2009) lacks some dinosauriforms from Carnian strata of south Gondwana, as *Guaibasaurus* and *Panphagia*, but the inclusion of them probably would reinforce their conclusions (Fig. 2). However, as discussed by several authors (Parker et al. 2005, Nesbitt et al. 2009, Langer et al. 2010), the South American origin hypothesis may be biased by the worldwide record of Ladinian-Carnian terrestrial vertebrates, which mainly encompasses localities from Argentina and Brazil (Rogers et al. 1993, Langer 2005a, b, Langer et al. 2007a). Accordingly, both relative diversity and abundance of basal dinosaurs across Pangaea are probably underestimated.

The distribution patterns of post-Carnian dinosaur faunas across Pangaea, including Laurasia (e.g., Rauhut and Hungerbühler 1998, Irmis 2005, Nesbitt et al. 2007), and their driven biogeographic processes, also remain elusive (Nesbitt et al. 2009), as the detection of vicariance or dispersal depends on distribution data for a well-sampled set of taxa. This is the case of the possible Norian herrerasaurids from North America, which are younger than South American members of this clade. The alleged coeval record of the group in South Africa (Galton 1985) has been refuted (Galton and Van Heerden 1998, Langer 2004, Yates 2007a). Thus, the unambiguous record of herrerasaurid suggests that this clade is restricted to western Pangaea, regardless their phylogenetic position within dinosaurs. Some records from India (Novas et al. 2009a), if confirmed, may expand the known distribution of this clade across south Pangaea. The recent reclassification of the herrerasaurids as basal theropods (Fig. 2, Nesbitt et al. 2009) overcomes the ghost-lineage problem of Theropoda, since sauropodomorphs are recorded since Carnian (Langer et al. 1999, Martinez and Alcober 2009). However, the phylogeny of basal Saurischia is far from consensual (Langer et al. 2010).



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TABLE I
List of Mesozoic dinosauriform taxa recorded in Brazil indented by taxonomic hierarchy.

Archosauria <i>sensu</i> Gauthier 1986	Theropoda <i>sensu</i> Gauthier 1986
cf. Dinosauria	<i>Guaibasaurus candelariensis</i>
<i>Spondylosoma absconditum</i>	Theropoda indet.
Dinosauriformes <i>sensu</i> Sereno and Arcucci 1994	Abelisauridae Bonaparte and Novas 1985
Silesauridae Langer et al. 2010	<i>Pycnonemosaurus nevesi</i>
<i>Sacisaurus agudoensis</i>	Abelisauridae indet.
Dinosauria <i>sensu</i> Padian and May 1993	Tetanurae Gauthier 1986
<i>Teyuwasu barberenai</i>	Tetanurae indet.
Dinosauria indet.	Spinosauridae <i>sensu</i> Sereno et al. 1998
Ornithischia <i>sensu</i> Butler et al. 2008	<i>Angaturama limai</i>
cf. Hadrosauridae	<i>Irritator challengeri</i>
Saurischia <i>sensu</i> Langer 2004	Spinosauridae indet.
cf. Saurischia	Carcharodontosauridae <i>sensu</i> Sereno et al. 1998
Herrerasauridae <i>sensu</i> Langer 2004	Carcharodontosauridae indet.
<i>Staurikosaurus pricei</i>	Coelurosauria <i>sensu</i> Gauthier 1986
Eusaurischia <i>sensu</i> Padian et al. 1999	Compsognathidae <i>sensu</i> Holtz et al. 2004
<i>Saturnalia tupiniquim</i>	<i>Mirischia asymmetrica</i>
Sauropodomorpha <i>sensu</i> Langer 2003	Tyrannoraptora Sereno 1999b
<i>Unaysaurus toletinoi</i>	<i>Santanaraptor placidus</i>
Sauropoda <i>sensu</i> Yates 2007a	Maniraptora Gauthier 1986
Sauropoda indet.	Maniraptora indet.
Nemegtosauridae Upchurch 1995	cf. Aves
Nemegtosauridae indet.	Deinonychosauria <i>sensu</i> Gauthier 1986
Diplodocoidea <i>sensu</i> Wilson 2002	cf. Troodontidae
<i>Amazonsaurus maranhensis</i>	cf. Dromaeosauridae
<i>Rayososaurus</i> sp.	cf. Velociraptorinae
Diplodocoidea indet.	Aves <i>sensu</i> Padian and Chiappe 1998
Titanosauria <i>sensu</i> Upchurch et al. 2004	Aves indet.
<i>“Antarctosaurus” brasiliensis</i>	Enantiornithes indet.
<i>Adamantisaurus mezzalirai</i>	
<i>Baurutitan brittoi</i>	
<i>Maxakalisaurus topai</i>	
Titanosaurus sp.	
<i>Trigonosaurus pricei</i>	
<i>Uberabatitan ribeiroi</i>	
Titanosauria indet.	
Andesauridae indet.	
Aeolosaurini Franco-Rosas et al. 2004	
<i>Aeolosaurus</i> sp.	
<i>Gondwanatitan faustoi</i>	

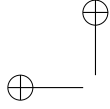
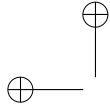


TABLE II
Summary of the osteological record of Mesozoic dinosauriforms in Brazil. Abbreviations: Gr. = Group, Fm. = Formation, Mb. = Member.

