Bruno Albert Navarro

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titanossauro do Cretáceo Inferior *Tapuiasaurus macedoi*
Zaher *et al.* 2011

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Advisor: Prof. Dr. Hussam El Dine Zaher

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Dedictory

To my family and many friends who have always
believed in my potential and encouraged me.

Epigraph

“Quem elegeu a busca não pode recusar a travessia”.

"Who elected the search, cannot refuse the crossing"

Guimarães Rosa, *Primeiras Estórias*

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1 - Introduction

More than a decade ago, the Paleontology Laboratory from the Museu de Zoologia da Universidade de São Paulo (MZUSP) opened a new frontier in dinosaur research in Brazil. The MZUSP team started several field seasons in the deposits of Sanfranciscana Basin, located at the outskirts of Coração de Jesus Municipality, north of the Minas Gerais State, South-eastern Brazil (Pires Domingues 2009). The fieldwork was carried in outcrops of the Early Cretaceous Quiricó Formation, which yielded remarkable specimens unexpected for this geological unit at this point, such as the remains of sauropod (Titanosauria) and theropod (Abelisauroidae) dinosaurs (Pires Domingues 2009, Zaher *et al.* 2011, Da Silva 2013).

Among the collected individuals, there is one the most complete titanosaur specimens recovered from Brazil so far: *Tapuiasaurus macedoi* Zaher *et al.* 2011. This finding stands out because, among the recovered materials, the skull and jaws are complete, articulated and exceptionally preserved, a rare fact in the fossil record of this group, representing one of the most complete skulls recovered in the world and the first for a Brazilian titanosaur (Zaher *et al.* 2011, Bittencourt *et al.* 2015, Wilson *et al.* 2016).

Over a sesquicentennial history of titanosaur research, just other four species with almost complete skulls have been described until now. They consist in the partial skulls of *Nemegtosaurus mongoliensis* and *Quaesitosaurus orientalis* from the latest Cretaceous (Maastrichtian and Campanian respectively) Nemegt and Bayun Goyot formations, Mongolia (Nowinski 1971, Kurzanov & Bannikov 1983, Wilson 2005); the disarticulated skulls of *Rapetosaurus krausei* from the Maastrichtian Maevarano Formation of Madagascar (Curry Rogers & Forster 2001, 2004); and the complete skull of *Sarmientosaurus musacchioi* (Martínez *et al.* 2016) from the early Late Cretaceous (Cenomanian-Turonian) Bajo Barreal Formation of Argentina. Hence, *Tapuiasaurus* constitutes the first and only complete titanosaur skull from the Early Cretaceous time-interval known up to date (Wilson *et al.* 2016).

Beyond the skull remains, the holotype of *Tapuiasaurus* (MZSP-PV 807) preserves anatomical regions of great significance for the knowledge of general titanosaurian anatomy, such as an articulated part of its cervical sequence, dorsal and caudal vertebrae, as well as almost complete fore and hindlimbs, including one nearly complete left foot, which is

another region poorly sampled for Sauropoda as whole. Although recent works have been focused on this part of the appendicular skeleton (e.g. González Riga *et al.* 2008, 2016), due to limited sampling, the evolution of sauropod pedal anatomy remains poorly understood, allowing *Tapuiasaurus* to become a good model for character polarization.

The importance of this taxon to the knowledge of titanosaurian morphological evolution does not lie only in the preservation of poorly sampled anatomical regions, but also because *Tapuiasaurus* is one of the oldest representatives of this group, filling a crucial gap (*i.e.* Berriasian to Barremian) in the early stages of the titanosaurian dispersion around the world (Carballido *et al.* 2017, Poropat *et al.* 2017, Sallam *et al.* 2018). *Tapuiasaurus*, being also one of the first “true” titanosaurians, which broadens the understanding about initial steps in the titanosaur evolution, even if the ichnological record supports an earlier titanosaur cladogenesis, placing the group origins into the Middle Jurassic (Wilson & Carrano 1999, Curry Rogers 2005).

The enigmatic African taxa *Janenschia robusta* and *Tendaguria tanzaniensis* (Wild 1991, Bonaparte *et al.* 2000), from the Late Jurassic Tendaguru Beds of Tanzania, may correspond to putative Jurassic titanosaurians (McIntosh 1990, Curry Rogers 2005), despite these taxa being likely related to non-titanosauriform sauropodans according some authors (Santucci 2005, Upchurch *et al.* 2015, Mannion *et al.* 2019). Even if these species correspond to true early titanosaurians or immediate sister-groups, a significant temporal and morphological gap exists between the limited Jurassic forms and the diverse and widespread titanosaurs from the Late Cretaceous, creating a ghost-lineage of, at least, 50 My. *Tapuiasaurus* is there at the midst of this unclear period of titanosaur evolution, given that available occurrences from this age are limited to punctuated and highly fragmentary specimens.

Contrasting with the abundance of later forms, titanosaurians from the earliest Cretaceous are scarcer and represented mostly by very fragmentary or dubious taxa. From South America, the oldest titanosaurian record for a long time comprised by an isolated procoelous caudal vertebra of an undetermined form recovered from the Aptian Rayoso Formation (Neuquén Basin), Argentina (Bonaparte 1996). Recently, Ghilardi *et al.* (2016) and Carvalho *et al.* (2017) described older titanosaurian remains, recovered from the Hauterivian-Barremian Rio Piranhas Formation (Rio do Peixe Basin Complex), Northeastern of Brazil. They consist of the isolated fibula of an unnamed form and by the

putative early titanosaur *Triunfosaurus leonardii* (composed by an ischium, chevrons and three partial mid caudal vertebrae). However, some authors suggests that *Triunfosaurus* represents a non-titanosaurian somphospondyliian, such as *Wintonotitan wattsi* (Poropat *et al.* 2014, 2017).

Outside South America, titanosaurs prior to Aptian time-interval are represented by an undetermined form composed by two large procoelous mid-caudal vertebrae, and by the *nomen dubium* taxon *Iuticosaurus valdensis*, both recovered from the Barremian-Aptian Wessex Formation (Wealden Group) of England (Le Loeuff 1993, Upchurch *et al.* 2011). The coeval taxa *Eucamerotus foxi* and *Haestasaurus becklesii*, composed by several non-associated dorsal neural arch and vertebrae and a nearly complete forelimb respectively, may correspond to another putative titanosaurs from the earliest Cretaceous (Berriasian-Valanginian, Santucci 2005), although it being likely related to brachiosaurids rather than titanosaurs (Blows 1995, Upchurch *et al.* 2011, 2015).

