Bruno Albert Navarro

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Advisor: Prof. Dr. Hussam El Dine Zaher

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Dedicatory

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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Summary

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 (Abelisauroidea) 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 it 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 somphospodylian, 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 titanosaurians from the earliest Cretaceous (Berriasian-Valanginian, Santucci 2005), although it being likely related to brachiosaurids rather than titanosaurians (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 titanosaurians 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 titanosaurian 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 titanosaurians. 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 (Titanosauroidea, 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 amphyplatyan 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 Titanosauroidea 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 Titanosauroidea. Within Titanosauroidea, 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, Titanosauroidea) 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 titanosaurians, 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 Titanosauroidea, Eutitanosauria, Saltasaurinae and Opisthocoelicaudinae, as well as creating the stem-based clades Epachthosaurinae and Andesauroidea.

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).

1.2. The Brazilian titanosaur fossil record

1.2.1. Historical background

Titanosaurs represent the most expressive group (Figure 10), in terms of number of occurrences and species diversity, among Brazilian dinosaurs (Santucci & Bertini 2001). However, most of its numerous findings consist mainly of axial materials, often found as isolated or disarticulated bone elements (Santucci & Bertini 2001, Santucci 2002). Another particularity of the forms found in Brazil, is that most of the species come from the Late Cretaceous deposits.

The first mention of titanosaur fossils in the country dates back to 1883 (Kellner & Campos 2000). Skeletal remains were found in deposits of the Parecis Basin, outcropping northeast of the city of Cuiabá and in the locality called "Morro do Cambambe", Mato Grosso state, being also cited by Derby (1890). In the Bauru Basin, the most prolific Brazilian unit regarding the number of titanosaurian species, the first record of these animals probably corresponds to the fragments of bones and teeth initially referred to *Thecodontosaurus* by Woodward (1910).

In addition, also from the Bauru Basin deposits, Pacheco (1913) reported the discovery of a procoelous caudal vertebra found near the Colina train station, São Paulo state. However, the author interpreted this material as belonging to a crocodiliform (Mezzalira, 1966). The same specimen was posteriorly identified as belonging to "*Titanosaurus*" (= *Neuquensaurus*) *australis* by Huene (1929). Subsequently, Huene (1931) made mentions of the occurrence of several undetermined vertebrae and bones of titanosaurs in the Municipality of Monte Alegre de Minas, Minas Gerais state, and a partial postcranial skeleton coming from Pedras locality, Mato Grosso state, which is sent to the London Natural History Museum. The latter occurrence may correspond to the specimen reported by Derby (1890).

In the late 1940s, Price (1947) related the discovery of some sauropod caudal vertebrae, which may correspond to remains of titanosaurs, at the deposits of the "Itapecuru Formation" (previously considered with a Tertiary age), São Marcos Bay, Maranhão state. According to Price (1961), in 1948 the first remains of titanosaurians were found in the region of Peirópolis, Uberaba (Minas Gerais state), recovered from a railway section of the former Estrada de Ferro Mogiana, on sediments corresponding to the Marília Formation of the Bauru Basin (Santucci 2002).

Mezzalira (1948, 1959, 1966) reported the presence of titanosaurian remains from the western region of the São Paulo state, at the Florida Paulista and Pacaembu Paulista municipalities also on rocks of Bauru Basin. One of these specimens (six caudal vertebrae and a femur) were collected during the construction of the railroad stretch between Adamantina and Irapurú municipalities. Nonetheless, they were only described in detail 50 years later by Santucci and Bertini (2006a) that erected the new species *Adamantisaurus mezzalirai* (see below). Mezzalira (*op. cit.*) still cites several titanosaur occurrences in the west and north of São Paulo state (*e.g.* Pacaembú, Catandúva).

Arid *et al.* (1962) reported the discovery of fragmentary titanosaur bones on the outskirts of São José do Rio Preto Municipality and according to these authors would be related to the same individual. This occurrence, posteriorly, it would be the first titanosaur formally described in Brazil: "*Antarctosaurus brasiliensis*" (Arid & Vizotto 1971). In addition, Arid and Vizotto (1963) mentioned the discovery of a large amount of fossils in Ibirá, São Paulo, mostly disarticulated and poorly preserved, and associated them with titanosaurians.

During the last half of the 20th century, several titanosaur specimens are reported for the Bauru Basin, mainly from the São Paulo state (Maciel 1962, Arid & Vizotto 1971, Leonardi & Duszczac 1977, Bertini & Campos 1987, Cunha *et al.*, 1987). However, the most significant advance in the study of Brazilian titanosaurs was observed from the 1990s. New taxa were described for the Bauru Basin (see below), many of them resulting from Price's collection campaigns between the decades of 1940-1970 (Bittencourt & Langer 2012).

The most extensive works done so far with the Brazilian titanosaurs, mainly from the Bauru Basin, comes from Santucci (1999, 2002). The author cataloged approximately 130 occurrences through a study of previous literature (Santucci 1999), as well as visits to collections and field works (Santucci 2002). The same author was the first to perform a cladistic analysis with the main objective of studying the phylogenetic relationships between the forms found in the Bauru deposits.

Finally, in the last decade, titanosaurs have been described in other Brazilian basins, such as the Sanfranciscana, Rio do Peixe and Potiguar Basins (Zaher *et al.* 2011, Carvalho *et al.* 2017, Pereira *et al.* 2018). These findings place the study of Brazilian titanosaurs at a new level, given that the forms found in the northernmost regions of the country come from the Lower Cretaceous strata, broadening the understanding of the evolution of the first titanosaurs.

1.2.2. Brazilian titanosaurians

In this chapter, were compiled a basic data set of previously published information regarding to the nominal titanosaur species from Brazil, as well as of some unpublished taxa whose are still under study by several Brazilian researchers. These specimens were employed in the comparisons and phylogenetic analyses performed by this study (see Table 3.5.). The descriptions and comparisons presented in this chapter were based on the literature and personal observation of the specimens, and are accompanied by a brief diagnosis that had been used by the authors to establish these taxa. Additionally, was provided general remarks about your diagnosis, as well as its anatomy, phylogenetic relationships and proposed taxonomic assessments. For ethical reasons the cited new genus and species that still under study were distinguished in the text, having only the most relevant information compiled and not being figured in a way does not to prejudice the subsequent publications and descriptions.

1.2.2.1. Systematic Paleontology

DINOSAURIA Owen 1842
SAURISCHIA Seeley 1887
SAUROPODOMORPHA Huene 1932
SAUROPODA Marsh 1878
NEOSAUROPODA Bonaparte 1986
TITANOSAURIFORMES Salgado, Coria & Calvo 1997
SOMPHOSPONDYLI Wilson & Sereno 1998
aff. TITANOSAURIA Bonaparte & Coria 1993
incertae sedis muttabilis

Triunfosaurus Carvalho, Salgado, Lindoso, Araújo-Júnior, Nogueira & Soares 2017

Type species:
Triunfosaurus leonardii Carvalho *et al.* 2017
Type by monotypy

Figure 11

Etymology. The genus name derives of the locality where the type specimen comes from, the Triunfo Basin (Rio do Peixe Basins Complex), plus *saurus*, which is the Greek word for lizard or reptile. The species name is in honor of the paleontologist Giuseppe Leonardi, which dedicated to the study of the reptile ichnofauna from the northeastern Brazil, especially the record of Rio do Peixe Basins Complex (Carvalho *et al.* 2017).

Type material. A fragmentary postcranial skeleton, composed of three articulated middle-posterior caudal vertebrae (UFRJ-DG 498-K-R), one right ischium (UFRJ-DG-498-a-R), three isolated haemal arches (UFRJ-DG-498-b-R, UFRJ-DG-498-d-R and UFRJ-DG-498-f-R) and three isolated neural spines (UFRJ-DG-498-g-R, UFRJ-DG-498-h-R and UFRJ-DG-498-i-R), belonging to the same individual (Carvalho *et al.* 2017). These materials are deposited at Departamento de Geologia of the Universidade Federal do Rio de Janeiro (UFRJ-DG).

Diagnosis. *Triunfosaurus* is characterized by the following combination of characters, which the indicated with asterisks are potential autapomorphies recovered in the phylogenetic analysis carried by Carvalho *et al.* (2017): (1) mid-anterior caudal vertebrae with short and robust prezygapophyses, directed anteriorly and slightly inclined upward; (2) low caudal neural spines, possessing a sagittal process expanded at its posterodistal ends; (3) transverse process inclined upward and slightly oriented posteriorly; (4) posterior half of the centrum with lateral faces strongly concave and having small pneumatophores; (5) straight anterior chevrons with articular surfaces dorsally directed; (6) middle chevrons anteroposteriorly compressed, with articular surfaces of the proximal processes directed posterodorsally and distal processes reduced; (7)* anteroposterior pubic pedicel of the ischium divided by the total length of the ischium larger than 0.5; (8)* close angle (less than 70º) formed between the shaft and the acetabular line of the ischium.

Horizons and type locality. The bone remains of *Triunfosaurus* were collected at Areias Farm, located in the Triunfo Municipality , Paraíba State. In this region, outcrops facies of the Rio Piranhas Formation, Triunfo Basin, composed by coarse grained immature sandstones, medium grained sandstones, breccias and polymictic conglomerates (Carvalho *et al.* 2017). The Lower Cretaceous Rio Piranhas Formation is aged at Late Hauterivian to Early Barremian time-interval based on ostracodan and palynozones associations (Arai 2006).

General remarks. *Triunfosaurus* represents the first named tetrapod taxon from Rio do Peixe Basins Complex based on body-fossils (Carvalho *et al.* 2017). Alongside *Triunfosaurus*, Ghilardi *et al.* (2016) earlier described an isolated left fibula from the same horizons at Lagoa do Forno locality, Sousa Municipality , which is informally nicknamed of "*Sousatitan*" in the media. According to the senior author (A. M. Ghilardi, personal communication 2017), both occurrences may pertain to the same taxon, although is needed more materials with anatomical overlapping to evaluate this issue.

Triunfosaurus is diagnosed based on a combination of eight characters, in which two of them may be autapomorphic according the phylogenetic analysis carried by the authors (chars. 7 and 8, Carvalho *et al.* 2017). The first and second characters (*i.e.* short and robust prezygapophyses on mid caudal vertebrae directed anteriorly and slightly inclined upward, and the sagittal process expanded at its distal ends) are homoplastic for some late titanosaur lineages (lognkosaurians, aeolosaurines and rinconsaurians), such as the Brazilian taxa *Gondwanatitan, Trigonosaurus, Adamantisaurus, Uberabatitan* and "*Aeolosaurus*" *maximus* (Kellner & Azevedo 1999, Campos *et al.* 2005, Santucci & Bertini 2006a, Carvalho & Salgado 2008, Santucci & Arruda Campos 2011).

The third character (transverse process inclined upward and oriented posteriorly) is also shared with several other titanosaurians, such as *Trigonosaurus* (DGM) and "*Aeolosaurus*" *maximus* (Campos *et al.* 2005, Santucci & Arruda Campos 2011). *Triunfosaurus* additionally share with *Trigonosaurus, Adamantisaurus* and "*Aeolosaurus*" *maximus* laterally enlarged neural spines those forming dorsolateral bulges, thick PRSL and POSL, well-developed SPRL and dorsally projected postzygapophyseal processes. Nonetheless, *Triunfosaurus* also displays a set of plesiomorphic features as a platycoelous type articulation, relating this taxon to early titanosaurians such as *Mnyamawamtuka* (Gorscak & O'Connor 2019). Additionally, *Triunfosaurus* exhibit a bulge on the anterior surface of posterior chevron, which can be autapomorphic for this taxon.

Although fragmentary, *Triunfosaurus* is very important for the understanding of macroevolutive and paleobiogeographical patterns in early titanosaur evolution, supporting the hypothesis of a Gondwanan origin for Titanosauria during the earliest Cretaceous (Neocomian), maybe in South America or Africa (Gorscak & O'Connor 2016), also corroborated by other fragmentary occurrences, such as *Algoasaurus* from Valanginian-Hauteriavian Kirkwood Formation (McPhee *et al.* 2016).