Taxon	Material	Horizon	Location	Age	References
cf. Dinosauria	Isolated vertebrae	Recôncavo Basin	Bahia (East)	Cretaceous	Marsh (1869), Mawson and Woodward (1907)
	Partial skeleton	Santa Maria Fm.	Rio Grande do Sul	Carnian-Norian	Cabreira et al. (2007), Langer et al. (2007a)
<i>Spondylosoma absconditum</i>	Partial skeleton	Santa Maria Fm.	Rio Grande do Sul	Ladinian	Huene (1942), Galton (2000), Langer (2004)
<i>Sacisaurus agudoensis</i>	Isolated remains	Caturrita Fm.	Rio Grande do Sul	Norian	Ferigolo and Langer (2007)
<i>Teyuwasi barberenai</i>	Femur and tibia	Santa Maria Fm.	Rio Grande do Sul	Carnian	Kischlat (1999), Langer (2004)
Dinosauria indet.	Partial pelvis/ vertebrae	Caturrita Fm.	Rio Grande do Sul	Norian	Kischlat and Barberena (1999)
cf. Hadrosauridae	Caudal vertebra	Iapecuru Fm.	Maranhão (North)	Aptian-Albian	Avilla et al. (2003)
cf. Saurischia	Partial postcranium	Caturrita Fm.	Rio Grande do Sul	Norian	Beltrão (1965), Lyrio et al. (2004)
<i>Staurikosaurus pricei</i>	Partial skeleton	Santa Maria Fm.	Rio Grande do Sul	Carnian	Colbert (1970), Galton (1977), Bittencourt and Kellner (2009)
Theropoda indet.	Partial tibia	Alcântara Fm.	Maranhão (North)	Early Cenomanian	Van Tomme et al. (2008)
	Partial sacrum	Santana Fm. (Romualdo Mb.)	Chapada do Araripe	Albian	Frey and Martill (1995)
	Partial vertebra	Santana Fm. (Romualdo Mb.)	Chapada do Araripe	Albian	Campos (1985), Kellner and Campos (2000)
	Isolated teeth	Iapecuru Fm.	Maranhão (North)	Aptian-Albian	Ferreira et al. (1992), Carvalho et al. (2003)
		Alcântara Fm.	Maranhão (North)	Early Cenomanian	Medeiros et al. (2007)
		Parecis Gr.	Mato Grosso (South)	Late Cretaceous	Azevedo et al. (1995), Kellner and Campos (2002), Kellner et al. (2004)
		Adamantina Fm.	São Paulo (West)	Campanian-Maastrichtian	Bertini et al. (1993), Candeiro et al. (2002, 2004, 2006a), Azevedo et al. (2007a)
<i>Guaibasaurus candelariensis</i>	Three partial skeletons	Adamantina Fm.	Triângulo Mineiro	Campanian-Maastrichtian	R. Candeiro (unpublished data)
<i>Pycnonemosaurus nevesi</i>	Partial post- cranium/teeth	Marília Fm.	Triângulo Mineiro	Maastrichtian	Kellner (1996b), Candeiro et al. (2004)
	Premaxilla with teeth	Alter do Chão Fm.	Amazonas	Late Cretaceous	Price (1960)
	Postcranial remains	Caturrita Fm.	Rio Grande do Sul	Norian	Bonaparte et al. (1999, 2007), Langer et al. (2007b)
Abelisauridae indet.	Isolated teeth	Parecis Group	Mato Grosso	Campanian-Maastrichtian	Bittencourt and Kellner (2002), Kellner and Campos (2002)
	Isolated teeth	Adamantina Fm.	São Paulo (West)	Campanian-Maastrichtian	Bertini (1996), Bertini et al. (2003)
		Marília Fm.	Triângulo Mineiro	Maastrichtian	Novas et al. (2008)
		Adamantina Fm.	São Paulo (West)	Campanian-Maastrichtian	Candeiro et al. (2002, 2004, 2006a)
		Marília Fm.	Triângulo Mineiro	Maastrichtian	Candeiro et al. (2006b)
			Triângulo Mineiro	Maastrichtian	Candeiro et al. (2004, 2006a)