From the Murtoi Formation, Transbaikalia, Russia, Averianov and Skutschas (2017) describes three procoelous mid caudal vertebrae, which assigned to a new species, *Tengrisaurus starkovi*, representing the first unequivocal Early Cretaceous lithostrotian from Asia. More recently, Averianov and Efimov (2018) described, from marine deposits located nearly the Volga River, Russia, the species *Volgatitan simbirskiensis*, composed by seven anterior and middle caudal vertebrae. With ages ranging the upper Hauterivian to Barremian, these taxa denotes the occurrence of a true titanosaurs in the earliest Cretaceous of Asia, raising several biogeographical implications, such as the timing and center of origin of the group, given the synchronous records in the southern Gondwana.

Finally, the problematic taxon *Algoasaurus bauri* (Broom 1904) from the Valanginian to Hauterivian Kirkwood Formation (Algoa Basin), South Africa, may represent the oldest Cretaceous titanosaur known. This taxon is comprised by incomplete postcranial remains (*e.g.* opisthocoelian cervical and dorsal vertebrae, caudal vertebrae, ribs, scapula, femur and an ungual phalanx) unfortunately now lost (Broom 1904, McPhee *et al.* 2016). However, their fragmentary nature and the scarcity of coeval taxa hinders major comparisons.

According McPhee *et al.* (2016) *Algoasaurus* has been considered possessing titanosaurian, diplodocoid (including rebbachisaurid) and camarasaurid affinities (Huene 1932, Jacobs *et al.* 1996, Canudo *et al.* 2003) and, actually, it is considered a *nomen dubium* by some authors (McIntosh 1990, Upchurch *et al.* 2004, McPhee *et al.* 2016), making *Tapuiasaurus* the most complete and the best-representative Early Cretaceous titanosaur known at this point.

Nonetheless, although *Tapuiasaurus* has been incorporated into numerous recent phylogenetic analyses (*e.g.* Zaher *et al.* 2011, Carballido & Sander 2014, Gorscak *et al.* 2014, Lacovara *et al.* 2014, Poropat *et al.* 2015, Bandeira *et al.* 2016, González Riga *et al.* 2016, Martínez *et al.* 2016, Wilson *et al.* 2016, Averianov & Skutschas 2017, Tykoski & Fiorillo 2017, Carballido *et al.* 2017, Gorscak *et al.* 2017, Averianov & Efimov 2018, González Riga *et al.* 2018, Sallam *et al.* 2018), its postcranial skeleton has not been previously fully described and illustrated in the literature.

Therefore, the present research aimed a full description of the postcranial osteology of *Tapuiasaurus*, comparing it with several other early titanosaurs. This study increases our knowledge of a key taxon, substantial to the understanding of the origins, phylogenetic relationships and first steps in titanosaurian diversification. Furthermore, this research also provides an increase in the understanding of the vertebrates that were present in the Sanfranciscana Basin during the Early Cretaceous, giving a solid basis for future paleoecological, biostratigraphical and paleobiogeographical studies.

1.1. A brief review of titanosaurian anatomy, systematics and taxonomy

Widespread and remarkably diverse, Titanosauria represents a successful lineage among sauropod dinosaurs (Curry Rogers 2005, Mannion *et al.* 2011, Carballido *et al.* 2017). Titanosauria constitutes a taxonomically numerous fossil group and, currently, comprises at least 100 valid species between the approximately 135 yet reported forms (Table 3.1.). According some authors (Curry Rogers 2005, Mannion *et al.* 2011) this diversity corresponds to more than a third of all sauropod dinosaur taxa described until now. The titanosaur records were present on entire Cretaceous time-interval, at rocks distributed throughout all the continents, including Antarctica (Wilson 2006a, Cerda *et al.* 2012). For this reason, this group represents a useful tool to studies regarding the Cretaceous paleobiogeography, as well as for stratigraphic correlations of continental deposits (Santucci 2005).

Hugh Falconer in 1868 has made the first mention of titanosaur bones in the literature (Wilson & Upchurch 2003), reporting the remains that later would represent the first named species of the group: *Titanosaurus indicus* Lydekker 1877. However, other mentions that correspond to titanosaurs or, at least, very close related taxa has been previously made, such as the occurrences of *Aepisaurus elephantinus* (Gervais 1848), *Pelorosaurus* (= *Haestasaurus*) *becklesii* (Mantell 1853, Upchurch *et al.* 2015), *Hypselosaurus priscus* (Matheron 1869), *Eucamerotus foxii* (Hulke 1871, Blows 1995) and *Macrurosaurus semnus* (Seeley 1876).

Lydekker (1877) established *Titanosaurus indicus* based on two mid-posterior caudal vertebrae and a left femur (Figures 1-2), recovered from the latest Cretaceous strata of Lameta Formation (India), basing its diagnosis only in the procoelous nature of the caudal remains. Posteriorly, Titanosauridae was erected to encompass the numerous taxa that also shared procoelous caudal vertebrae, making *Titanosaurus* the first dinosaur taxon with global distribution, since fourteen species have been referred to this genus, distributed across South America, Europe, Madagascar, India and Asia (Wilson & Upchurch 2003, Wilson 2006a). This fact making “*Titanosaurus indicus*”, as well as the subordinates that derives from it (Titanosauroidae, Titanosauridae and, Titanosaurinae) have long been recognized as a "wastebasket taxa" (Wilson 2006a).

Despite the numerous titanosaur discoveries has been made earlier in the history of dinosaur research, their relationships within other sauropods have long remained uncertain until the end of XX century, which began to be understood only in the late 1990s (Calvo & Salgado 1995, Upchurch 1995, Salgado *et al.* 1997). Although non-cladistic, Huene (1929) made the first inference regarding the titanosaurian relationships (Figure 3), which hypothesized that titanosaurs compose the last lineage of the paraphyletic “Cetiosauridae”, representing the descendants from this “basal stock” group (Huene 1929). This author also recognized *Pleurocoelus* as the “link” between cetiosaurids and titanosaurids (Salgado *et al.* 1997). As explained by Salgado *et al.* (1997), some authors disagree that hypothesis (Janensch 1929, Nopcsa 1930, Steel 1970, Kues *et al.* 1980), suggesting that titanosaurids are related to diplodocoids due the resemblance between the skull materials of *Antarctosaurus* and *Diplodocus*.

This hypothesis has persisted for a long time, gaining ground mainly due the corroboration of the first cladistic studies involving sauropods (*e.g.* Gauthier 1986, McIntosh 1990). Upchurch (1995) consolidated this view (Figure 4) given the specific focus and inclusion of new cranial material on his analyses, such as the isolated skulls of *Nemegtosaurus* and *Quaesitosaurus* (Nowinski 1971, Kurzanov & Bannikov 1983). Nonetheless, Calvo and Salgado (1995) in the same epoch recovered for the first time a different topology (Figure 5) in which titanosaurs and brachiosaurids representing a monophyletic group. It should be noted that, in this analysis, the authors did not include data from the *Nemegtosaurus* and *Quaesitosaurus*.