TITANOSAURIA Bonaparte & Coria 1993

incertae sedis muttabilis

Antarctosaurus Huene 1929

Type species*:*
Antarctosaurus wichmannianus Huene 1929

Included species*:*
Antarctosaurus giganteus Huene 1929 (*nomen dubium*)
Antarctosaurus septentrionalis Huene & Matley 1933
(= *Jainosaurus septentrionalis* gen. nov. Hunt *et al.* 1994)
Antarctosaurus jaxarticus Riabinin 1933 (*nomen dubium*)

Antarctosaurus brasiliensis Arid & Vizotto 1971

Figure 12

Taxonomical assessments:
Antarctosaurus brasiliensis gen. et sp. nov. (Arid & Vizotto 1971)
"*Antarctosaurus*" *brasiliensis nomen dubium* (Santucci & Bertini 2001)
"*Antarctosaurus brasiliensis*" *nomen dubium* (Powell 2003)
Antarctosaurus sp. indet. (Santucci 2002)

Etymology. The generic epithet derives from the Greek words *anti* (which means "opposite of"), plus *arktos* ("north") and *sauros* ("lizard"), and refers to geographical location of those species (*A. wichmannianus* and *A. giganteus*), on a southern continent. Likewise, the specific name refers to the provenance of this species, Brazil.

Type material. A very fragmentary postcranial skeleton composed of a proximal half of a right humerus (GP-RD-3), a fragmentary dorsal vertebra (GP-RD-4) and a left femur lacking the proximal end (GP-RD-2) that may belong to the same individual. This specimen is deposited in the collection of the Museu de Geologia of the Universidade Estadual Paulista Julio de Mesquita Filho (MG-UNESP). Additionally, the authors cite the presence of other undetermined associated materials, but do not provide images or descriptions.

Referred material. An additional specimen, known by an isolated dorsal centrum may pertain to the same form, and is deposited at Laboratório de Paleoicnologia e Paleoecologia (LPP-UFSCar) of the Universidade Federal de São Carlos.

Diagnosis. Arid and Vizotto (1971) diagnosed this species based solely by the robustness indexes of the type specimen, in which it is slenderer than the specifier of the genus.

Horizons and type locality. The type specimen was found in the São José do Rio Preto Municipality , northern part of São Paulo State, in an outcrop located at the kilometer 5 of the São José do Rio Preto - Barretos State Highway. In this region, outcrop sediments of the homonymous unit São José do Rio Preto Formation and, according to the authors, the materials were found by laborers working on this highway, in facies of a fine and massive sandstones intercalated with siltstones (Arid & Vizotto 1971). The additional specimen was found in the same unit at Vila Ventura, Ibirá Municipality , São Paulo State, at conglomeratic sandstones. This unit is aged on Santonian - Campanian time-interval based on carophyta algae and palynomorphs (Dias Brito *et al.* 2001).

General remarks. "*Antarctosaurus brasiliensis*" was the first titanosaur formally described in Brazil. The material was initially reported by Arid *et al.* (1962) and subsequently described by Arid and Vizotto (1971). "*A. brasiliensis*" is a large-sized titanosaur, which its humerus is estimated in 0,95m in length and the femur at 1,55m (*op. cit.*). However, this taxon was based on very fragmentary remains, lacking apomorphies that differentiates it from other titanosaurs (Santucci 2002). Powell (2003) considers that the morphological characteristics observed in the three bones that compose the type material are insufficient for the recognition of a new taxon, considering it a *nomem dubium*.

According to Arid and Vizotto (1971) and Santucci (2002), the attribution of this specimen to the genus *Antarctosaurus* is due to similarities that the Brazilian material shares with the type material of *Antarctosaurus wichmannianus* Huene 1929, from the Upper Cretaceous (Santonian-Campanian) Anacleto Formation of Argentina. The main similarities are observed in the morphology of the humerus that has a straight dorsolateral contour at the proximal margin, as well as by position of the fourth trochanter, which is located just above its middle portion. Additionally, Arid and Vizotto (1971) remark that specimen are virtually slenderer than other titanosaurs known at the epoch.

Comparisons with dorsal elements cannot be performed due to the absence of that records for the type specimen of *Antarctosaurus* (Huene 1929, Arid & Vizotto 1971) and according Bertini (1993 *apud* Santucci 2002), especially for this reason, the allocation of the specimen in this genus becomes dubious. Despite the similarities, due to the low preserved sampling is very tentative to evaluate if these characteristics represent synapomorphies, as well as if the differences of the robustness indexes observed by the authors are sufficient to differentiate the Brazilian form of other *Antarctosaurus* occurrences (Santucci 2002).

Nevertheless, "*A. brasiliensis*" shares with *Jainosaurus septentrionalis* some characters, such as an obliquely oriented insertion of the deltopectoral crest and a proximolateral bulge on the deltopectoral crest (Wilson *et al.* 2009), the latter also shared with other titanosaurs such as *Tapuiasaurus.* In addition, "*A. brasiliensis*" shares with *Tapuiasaurus* taxon a vertical fossa, between the deltopectoral crest and the lateral margin of the humerus. The "*A. brasiliensis*" humerus also bears an anterior protuberance proximomedially.

The position of the fourth trochanter of the femur, allied to its gracile constitution, are indicative of it represents, at least, a closely related taxon to *Antarctosaurus* (Huene 1929). In summary, the main characteristics presented by this specimen are shared among several titanosaurs, not being sufficient to attribute a diagnosis of generic or specific level and new findings are needed to better evaluate their phylogenetic relationships and the validity of this taxon.

LITHOSTROTIA Upchurch, Barret & Dodson 2004
LOGNKOSAURIA Calvo, Porfiri, González-Riga & Kellner 2007

Austroposeidon Bandeira, Simbras, Machado, Campos, Oliveira & Kellner 2016

Type species:
Austroposeidon magnificus Bandeira *et al.* 2016
Type by monotypy

Figure 13

Etymology. The generic epithet is formed by the words "*Austro*", which means "Southern" in allusion to South America, and "*Poseidon*", in reference to the Greek God responsible for earthquakes. The specific epithet is composed of Latin adjective "*magnificus*", meaning "great, elevated, noble" in allusion to the large size of this species (Bandeira *et al.* 2016).

Type material. A fragmentary disarticulated postcranial skeleton belonging to the same individual, which is composed by remains of two incomplete cervical vertebrae, one cervical rib, one dorsal vertebra, seven fragments of dorsal vertebrae and a fragment of a sacral vertebra (MCT 1628-R), deposited at Museu de Ciências da Terra of the Companhia de Pesquisa de Recursos Minerais (CPRM, anteriorly known as DNPM).

Diagnosis. Bandeira *et al.* (2016) diagnosed this species by the following autapomorphies: (1) columnar-like centropostzygapophyseal laminae (CPOL) in the last cervical vertebrae (Cv-13); (2) last cervical vertebra bearing a bifurcated posterior centrodiapophyseal lamina (PCDL); (3) first dorsal vertebra with the anterior and posterior centrodiapophyseal laminae (ACDL and PCDL) curved ventrolaterally and with the diapophysis reaching the dorsal margin of the centrum; (4) the anteriormost portion of the spinoprezygapophyseal laminae (SPRL) forked in the posterior dorsal vertebra.

Additionally, the authors distinguished *Austroposeidon* from other titanosaurs by the following combination of characters: (5) presence of medial ventral kell in the last cervical centrum; (6) presence of a lamina on pleurocoel, limiting it from the centrodiapophyseal fossae (CDF) in the last cervical vertebrae; (7) presence of developed centrodiapophyseal fossa (CDF) in the posterior cervical vertebra; (8) posterior cervical vertebrae with tall neural spines; (9) presence of triangular centropostzygapophyseal fossae (CPOF), around the neural channel in the posterior cervical vertebra; (10) thick SPRL in the anterior dorsal vertebrae; (11) developed SPDL in the anterior dorsal vertebrae; (12) strongly developed postzygaphophysis in the first dorsal vertebra; (13) neural spine of the first dorsal vertebrae in vertical position and anteriorly located; (14) PRSL in the anterior dorsal vertebrae well-developed, present entire in the neural spine; (15) diapophyses in the anterior dorsal vertebrae expanded anteroposteriorly and strongly inclined ventrolaterally; (16) presence of well-developed pneumatizated internal bone tissue in presacral vertebrae; (17) absence of hyposphene-hypantrum compex in the dorsal vertebra; (18) short and robust cervical ribs (Bandeira *et al.* 2016).

Horizons and type locality. According to Bandeira *et al.* (2016) the specimen was found at the Raposo Tavares highway (BR-374), close to intersection with the Assis Chateaubriand State Road (SP-425), vicinities of the Presidente Prudente Municipality, southwestern São Paulo State. At this region, outcropping sandstones and mudstones referred to the Campanian-Maastrichtian Presidente Prudente Formation.

LITHOSTROTIA Upchurch, Barret & Dodson 2004
RINCONSAURIA Calvo, González-Riga & Porfiri 2007

emendavit

***Emended diagnosis*:** Calvo *et al.* (2007b) erected the clade Rinconsauria based on the following association of characters: (1) slender sub-oval teeth (nearly "D-shaped") with labial and lingual faces differentiated by well-developed carinae which lacks denticles; (2) presence of bony processes supporting the postzygapophyseal articular surfaces (*i.e.* lateroposteriorly directed postzygapophyseal processes) in mid-caudal vertebrae; and (3) posterior caudal centra depressed posteriorly. Further, rinconsaurians also can be distinguished from others titanosaurs by possessing the following combination of characters: (4) dorsal vertebrae with low and acute neural spines, conspicuous in the anterior ones; (5) procoelous caudal vertebrae with restricted condyles ("ball-and-socket"); (6) procoelous mid to posterior caudal vertebrae intercalated by, at least, an amphicoelous and biconvex element.

***Included species*:** *Rinconsaurus caudamirus*, *Maxakalisaurus topai, Muyelensaurus pechenni*, *Pitekunsaurus macayai, Bonitasaura salgadoi*, *Uberabatitan ribeiroi,* and probably "*Titanosaurus indicus*".

***Temporal range*:** Late Cretaceous, Coniacian to Maastrichtian.

Maxakalisaurus Kellner, Campos, Azevedo, Trotta, Henriques, Craik & Silva 2006

Type Species:
Maxakalisaurus topai Kellner *et al.* 2006
Type by monotypy

Figure 14

Taxonomical assessments:

Titanosauridae gen. et. sp. indet. (Almeida *et al.* 2004)
Aeolosaurus sp. indet. (Candeiro *et al.* 2006)
Maxakalisaurus topai sp. nov. (Kellner *et al.* 2006)

Etymology. The generic name of this taxon is composed by the words "*Maxakali*", from the Macro-Jê stock language, honoring the Maxakali ethnic group that is present at the Minas Gerais State where this dinosaur was found, plus "*saurus*" which is the Greek word for lizard, commonly assigned to fossil reptiles. The specific name also derives from a Maxakali language, which "*Topa*" is a tribal god worshiped by the Maxakali ethnic group (Kellner *et al.* 2006).

Type material. A fragmentary partial skeleton of a juvenile individual (MN 5013-V), composed of an incomplete right premaxilla with teeth, the remains of 12 cervical vertebrae including several cervical ribs, part of seven dorsal vertebrae and ribs, one sacral neural spine, one sacral centrum, six caudal vertebrae, several chevrons, part of both scapulae, both sternal plates, the distal portion of a left ischium, both humeri, the second and forth right metacarpals, an incomplete fibula, one osteoderm, and several unidentified bones. This specimen is housed at the Museu Nacional of the Universidade Federal do Rio de Janeiro (MN-UFRJ).