MESOZOIC DINOSAURS FROM BRAZIL

TABLE II (continuation)

Taxon	Material	Horizon	Location	Age	References	
<i>Angaturama limai</i>	Partial rostrum	Santana Fm. (Romualdo Mb.)	Chapada do Araripe	Albian	Kellner and Campos (1996), Kellner (1996b)	
<i>Irritator challengeri</i>	Partial skull	Santana Fm. (Romualdo Mb.)	Chapada do Araripe	Albian	Martill et al. (1996), Kellner (1996b), Sues et al. (2002)	
	Partial postcranium	Santana Fm. (Romualdo Mb.)	Chapada do Araripe	Albian	Campos and Kellner (1991), Kellner (2001), Machado and Kellner (2005)	
	Sacral/ caudal vertebrae	Santana Fm. (Romualdo Mb.)	Chapada do Araripe	Albian	Kellner and Campos (1999), Bittencourt and Kellner (2004)	
		Santana Fm. (Romualdo Mb.)	Chapada do Araripe	Albian	Leonardi and Borgomanero (1981), Machado and Kellner (2007)	
	Spinosauridae indet.	Partial rib	Santana Fm. (Romualdo Mb.)	Chapada do Araripe	Albian	Machado et al. (2009), Kellner et al. (2011)
Partial rostrum		Alcântara Fm.	Maranhão (North)	Early Cenomanian	Ribeiro et al. (2003)	
Isolated teeth		Itapecuru Gr. (Unid. Indif.)	Maranhão (North)	Albian	Medeiros and Schultz (2002), Medeiros (2006)	
		Alcântara Fm.	Maranhão (North)	Early Cenomanian	Medeiros and Schultz (2002), Medeiros et al. (2007)	
Carcharodontosauridae indet.		Caudal vertebrae	Alcântara Fm.	Maranhão (North)	Early Cenomanian	Ribeiro et al. (2003)
	Isolated teeth	Itapecuru Gr. (Unid. Indif.)	Maranhão (North)	Albian	Vilas Boas et al. (1999), Medeiros and Schultz (2002), Medeiros et al. (2007)	
		Alcântara Fm.	Maranhão (North)	Early Cenomanian	Candeiro et al. (2006b)	
		Adamantina Fm.	Triângulo Mineiro	Campanian-Maastrichtian	Silva and Kellner (1999), Candeiro et al. (2002, 2004, 2006a)	
		Adamantina Fm.	São Paulo (West)	Campanian-Maastrichtian	Silva and Kellner (1999), Candeiro et al. (2004)	
		Marília Fm.	Triângulo Mineiro	Maastrichtian	Martill et al. (2000), Naish et al. (2004)	
	<i>Mirischia asymmetrica</i>	Partial postcranium	Santana Fm. (Romualdo Mb.)	Chapada do Araripe	Albian	Kellner (1999, 2001)
	<i>Santanaraptor placidus</i>	Partial postcranium	Santana Fm. (Romualdo Mb.)	Chapada do Araripe	Albian	Novas et al. (2005b)
Maniraptora indet.	Manual ungual phalanx	Marília Fm.	São Paulo (West)	Maastrichtian	Machado et al. (2008)	
	Scapula	Marília Fm.	São Paulo (West)	Maastrichtian	Bertini et al. (1997), Bertini and Franco-Rosas (2001)	
Deinonychosauria (cf. Troodontidae, Dromaeosauridae and	Isolated teeth	Bauri Gr.	São Paulo (West)	Campanian-Maastrichtian	Bertini and Franco-Rosas (2001), Franco-Rosas (2002)	
			Triângulo Mineiro	Campanian-Maastrichtian	Franco-Rosas (2001)	

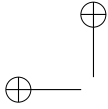
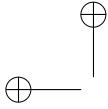