Salgado *et al.* (1997a) presented the first cladistic study with specific focus on titanosaurs. In this work, two equally most parsimonious trees were obtained, differing only in the position of *Epachthosaurus* and *Malawisaurus*. The strict consensus presented by these authors, depict *Chubutisaurus* as the sister group of Titanosauria, defined by only an unambiguous synapomorphy: the distal portion of the tibia wider transversely than anteroposteriorly. *Brachiosaurus* (= *Giraffatitan*) would correspond the sister-taxa of this clade, forming with *Chubutisaurus* and the other titanosaurs a group named of Titanosauriformes. This group would be supported by five synapomorphies: (1) mid-posterior caudal vertebrae with a neural arch occupying the anterior region of the center; (2) claw in the 1st digit of the anterior limbs reduced or absent; (3) highly developed iliac preacetabular lobe; (4) pubic pedicel perpendicular to the sacral axis; (5) the presence of a lateral protuberance below the great trochanter of the femur (Figure 6). This hypothesis was corroborated by several subsequent studies (*e.g.* Sereno 1998, Upchurch 1998, Wilson & Sereno 1998, Sanz *et al.* 1999), becoming widely accepted in the late 1990s.

Posteriorly, Wilson and Sereno (1998) identified in their analyses that titanosaurians would be more related to a more specific group of titanosauriforms from the Early Cretaceous, such as *Euhelopus*, *Phuwiangosaurus* and *Chubutisaurus*, than brachiosaurids, defining the most inclusive taxon Somphospondyli. The monophyly of Somphospondyli is mainly related to the pneumatization of the axial skeleton, being supported by the following synapomorphies: (1) cervical vertebrae with rudimentary laminae; (2) presacral vertebrae with spongy internal tissue (camellate or somphospondylous); (3) neural spine in the mid and posterior dorsal vertebrae inclined posteriorly; (4) medially deflected glenoid cavity on the scapula (Wilson & Sereno 1998). This hypothesis (Figure 7) is widely accepted today,

being recovered in several works (e.g. Carballido & Sander 2014, González Riga *et al.* 2018).

Regarding to the taxonomy, titanosaurians have already been defined as a stem-based and a node-based clade (Table 3.2.). Bonaparte and Coria (1993) erected Titanosauria to allocate Titanosauridae and the newly denominate Andesauridae, without, however, provide a phylogenetic definition, only listing the taxa included and their respective synapomorphies. This latter would encompassing all species whose characteristics do not apply to the taxa traditionally included in Titanosauridae, such as medium and posterior amphiplatyan caudal vertebrae and presence of hyposphene-hypantrum complex in the dorsal vertebrae (*i.e.* *Andesaurus*, *Malawisaurus*, *Argentinosaurus*, and *Epachthosaurus*). Subsequently, Upchurch (1998) defined the stem-based clade Titanosauroida to accommodate all taxa are more closely related to the "true" titanosaurians (e.g. *Saltasaurus*) in respect to the other titanosauriforms, such as brachiosaurids.

Nonetheless, in subsequent phylogenetic analyses (Salgado *et al.* 1997, Wilson & Sereno 1998, Wilson 2002), *Argentinosaurus* and *Epachthosaurus* appear within Titanosauridae. Additionally, Titanosauridae was defined based on apomorphic characters, while Andesauridae is based only in plesiomorphic characters in which, by definition, explain it as a paraphyletic group (Wilson & Upchurch 2003). Salgado *et al.* (1997a) in their cladistic analysis, provide the first robust taxonomic definition for Titanosauria, and defines it as being a nodal clade composed by the most recent common ancestor of *Andesaurus*, Titanosauridae and all his descendants.

Sanz *et al.* (1999), provided a cladistic study in the description of the Spanish taxon *Lirainosaurus*. Some differences can be observed in the single tree most parsimonious obtained when compared with previous analyses (Santucci 2005). In the work of Sanz *et al.* (1999) the Asian *Opisthocoelicaudia* occupies a basal position in the cladogram. In other contributions (e.g. Wilson & Sereno 1998), this taxon would be more related with saltasaurids, such as *Saltasaurus* and *Neuquensaurus* of Argentina. These authors also recovered a clade containing *Haplocanthosaurus* plus *Andesaurus* as sister-group of Titanosauroida. Within Titanosauroida, the authors have confirmed the titanosaurian monophyly, proposing the clade Eutitanosauria for a clade more derived titanosaurids, which is diagnosed, in part, by the presence of dermal armor.

However, Wilson and Upchurch (2003) contested the validity of Titanosauridae. These authors pointed out that the name of the Family Titanosauridae, as well as the genus *Titanosaurus* and all derivatives of this (*i.e.* Titanosaurinae, Titanosauroidae) should be invalidated because the type species on which it was based, *Titanosaurus indicus*, is not diagnosable. Thus, posteriorly, Upchurch *et al.* (2004) attributed erected the clade Lithostrotia to encompasses the apomorphic titanosaurs, which consists in the node composed by the most recent common ancestor of *Malawisaurus*, *Saltasaurus* and all of his descendants. On the other hand, Salgado (2003) argues that the Phylogenetic Code of Biological Nomenclature (Phylocode) favours the maintenance of the term Titanosauridae. In attempt to stabilize and unify the taxonomy of Titanosauria, the author bases the group on a nodal definition. Additionally, the same author redefines other taxa, as Titanosauroidae, Eutitanosauria, Saltosaurinae and Opisthocoelicaudinae, as well as creating the stem-based clades Epachthosaurinae and Andesauroidae.

Upchurch *et al.* (2004) considered the absence of the hyposphene-hypantrum articulations in dorsal vertebrae as a synapomorphy for Lithostrotia that, along with other characteristics such as the strong procoelous caudal vertebrae supports the monophyly of the group. Additionally, Lithostrotia is sustained by other 12 Synapomorphies (see D'Emic, 2012), for example, opisthocoelous presacral vertebrae (with pneumatic cavities in the centra and neural arch) and the presence of osteoderms. Nonetheless, the presence of osteoderms in less derivatives taxa (such as *Epachthosaurus* and *Opisthocoelicaudia*) and its absence in some basal members of Lithostrotia (as *Malawisaurus* and *Mendozasaurus*), have led some authors to question the usage of the term, and reuse the Titanosauridae definition proposed by Salgado (2003). Further, this proposal is associated with the fact that the taxon name Lithostrotia is giving in a previously proposed synapomorphy of Eutitanosauria, indicating a probable synonymy.

In the last decade, the number of titanosaur discoveries, and consequently more complete species described, increased considerably, leading to the identification of several less inclusive clades (*e.g.* Franco Rosas *et al.* 2004, Calvo *et al.* 2007a and 2007b). This indicates a greater diversity and complexity in the internal titanosaurian phylogenetic relationships, in which most recovered topologies are conflicting, being solely some clades recovered in different data sets (Figure 8), and the synapomorphies that support the titanosaurian monophyly vary substantially in each topology (Figure 9). Moreover, mostly of these studies have been hindered by high missing data indexes, until the osteology of

several titanosaurian species, as well as some important areas of the titanosaurian skeleton, remain poorly understood, particularly the skull, the most posterior caudal vertebrae, as well as the manual and pedal anatomy (González Riga *et al.* 2016).