Referred material. Kellner *et al.* (2006) also reported a distal end of a right scapula (MN 7048-V), two sternal plates (MN 7049-V and MN 7050-V) of a second animal and one caudal vertebra (MN 7051-V) that may or not pertain to *Maxakalisaurus topai,* both housed at the Museu Nacional of the Universidade Federal do Rio de Janeiro (MN-UFRJ); Additionally, França *et al.* (2016) assigned to this species an incomplete right dentary (MBC-42-PV), and an isolated teeth (MBC-38-PV), housed at the Zoological Collection of INBIO/UFU. Almeida *et al.* (2004) and Candeiro *et al.* (2006), earlier from the description of this taxon, described an isolated mid caudal vertebra associated with a partial chevron (UFRJ DG 270 R), a cervical and dorsal ribs (MMR/UFU-PV 0002 and MMR/UFU-PV 0003), and another posterior caudal vertebra (MMR/UFU-PV 0001) from the same site were the holotype material was recovered, which were associated with *Maxakalisaurus topai* hypodigm (Martinelli *et al.* 2011). These materials are housed at the Departamento de

Geologia of the Universidade Federal do Rio de Janeiro and the Museu de Minerais e Rochas of the Universidade Federal de Uberlândia, respectively.

Diagnosis. *Maxakalisaurus topai* was characterized by the following combination of features according to Kellner *et al.* (2006): (1) caudal series with the anterior and posterior surface of the centrum dorsoventrally compressed; (2) midposterior caudal vertebrae with the lateral surface of the centrum strongly concave ("spool-shaped"); (3) dorsal margin of neural spine in mid-posterior caudal vertebrae obliquely oriented; (4) presence of at least one mid-posterior caudal with biconvex centrum; (5) the metacarpal IV about 12% shorter than metacarpal II; and (6) sacral centrum with a keel-shaped ventral surface. Later, França *et al.* (2016) extended the *Maxakalisaurus topai* diagnosis with the following features: (7) Meckelian groove not enters at symphysis area on dentary; (8) U-shaped tooth row; (9) teeth with high-angled planar facets and sub-oval cross-section; (10) two replacement teeth per alveolus.

Horizons and type locality. All materials that assigned to *Maxakalisaurus topai* were collected from the same stratigraphic level of small outcrop located 45km west of the Prata Municipality, at the Prata-Campina Verde State Highway, in a region called Boa Vista Range, Minas Gerais State. In this locality outcrops a fine to medium-grained reddish sandstone that has been regarded as part of the Late Cretaceous (Santonian-Campanian) Adamantina Formation, Bauru Basin (Dias Brito *et al.* 2001).

LITHOSTROTIA Upchurch, Barret & Dodson 2004
RINCONSAURIA Calvo, González-Riga & Porfiri 2007

Uberabatitan Salgado & Carvalho 2008

***Type Species**:*
Uberabatitan ribeiroi Salgado & Carvalho 2008
Type by monotypy

Figure 15

Taxonomical assessments:
Aeolosaurus sp. indet. (Santucci 2002)

Etymology. The genus name derives from the Uberaba Municipality, located near the locality of the type specimens has been recovered, plus the suffix *titan*, which correspond to "giant" in Greek mythology. The species name is in honour of Luiz Carlos Borges Ribeiro, director of the Centro de Pesquisas Paleontológicas Llewellyn Ivor Price, for his support of palaeontological research in Minas Gerais State (Salgado & Carvalho 2008).

Type material. *Uberabatitan ribeiroi,* according Salgado and Carvalho (2008), is represented at least by three partial individuals (A, B and C). The most complete of them (A), has been regarded as the holotype specimen. However, a recent research (Silva Junior 2019) has identified a greater number of individuals than previously thought, as well as redefined the holotype specimen (indicated with asterisk): The Specimen A (CPPLIP-UrHo) originally is represented by a small individual and composed by four anterior cervical vertebrae (CPPLIP-914-UrHo, 919-UrHo, 1057-UrHo, 1058-UrHo) and two anterior cervical neural arches (1091-UrHo, 1104-UrHo); two mid-cervical vertebrae (992-UrHo, 1023-UrHo); two posterior cervical centra (915-UrHo and 993-UrHo); several cervical ribs (917-UrHo, 921-UrHo, 922-UrHo, 929-UrHo, 1081-UrHo, 1105-UrHo); an anterior dorsal (1077-UrHo); and a mid-dorsal neural arch (1068-UrHo); a dorsal rib (923-UrHo); a sacral centrum (1099-UrHo); an anterior caudal vertebra (1079-UrHo); a mid-caudal vertebra (1017-UrHo); four posterior caudal vertebrae (1009-UrHo, 1010-UrHo, 1011-UrHo, 1012-UrHo); an anterior (1056-UrHo) and a posterior chevron (1006-UrHo); a sternal plate (1027-UrHo); a right coracoid (1109-UrHo); a left humerus (1030-UrHo); the both radii (911-UrHo and 1032-UrHo); right metacarpal (1080-UrHo); pubes (1029-UrHo, 1103-UrHo); left tibia, fibula and astragalus * (912-UrHo, 1082-UrHo, 1107-UrHo).

The Specimen B (CPPLIP-UrB) is represented by a large individual, composed by anterior (CPPLIP-1022-UrB, 1075-UrB), mid (CPPLIP 994-UrB, 1070-UrB, 1085-UrB) and posterior (CPPLIP 1024-UrB, 1108-UrB) cervical vertebrae; cervical neural arches (CPPLIP 918-UrB, 991-UrB); a fragment of vertebra (CPPLIP 1078-UrB); a dorsal rib (CPPLIP 1065-UrB); mid (CPPLIP 1018-UrB, 1019-UrB, 1020-UrB), posterior caudal vertebra and a caudal centrum (CPPLIP 1014-UrB and1008-UrB respectively); chevrons (CPPLIP 1003-UrB, 1004-UrB, 1005-UrB); a left coracoid (CPPLIP 1120-UrB); fragment of right pubis (CPPLIP 913-UrB); a fragment of ischium (CPPLIP 1026-UrB), a distal end of a right femur (CPPLIP 898-UrB) and a left fibula (CPPLIP 1106-UrB). The Specimen C (CPPLIP-UrC) comprises solely of a mid-dorsal centrum (CPPLIP-1116-UrC) and a partial right femur (CPPLIP 894-UrC). The type series of this taxon is housed on Centro de Pesquisas

Paleontológicas Llewellyn Ivor Price, located at the Complexo Cultural e Científico de Peirópolis of Universidade Federal do Triângulo Mineiro (CCCP-UFTM), Peirópolis District, Minas Gerais State. More recently, Silva Júnior *et al.* (2019) identified six new specimens recovered from the type-locality of *Uberabatitan*: a partial mid cervical vertebra (CPPLIP-1690), a proximal chevron (CPPLIP-1691), complete (CPPLIP-1238) and partial (CPPLIP-1189) left femora, a metatarsal II (CPPLIP-1043) and an ungual phalanx (CPPLIP-971).

Referred material. Several other individuals, from multiple localities on Uberaba/Peirópolis, can be assigned to this genus: the specimen known as "Mumbuca Titanosaur" (MCT 1487-R, previously known as DGM Series A of Powell 2003), which is represented by a complete cervical series (atlas, axis and the remaining 11 cervical vertebrae), the three first dorsal vertebrae and a segment of posterior caudal vertebrae, composed by eight elements (see Trotta 2002); a large individual composed by a complete posterior dorsal vertebrae (CPPLIP-494), plus a dorsal centrum and an anterior portion of preacetabular process and iliac peduncle of the right ilium (Santucci 2002); an isolated partial posterior cervical vertebra (CPPLIP-1452); isolated anterior (CPPLIP-361) and mid (MCT) dorsal vertebrae; several partial caudal series (MCT 1664-R, CPPLIP-91 to 96, 393 to 402), as well as isolated anterior (CPPLIP), mid (CPPLIP-45 to 47, 248) and posterior (MCT 1666-R) caudal vertebrae.

Diagnosis. According Salgado and Carvalho (2008), *Uberabatitan* is diagnosed by presenting the following autapomorphies: (1) anterior and mid-cervicals with postzygodiapophyseal lamina (PODL) segmented in two unconnected laminae, zygapophyseal and diapophyseal, of which the zygapophyseal segment extends anterodorsally over the diapophyseal; (2) mid-dorsal vertebrae with a robust composite lateral lamina formed mainly by a diapophyseal lamina, probably homologous to the postzygodiapophyseal lamina (PODL) and, to a lesser extent, by a relic of spinodiapophyseal lamina (SPDL); (3) mid (and possibly posterior) dorsals with neural accessory laminae parallel to the prespinal lamina, which are probably the spinoprezygapophyseal laminae (SPRL); (4) mid-caudal centra with deeply excavated lateral faces; (5) pubis notably thick and robust, with a very stout longitudinal crest on its external (ventral) face; (6) proximal end of the tibia with a very robust lateral protuberance that articulates with an equally robust medial knob of the fibula.

Horizons and type locality. All individuals referred to *Uberabatitan* comes from upper section of the Serra da Galga Member, Marılia Fomation, located at the BR-050 Highway site B, km 153, Uberaba Municipality, Minas Gerais State (Salgado & Carvalho 2008).

LITHOSTROTIA Upchurch, Barret & Dodson 2004

TRIGONOSAURINAE tax. nov.

Proposed definition**:** The most recent common ancestor of *Trigonosaurus pricei* Campos *et al.* 2005, *Adamantisaurus mezzalirai* Santucci & Bertini 2006a and all of its descendants.

Proposed diagnosis**:** trigonosaurines can be distinguished from others titanosaurs by possessing the unique following combination of synapomorphies: Cervical vertebrae with (1) SPRL processes on top of prezygapophyses; (2) anterior margin of neural spines with a faintly step; (3) prominent lateral bulges at the end of neural spines; (4) absence of EPRL; Anterior to mid caudal vertebrae with (5) neural archs with well-developed laminae (SPRL, PRSL, SPOL and POSL); (6) relatively elongated and robust prezygapophyses, directed upward and slightly inclined anteroventrally; (7) very widened prezygapophyseal articular facets with laminar borders, which extends close to the mid of prezygapophyses; (8) presence of postzygapophyseal processes, which the development of lateral expansion, at dorsal portion, is curved downward creating concave articular facets, mainly in the mid-caudal vertebrae; (9) neural spine height equals or greater than centrum height, slightly straight or backward-projected, with the distal ends anteriorly deflected; (10) neural spines strongly expanded laterally, which the distal ends forming rounded dorsolateral bulges; and (11) chevron articular facets placed posteriorly, at the condyle surface, and not ventrally to the centrum (Figure 16).

Included species*: Trigonosaurus pricei***,** *Adamantisaurus mezzalirai* and *“Aeolosaurus” maximus*.

Temporal range*:* Late Cretaceous, Santonian to Maastrichtian.

Trigonosaurus Campos, Kellner, Bertini & Santucci 2005

Type species:

Trigonosaurus pricei Campos *et al.* 2005

Type by monotypy

Figure 17

Taxonomical assessments:

Titanosaurinae indet. "DGM Series B" (Powell 2003)

Titanosaurinae gen. et. sp. nov. (Bertini 1993)

Titanosauridae gen. et. sp. nov. B (Campos & Kellner 1999)

Titanosaurinae gen. et. sp. nov. E (Santucci 2002)

Etymology. The genus epithet comes from the Greek word "*trigónos*" (triangle) in allusion to the region called as "Triângulo Mineiro" at Minas Gerais State, where the specimen was collected, and "*saurus*" which meaning reptile. The specific name is given in honor of Llewellyn Ivor Price, a very important vertebrate paleontologist, who has collected this and several other Brazilian dinosaur specimens (Campos *et al.* 2005).