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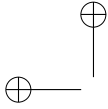
Taxon	Material	Horizon	Location	Age	References
cf. Aves	Feathers (various types)	Santana Fm. (Crato Mb.)	Chapada do Araripe	Aptian-Albian	Martins Neto and Kellner (1988), Martill and Frey (1995), Kellner (2002b)
	Carpal(?) and feather	Santana Fm. (Crato Mb.)	Chapada do Araripe	Aptian-Albian	Naish et al. (2007)
	Phalanx	Adamantina Fm.	São Paulo (West)	Campanian-Maastrichtian	Azevedo et al. (2007a)
Enantiornithes indet.	Partial skeletons	Adamantina Fm.	São Paulo (West)	Campanian-Maastrichtian	Alvarenga and Nava (2005)
	Partial skeleton	Santana Fm. (Crato Mb.)	Chapada do Araripe	Aptian-Albian	Naish et al. (2007)
	Partial postcranium	Santa Maria Fm.	Rio grande do Sul	Camian	Da Rosa et al. (2006)
Sauropodomorpha indet.	Three partial skeletons	Santa Maria Fm.	Rio Grande do Sul	Camian	Langer et al. (1999, 2007c), Langer (2003)
<i>Saurnalia tupiniquim</i>	Partial skeleton	Caturrita Fm.	Rio Grande do Sul	Norian	Leal et al. (2004)
<i>Unaysaurus toletinoi</i>	Teeth	Alcântara Fm.	Maranhão (North)	Early Cenomanian	Freire et al. (2007), Medeiros et al. (2007)
Sauropoda indet.	Vertebra	Alcântara Fm.	Maranhão (North)	Early Cenomanian	Medeiros and Schultz (2002), Medeiros et al. (2007)
	Osteoderms	Adamantina Fm.	São Paulo (West)	Campanian-Maastrichtian	Bergqvist et al. (2002)
	Vertebrae and humerus	Iapecuru Gr. (Unid. Indif.)	Maranhão (North)	Albian	Castro et al. (2007)
Titanosauria indet.	Vertebral centra	Alcântara Fm.	Maranhão (North)	Early Cenomanian	Medeiros and Schultz (2002), Medeiros et al. (2007)
	Trunk vertebrae	Marília Fm.	Triângulo Mineiro	Maastrichtian	Santucci and Bertini (2006a)
	Caudal vertebrae	Uberaba Fm.	Triângulo Mineiro	Campanian-Maastrichtian	R.M. Santucci (unpublished data)
		Adamantina Fm.	São Paulo (West)	Campanian-Maastrichtian	Santucci and Bertini (2001)
		Marília Fm.	São Paulo (West)	Maastrichtian	R.M. Santucci (unpublished data)
	Cervical vertebrae (series)	Marília Fm.	Triângulo Mineiro	Maastrichtian	R.M. Santucci (unpublished data), Trotta et al. (2002)
	Osteoderms	Marília Fm.	Triângulo Mineiro	Maastrichtian	Powell (2003), R.M. Santucci (unpublished data)
Andesauridae indet.	Partial postcranium	Parecis Gr.	Mato Grosso (South)	Campanian-Maastrichtian	Azevedo and Kellner (1998), Marinho and Candeiro (2005)
	Postcranial elements	Adamantina Fm.	São Paulo (West)	Campanian-Maastrichtian	Kellner and Campos (2000), Kellner et al. (2004)
		Marília Fm.	Triângulo Mineiro	Maastrichtian	Azevedo et al. (2007b)
		Parecis Gr.	São Paulo (West)	Maastrichtian	Campos and Kellner (1999), Santucci and Bertini (2001)
	Isolated teeth	Parecis Gr.	Mato Grosso (South)	Late Cretaceous	Bertini et al. (2001)
	Vertebral centra	Adamantina Fm.	São Paulo (West)	Campanian-Maastrichtian	Azevedo et al. (1995), Kellner (1996b)
		Alcântara Fm.	Maranhão (North)	Early Cenomanian	Candeiro et al. (2004, 2006a) Medeiros and Schultz (2002), Medeiros et al. (2007)



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TABLE II (continuation)