1.3. Geologic settings

1.3.1. Sanfranciscana Basin stratigraphy

The Sanfranciscana Basin (SFB) comprises in an Interior *Sag* (intracratonic unit *sensu* the terminology proposed by Kingston 1983), corresponding to the Phanerozoic sequence of the São Francisco-Congo Craton (Campos & Dardenne 1997a, Bittencourt *et al.* 2015). This unit had its tectonic origin since the Paleozoic, with the formation of small rifts and grabens, whose the subsidence is intensified during the Lower Cretaceous due to distensive efforts in the Brazilian Shield occurred in the opening of the South Atlantic Ocean (Campos & Dardenne 1997b, Silva *et al.* 2003).

This basin is elongated in-shape, with an axis in the N-S direction, and occupies a total area of 550,000 km² that extends through the Piauí, Maranhão, Tocantins, Bahia, Goiás and Minas Gerais states (Sgarbi 1993, Campos & Dardenne 1997a and 1997b). The SFB unit are delimited to the North by the Rio Preto Belt and the Paranamirim Aulacogen, to the East by the Araçuaí Belt and to the West by the Brasília Belt (Pires-Domingues 2009, Bittencourt *et al.* 2015). To the South, the Alto Paranaíba Uplift, besides delimiting the basin, contributed substantially to the deposition of the igneous units of the Upper Cretaceous sequence (Sgarbi *et al.* 2001).

The SFB (Figure 23) is divided into two restricted structural units, the Abaeté (to the south) and Urucuia (to the north) sub-basins, separated by a middle structural high, the Paracatu Uplift (Campos & Dardenne 1997a and 1997b, Sgarbi *et al.* 2001, Pires-Domingues 2009, Bittencourt *et al.* 2015). Several stratigraphic charts were proposed for the sedimentary succession of SFB, assessed by traditional stratigraphic approaches (*e.g.* Sgarbi 1989, Campos & Dardenne 1997b, Sgarbi *et al.* 2001) as well as by sequence stratigraphy (*e.g.* Kattah 1991, Mendonça 1999, 2003). This research followed the stratigraphy scheme proposed by Campos & Dardenne (1997b) due his consensual lithologic and facilogic association, which are detailed below. According to these authors, the tectonic evolution of SFB consists of five sedimentary sequences, which are disconnected by regional unconformities.

The carbonatic Neoproterozoic units of the Bambuí Group represent the basement of the SFB. The basal unit consists of the Santa Fé Group, comprised by the Floresta and Tabuleiro Formations. Some authors (*e.g.* Kattah 1991, Kattah & Carvalho 1997), however, consider invalid the inclusion of this group as part of SFB sedimentary sequence and regards

the Areado Group as the basal unit. The Floresta and Tabuleiro formations are composed of diamictites, shales and massive sandstones with claystone intercalations, deposited under glaciogenic regime. These units may be correlated to the Itararé and Passa-Dois Groups of the Paraná Basin (Gondwana I Supersequence *sensu* Milani & De Wit 2008) and the Balsas Group of the Parnaíba Basin, of Carboniferous-Permian age. Nevertheless, some authors suggest a Middle to Late Permian age for these formations based in magnetostratigraphy data (Brandt & Ernesto 2006).

The Cretaceous volcanosedimentary fill of the SFB is subdivided into the lower, Early Cretaceous Areado Group, and the upper, Late Cretaceous Urucuia and Mata da Corda Groups. The latter, is laterally interfingered with the top of Areado Group and includes alkaline lavas and volcanoclastic rocks (Zaher *et al.* 2011). The Lower Cretaceous Areado Group consists of the Abaeté (Late Valanginian- Early Barremian), Quiricó (Late Barremian-Early Aptian) and Três Barras (Late Aptian-Albian?) Formations. They represent a succession of interfingered sediments deposited under alluvial, braided-fluvial (Abaeté), lacustrine (Quiricó), aeolian and fluvial-deltaic cycles (Três Barras). The Areado group covers a large area of occurrence throughout the basin, since the south to north, being continuously in the Abaeté Sub-Basin and discontinuous in the Urucuia Sub-Basin (Campos & Dardenne 1997). Most of the fossil record recovered in SFB is limited to the units of the Areado Group, mainly in the Quiricó Formation

The Abaeté Formation is divided into Carmo and Canabrava Members, represented mainly by conglomerates and massive sandstones, respectively, and deposited in alluvial and fluvial system tracts under arid environments. The lacustrine Quiricó Formation is marked by intense variation of lacustrine lithologies, including mudstones, siltstones, marls, limestones, turbidites and shales intercalated by sandstones. The Três Barras Formation comprises mainly of through-cross-bedding sandstones deposited at successive system tracts (aeolian, fluvial and fluvial-deltaic). In this formation also occur a thin *chert* level intercalated with aeolian sandstones in the top of the sequence, indicative of a transgressive event (Kattah 1991, Arai 2000 and 2009).

The Urucuia Group, non-fossiliferous until now, is comprised mainly of aeolian sandstones deposited in a desert system from the south of the basin, being covered by epiclastic sediments in the northern portion. It is subdivided into the Posse and Serra das

Araras Formations, which are probably correlated with the Araripe Basin fluvial-aeolian sequence represented by the Arajara and Exu Formations (Cenomanian).

The Mata da Corda Group, also non-fossiliferous, consists of the Patos and Capacete Formations. The first consists of ultramafic rocks of alkaline nature, while the second is represented by epiclastic and distal pyroclastic rocks deposited from volcanic sources with the contribution of an aeolian system. Finally, the Chapadão Formation, of Pliocene-Pleistocene age, represents the Cenozoic cover and is composed of unconsolidated sediments, such as alluvial, colluvial and elluvial deposits (Silva *et al.* 2003, Bittencourt *et al.* 2015).

1.3.2. Fossil record of Areado Group

The fossil record of the Sanfranciscana Basin, specifically of Areado group (Table 3.3.), contrasts with the geographic and temporal range of this unit, which encompasses most of the entire Cretaceous interval. For a century, the only fossil occurrences from this unit consisted of palynomorphs and plants, mainly recovered from the shales deposits of Quiricó Formation. According to Bittencourt *et al.* (2015 and references therein) the first fossil discoveries at Areado Group were made by Liais (1872) represented by undetermined dicotyledoneous silicified logs. Later, Freyberg (1965) also reported other incomplete logs and referred to the genus *Araucarioxylon*, suggesting a Triassic age for the “Areado Sandstone” (*op. cit.*).