Type material. According to Campos *et al.* (2005), *Trigonosaurus* is represented by two individuals: the holotype (MCT 1488-R) which consist in an incomplete articulated axial series formed by the five last cervical vertebrae, ten dorsal vertebrae, sacrum and right ilium; and a paratype (MCT 1719-R) composed by ten anterior to mid caudal vertebrae. However, previously, Powell (2003) considers both materials belonging to the same individual (The DGM Series B) which is followed by this study. Both materials assigned to *Trigonosaurus* are deposited at Museu de Ciências da Terra of the Companhia de Pesquisa de Recursos Minerais (MCT).

Referred material. Other specimens recovered from adjacent quarries of Peirópolis, such as the "Rodovia Site", can be associated with *Trigonosaurus.* They consists in a single posterior dorsal vertebra (MCT 1621-R), a partial caudal sequence represented by anterior and mid-anterior elements (MCT 1625-R, 1667-R to 1670-R) and an isolated anterior caudal vertebra (CPPLIP-102).

Diagnosis. *Trigonosaurus* is characterized by the following combination of characters (Campos *et al.* 2005): (1) elongated mid-cervical vertebrae, with low neural spine and concave ventral margin; (2) elongated mid-dorsal vertebrae with strongly posteriorly inclined neural spine; (3) dorsal vertebrae 9 and 10 with incipient postzygodiapophyseal lamina (PODL); (4) anterior caudal vertebrae with thin base broadening towards the top; (5) anteriormost caudals (2-5), with two and middle caudals with one pronounced dorsal depression on the transverse process; (6) prezygapophyses on the caudal vertebrae extended forward, with wide articular faces; (7) articulation surfaces for haemal arches strongly developed starting on caudal 3 until the last preserved element (caudal 20); (8) transverse processes well developed throughout the sequence formed by anterior and medial caudals (until at least caudal 20).

Horizons and type locality. The remains of *Trigonosaurus* were collected at the site known as "Caieira", an abandoned quarry from the São Luís Farm, Veadinho Range, situated about 2 km north of Peirópolis District, Uberaba Municipality, Minas Gerais State (Campos & Kellner 1999, Campos *et al.* 2005, Kellner *et al.* 2005). The specimen was found in fine to medium-grained white and yellow sandstones, with conspicuous siltic-argillaceous matrix, from the Marília Formation, Serra da Galga Member, Bauru Basin. The age of this stratigraphic unit is regarded as Late Maastrichtian (Gobbo Rodrigues *et al.* 1999).

LITHOSTROTIA Upchurch, Barret & Dodson 2004
TRIGONOSAURINAE tax. nov.

Adamantisaurus Santucci & Bertini 2006a

Type species:
Adamantisaurus mezzalirai Santucci & Bertini 2006a
Type by monotypy

Figure 18

Taxonomical assessments:
Titanosauridae indet. (Mezzalira 1959, 1966, 1989)
Titanosaurinae gen. nov. sp. nov. F (Santucci 2002)

Etymology. The genus name come from the Adamantina Formation, from which this specimen was collected, and *saurus*, the Greek for lizard. The species name is in honour of Dr. Sérgio Mezzalira, the researcher who collected and first mentioned the remains in the literature (Santucci & Bertini 2006a).

Type material. The holotype specimen of *Adamantisaurus* is composed by six articulated anterior caudal vertebrae (MUGEO 1282) and two chevrons (MUGEO 1289-1295), deposited at the Museu Geológico Valdemar Lefèvre of the Geological Institute of São Paulo State (Santucci & Bertini 2006a).

Referred material. A complete left femur, found at the same outcrop, may pertain to the type specimen. However, due the absence of a stratigraphic control in the collect campaign, Santucci and Bertini (2006) do not associated this material to the type series.

Diagnosis. *Adamantisaurus* is characterized by Santucci and Bertini (2006a) through the following combination of characters: (1) anterior caudal vertebrae with straight or slightly backward-projecting neural spines, with distal end strongly expanded laterally; (2) stout prespinal lamina; (3) pre and postzygapophyses with very wide articular facets; (4) concave postzygapophyseal articular facets on anterior caudal vertebrae.

Horizons and type locality. *Adamantisaurus* was recovered in the railway cut located between the Adamantina and Irapurú municipalities, at near the Flórida Paulista Municipality, western part of São Paulo State. In this site, occurs the sandstones of the Upper Cretaceous (Santonian-Campanian) Adamantina Formation (Dias Brito *et al.* 2001).

LITHOSTROTIA Upchurch, Barret & Dodson 2004
AEOLOSAURINI Franco-Rosas, Salgado, Rosas & Carvalho, 2004
sensu Casal *et al.* 2007

Aeolosaurus Powell 1987

Type species: *Aeolosaurus rionegrinus* Powell 1987

***Included species**:*
Aeolosaurus colhuehuapensis Casal *et al.* 2007
Aeolosaurus maximus Santucci & Arruda Campos 2011

Figure 19

Taxonomical assessments:

Aeolosaurus sp. nov. (Bertini *et al.* 1999a)
Aeolosaurus sp. nov. H (Santucci 2002)
Aeolosaurus maximus gen. et sp. nov. (Santucci & Arruda Campos 2011)
"*Aeolosaurus*" *maximus* (Martinelli *et al.* 2011)

Etymology. Santucci and Arruda Campos (2011) give the name "*maximus*", which means large in Latin, to this *Aeolosaurus* species in reference to the size of the specimen. Nonetheless, several authors questioned the inclusion of that species into the *Aeolosaurus* genus due the phylogenetic relationships recovered through subsequent phylogenetic analyses, which is pending a revision of this species and the creation of a new genus to comport it.

Type material. "*Aeolosaurus*" *maximus* is based on a large individual (MPMA 12-0001-97), composed by two incomplete posterior cervical vertebrae, seven incomplete cervical ribs, a fragmentary anterior dorsal centrum, a probable fragment of a middle dorsal vertebra, a fragmentary posterior dorsal vertebrae, several incomplete diapophysis of dorsal vertebrae, 12 incomplete dorsal ribs, six articulated anterior caudal vertebrae, a mid-caudal centrum, two posterior caudal vertebrae, six anterior, one mid and one posterior chevrons, a probable fragmentary scapula, an incomplete right humerus, a probably fragmentary left humerus, a probably incomplete radius, incomplete right femur, a complete left femur, left ischium and several unidentified fragments. The holotype material is housed in the Museu de Paleontologia de Monte Alto, São Paulo State (MPMA).

Diagnosis. Santucci and Arruda Campos characterized this species by the following unique association of characters: (1) well-developed posterior protuberance below the articular area on the anterior and middle chevrons, and a lateral bulge on the distal portion of the articular process of the mid-posterior chevrons. Further, an additional set of ambiguous synapomorphies includes: (2) presence of posterior centrodiapophyseal lamina (PCDL) at least 50% thicker than the postzygodiapophyseal lamina (PODL) in posterior cervical vertebrae; (3) posterior dorsal vertebrae with intrapostzygapophyseal lamina (TPOL) and an oblique medial centropostzygapophyseal lamina (mCPOL), which bifurcates from the proximal portion of the centropostzygapophyseal lamina (CPOL); (4) mid-thoracic ribs bearing well-developed anterior and posterior crests with a D-shaped cross section.

As explained by the authors, these features are considered ambiguous because they cannot be assessed in other *Aeolosaurus* species so far, and may correspond to a set of synapomorphies of *Aeolosaurus* or even Aeolosaurini (Santucci & Arruda Campos 2011).

Horizons and type locality. The holotype specimen of "*Aeolosaurus*" *maximus* was recovered in reddish massive sandstones locally with carbonatic cementation, which corresponds to the top of the Upper Cretaceous (Santonian-Campanian) Adamantina Formation, approximately 12 Km SW far from the Monte Alto Municipality, São Paulo State.

LITHOSTROTIA Upchurch, Barret & Dodson 2004
AEOLOSAURINI Franco-Rosas, Salgado, Rosas & Carvalho, 2004

Gondwanatitan Kellner & Azevedo 1999

Type species: *Gondwanatitan faustoi* Kellner & Azevedo 1999
Type by monotypy

Figure 20

Taxonomical assessments:
Titanosaurus sp. indet. (Cunha *et al.* 1987)
Titanosaurus sp. indet. (Bertini 1993)
Aeolosaurus faustoi (Santucci & Bertini 2001)
Aeolosaurus faustoi (Santucci 2002)
Gondwanatitan faustoi (Martinelli *et al.* 2011)

Etymology. The generic epithet is formed by "*Gondwana*", the ancient supercontinent that once united all southern landmasses (plus the Indo-Pakistan block), and "*Titan*" which relates to the gigantic Greek deities. The specific epithet is given in honor of Dr. Fausto L. de Souza Cunha, a Brazilian paleontologist and former curator at MN-UFRJ, who collected and recognized the importance of this specimen (Kellner & Azevedo, 1999).

Type material. The *Gondwanatitan faustoi* holotype (MN 4111-V) consists in an incomplete (semi articulated) postcranial skeleton, composed by two cervical vertebrae, seven dorsal vertebrae, six sacral vertebrae, twenty four caudal vertebrae, proximal portion of the left scapula, left ilium, medial portions of both pubis, both incomplete ischia, both humeri, both tibiae, multiple fragments of ribs and indeterminate fragments (Kellner & Azevedo 1999). All bones were found at the same outcrop and are regarded as belonging to a single individual, and are deposited at Museu Nacional of the Universidade Federal do Rio de Janeiro (MN).

Referred material. A very fragmentary postcranial skeleton composed by an incomplete anterior caudal centrum (MP 285), a caudal neural arch (MP 288), an incomplete mid caudal vertebra (MP 287); a complete posterior caudal vertebra (MP 284), and a complete left tibia (MP 286). This individual is designed as *Gondwanatitan* sp., needing more complete specimens for evaluate this assignation. The remains were recovered from the Upper Cretaceous Cambambe Formation, at Mato Grosso State, and are deposited at the Museu de Paleontologia da Universidade Federal do Mato Grosso (MP).

Diagnosis. *Gondwanatitan* is diagnosed by the follow combination of characters: (1) condyle in anterior and mid caudal vertebrae with "heart-shaped" outline; (2) humeral deltopectoral crest strongly developed and deflected medially; (3) proximal articulation of tibia projecting dorsally; and (4) cnemial crest of tibia almost straight, only slightly curved laterally.

Horizons and type locality. According with Kellner and Azevedo (1999), *Gondwanatitan* is recovered at a mudstone layer truncated by cross laminated sandstones, and overlain by a conglomerate. These strata is regarded as part of the Late Cretaceous (Campanian-Maastrichtian) Presidente Prudente Formation. The skeleton was found on a farm called "Sítio Myzobuchi", located near the Álvares Machado Municipality, São Paulo State.

LITHOSTROTIA Upchurch, Barret & Dodson 2004

ANTARCTOSAURINAE Powell 2003

emendavit

***Proposed definition*:** All titanosaurians more closely related to *Antarctosaurus wichmannianus* Huene 1929 than to *Saltasaurus loricatus* Bonaparte & Powell 1980.

***Proposed diagnosis*:** antarctosaurines can be distinguished from others titanosaurs by possessing the following combination of characters: (1) slenderer cylindrical (pencil-like) teeth crowns (2) strongly L-shaped mandibular rami; (3) well-developed postdentigerous ridge on dentary, which extends posteriorly to dorsal process of splenials; (4) very elongated mid-cervical vertebrae with low neural spines; (5) anteroposteriorly shorter first caudal centrum with a biconvex type articulation.

***Included species**: Antarctosaurus wichmannianus, Baalsaurus mansillai, Brasilotitan nemophagus* and *Pellegrinisaurus powelli*.

***Temporal range**:* Latest Cretaceous, Campanian to Maastrichtian.

Brasilotitan Machado, Avilla, Nava, Campos & Kellner 2013

Type species: *Brasilotitan nemophagus* Machado *et al.* 2013
Type by monotypy

Figure 21

Etymology. The generic epithet is formed by "*Brasilo*"*,* a Latin name that means "relative to the Brazil", the country where the new species was found, and *titan*, which is related to the Greek giant divinities. The specific name is composed by the union of two Greek words: "*némos*", meaning pasture or wood, plus "*phagos*", which means to eat, in allusion to the herbivorous nature of this species (Machado *et al.* 2013).