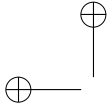
Taxon	Material	Horizon	Location	Age	References
<i>Antarctosaurus' brasiliensis</i>	Trunk vertebra, femur, and humerus	Adamantina Fm.	São Paulo (West)	Campanian-Maastrichtian	Arid and Vizotto (1971), R.M. Santucci (unpublished data)
<i>Amantissaurus mezzalrai</i>	Caudal vertebrae	Adamantina Fm.	São Paulo (West)	Campanian-Maastrichtian	Santucci and Bertini (2006b)
<i>Urubatan brittoi</i>	Sacral/caudal vertebrae	Marília Fm.	Triângulo Mineiro	Maastrichtian	Kellner et al. (2005)
<i>Axakalisaurus topai</i>	Partial skeleton	Adamantina Fm.	Triângulo Mineiro	Campanian-Maastrichtian	Kellner et al. (2006)
<i>anosauros</i> sp.	Isolated postcranial elements	Marília Fm.	Triângulo Mineiro	Maastrichtian	Bertini et al. (2001), Santucci and Bertini (2001)
			São Paulo (West)	Maastrichtian	Bertini et al. (2001), Santucci and Bertini (2001)
<i>igonosaurus pricei</i>	Partial column and pelvis	Marília Fm.	Triângulo Mineiro	Maastrichtian	Campos et al. (2005)
<i>perabatitan ribeiroi</i>	Three partial skeletons	Marília Fm.	Triângulo Mineiro	Maastrichtian	Salgado and Carvalho (2008)
<i>olosaurini</i> indet.	Caudal vertebra	Adamantina Fm.	Triângulo Mineiro	Campanian-Maastrichtian	Almeida et al. (2004), Candeiro et al. (2006b)
<i>olosaurus</i> sp	Partial postcranium	Adamantina Fm.	São Paulo (West)	Campanian-Maastrichtian	Bertini et al. (1999a), Santucci and Bertini (2001)
	Caudal vertebra	Adamantina Fm.	Triângulo Mineiro	Campanian-Maastrichtian	Candeiro et al. (2006b)
	Caudal vertebra	Marília Fm.	Triângulo Mineiro	Maastrichtian	Santucci and Bertini (2001)
<i>ondvanatitan faustoi</i>	Partial postcranium	Adamantina Fm.	São Paulo (West)	Campanian-Maastrichtian	Kellner and Azevedo (1999), Santucci and Bertini (2001)
<i>ondvanatitan</i> sp.	Vertebrae and tibia	Paracis Gr.	Mato Grosso (South)	Late Cretaceous	Franco-Rosas et al. (2004)
<i>megosauridae</i> indet.	Dentary and postcranium	Adamantina Fm.	São Paulo (West)	Campanian-Maastrichtian	Avilla et al. (2005)
<i>azonsaurus maranhensis</i>	Partial postcranium	Itapicuru Fm.	Maranhão (North)	Aptian-Albian	Carvalho et al. (2003)
<i>yososaurus</i> sp.	Isolated vertebrae	Alcântara Fm.	Maranhão (North)	Early Cenomanian	Medeiros and Schultz (2004)
<i>plodocoida</i> indet.	Isolated vertebrae	Itapicuru Gr. (Unid. Indif.)	Maranhão (North)	Albian	Castro et al. (2007)



Cretaceous age (Carvalho and Kattah 1998); 2 – Botucatu Formation, Paraná Basin (Leonardi 1980, Leonardi and Oliveira 1990), a massive aeolian sequence of possible Late Jurassic-Early Cretaceous age (Assine et al. 2004) that crops out in an extensive area in east-central South America (Scherer 2000). The ichnofaunas includes possible theropod and ornithopod footprints recovered mainly in São Paulo State (Leonardi 1994, Leonardi et al. 2007, Fernandes and Carvalho 2007). Some authors have noted that the dinosaur fauna from Botucatu Formation is restricted both ecologically, as it is mainly composed of small to medium-sized animals, and taxonomically, with the virtual absence of sauropods (Leonardi 1989, Novas 2007, 2009). The interpretation of the Botucatu Formation as a paleodesert (Assine et al. 2004) suggests that environmental stress could be responsible for this pattern (Novas 2007, 2009). Late Jurassic dinosaur-bearing rocks in Gondwana are rare, with significant records only from the Tendaguru beds, Tanzania, which includes several sauropods, theropods, stegosaurs, and basal iguanodonts (Janensch 1914, Bonaparte et al. 2000, Tykoski and Rowe 2004, Upchurch et al. 2004, Rauhut 2005, Remes 2006, 2007), and the Cañadon Calcáreo Formation, Argentina, with sauropod records (Rauhut et al. 2005, Rauhut and Lopez-Arbarelo 2008). Other records (see Novas 2009 for review) include the Lower or Middle Jurassic strata of the La Quinta Formation, Venezuela, with ornithischians and saurischian incomplete specimens (Barrett et al. 2008), La Matilde Formation from Middle or Late Jurassic of Argentina (Leonardi 1989), with theropod footprints (Novas 2009), and Baños del Flaco Formation, Tithonian of Chile (Moreno and Benton 2005), with sauropod tracks. The paucity of Jurassic dinosaurs in Brazil has been discussed under a paleoecological framework (Novas 2007, 2009), and it adds few information from a historical biogeography point of view. Indeed, the same can be said about the ornithischian record, which includes the above-mentioned and additional footprints from the Early Cretaceous of Sousa and Uiraúna-Brejo das Freiras basins, northern Brazil (Leonardi and Carvalho 2002, 2007), and a preliminarily described vertebra from Itanecuru beds (see above)

ing hadrosauroid taxa (Coria and Cambiaso 2007, Novas 2007, 2009). These clades, along with those registered in the Jurassic-Cretaceous of Africa (Galton and Upchurch 2004b, Norman 2004, Norman et al. 2004, Weishampel et al. 2004), probably ranged throughout South America, and could possibly be found in Mesozoic strata of Brazil. Explanations for their paucity include insufficient fieldwork, scarcity of available outcrops due to extensive vegetal covering, and a possible ecological constraint, as ornithischians are rarer herbivorous components in the known Mesozoic Gondwanan terrestrial ecosystems compared to sauropods (Bonaparte 1996, Upchurch and Barrett 2005).