Duarte (1968, 1985a, 1985b, 1997) described gymnosperms and angiosperms from the Quiricó Formation black shale level, including, conifers of the genus *Brachyphyllum obesum* and *Podozamites lanceolatus*, the aquatic nymphaeaceae *Nymphaeites choffatii* and endemic poaceae *Paraleptaspis varjensis*. Except the later taxon, the remaining also occurs in several units from Northeastern of Brazil, such as Araripe (Crato and Romualdo Formations) and São Luís-Grajaú (Codó Formation) Basins.

Barbosa (1970), Lima (1979) and Arai *et al.* (1995) also identified several terrestrial palynomorph taxa in the black shale level, raising discussions about the age and environment of this unit.

Kattah (1991) registered the occurrence of a radiolarian fauna, dinoflagellates and sponge spicules in the *chert* level of Três Barras Formation. Posteriorly, from the samplings recovered in the same site, Dias-Brito and Pessagno (1996) identified the controversial

radiolarian genera *Parvincingula*, *Caneta* and *Noviforemanella*, whose its distribution ranges from Kimmeridgian (Late Jurassic) to Valanginian (Early Cretaceous) ages, hence setting the underlying formations (Quiricó and Abaeté) into the Jurassic or the earliest Cretaceous, at least. Additionally, Dias-Brito *et al.* (1999) also identified some foraminiferans also from the same samples, including records of the genus *Globigerinelloides*.

From the black shale level of Quiricó Formation, several arthropod microfossil genera have been described, such as the spinicaudatans *Cyzicus* and *Palaeolimnadiopsis* (Rohn & Cavalheiro 1996, Delicio *et al.* 1998) and the ostracodan genera *Heterocypris*, *Eucyproides*, *Candonopsis*, *Harbinia*, *Cypridea*, *Bisulcocypris*, *Brasacypris*, *Ilyocypris*, *Darwinula* and *Wolburgiopsis* (Barbosa *et al.* 1970, Carmo *et al.* 2004). Additional arthropodan fossils occurrences are represented by a solely record, of the endemic heteropteran *Saucrolus silvai* (Santos 1971).

Vertebrate records are scarcer and, for a long time, were represented only by two occurrences of the teleostean fishes: the gonorynchiform *Dastilbe moraesii* (a junior synonymous of *D. crandalli*) and the endemic osteoglossiform *Laeliichthys ancestralis* (Scorza & Santos 1955, Santos 1985). Posteriorly, remains of coelacanthiforms were assigned to the *Mawsonia gigas* (Carvalho & Maisey 2008). Other records include cephalic and fin spines associated with hybodontiforms sharks, amiid vertebrae, semiotitiform scales, isolated scales and a partial skeleton of a Lepisosteidae and, more recently, a dental plaque associated with a complete pterygopalatine bone of a Dipnoi, assigned to the genus *Ceratodus* (Carvalho & Maisey 2008, Bittencourt *et al.* 2015 and 2017, De Carvalho 2017).

Carvalho and Kattah (1998) describes theropod and ornithopod dinosaur footprints in aeolian facies. The authors pointed that these ichnological records came from the basal portion of the sedimentary sequence, equivalent to the Abaeté Formation. However, Bittencourt *et al.* (2015) correlate this occurrence as belonging to the Três Barras Formation. Recently, undescribed sauropod tracks have also been reported, probably from the Três Barras Formation (Mescolotti 2017). Pires Domingues (2009) made the first mentions of dinosaur body-fossils. Alongside the titanosaurian specimens, Zaher *et al.* (2011) cited the presence of an abelisauroid theropod associated to the *Tapuiasaurus* skeleton.

Additionally, Da Silva (2013) describes mesopodial and epipodial remains of another theropod right hindlimb with noasaurian affinities.

According to Bittencourt *et al.* (2015), some other dinosaur specimens from Quiricó Formation await for a detailed description. These isolated remains were recovered from the vicinities of the Coração de Jesus, in the Lagoa dos Patos and Ibiaí municipalities. They includes several isolated bone fragments (Vieira *et al.* 2015), as well as some isolated teeth were preliminary attributed to abelisaurids, carcharodontosaurids and dromaeosaurids (Carvalho *et al.* 2012, Santucci *et al.* 2014).

More recently, fragmentary remains of rebbachisaurids (a caudal neural spine and diapophysis), abelisaurid and carcharodontosaurid teeth are described for the Quiricó Formation (De Carvalho & Santucci 2018).

1.3.3. Reevaluation of the Quiricó Formation age

The deposition age of the Cretaceous sequence of SFB possesses a debated history, as well as other Brazilian continental deposits, such as Bauru and Parecis Basins (Batezelli *et al.* 2017). Nevertheless, as explained by Zaher *et al.* (2011), the SFB were constrained by two remarkable magmatic events, at the bottom and top of the sedimentary sequence respectively, which are helpful to constrain the interval between the beginning and the end of sedimentation (Campos & Dardenne 1997, Sgarbi 2001). The basal portion of this basin postdates the Paraná-Etendeka continental flood basalt event, dated at 138-128 My (Valanginian to Hauterivian time-interval, Turner *et al.* 1994). In the top, alkaline ultrabasic lavas and volcanoclastic rocks of Patos Formation, which possesses ages ranging from 95-76 My (Cenomanian to Campanian) based on the K/Ar method (Hasui & Cordani 1968, Sgarbi 2004, Riccomini 2005). The latter magmatic event are coeval to the Late Cretaceous sedimentation, which the volcanic rocks occurs intercalated with sandstones from the top of Mata da Corda Group (Sgarbi 2001). These ages are also contemporaneous to the magmatic activity occurring in Southeastern Brazil, relative to the Alto Paranaíba Uplift, that derives from the Trindade Mantle Plume Event (Thompson *et al.* 1998).

Until the last decade, only few macrofossils occurrences have been previously reported for the lacustrine deposits of the Quiricó Formation, hampering major biostratigraphical correlations. The fossil records that began to elucidate a more specific age for this formation, and the Cretaceous Sequence of SFB as well, was represented by the

teleostean fishes remains recovered in limestones facies. They includes the ostariophysian *Dastilbe moraes* (now a junior synonymous of *D. crandalli sensu* Brito & Amaral 2008). The record of *Dastilbe* is important for biostratigraphic correlations, because it indicate for a first time a minimum Aptian age for these deposits. This taxon also occurs in other Brazilian units, such as the Codó (Parnaíba Basin), Crato (Araripe Basin) and Maceió formations (Sergipe-Alagoas Basin) with occurrences also in the Equatorial Guinea (Santos & Carvalho 2004), indicative of a probable contemporaneity between these units (Carvalho & Masey 2008, Bittencourt *et al.* 2015).