Type material. A fragmentary skeleton belonging to a single individual (MPM 125R), composed by a right dentary, two cervical vertebrae, three incomplete sacral vertebrae, fragment of an ilium, fragments of an ischium, one ungual and fragmentary elements, all housed at the Museu de Paleontologia de Marília, São Paulo state (Machado *et al.* 2013).

Referred material. An isolated tooth (MPM 126R) found in association with the holotype, also deposited at the Museu de Paleontologia de Marília.

Diagnosis. *Brasilotitan* was diagnosed by Machado *et al.* (2013) with the following autapomorphies: (1) dorsal symphyseal region of the dentary twisted medially; (2) dorsal portion of the symphyseal contact anteroposteriorly thicker than the ventral part; (3)

presence of anteriorly directed accessory prezygapophyseal articulation surface on cervical vertebrae; (4) intraprezygapophyseal laminae (TPRL) of cervical vertebrae with a V-shape in dorsal view.

The authors further distinguished *Brasilotitan* from other titanosaurs by the following combination of characters: (5) mandibular ramus in dorsal view with an “L-shaped” morphology; (6) a sharp anteroposteriorly oriented crest on the dorsal margin at the posterior region of the mandibular ramus (=postdentigerous crest); (7) cervical vertebrae with dorsoventrally low neural spines (approximately 36% and 38% of the total size of the vertebrae); (8) ventral portion of the cervical centrum arched dorsally; (9) prezygapophyses of cervical vertebrae placed anteriorly relative the condyle.

Horizons and type locality. According Machado *et al.* (2013) the remains of *Brasilotitan* was collected at the kilometer 571 of the Raposo Tavares state road (SP-270), near the Presidente Prudente Municipality, São Paulo State. It was recovered from a reddish fine-grained sandstone that is part of the Presidente Prudente Formation, whose is aged as Campanian to Maastrichtian interval (Gobbo Rodrigues *et al.* 1999).

LITHOSTROTIA Upchurch, Barret & Dodson 2004
SALTASAURIDAE Sereno 1998
SALTASAURINAE Powell 1992 *sensu* Sereno 1998

Baurutitan Kellner, Campos & Trotta 2005

***Type species*:**
Baurututan britoi Kellner, Campos & Trotta 2005
Type by monotypy

Figure 22

Taxonomical assessments:
Titanosaurus sp. indet. (“DGM Series C”) Powell 2003
“Peirópolis Titanosaur” Sanz *et al.* 1999
Titanosaurus sp. nov. G Santucci 2002

Etymology. The generic epithet is formed by the sum of the words "*Bauru*", in allusion to the Bauru Basin of Southeastern Brazil, plus "*titan*" from the giants of the Greek myths. The specific name is given in honor of Ignacio Aureliano Machado Brito (1938-2001), an important Brazilian paleontologist (Kellner *et al.*, 2005).

Type material. The holotype, and probably only specimen known until now, of *Baurutitan britoi* (MCT 1490-R) is composed by the last sacral vertebrae articulated with a sequence of 18 caudal vertebrae, belonging to a single individual, and housed at the Museu de Ciências da Terra of the CPRM, Rio de Janeiro State.

Referred material. Possible additional specimens, composed by a second caudal vertebra, one anterior, one mid and two posterior caudals, may correspond to *Baurutitan britoi*. These materials were deposited at MCT and are unnumbered.

Diagnosis. *Baurutitan britoi* is characterized, according with Kellner *et al.* (2005), by the following potential autapomorphies: (1) strongly pointed laterally directed process intercepting the spinoprezygapophyseal lamina on the fisrt caudal vertebra and (2) an anterolaterally directed spinoprezygapophyseal lamina. These authors further distinguished *Baurutitan* from other titanosaurians by the following combination of characters: (1) first caudal vertebra with biconvex articulations; (2) a developed dorsal tuberosity on the neural arch, which turns into a lateral ridge on the mid-caudal vertebrae; (3) neural spines in the most anterior caudals (Cd1 to Cd4) posteriorly turned, changing to a more vertical to sub-vertical inclination in caudal 5 to 10; (4) prezygapophyseal tuberosity on the lateral margin of the prezygapophysis of caudals two to four, which becomes less developed in the posterior elements and smoothing out in the middle caudals; and (5) sub-rectangular cotyle outline, getting more square-shaped towards the end of the caudal series.

Horizons and type locality. The remains of *Baurutitan britoi* was collected in the Peirópolis District area, at the site known as "Caieira" which is an abandoned quarry at the São Luis Farm, located at the Serra do Veadinho (Veadinho Range). This point is situated about 2km North of Peirópolis, Uberaba Municipality, Minas Gerais State. The specimen has found in fine to medium grained white and yellowish sandstones from the Serra da Galga Member of Marília Formation, associated with *Trigonosaurus* and several others titanosaur remains. The age of this stratigraphic unit is regarded as Late Maastrichtian (Gobbo-Rodrigues *et al.* 1999, Kellner *et al.* 2005).

1.2.2.2.Unnamed forms

1.2.2.2.1. Quiricó titanosaur

The Quiricó titanosaur is represented by a disarticulated, but associated, postcranial skeleton of a mid to large-sized individual, which is composed by a complete posterior cervical vertebra with rib, and a nearly complete forelimb (right humerus, radius and manus). Other materials still wait a preparation, such as a sternal plate, a possible coracoid, cervical and dorsal ribs. These materials were recovered from lacustrine siltstones of the Early Cretaceous (Barremian-Aptian) Quiricó Formation at the outcrop CJ-01, far around 2 km from the site that yielded the specimens of *Tapuiasaurus macedoi* (CJ-04 A), and were found associated within a partial hindlimb of a noasaurian (Pires Domingues 2009, Da Silva 2013). This specimen is housed at the Museu de Zoologia of the Universidade de São Paulo (MZSP-PV 831).

1.2.2.2.2. Campina Verde titanosaur A

From the Late Cretaceous (Campanian-Maastrichtian) Echaporã Member of Marília Formation at Campina Verde, two titanosaur partial skeletons were recovered, designated here as Form A and Form B (see below). The Form A is represented by a semiarticulated partial cervical series of a large-sized individual, composed by an anterior (Cv4?), two mid (Cv 6 and Cv7?), a posterior cervical vertebrae (Cv9 or Cv10?) and probably a fragmentary right scapula. This specimen is housed at the Museu de Biociências of the Universidade Federal de Uberlândia (MBC-PV 032).

1.2.2.2.3. Campina Verde titanosaur B

The form B, also recovered at Campina Verde outcrop, is represented by a partial postcranial skeleton of a small-sized individual. This specimen is composed by four articulated and almost complete anterior to mid-dorsal vertebrae (D2 to D5), a broken dorsal vertebra (D6 or D7), one anterior and one mid caudal vertebra, one anterior chevron, a left coracoid, a probable distal end of a scapula and a partial proximal half of a dorsal rib. The Form B is recovered above and associated to the remains of Form A. This specimen also is deposited at the Museu de Biociências of the Universidade Federal de Uberlândia under the acronym MBC-PV 033.

1.2.2.2.4. Ibirá titanosaur

The material associated to this form consists mainly of a disarticulated postcranial skeleton, composed by a moderately preserved posterior dorsal vertebra (LPP-PV 200), fragmentary radius and ulna (LPP-PV 201 and LPP-PV 202), a distal half of a metacarpal (LPP-PV 203), partial anterior and posterior caudal vertebrae (LPP-PV 204 and LPP-PV 205). All materials were referred to the same individual because they were found on a single layer and in close association at a small area (6.60m^2). Additionally, other individuals recovered from adjacent outcrops are assigned to the same morphotype. They consists in a cervical centrum (MPPC 02-012), a nearly preserved posterior cervical vertebrae (MPMA 08-0049-02), a partial anterior dorsal vertebra (MPMA 08-0050-01), two neural arch of anterior dorsal vertebrae (MPPC 02-013 and), a mid to posterior dorsal centrum (MPPC), a complete mid-caudal vertebra (MPMA 08-0060-07), a partial neural arch of mid-caudal vertebra (LPP-PV 206), and a nearly complete fibula (MPMA 09-0001-99). All materials are referred to the same taxon due its sharing several characters and compatible morphology. These specimens has been recovered from the Santonian-Campania São José do Rio Preto Formation at Vila Ventura, Ibirá Municipality.

1.2.2.2.5. Prata titanosaur

This titanosaurian specimen is represented by some axial and appendicular elements, which were collected in the 1970's on deposits of Adamantina Formation (Santonian-Campanian), on a farm around Prata municipality, and deposited posteriorly on CPRM collection (RJ). The specimen includes: a cervical centrum (DGM 756-R), a partial anterior dorsal vertebra (DGM 759-R), a dorsal centrum (DGM 762-R), two partial neural arches (DGM 760-R & DGM 761-R), the three last dorsal vertebrae articulated (DGM 775-R), one posterior caudal vertebra (DGM 767-R), one cervical rib (DGM 769-R), one dorsal rib (DGM 770-R), the right humerus (DGM 758-R), and the right femur (DGM 757-R).

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 faciologic 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 are 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 suggests a Middle to Late Permian ages 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 volcaniclastic 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 systems 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 moraesi* (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, assignated 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 moraesi* (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 Paranaíba and Rio do Sono localities. Them consists of the controversial-aging spinicaudatans *Cyzicus* and *Palaeolimnadiopsis* (Rohn & Cavalero 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 peebles 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 occured, 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.

4 - Results

4.1. Systematic Paleontology

DINOSAURIA Owen 1842
SAUROPODA Marsh 1878
TITANOSAURIFORMES Salgado *et al.* 1997
SOMPHOSPONDYLI Wilson & Sereno 1998
TITANOSAURIA Bonaparte & Coria 1993
LITHOSTROTIA Upchurch *et al.* 2004
TAPUIASAURINAE tax. nov.

Proposed definition**:** The most recent common ancestor of *Tapuiasaurus macedoi* Zaher *et al.* 2011*, Yongjinglong datangi* Li *et al.* 2014 and all of its descendants.

Proposed diagnosis**:** Tapuiasaurines can be distinguished from others titanosaurians by possessing the following combination of synapomorphies: mid to posterior dorsal vertebrae with: (1) almost flat anterior surface; (2) pneumatophores close to the neurocentral joint; (3) centroprezygapophyseal laminae splited at the mid-height (creating the lCPRL and mCPRL), due the internal development of the centroprezygapophyseal fossa (CPRF), which the lateral ramus is merged with the anterior centroparapophyseal lamina (ACPL) and contacts directly ventral to prezygapophyses, while the medial ramus contacts ventrally with the TPRL; (4) retaining the anterior centrodiapophyseal laminae (ACDL); (5) posterior centrodiapophyseal laminae (PCDL) not bifurcated ventrally, only slightly expanded; (6) accessory spinodiapophyseal laminae (aSPDL) absent on almost elements; (7) aliform processes limited to a small lateral protuberances; and (8) humeral head with an anteroproximal tuberosity, on medial corner of the deltopectoral fossa; (Figure 27).

Included taxa*: Tapuiasaurus macedoi***,** *Yongjinglong datangi,* the Prata titanosaur and probably *Gobititan shenzhouensis*.

Temporal range*:* Early (Hauterivian-Aptian) and Late (Santonian-Campanian) Cretaceous.

Tapuiasaurus Zaher *et al.* 2011

(Figure 28)

Type species. *Tapuiasaurus macedoi*

Diagnosis. As for type and only known species (type by monotypy).

Etymology. The generic epithet derives from ''*Tapuia*'', a common name from the Jês indigenous language family, used by the tribes of the Brazilian coast to designate the people that inhabited the inner regions of the country, plus "*sauros*" which is the ancient Greek word for lizard, commonly used for fossil reptiles (Zaher *et al.* 2011).