Bonaparte (1986) proposed that the Cretaceous dinosaur faunas from Gondwana and Laurasia might be differentiated by their endemism following the separation of both landmasses in the Jurassic. In general, Laurasia would be dominated by ornithischians and some theropod taxa such as tyrannosauroids, ornithomimids, therizinosaurs and dromaeosaurids, while Gondwana would be inhabited by sauropods, specially titanosaurs (e.g., Bonaparte and Kielan-Jaworowska 1987), and other theropod taxa such as abelisaurids and alvarezsaurids (Bonaparte 1991b, 1996). This proposition has been weakened by novel findings that expand the distribution of several dinosaur clades (Fig. 2). Non-tyrannosaurid tyrannosauroids, possibly including *Santanaraptor*, are recorded in southern landmasses (Benson et al. 2010), and dromaeosaurids have been recovered in several localities from Gondwana (see above). On the other hand, theropod clades once thought to be endemic of Gondwana were more recently recovered from Laurasian terrains, including carcharodontosaurids from the Early Cretaceous of North America and Europe (Holtz et al. 2004, Sereno and Brusatte 2008), Late Cretaceous of Asia (Brusatte et al. 2010), and alvarezsaurids from the Late Cretaceous of Mongolia and North America (Chiappe et al. 2002). Abelisaurid remains from Laurasia are dubious (e.g., Le Loeuff and Buffetaut 1991, Sampson et al. 1998, but see Pereda-Suberbiola 2009), and titanosaur sauropods have representatives in both landmasses (Taylor and Naish 2007), although they are more common in Gondwanan (Fig. 2 4b-c) (Upchurch



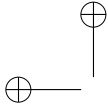
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also Sereno et al. 1998). Indeed, several dinosaur clades recovered in northeastern Brazil in Albian-Cenomanian strata, e.g., Rebbachisauridae, Spinosauridae, Carcharodontosauridae, and Compsognathidae, have older Laurasian records (see above). However, strata of the lowest Cretaceous are rare in northern Gondwana.

Several authors suggested that the similarities between the dinosaur fauna of northeastern Brazil and North Africa (Novas 2007, 2009) in this period may be explained by continuous land connections until the Cenomanian (Calvo and Salgado 1995, Sereno et al. 2003, 2004, Sereno and Brusatte 2008). Evidences supporting this hypothesis (named ‘Pan-Gondwana’), include paleogeographic reconstructions (Smith et al. 1994) and shared Cretaceous taxa as the crocodyliforms *Araripesuchus* (Turner 2006, Sereno and Larsson 2009), *Sarcosuchus* (Buffetaut and Taquet 1977, 1979, Sereno et al. 2001), and notosuchians (Sereno et al. 2003, Turner 2006); araripemydid turtles (Fuente and Broin 1997, Gaffney et al. 2006); the coelacanthiform *Mawsonia* (Maisey 1991, Yabumoto and Uyeno 2005); abelisaurid (Sereno et al. 2004, Sereno and Brusatte 2008) and diplodocoid (Calvo and Salgado 1995, Medeiros and Schultz 2004) dinosaurs. However, the separation between Africa and South America is often considered older (Hay et al. 1999, Sampson et al. 1998, Scotese 2002, Krause et al. 2006, 2007), and geologic data from northeastern Brazil point towards the existence of openly marine deposits in Albian times (Petri 1987, Mohriak 2003). In this scenario (‘Africa-first’ hypothesis), the closer similarity of the turtle and crocodyliform faunas could be explained by the possibility for semi-aquatic forms to disperse across restrict oceanic barriers. Whatever separation date between these landmasses is correct, Upchurch et al. (2002) objectively suggested that vicariance rather than dispersal played a major role in the biogeographic evolution of dinosaurs at least for Middle Jurassic to mid-Cretaceous times. Turner (2004) performed an analysis of crocodyliform biogeography during the Cretaceous and also concluded that vicariance driven by the fragmentation of Gondwana was a major factor affecting the distribution of this clade during mid to Late Cretaceous.

saurids from the Bauru Group. The phylogenetic analysis presented by this author shows *A. gomesi* to *A. patagonicus*, from Argentina, than to *A. we* from Africa. This is congruent with the presence of sauropod *Rayososaurus* in mid-Cretaceous strata both Argentina and Brazil. On the other hand, additional archosaurian records suggest a closer affinity between the northern fauna of the mid-Cretaceous of Brazil and African faunas (Medeiros and Schultz 2002, 2009). This includes the spinosaurids from the Bauru Basin/Itapecuru Group, and the crocodyliform *Itapetodus itapetecurui* from the Itapecuru Group (Sereno et al. 2004), which is closely related to the African *Wisuchus* (Zaher et al. 2006). This conundrum alternatively suggests a closer similarity between eastern and western Gondwanan faunas than previously thought. Accordingly, the close relationship between the crocodyliforms from Itapecuru group with Gondwanan (i.e. notosuchians) (Zaher et al. 2006, Kellner et al. 2009), along with the occurrence of peirosaurid baurusuchids in the Late Cretaceous, reinforces the existence of a vicariant pattern in crocodyliform distribution (Turner 2004). This scenario is also compatible with the distribution of dinosaurs in southern landmasses (Upchurch et al. 2002, Novas 2007, 2009).