Bones of the coelacanthid sarcopterygian *Mawsonia gigas* were found at black shale facies (Carvalho & Masey 2008). However, this taxon have an extensive temporal range (Berriasian to Cenomanian), incompatible with the volcanic ages that beacon the SFB (Zaher *et al.* 2011). In addition, other age-informative “fish” records from the top of Quiricó Formation includes a dental plaque associated with a pterygopalatine bone of a Dipnoi, which were assigned to the genus *Ceratodus* (De Carvalho 2017), This taxon have been also recorded in other Brazilian units, such as the Albian-Cenomanian Alcântara Formation (São Luís-Grajaú Basin).

Further, besides the previously reported dinosaur remains (Kattah & Carvalho 1997, Zaher *et al.* 2011, Da Silva 2013), additional fragmentary specimens (*e.g.* rebbachisaurid bones and carcharodontosaurid teeth) has been described for the Quiricó Formation (De Carvalho & Santucci 2018). These two dinosaur groups were typical faunal components of Early to “Mid-Cretaceous” (Aptian-Cenomanian) dinosaur communities, especially in North Africa and Argentina (Bittencourt & Langer 2011 and 2012). Therefore, except for the *Dastilbe* occurrence, the vertebrate record of Quiricó Formation cannot constrain an age more restricted than the Early Cretaceous time-interval.

The micropaleontological data was useful to constrain specific ages for the dinosaur-bearing beds of the Quiricó Formation (Figure 24), pointing this unit into the Barremian-Aptian boundary. Several arthropod microfossil genera have been described in claystones facies below and above of the black shale level at Carmo do Parnaíba and Rio do Sono localities. Them consists of the controversial-aging spinicaudatans *Cyzicus* and *Palaeolimnadiopsis* (Rohn & Cavaleiro 1996, Delício 1998) and ten non-marine ostracodan genera (*e.g.* *Heterocypris*, *Eucyproides*, *Candonopsis*, *Harbinia*, *Cypridea*, *Bisulcocypris*, *Brasacypris*, *Ilyocypris*, *Darwinula* and *Wolburgiopsis*; Barbosa 1970, Carmo *et al.* 2004).

The association of three ostracodans (*Darwinula martinsi*, *Brasacypris* sp. 1, and *Harbinia symmetrica*?) supports the Barremian-Aptian age, due these taxa have been previously recorded in Codó and Crato Formations. One of them (*Brasacypris ovum*), are earlier recognized from older units (the Neocomian Itaparica and Candeias formations of Recôncavo-Tucano Basin). Three others (*Ilyocypris* sp., *Wolburgiopsis plastica* and *Wolburgiopsis chinamuertensis*) were previous recovered from La Amarga Formation (Neuquén Basin), Argentina. The occurrence of *Wolburgiopsis plastica* and *Wolburgiopsis chinamurtensis* also supports a Barremian age for these deposits because they are restricted to this time-interval (Carmo *et al.* 2004).

Terrestrial palynomorph taxa have been also recovered from the black shale level of Quiricó Formation. Among them, the record of *Transitoripollis* (= *Tucanopollis*) *crisopolensis* palynozone supports the previous hypothesis of a Late Barremian maximum age, at least for this level of the Quiricó Formation (Lima 1979, Bittencourt *et al.* 2015), due this pollen disappeared in the mid-Aptian time-interval (Maysei 2000). Furthermore, the remarkable record of *Afropollis*, recovered from the upper levels above the *Dastilbe* site, suggests an Early Aptian age for the strata overlaying the black shale (Arai *et al.* 1995, Bittencourt *et al.* 2015). Additionally, the Quiricó Formation contains a high count of other angiosperm pollen grains characteristic of the Barremian-Aptian boundary (*e.g.* *Sergipea* cf. *naviformis*; Arai *et al.* 1995, Zaher *et al.* 2011).

1.3.4. The *Tapuiasaurus macedoi* type locality

According Pires Domingues (2009) and Zaher *et al.* (2011), in the region where *Tapuiasaurus* specimens coming (Figure 25), the Early Cretaceous Areado Group comprises, from the bottom to the top, into the Abaeté, Quiricó and Três Barras Formations. The Abaeté Formation at Coração de Jesus outcrops is represented by a thin, up to 8 m thick, package of conglomerate and sandstones deposited under alluvial fans to braided fluvial systems. The Quiricó Formation is present as a succession of typical lacustrine deposits, composed by claystones, siltstones, limestones and minor shale with sandstone intercalations facies, which reaches up to 100 m in thickness. The upper and overlaying Três Barras Formation is a thick, up to 140 m, succession of aeolian, fluvial-deltaic and fluvial meandering sandstones and minor conglomeratic sandstones, with scarce centimetric pebbles of quartz (*op. cit.*).

The occurrence of the silt-clayey levels with convolute bedding, associated with calcrete horizons and sandstone lenses, led some authors to interpret that the lacustrine deposits of Coração de Jesus may represent a new lithostratigraphic unit (Pires Domingues 2009, Bittencourt *et al.* 2015). However, the presence of the Abaeté and Três Barras formations associated, at the base and overlaying respectively, confirms that these deposits are correlate with the Quiricó Formation. A possible explanation of the discrepant pattern of these levels from the typical Quiricó Formation lithology (*e.g.* shales and mudstones), consists of these levels represent deposits generated in the margin of the lacustrine body and the typical lithology of Quiricó Formation derived from basal levels of the lacustrine system, evidenced by the presence of black shale levels.

1.3.5. Taphonomical remarks

Pires Domingues (2009) has provided an extensive taphonomic study from the Quiricó Formation dinosaur-beds. The data obtained by this author indicate that the studied fossil accumulations in Coração de Jesus outcrops occur in alluvial fans sediments of a marginal lacustrine environment, representing an autochthonous concentration with possible temporal mixing. In the main outcrops were present sauropod and theropod associations (CJ-01 and CJ-04). *Tapuiasaurus* has been found in the CJ-04 outcrop associated with an articulated abelisaurid theropod skeleton, found below its cervical series (Zaher *et al.* 2011).

According to Pires Domingues (2009), the direction and the dip of the bony elements indicates that the history of this accumulation included a prolonged biostratinomic phase, occurring the biodegradation of carcasses on the border of the lacustrine system (*e.g.* presence of drying cracks). A partial disarticulation of the skeletons of some individuals occurred, especially those of large size, by biotic factors such as necrophagy (*e.g.* presence of teeth marks in long bones and ribs). Subsequently, there was partial burial and bone reorientation, mainly in the anterior and posterior limbs, by debris flows that reached the lacustrine system. The neck of *Tapuiasaurus* were found almost articulated (Figure 26), displaying the typical posteriorly turned *rigor mortis*, indicative that this part of the skeleton stay exposed from a determined period before the total burial. On the other hand, the base of the neck and rib cage of this individual is disposed in a chaotic way. The processes related to the fossil diagenesis included the plastic deformation of the bones due to the lithostatic pressure, the fracture of the bones due to the rearrangement of the deposits and, finally, the subaerial exposure and weathering by the current environment, causing some modules to be lost, such as the pelvis (Pires Domingues 2009).