Tapuiasaurus macedoi Zaher *et al.* 2011

Derivation of name. The specific epithet honors Ubirajara Alves Macedo, who first discovered the fossil localities in Coração de Jesus Municipality (Zaher *et al.* 2011).

Hypodigm. The holotype specimen of *Tapuiasaurus macedoi* (MZSP-PV 807) comprises in a partial articulated skeleton of a sub-adult individual (Figure 28), composed by a complete skull, mandibles and hyoid apparatus (right and left ceratobranchials); both proatlas, atlas, axis and the remaining five articulated cervical vertebrae (3rd to 7th) with their respective ribs; two mid to posterior cervical vertebrae (8th or 9th and 10th or 12th); at least two anterior, one mid and one posterior dorsal vertebrae; a posterior dorsal neural arch; complete dorsal ribs and several fragments of others; one fragment of a probable sacral rib; seven partial mid to posterior caudal vertebrae and six fragments of posterior elements; remains of caudal neural arches; one complete anterior chevron and fragments of two posterior; a right sternal plate; left coracoid; right humerus; ulnae; left radius; partial remains of both manus, including a manual phalanx and ungual of right metacarpal-I; partial femora; left tibia and fibula; and a nearly complete left pes.

A smaller second individual (MZSP-PV 831) is designated here as topotype of *Tapuiasaurus macedoi*. This individual shares overlapped bone elements with the holotype and was recovered few meters (*c.a.* 4m) close from to the point where the MZSP-PV 807 specimen were collected. It comprises in a nearly preserved forelimb, represented by a partial right humerus, fragmentary ulna, a probable radius and metacarpals. Additionally, an almost complete isolated femur of a large individual (MZSP-PV 1324) is designed as referred specimen of *Tapuiasaurus macedoi*.

Horizons and type locality. The specimens assigned to *Tapuiasaurus macedoi* were found in two different outcrops (CJ-04 and CJ-06) at the Mucambo Farm, situated on the Embira Branca Range, a countryside near Coração de Jesus Municipality, northern region of Minas Gerais state. These deposits are assigned to the Early Cretaceous Quiricó Formation, Areado Group, Sanfranciscana Basin (Zaher *et al.* 2011).

The lacustrine sequence of Quiricó Formation are constrained to the Late Barremian to Early Aptian time-interval (Buracica and Jiquiá Local Ages), based on stratigraphical correlation (Zaher *et al.* 2011), by the presence of the gonorynchiform actinopterygian *Dastilbe crandalli* (Brito & Amaral 2008), the *Tucanopollis crisopollensis*, *Afropollis* sp., *Sergipea* cf. *naviformis* palynozones (Arai *et al.* 1995), and by the ostracodan association of *Bisulcocypris* sp., *Brasacypris* sp. 1, *Darwinula martinsi, Ilyocypris* sp., *Harbinia symmetrica, Wolburgiopsis plastica* and *W. chinamuertensis* biozones (Carmo *et al.* 2004).

4.1.1. Diagnosis

4.1.1.1. Original diagnosis provided by Zaher *et al.* (2011)

In the original diagnosis, based mainly in the cranial material, Zaher *et al.* (2011) identified three autapomorphies that distinguish *Tapuiasaurus macedoi* among the "advanced titanosaurians" (or eutitanosaurians): (1) a hook-shaped posteroventral process of the quadratojugal; (2) anterior process of the jugal tapering and forming most of the ventral margin of the antorbital fenestra; and (3) the anterolateral tip of the pterygoid contacting with the medial surface of the ectopterygoid.

Additionally, these authors diagnosed the taxon by the following unique combination of characters, such as a deep fossa on the lateral surface of the maxilla between the antorbital fenestra and the subnarial foramen (=preantorbital fenestra); elongated middle cervical vertebrae; posterior dorsal vertebrae with well-developed prespinal lamina; absence of hyposphene-hypantrum complex; a deep fossae located below intraprezygapohyseal lamina (= centroprezygapophyseal fossa); crescentic-shaped sternal plates; proximodistally long coracoid; elongated ulna; and a distally expanded radius (*op. cit.*).

4.1.1.2. Emended diagnosis provided by Wilson *et al.* (2016)

Later, Wilson *et al.* (2016), in the full description of the skull and mandible material of this species, added more eight diagnostic features for *Tapuiasaurus macedoi*: (4) maxilla with a tapering post-dentigerous process that is elevated above the alveolar margin; (5) jugal with an elongate lacrimal process forming much of the posteroventral border of the antorbital fenestra; (6) lateral temporal fenestra divided by a second squamosal-postorbital contact, forming a small posterodorsal opening and an elongate anteroventral opening; (7) quadrate and quadratojugal with a narrow (*c.a.* 2 mm), end-on articulation; (8) maxillary teeth with labial wear; (9) absence of a post temporal foramen; (10) flat overlapping articulation between squamosal and quadratojugal; and, finally, (11) basisphenoid with median ridge extending from contact with basiocciptal onto ventral surface.

4.1.1.3. Remarks

Although it is not the central issue of this research, during the analysis of the MZSP-PV 807 (holotype specimen) was observed that the skull and mandibles of *Tapuiasaurus macedoi* still features more four additional putative autapomorphies (Figure 29): (12) preantorbital fossa anteriorly segmented by a bone septum, forming an anterior foramen that is also perforated interiorly and separated from the internal preantorbital opening; (13) a thin maxila-quadratojugal contact; (14) maxillary ascending process dorsally bifurcated, with a narrow posterolateral process contacting to the prefrontal; (15) posterior processes of the surangular and angular strongly downward turned.

4.1.5. Extended diagnosis

Based on postcranial skeleton, *Tapuiasaurus macedoi* represents a medium-sized (*c.a.*12m in length) early lithostrotian titanosaur, which can be diagnosed by 12 additional putative autapomorphies (Figure 30) that differentiates it from other titanosaurian taxa: (1) atlantal neurapophyses with developed zygapophyses; (2) cervical vertebrae with postzygapophyseal lamina (PODL) and posterior centrodiapophyseal lamina (PCDL) connecting posteriorly in respect to the diapophyseal process; (3) anterior and mid cervical vertebrae bearing a posterolateral tubercle on the spinodiapophyseal fossa (SPDF) that is associated with a sulcus in each spinopostzygapophyseal laminae (SPOL); (4) mid and posterior cervical vertebra with accessory rami on medial spinoprezygapophyseal laminae (mSPRL); (5) mid to posterior cervical vertebrae with a sharp and well-developed medial spinopostzygapophyseal laminae (mSPOL); (6) expanded neural spine on last cervical vertebrae slanted posteriorly and exhibiting small accessory fossae between the medial spinoprezygapophyseal laminae branches; (7) posterior dorsal vertebrae with a medial prezygodiapophyseal laminae (PRDL) that contacts anterodistally to the spinodiapophyseal laminae (SPDL); (8) medially deflected humeral deltopectoral crest with a flat and rugose anterior surface, which exhibit sharp anterior and lateral crests. Additionally, a shallow fossa is present between the lateral and posterior margins; (9) fourth trochanter with a sagittal groove, dividing it into two small ridges; (10) very reduced, “ball-shaped”, phalanx I-1, whose shows less than the half breadth rather the others phalanges, and displays a hemispherical surface on distal articulation; (11) the metatarsal-II longer than the metatarsal-III.

4.1.6. Revised and comparative diagnosis

Further, *Tapuiasaurus macedoi* is also distinguished from other titanosaurians (see discussion below) by the following unique autapomorphic combination of characters: Proatlases with narrow and elongated posterior tip, lacking prominent expansions in the ventral processes; Anterior cervical neural spines in lateral view with a remarkable step on anterior edge; Middle cervical neural spines bearing incipient lateral bulges and thick spinoprezygapophyseal and spinopostzygapophyseal laminae; Posterior cervical neural spines with lateral and medial spinoprezygapophyseal laminae (lSPRL and mSPRL); Posterior cervical neural spines with lateral expansion formed by the lateral spinoprezygapophyseal laminae (lSPRL); Presence of an incipient epipophyseal-prezygapophyseal laminae (EPRL) on almost entire cervical series; Paired restrict centroprezygapophyseal fossa (CPRF) on posterior dorsal vertebrae located between the centroprezygapophyseal laminae (lCPRL and mCPRL); Absence of hyposphene-hypantrum complex; Posterior dorsal vertebrae with single and well-developed prespinal lamina; Diapophysis on posterior dorsal vertebrae strongly directed dorsally, with a flattened dorsal surface; Absence of postzygodiapophyseal laminae (PODL) on posterior dorsal vertebrae; Broader spinopostzygapophyseal laminae (SPOL) on cervical and dorsal vertebrae; Middle and posterior caudal centra with platycoelous to slightly procoelous type articulation; Distal caudal centra with a procoelous type articulation; Middle and posterior caudal centra with flattened lateral and ventral surfaces; Anterior chevrons lacking a crus; Crescentic-shaped sternal plates; Proximodistally long coracoid, which the coracoid foramen is almost there on scapula; A posterolateral tuberosity in the proximal portion of humeral deltopectoral crest; Elongated ulna with very expanded proximal end; Olecranon process strongly developed; Ulna with an anteromedial excavated fossa; Radius with a prominent anteromedial process; Distally expanded radius; Presence of phalanges only in the metacarpal-I, including an ungual; Femoral distal end with a prominent epicondyle; Developed lateral trochanter and interosseous ridge on fibula; Entaxonic pes, which the 1st digit has the half size of the others; Pes with phalangeal formula 2-2-2-2-2.

4.2. Postcranial osteology

The following description includes all preserved materials from the holotype specimen of *Tapuiasaurus macedoi* (MZSP-PV 807), although some elements of this individual (*e.g*. anterior dorsal vertebrae, tibia) were not included because they are in preparation until the end of this study. The topotype and referred specimens, beyond its fragmentary state, likewise had some elements in restoration. For this reason, only some overlapped elements of these specimens were included.

4.2.1. Axial bones

4.2.1.1. Cervical series

The skull and cervical series of *Tapuiasaurus macedoi* was found articulated, ranging from the proatlas to the seventh element (Figure 31). The remaining cervical vertebrae were recovered disarticulated and far from the other elements. They comprises into two vertebrae: a possible ninth or tenth and the eleventh or twelfth vertebra. These assignations was made based on the development of some characteristics, such as the lateral bulge in the neural spines, their sizes, as well as comparisons with more complete cervical series, such as the Mumbuca titanosaur (DGM Series A of Powell 2003), *Futalognkosaurus* (Calvo *et al.* 2007c), *Rapetosaurus* (Curry Rogers 2009) and *Malawisaurus* (Gorscak 2016).

4.2.1.1.1. Proatlas and Atlas-Axis complex

Both left and right proatlases were recovered complete and well preserved. The right proatlas were found, although slightly shifted, in living position and articulated in the occiput, whereas the left one was disarticulated during the specimen preparation. These elements has a narrow shape, where the posterior tip is elongate, almost pointed (Figure 32). Dorsally and ventrally, the medial margin exhibit a sigmoid profile. Medially, the anterior end displays a marked flat articular surface, while the lateral surface is slightly convex and exhibit a broad ventral expansion. On the ventral face, there a conspicuous fossa close to the anterior end, followed by a longitudinal groove that accompanies along the ventral side of the posterior tip. This groove may represent the articulation with the anterior processes of atlantal neurapophyses.

The atlas is complete but none of its elements is fully fused (Figure 33). Additionally, the atlas have a much-accentuated taphonomical distortion, from left to right side of the neural arches, and dorsoventrally at the atlantal intercentrum. The atlantal intercentrum is fused with the left atlantal neurapophysis by rock matrix. However, the latter is dislocated medially, evidencing that neurocentral joint is broad and sharped on anterior portion, whereas in the lateral view the suture is straight. In turn, the right neurapophysis is bounded, also by rock matrix, with de atlantal pleurocentrum.