The Brazilian fossil record of dinosaurs adds relevant data to the biogeographic comparison with Argentina. Early Cretaceous taxa shared between these areas include diplodocoids, carcharodontosaurid titanosaurs. On the contrary, clades recorded in the Bauru and São Luís-Grajaú basins, such as Spinosauridae and Compsognathidae, were not found in chronologically equivalent strata in Argentina (Novas et al. 2009), while abelisauroids, with a well-known record in that country, are not recorded in the Aptian-Cenomanian of Brazil. This pattern may reflect either the incompleteness of the fossil record, inaccessibility to fossil species due to vegetal covering, insufficient fieldwork, or endemism, although evidence supporting the latter is scarce. The Late Cretaceous from both areas exhibits a very similar dinosaur fauna, including carcharodontosaurids and aeolosaurine titanosaurs, even at a generic level (*Aeolosaurus* (see below)).



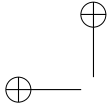
currence of more derived forms of this clade (Carnotaurinae *sensu* Sereno et al. 2004, see also Carrano and Sampson 2008) in South America, Indo-Pakistan, and Madagascar leaded some authors (Sampson et al. 1998) to suggest that abelisaurids might have radiated across Gondwana after the separation of continental Africa in the Early Cretaceous (Krause et al. 2007). Yet, recent records of basal abelisauroids in the Early Cretaceous of Niger (Sereno et al. 2004, Sereno and Brusatte 2008), along with fragmentary material from the Aptian-Albian of Libya (Smith and Dalla Vecchia 2006), Cenomanian of Morocco (Mahler 2005), and Maastrichtian of Egypt (Smith and Lamanna 2006), indicate a wider distribution of this group in southern landmasses than previously thought. These findings suggest a later separation of continental Africa from Gondwana (‘Pan-Gondwana’ model), and the absence of carnosaurines in northern Africa in the Late Cretaceous could be explained by the incompleteness of the fossil record (Sereno and Brusatte 2008). However, recent findings suggest that carnosaurines are restricted to Gondwana and at least one clade within it (Brachyrostra) is endemic to South America (Canale et al. 2009). The recent discovery of a *Megaraptor*-like theropod in the Early Cretaceous of Australia is congruent with a connection between South America and Australia until the Late Cretaceous (Krause et al. 2006), but it is uncertain if the separation of Africa occurred earlier than this period (Sereno et al. 2004).

The sauropod fossil record in Brazil (Table I, II) is also relevant for paleobiogeographic studies because of its rich titanosaur record. In the context of some phylogenetic hypotheses (Wilson 2002, Upchurch et al. 2004, Curry Rogers 2005), the Late Cretaceous cosmopolitanism of this clade (Fig. 4b-c) cannot be explained only by cladogenesis associated with the splitting of Pangaea. For some authors (e.g., Bonaparte 1984, Sullivan and Lucas 2000), the Maastrichtian record of the titanosaur *Alamosaurus* in North America (Montellano-Ballesteros 2003, Upchurch et al. 2004) is congruent with a land connection with South America in the Late Cretaceous (Simpson 1950, 1978), which would also be responsible for the presence of hadrosaurids and ankylosaurs in southern latitudes (Bonaparte et al. 1984,

generic level (Bertini et al. 1993) or for small-bodied animals relative to sauropod dinosaurs (e.g., crocodylomorphs and turtles, Santucci and Bertini 2001). These alleged taxonomic and/or ecological partitioning may be related to the formation of biogeographic barriers at the borders of the ‘basin’ originated with the lithostatic load of the basalt floods referred to as the Serra Geral Formation (Santucci and Bertini 2001). However, the existence of geologic barriers at the borders of Bauru Group is questionable (see Milani 2001). Besides, no tetrapod taxon is endemic to the Bauru Group at a suprageneric level, and even genera such as *Aeolosaurus*, *Peirosaurus*, *Roxochelys*, plus baurusuchids closely related to Brazilian forms are recorded in Argentinean strata (Gasparini 1972, Broin 1991, Gasparini et al. 1991, Riff and Kellner 2001, Franco-Rosas et al. 2004). In addition, taxa recorded only in the Bauru Group are closely related to forms recorded in widespread localities across southern landmasses (Franco-Rosas et al. 2004, Carvalho et al. 2004, Turner and Calvo 2005, Zaher et al. 2006, França and Langer 2006, Evans et al. 2008). Although less diverse and abundant than some faunas of equivalent age in South America (e.g., Neuquena Basin, Novas 2009), the dinosaur assemblages of the Bauru Group is rather similar to the Late Cretaceous assemblages from other parts of Gondwana, especially Argentina.