2 - Objectives

This research was divided into three main objectives:

- (I) To describe in detail the postcranial skeleton of the holotype specimen of *Tapuiasaurus macedoi* (MZSP-PV 807), because it is the most complete titanosaur recovered in the Lower Cretaceous Quiricó Formation so far, and one of the most complete Early Cretaceous titanosaurs known to date;
- (II) To compare the holotype specimen of *Tapuiasaurus macedoi* (MZSP-PV 807) with other individuals from the same locality and from coeval deposits, as well as with different taxa previously described for other Brazilian (*e.g.* Bauru Basin) and South American (*e.g.* Neuquén Basin) Cretaceous units;
- (III) Submit the studied specimens to a cladistic analysis, in order to assess the phylogenetic relationships of *Tapuiasaurus macedoi* and the associated forms within Titanosauria, as well as to identify patterns in early titanosaurian evolution.

3 - Material and Methods

3.1. Material

3.1.1. Studied specimens

The specimens whose constitute the study-object of this research, were collected in several field seasons, occurred between 2005 and 2012, in the vicinities of Coração de Jesus Municipality, northern region of Minas Gerais State (Pires Domingues 2009, Zaher *et al.* 2011, Silva 2013). These collecting campaigns were included in the scope of the thematic project “Evolution of reptile fauna in Southeastern Brazil from the Late Cretaceous to the Recent: paleontology, phylogeny and biogeography”, under the coordination of Prof. Dr. Hussam El Dine Zaher and promoted by FAPESP - Fundação de Amparo à Pesquisa do Estado de São Paulo (Foundation for Research Support of the São Paulo State; grant 02/13602-4). The Table 3.4. presents the detailed list of all specimens collected and those that be used in this study.

3.1.2. Specimens employed in comparisons

The taxonomic sampling has chosen due their relevance to phylogenetic objectives of this study, and because they represent a set of taxa with the preservation of anatomical regions of interest as well. They are deposited in institutions in Brazil and Argentina (Table 3.5.). In addition, the specimens studied here has been also compared with taxa described in the literature that belongs to other localities (*i.e.* Africa-Madagascar, North America, Asia, Australia, Europe and India). Given the logistical limitations and the short period of thesis, these specimens should not be examined in person and were compared based on the published information (see cap. 3.4. on the volume II).

3.2. Methods

3.2.1. Osteological and directional terminology

For anatomical and directional nomenclature, the traditional “Romerian” terminology have been chosen over the veterinarian and avian alternatives, as proposed by Wilson (2006a, 2012). In this nomenclature “anterior” and “posterior” were used as directional terms rather than the veterinarian alternatives “cranial” (or “rostral”) and “caudal”, and anatomical structures are standardized (*e.g.* “centrum” or “centra”, not “corpus”). Additionally, the Romerian terminology considers the division of the vertebral bones into anterior, posterior, ventral, dorsal and lateral portions (left and right). Likewise, the appendicular bones (represented by propodial, mesopodial, metapodial and epipodial bones) are divided into the anterior, posterior, medial, lateral, proximal and distal portions.

Regarding to the identification and designation of vertebral laminae and fossae for Sauropoda (and other saurischian dinosaurs), was followed the landmark-based scheme proposed by Wilson (1999, 2012) and Wilson *et al.* (2011) respectively, with the addition of a few laminae suggested or redefined by other authors (Apesteguía 2005, Salgado & Powell 2010, Gallina 2011). For internal pneumatic bony tissue arrangement, this study followed the nomenclature proposed by Wedel *et al.* (2000).

3.2.2. Preparation and measurements of the specimens

The excavation and recovering of the studied specimens followed the traditional procedures and techniques largely used in field campaigns, such as the jacketing process, plaster using, plaster bandage and tow (Feldmann 1989, Leiggi *et al.* 1994, May *et al.* 1994). A separating layer of toilet paper and aluminium foil were used to prevent the plaster from sticking to the fossil bones. Part of the skeleton was partially prepared in the field to determine the position and composition of each specimen, to ensure that all of it was entire collected. To protect and preserve the integrity of the bones was used the resin Paraloid b-72 dissolved in acetone. The removal of rock matrix was done in the Laboratório de Paleontologia of the Museu de Zoologia of Universidade de São Paulo, Brazil, using several tools such as pneumatic hammers, air blasting systems, needles and pin vises. Measurements of the bone elements of the specimens were obtained using a digital calliper. Three acquisitions of each measure was taken in order to estimate a mean and avoid discrepant data.

3.2.3. Phylogenetic inference

The methodology applied to determine phylogenetic relationships is the cladistics, following the parsimony principles enunciated by Hennig (1966) and Nelson and Platnick (1991). The character were structured and scored following the logical basis proposed by Sereno (2007), and polarized through outgroup comparisons (Farris 1982). An equally weighted parsimony analysis (Kluge & Farris 1969, Farris 1970) were conducted using the software TNT v1.5, a program made freely available (www.lillo.org.ar/phylogeny/tnt) through the Willi Hennig Society (Goloboff *et al.* 2008, Goloboff & Catalano 2016).

3.2.3.1. Data matrix construction

In order to assess the phylogenetic relationships of *Tapuiasaurus* within Titanosauria, the type specimen (MZSP-PV 807) were scored in the matrix of Carballido *et al.* (2017), because this dataset is currently one of the most comprehensive in number of characters and taxa of interest. Additionally, new unpublished characters were chosen to incorporate the data-set (see cap. VI on Volume II). The incorporation of new characters was made under the Character Distribution Map method, as suggested by Whitlock and Wilson (2013). The proportion of character data included from different anatomical modules can often have major impact on the tree topologies. This method is helpful to the identification of patterns in character inclusion by body region (Whitlock & Wilson 2013).

3.2.3.2. Operational Taxonomic Units scoring

The Operational Taxonomic Units (OTUs) are equivalent to the studied specimens (specimen-level analysis), for this analysis that can incorporate and test phylogenetic signals derived from distinct morphological complexes. The taxa scoring are be done based on the suggestions made by Tschopp *et al.* (2017), in which an OTU consist of more than one specimen only when there a substantial anatomical overlap. The scoring of the studied specimens were made in the Mesquite software v3.6 (Maddison & Maddison 2017).

3.2.3.3. Heuristic tree search protocol

Due the large sampling, were employed the more elaborate search procedures known as “New Technology Search” under the command ‘*xmult = consense5;*’. A final round of TBR have been also performed to the best trees found during the replicates (command ‘*bb*’), in order to find all most parsimonious trees (MPTs). Unstable taxa in the MPTs were detected *a priori* using the “iterpcr” method in order to recover a reduced strict consensus that ignores the alternative positions of the highly fragmentary or unstable taxa (Pol & Escapa 2009).