The atlantal intercentrum is dorsoventrally low, in which its lateromedially breadth is three times longer than the anteroposteriorly height, occupying less than the half of the occipital condyle (Table 4.1-A). Laterally, the atlantal intercentrum exhibit an “eye-shaped” fossa that may be homologous to the presacral pneumatophores. The articulation surface type is procoelous, given that his posterior face has a slightly developed condyle-like structure. Posteroventrally, the intercentrum bears two prominent apophyses with concave surfaces for articulation of the atlantal ribs. The only preserved atlantal rib correspond to a slim and cylindrical narrow bone with longitudinal stretch marks, which its posterior distal end is slightly flattened.

The neurapophyses, mainly on the left ones, are segmented into two non-fused parts: the neural arch pedicel articulated to the distal expanded neural spine, and an anterior bone that articulate on the neural spine. This latter consist in a thin crescentic bone with a sulcate ventral margin which fits medially onto anterior margin of neural spine. Laterally, can be observed that the neural arch pedicels are ventrally expanded and bears a sharply anterior “foot”, which its oblique anterior margin make a 45° angle in respect to the neurocentral joint and, posteromedially, the ventral end also displays a conspicuous foramen. The pedicel has an anteroposterior-compressed format, with asymmetrically accentuated concave margins with sharp edges, but towards dorsally, which again expands and projects posterolaterally. The expansion of neural spines has marked by possessing a wing-like morphology.

The neurapophyses also shows strongly prominent anterior processes that may correspond to incipient prezygapophyses. This assumption is due the fact of the medial side of left expanded neural spine also displays an incipient postzygapophysis. In addition, on the anterolateral surface of neural spines, along the axis of the anterior process, is there a marked ridge for articulation of proatlas, as well as the proatlas bears a conspicuous ventral fossa, that reinforces the hypothesis of the anterior processes on neurapophyses correspond to incipient prezygapophysis. This setting is regarded here as an autapomorphy of *Tapuiasaurus*.

The atlantal pleurocentrum consists in a wedge-shaped bone, with an ellipsoid transverse section, which is disarticulated from the odontoid process of the Axis. The anteroventral surface is convex while the dorsal ones is slightly concave due the dorsally bevelled anterior portion and, likewise the dorsal surface, the posterior face is slightly concave.

The Axis is almost complete, lacking solely the anterior part of the neural arch (Figure 34). Unfortunately, for this reason, it is not possible to evaluate how the prezygapophyses contacting with the atlantal postzygapophyses. The axial intercentrum and pleurocentrum are disarticulated by crushing, due the taphonomical distortion and/or *rigor mortis* presented by the holotype specimen (MZSP-PV 807).

The axial intercentrum is concave in anterior view, displaying a "tongue-shaped" odontoid process, and hardly perforated anterolaterally by pneumatic pits, including a small foramen. Laterally, the intercentrum exhibit three major fossae that ranges from sub-rectangular to sub-triangular shapes. The parapophysis are strongly posterolaterally projected, bearing a flat and circular articular surface to the axial ribs. Ventrally, the intercentrum is almost flat and its external edges has sharply margins. A median prominence is clearly visible on ventral surface, as well as small circular pneumatic pits along the external edges. Additionally, an elongated paramedian ventral fossa is present that reaches the anterior portion of the axial pleurocentrum. The pleurocentrum is elongated and low than the third cervical centrum, whereas the axial neural arch is two-and-a-half times greater than to the its height (Table 4.1-A). The pleurocentrum lacks evident lateral pneumatophores.

The neural arch is fused to the axial centra, but the neurocentral joint is visibly since the intercentrum. The PRDL is broad and merges with the ACDL. Above from this lamina, a ridge is present, and could accommodate the ventral margin of atlantal neural spine. The diapophysis is strongly directed ventrally, bearing a rounded posterior projection. Posteriorly, the diapophysis is connected to the posterior half only by the PCDL, due the PODL contacts directly on the first laminae. This pattern is discernible in all cervical vertebrae of *Tapuiasaurus*, being related to an autapomorphic condition.

The postzygapophyses has wide articular surfaces and dorsally exhibit small tubercles on epipophyseal region. An incipient EPRL is also present along the mid anteroposterior axis of the SPDF, but this lamina do not contacts anteriorly with the CPRL. On the dorsal part of this fossa, another autapomorphy of this taxon can be assessed, which comprises in prominent posterolateral tubercle and, similarly to the PODL+PCDL setting, this condition extends to the most posterior elements. Wide SPOL connect the postzygapophyses to the neural spine, and borders a wide, triangular-shaped deep POSF. Small lateral bulges give a transversally inflate aspect to the neural spine. Anterolaterally, the neural spine also displays an incipient SPRL.

The both axial ribs were found articulated and well preserved. The ribs comprises in elongated bones with convex lateral and concave ventromedial surfaces, but the distal end has a plank-like shape. Additionally, the ventro and dorsomedial edges are bordered by flanges, mainly in the latter. The proximal and distal ends are marked by rounded margins, which the capitulum and tuberculum are anteriorly facing. On the lateral side, several striae were visible in the proximal end. The lateral surface also bears grooves that accommodated the atlantal rib, creating the dorsal flange. The ventromedial side is smooth, excepting for a beveled and striated portion in the anterior end, also exhibiting a pneumatic foramen.

4.2.1.1.2. Anterior cervical

Articulated to the previous elements, remains of two cervical vertebra (the 3rd and 4th) were recovered complete (Figure 35). The third element of this block (the 5th cervical) only preserved a part of his anterior face, such as the tip of prezygapophyses and the centrum. One fact that deserves note is the length of the third in respect to the fourth vertebrae. While the third vertebra has a similar length to that of the axis (Table 4.1-B), the fourth is quite elongated, exhibiting a sub-equal length to that of the skull. Given the paucity of articulated, or at least associated, cervical and cranial elements it is difficult to assess whether this corresponds to an allometric pattern.

The both cervical vertebrae share several characters. All possesses elongated and dorsovetrally-compressed centra, marked by conspicuously ventrolateral rims. Pneumatophores are almost absent, limited to small lateral concavities. Deep fossa (PRSF and POSF) are present in the anterior and posterior views of neural spines, but the corresponding laminae (PRSL and POSL) are absent. Parapophyses and diapophyses are strongly downward projected, and the latter are supported by thicker PRDL and PODL+PCDL. In addition, the diapophyseal posterior processes on these vertebrae are limited to small tuberosities and in the third element is possible to observe that process is mostly formed by a development of the PODL. Still, the PODL in fourth cervical is broader on its anterior end displaying paired foramina.

The prezygapophyses are dorsally projected, but surpassing the condyle limit and its articular surfaces are dorsally directed. On the 3rd cervical, the prezygapophysis is pierced ventrolaterally by a foramen, which cannot be verified in the 4th vertebrae because this region is damaged. In lateral view, the SPRL are thicker and expands toward approach to the neural spine, merging with the lateral bulge. Also in this view, the neural spines displays a strongly angled sloping or step, which the at its corner the SPRL contacts to the EPRL. Although incipient the EPRL are well marked on the postzygapophyses, connecting dorsomedially to a rhomboid-shaped epipophysis. Similarly to the SPRL, the SPOL are widened, but the neural spine continues smoothly on the posterior edge lacking a remarkable step. The SPOL are marked by sulcus arranged obliquely towards SPDF, which may correspond to pneumatic tubes or to the ligament marks that were attached to the posterolateral tubercles present in this fossa.

4.2.1.1.3. Middle cervical

Like the anterior, two of the mid cervical elements were found nearly articulated (the 6th and 7th elements), but detached from the anterior vertebrae because the fifth cervical was destroyed by weathering prior to collection. The mid to posterior cervical (8th? - 9th?) was recovered close to the fore and hindlimb materials (Figure 26). The sixth vertebrae is very damaged, lacking mostly of the anterior part of the centrum, prezygapophyses and neural spine (Figure 36-A), while the seventh cervical lacks only the prezygapophyses and the tip of right postzygapophysis (Figure 36-B). The mid to posterior element, in turn, preserved almost of the neural arch and the right parapophyses (Figure 36-C).

The sixth cervical vertebra retains the features present in the previous elements, such as a marked neurocentral joint, an EPRL crossing transversely along the SPDF, as well as thick PRDL, SPRL and SPOL. Nevertheless, other characters were obliterated due to their poor preservation state, hampering major observations and comparisons.

In other hand, the seventh cervical vertebra differs from the anterior ones in some points. Given the fact that it was preserved with its ventral portion upwards, is possible to observe significant characters, such as the strongly development of ventrolateral edges forming sharp ridges, possible parapophyseal sutures, as well as pneumatic structures. Its ventral face displays a singular setting, which the medial point is strongly concave and displays a sagittal ridge that divides into two grooves pierced by foramina on posterior end.

Laterally to the medial concavity also is present two paramedial pneumatic foramina. Due preservational issues, these characters cannot be assessed on other cervical elements.

In addition, the seventh cervical shares with the axis a prominent diapophyseal process. With the fourth cervical, this vertebra share a widening in the anterior portion of the PODL formed by two foramina, a possible “U-shaped” fossa on SPOL and the paired sulcus. Nonetheless, in the seventh additional grooves appear at PODL and it is possible to observe that the TPRL extends close to the condyle limit. This vertebra, as well as the next described below, also displays a more tall neural spine, lacking the typical step presented by the anterior cervical vertebrae.

The mid to posterior vertebra besides the characteristics mentioned above also presents some differences. The first one is that many of the characters presented are more developed in this element than the previous one, such as the thick SPRL and SPOL, the lateral bulge on neural spine and the lateral tubercle on SPDF. This is a common fact due to the transition from anterior to posterior elements in the axial series. However, the differences are singular to the point of not enable comparisons of its development and extending along the series. The first one is that the SPRL is bifurcated, creating a lateral and a medial branch (lSPRL and mSPRL). Additionally, each of the mSPRL exhibit accessory medial rami towards the PRSF. Likewise, the SPOL is formed by lateral and medial branches, which the medial ones are sharply developed and converges at the top of neural spine, making a “V-shaped” profile to the POSF border. These characters are regarded here as autapomorphies of *Tapuiasaurus.*

4.2.1.1.4. Posterior cervical

The most-posterior cervical (10th? - 11th?) preserves mostly of the neural arch and anterior portion of centrum (Figure 37), lacking parts of the pre and postzygapophyses, diapophyses and parapophyses. This vertebra is considered as a posterior element due its proportions, such as anteroposterior length in respect to the other cervical material, as well as by the its morphology, such as the PRDL and CPOF shapes, which resembles the pattern present in the dorsal vertebrae (*i.e.* vertically oriented laminae, a restricted fossa). Even so, this vertebra does not represent the last cervical vertebra because it also retains a laminae/fossae setting (mainly in the SPOL, PODL, PCDL and SPDF) similar to observed in the other cervical.

In anterior view, the condyle is wide and dorsoventrally compressed. The neural arch pedicel is low, which the TPRL is very appressed to the neural canal. This lamina is stout and not develops beyond the neural canal border. The CPRL cannot be observed due preservation bias, but seems that the same is not divided. Equally the POSF on the mid to posterior cervical, the PRSF is deep and has a "V-shaped" profile, lacking a PRSL. Another common character shared with the previous vertebra is the SPRL divided into two branches. However, in the posterior one, there is a fossa between in each the mSPRL rami. This feature is unique among the titanosaurs known up to date, being a more autapomorphy of *Tapuiasaurus*.

The neural spine is well-expanded laterally through the development of the lCPRL and lateral bulge, but do not surpass the width of the centrum or extends far as the zygapophyses. Additionally, the lateral bulge in this vertebra is formed by the dorsal development of the SPOL, differing from the anterior cervical vertebrae. In lateral view, even though the material has a taphonomical distortion, it is possible to observe that the neural spine is posteriorly slanted. This pattern is considered here as a valid feature, and not as a bias, since the CPOLs are not distorted. In the lateral view also can be observed that the most posterior element recovered lacks a series of features well marked on the remaining cervical, such as the posterolateral tubercle and EPRL on SPDF and the SPOL sulcus.