CONCLUSIONS

- i) The dinosaur record of the Brazilian Mesozoic, although rather incomplete, has added significant data to biogeographic studies. This record is incongruent with the continental dimension of the country, and the scarcity of Jurassic and ornithischian forms may be related to deficient fieldwork, inaccessibility to the fossiliferous strata, lack of strata of appropriate age, or a true biogeographic pattern. On the other hand, most descriptive works (80%) are concentrated in the last decade, suggesting further increase of this record in the near future.
- ii) Triassic dinosaur faunas from south Brazil are specially correlated with others from south Gondwana



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ably restricted to western Pangaea (i.e., South and probably North America).

- iii) Various biogeographic models have been proposed to explain the distribution of Cretaceous dinosaur faunas in Gondwana. However, some of them do not incorporate vicariance as a fundamental process of biogeographic evolution, and barely take into consideration the scarcity of the fossil record of several key areas, as northern Brazil and Africa. Nonetheless, the ‘Pan-Gondwana’ hypothesis is partially supported by the faunal similarities among Argentina, Brazil and North Africa until the Cenomanian. Recent works suggests that vicariance driven by the fragmentation of Gondwana was an important process of dinosaurs and crocodyliform biogeographic evolution in the Cretaceous, which is consistent with the fossil record of these groups in South America. More conspicuous similarities in dinosaur and crocodyliform faunas from South America and India-Madagascar rather than continental Africa may be result of land connection between these areas well into the Late Cretaceous.
- iv) The comparable distribution of non-avian dinosaurs in Brazil and Argentina is noted from the Late Triassic to Late Cretaceous. However, some peculiarities as the absence of spinosaurids and compsognathids in Argentina, and ornithischians and abelisauroids in the Early Cretaceous of Brazil remain to be fully clarified. In this context, the endemism of the Bauru Group fauna, as proposed by some authors, is jeopardized by the occurrence of several of its taxa in various localities in South America and other Gondwanan areas.

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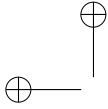
RESUMO

O registro osteológico de dinossauros no Mesozóico brasileiro está restrito a rochas triássicas do Rio Grande do Sul e a depósitos cretáceos de várias partes do país. Isto inclui 21 espécies, sendo duas referidas como *nomina dubia*, e 19 atualmente classificadas como dinossauros. Oito táxons específicos adicionais baseados em material fragmentado e diversas pegadas são conhecidos no Brasil. De fato, a maioria dos espécimes é composta de dentes isolados e vértebras. Apesar do aumento em trabalhos de campo na última década, não há exemplar esquelético de dinossauro no Jurássico brasileiro, e é escassa a evidência de Ornithischia. Faunas de dinossauros aqui registradas são em geral correlatas com as da Pangéia durante o Mesozóico. No Triássico Superior, há uma correspondência próxima com a Argentina e outras regiões sul-gondwânicas. Faunas do Cretáceo médio do nordeste brasileiro são semelhantes às dos depósitos coevos do norte da África e Argentina. Registros de espinosaurídeos no Cretáceo sul estão restritos à África e Brasil, enquanto que os de abelisaurídeos não são conhecidos no Cretáceo Inferior do Brasil. Assembleias de dinossauros da região sul e central do Brasil são endêmicas apenas em nível de gênero e, mais raramente, espécie, compartilhando táxons proximamente relacionados com assembleias da Argentina, Índia-Paquistão e, num menor grau, África continental.

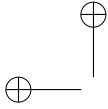
Palavras-chave: Brasil, Dinosauria, Triássico, Jurássico, Cretáceo, paleobiogeografia.

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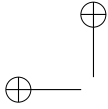


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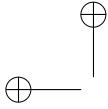


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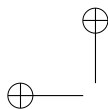


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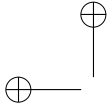


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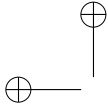


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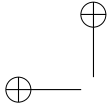


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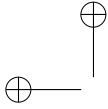


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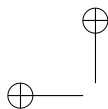


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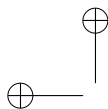


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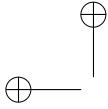


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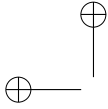


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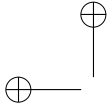


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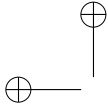


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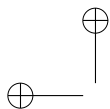


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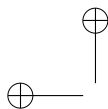


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