The branch relative support for the MPT's has been calculated by statistical resampling methodologies, such as Bootstrap (Felsenstein 1985), and by the Decay Index or direct support measure method (Bremer 1994). Resultant trees were processed in FigTree (v.1.4.2).

3.2.4. Taxonomy

Since its first mention, over 150 years ago, Titanosauria had a complex taxonomic history (see Wilson & Upchurch 2003, Wilson 2006b, Tykoski & Fiorillo 2016). Recently, due the advance in inclusion of more complete taxa and well-structured characters into sauropod phylogenies, the identification of new titanosaurian clades generate several propositions of new names (*e.g.* Aeolosaurini, Rinconsauria, Lognkosauria, Lirainosaurinae; Salgado *et al.* 1997, Sereno 1998, Wilson & Sereno 1998, Sanz *et al.* 1999, Franco Rosas *et al.* 2004, Calvo *et al.* 2007a and 2007b, Díez Díaz *et al.* 2018), as well as re-definitions and arguments to abandon or not previously established names (*e.g.* Titanosauridae; Wilson & Upchurch 2003, Salgado 2003, Upchurch *et al.* 2004).

For this reason, this work compiled all taxonomic definitions yet proposed regarding to the titanosaur systematics (Table 3.2.) as well as of the immediate ancestor clades, in order to accommodate the recovered groups through the phylogenetic analysis.

6 - Conclusions

1. *Tapuiasaurus* was previously diagnosed through 11 autapomorphies present in their cranial skeleton, as well as by an autapomorphic combination of characters which is revised here. In this study, four more putative autapomorphies are added to the skull and mandible diagnosis of this taxon;
2. Based on its postcranial skeleton, *Tapuiasaurus* is diagnosed by 12 additional putative autapomorphies that differentiates it from other titanosaurian taxa. Additionally, this taxon can be diagnosed by the unique autapomorphic combination of approximately 30 characters;
3. The phylogenetic analysis results, as well as the extensive osteological analysis of its postcranial skeleton, refute the hypothesis of *Tapuiasaurus* is deeply nested among advanced eutitanosaurian clades. This study recovered *Tapuiasaurus* as basal lithostrotian titanosaur, being more related to Early Cretaceous forms;
4. Through osteological comparisons, was identified that *Tapuiasaurus* shares eight synapomorphic characters with other two taxa (*Yongjinglong* and the Prata titanosaur), which was also recovered posteriorly by the phylogenetic analysis performed, supporting this clade by 11 additional synapomorphies. Here this group is provisionally named as Tapuiasaurinae. In addition, this study also recovered another group composed by endemic Brazilian titanosaurs, called as Trigonosaurinae, and supported by a unique combination of 11 characters;
5. The age of the Quiricó formation, unit that *Tapuiasaurus* comes, is reviewed here, in which it assumes a Barremian-Aptian age for these deposits;
6. Based on actual knowledge about titanosaur fossil record and paleogeographic data, true-titanosaurs already are well-dispersed at the beginning of Cretaceous, supporting a Late Jurassic cladogenesis for the group or, at least, at the Jurassic-Cretaceous boundary;
7. This study reveals that the stepwise acquisition of the typical titanosaurian characters possesses a mosaic pattern, in which the apomorphic anatomy presented by the advanced titanosaurians was acquired along the last part of the Late Cretaceous, probably in the post Turonian time-interval (89.8 My).

Resumo

É apresentada aqui uma abrangente descrição do esqueleto pós-craniano e análise filogenética do titanossauro do Cretáceo Inferior *Tapuiasaurus macedoi* Zaher *et al.* 2011. *Tapuiasaurus* representa um táxon-chave devido à sua alta completude, lançando novas luzes nos primeiros passos na evolução dos titanossauros. As novas informações coletadas por este estudo revelam que a anatomia das vértebras pré-sacrais de *Tapuiasaurus* possui uma típica morfologia litoestrotiana apomórfica (*e.g.* espinhos neurais não divididos, ausência do complexo hiposfeno-hipantro e de processos aliformes), enquanto que a arquitetura dos membros anteriores e posteriores retém caracteres plesiomórficos, como a presença de falanges manuais, bem como um pé com alta contagem falangeana (=10). Contrariando estudos anteriores, a análise filogenética realizada recuperou *Tapuiasaurus* como um litoestrotia basal, táxon-irmão do grupo formado por *Yongjinglong datangi*, do Cretáceo Inferior da China, mais um táxon relictual não nomeado do Cretáceo Superior do Estado de Minas Gerais, a mesma região geográfica na qual *Tapuiasaurus* provém. O novo clado reconhecido representaria uma das primeiras irradiações de litoestrotios em todo o mundo, fornecendo dados adicionais que ajudarão a elucidar os padrões de dispersão do grupo. Este estudo revela que a aquisição dos caracteres titanossaurianos típicos foi gradual, possuindo um padrão de mosaico, no qual a anatomia apomórfica apresentada pelos titanossauros avançados foi adquirida ao longo da última parte do Cretáceo Superior, provavelmente a partir do intervalo pós-Turoniano (89,8 M).

Palavras-chave: Cretáceo Inferior, Titanosauria, *Tapuiasaurus macedoi*, Osteologia, Filogenia.

Abstract

Herein is presented a comprehensive description of the postcranial skeleton and phylogenetic analysis of the Early Cretaceous titanosaurian *Tapuiasaurus macedoi* Zaher *et al.* 2011. *Tapuiasaurus* becomes a key-taxon due its completeness, shedding new lights on the first steps in the early titanosaur evolution. The new information gathered by this study reveals that the presacral vertebrae anatomy of *Tapuiasaurus* possesses the typical apomorphic lithostrotian morphology (*e.g.* single neural spines, absence of hyposphene-hypantrum complex and aliform processes), whereas the architecture of fore and hindlimbs retains plesiomorphic characters, such as the presence of manual phalanges, as well as a pes with greater phalangeal count (=10). Contrasting with previous studies, the phylogenetic analysis retrieved *Tapuiasaurus* as an early lithostrotian, sister-taxon of the group formed by *Yongjinglong datangi*, from the Early Cretaceous of China, plus a relictual unnamed taxon from the Late Cretaceous of Minas Gerais State, the same region that in which *Tapuiasaurus* comes. The new recognized clade that would represents one of the first lithostrotian irradiations around the world, providing additional data that will help elucidate dispersion patterns in the group. This study reveals that the stepwise acquisition of the typical titanosaurian characters possesses a mosaic pattern, in which the apomorphic anatomy presented by the advanced titanosaurians was acquired along the last part of the Late Cretaceous, probably in the post Turonian time-interval (89.8 My).

Key-words: Early Cretaceous, Titanosauria, *Tapuiasaurus macedoi*, Osteology, Phylogeny.

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