4.2.1.2. Dorsal series

4.2.1.2.1. Middle dorsal

The middle dorsal vertebra is moderately complete but very-damaged (Figure 38), lacking mostly of neural spine, the right ventral and posterior parts of the centrum. Nonetheless, the centrum preserves its opisthocoelous articulation and exhibit a pneumatized internally tissue. Pneumatophores has not been preserved. This vertebra probably corresponding to the fourth or fifth element of the series, based on the development of diapophysis in respect to the parapophyses, which are arranged almost on the same horizontal axis.

In anterior view, although distorted, the neural arch preserves a flat surface and is pierced by the two restricted CPRF. The prezygapophyses has a sub-oval articular surface, and there at the same level that the parapophyses, connected to them by a stout and columnar-like PRPL. The prezygapophyses also are bounded from each other by an incipient TPRL, but lacks a ventral bulge or a hypantrum.

The parapophyses has a rounded shape, and are connected to the diapophyses through a well-developed PRDL that expands laterally creating a wide roof to the PACDF. The diapophyses are strongly laterally directed and slightly dorsally, displaying an ellipsoid shape and its distal tip makes a "wing-like" that projects posteriorly. Laterally, the parapophyses are supported by a well-developed ACPL and an incipient PCPL. The diapophyses, in turn, bears well-developed ACDL and PCDL, which the first is thicker than the anterior one. The ACDL together the PCDL, encircles a deep excavated and triangular-shaped CDF.

The preserved portion of the neural spine indicates that it is strongly posteriorly turned, and displays on this basis a ventrally bipartite PRSL. The neural spines link to the diapophysis by a poorly accentuated SPDL, indicating that de non-preserved portion displays lateral margins that converge it. In the posterior view, the only preserved portion is there below the TPOL, lacking it and the postzygapophyses. The only preserved CPOL has a columnar shape and makes an opposite angle with PCDL, which both laminae contacts ventrally surrounding the POCDF. Inside on this latter, several undefined laminae arisen from the ventral to dorsal direction.

4.2.1.2.2. Posterior dorsal

Two posterior dorsal elements has been recovered. The first represents only a complete neural arch, disarticulated on neurocentral joint, and the second comprises in a well-preserved complete vertebra. These dorsal vertebrae was regarded as posterior elements due the position observed in the field, by their morphology (*e.g.* position of the parapophysis in respect to diapophysis), as well as comparisons with more complete dorsal series such as *Trigonosaurus, Futalognkosaurus* and *Overosaurus* (Campos *et al.* 2005, Calvo *et al.* 2007c, Gallina 2011, Coria *et al.* 2013).

The complete vertebra (Figure 39) has a slightly opisthocoelous and anteroposteriorly shortened centrum, which is equally higher than wide (circular in-shape), lacking a dorsoventral compression. The centrum also lacks a ventral keel, as well as a dorsal notch in the cotyle. The anterior face of the centrum is partially eroded, allowing the observation of a highly pneumatized somphospondylous internal tissue. In addition, the centrum displays as in other titanosaurians the characteristic narrow and deep lateral pneumatophores with acuminate posterior border ("eye-shaped pleurocoels") , which the anterodorsal portion is directed obliquely in respect to the transversal axis and the ventral outline is straight. The lateral pneumatophores are located very close to the dorsal edge of the centrum. The neural arch pedicel is tall as the centrum height, displaying developed laminae and a well-marked saw-like neurocentral joint. The neural spine, likewise, is tall and straight, giving a dorsoventral elongated aspect to the vertebra, bearing a slightly rugose dorsal surface.

The anterior face of neural arches has a flat aspect, and exhibit two sub-triangular (nearly D-shaped) deep CPRF, located dorsolaterally above to the neural canal. Inside the CPRF, also is present enlarged internal pneumatic foramina. Laterally, the CPRF is bordered by the lCPRL, which comprises in a smooth and laterally developed single lamina that is merged at its mid-height with the ACPL. Medially, this fossa is surrounded by the mCPRL, whose is connected ventrally with the TPRL. A beveled bulge below the TPRL is absent.

The prezygapophyses are small, and the articular surfaces obliquely oriented with a sub-oval outline. Accessory articulations, such as hyposphene-hypantrum complex, are absent. Dorsolaterally, the prezygapophyses are connected with parapophyses by a thick PRPL. Likewise, dorsomedially, the prezygapophyses connects on the medial side of diapophyses by an aPRDL. These laminae, PRPL and PRDL, to separate the SPRF to the PRSDF, whose both are anteroposteriorly elongated. The PRSL is narrow, but well-developed, being connected to the prezygapophyses by restrict SPRL that makes a bifurcated profile to ventral portion of that lamina. This lamina extends to the mid-height of neural spine, at the level of aSPDL, being broader at the dorsal end.

Parapophyses are ellipsoid in-shape and placed just below to diapophysis, on the same level of prezygapophyses. In the lateral view, the parapophyses are ventrally sustained by a robust and thick ACPL whereas, at the dorsal portion, displays a PPDL laterally projected. The PPDL forms a roof to the PRPADF, whose the latter is deeper and divided by an internally PPDL. The SPPL are absent.

The diapophyses are rectangular shaped and strongly dorsolaterally oriented, with flattened and smooth dorsal surfaces. Ventrally, are sustained by thin but well developed ACDL and PCDL in which holds a deep and triangular CDF. The PCDL is posterodorsally pierced by a groove, indicating a possible split development, while its ventral portion lacks an accessory ramus. Dorsally, the diapophyses connect to neural spine also by two robust laminae, the SPDL and aSPDL. The first lamina occurs asymmetrically on right portion of the neural arch, whose is splited close to the neural spine and holds a deep and restricted

SPDF. Nevertheless, on the left side, the aSPDL and SPDL are slightly divided near to the diapophysis by a restricted sulcus, indicating different timings and positions in the laminae development. The SPDL is thick and strongly upturned, following the curvature of neural spine. Both SPDL ends exhibit acute processes on the anterior portion of the aliform processes that are abruptly terminated by a marked step, making the neural spine transversely thinner on its dorsal half. The aliform processes are horizontally oriented, contacting posteroventrally with the lSPOL. A PODL connecting lateroposteriorly the diapophyses with postzygapophyses are absent.

The postzygapophyses are connected medially with the neural spines by a broad mSPOL, which is separated for the lateral ramus by a shallow and restrict vertical depression. Between the postzygapophyses, a poor developed SPOF are present, bearing an incipient POSL at the mid height of neural spine. A restrict TPOL contacts the postzygapophyses medially, and ventrally they are supported by broad CPOL. The CPOL are obliquely oriented and expanded at terminal ends, in which the dorsal ends are medially orientated. These laminae delineates a moderately deep sub-triangular CPOF above the neural canal.

4.2.1.3. Caudal series

Several partial caudal remains was found associated with the MZSP-PV 807 individual, and between them were identified one mid caudal element, seven partial mid to posterior caudal centra, six fragments of distal-most elements, numerous remains of neural arches, spines and zygapophyses (Figure 40).

The most-anterior mid caudal element lacks all the neural arch, which is disarticulated on the neurocentral joint. The centrum displays a platycoelous type articulation and has a solid internal tissue. The cotyle is shallow concave, and has a circular outline. On other hand, the posterior face is strongly flat and exhibit a sub-quadrangular shape. Shallow concavities are present, laterally and ventrally, however, the centrum lacks a longitudinal hollow. Additionally, the centrum features small and almost pointed incipient transverse processes, which are shifted down and towards.

Two mid-posterior vertebrae are recovered articulated, displaying a slightly procoelous morphology. The centrum is strongly compressed laterally due taphonomical loading, hampering the visualization of ridges or other processes. The first element also preserve almost of its neural arch, which exhibit poorly developed prezygapophyses.

Likewise, the postzygapophyses are small, lacking postzygapophyseal processes supported by bony projections.

The reminiscent elements lacks major morphological characters, except for the fact that the caudal centra acquires a more cylindrical shape and the procelia converts evident to the extent that the elements become more posteriorly, which the most-distal centra possess a fully procoelous articulation.

4.2.1.3.1. Chevrons

Several chevron fragments has been also identified, but only one them is almost complete (Figure 41). The most complete chevron had the open Y-shaped morphology *sensu* Otero *et al.* (2012), and represents an anterior to mid element, although its correspondent vertebra has been not preserved. The proximal rami are constricted medially and elongated, owning an equal length in respect to the distal ramus, which the haemal canal depth occupies almost 50% of the chevron height. The articular surfaces are convex, laterally expanded and posteroventrally turned. Posteriorly, the proximal rami bears interosseous ridges that extends from the articular surfaces to the distal blade, with converges to it. The distal ramus is straight in lateral view, having a sub-oval cross-section. The distal blade is poor developed, not reaching to the distal end of distal ramus.

4.2.2. Appendicular bones

4.2.2.1. Scapular girdle

4.2.2.1.1. Coracoid

A nearly complete left coracoid is present among the holotype material (Figure 42). The coracoid is more proximodistally long than anteroposteriorly, in other words, the dorsoventral length is greater than to its width. The coracoid exhibits a straight anterior outline while the dorsal and ventral ones are slightly convex, making a quadrangular aspect to the proximal half. The anterodorsally border on lateral portion is strongly ornamented by rugosities and bears a marked ridge at the anterodorsal corner, which extends posteroventrally, but lacks a marked glenoidal fossa due taphonomical distortion. In the posterior portion, above the glenoid process, an incipient obturator foramen is visible like as an invagination, indicating that the coracoid foramen extends posterodorsally onto the anterior end of scapular blade (although the latter is not preserved). The glenoid process is robust and strongly pronounced, possessing a sigmoidal profile on lateral border. Ventrally to it, the coracoid displays a well-developed and rugose infraglenoid lip, whose is slightly posteroventrally turned. Medially the coracoid is featureless, excepting for the anteroventral margin whose is ornamented by remarkable rugosities.

4.2.2.1.2. Sternal plate

A virtually complete right sternal plate has been recovered, and is connected to a dorsal rib on its internal (dorsal) surface (Figure 43). The sternal plate is a crescentic plate-like bone, with a slightly concave lateral and a strongly convex medial margin. Almost of the anterior portion is lacking whereas the posterior ones preserves a sub square outline. Additionally, the medial and posterior margins exhibit a remarkable rugosities. The external surface (ventral) is almost featureless, excepting by an incipient ridge near the anterior corner.

4.2.2.2. Limbs

4.2.2.2.1. Forelimb

4.2.2.2.1.1. Humerus

Solely a moderately preserved right humerus (Figure 44) has been recovered with the holotype specimen (MZSP-PV 807). The topotype specimen (MZSP-PV 831) was also recovered with a right humerus and, although it is poorly preserved, is possible to visualize the characters that allow its assignment to *Tapuiasaurus*. The both elements has a gracile shape, also evidenced by the low robustness index presented by the holotype (Table 4.5-A).

The proximal end is well expanded, in which its width is two times greater than to the mid-shaft, and displays an almost straight outline its dorsal margin. A beveled bulge is present on medial corner of both humeri, which is interpreted here as an synapomorphic condition for Tapuiasaurinae. Inside the broad deltopectoral fossa, other two small tuberosities are present close to the medial margin.

The diaphysis is lateromedially compressed, but even so had its width is three times greater than the anteroposterior width, giving an ellipsoid aspect to the transversal section of the mid-shaft. The lateral and medial margins are concaves, and the lateral ones exhibit a medially deflected deltopectoral crest. In the anterior view, the deltopectoral crest exhibit a rugose flattened surface, which develops a remarkable ridge anterodistally and a large bulge posteroproximally. The posterodistal bulge extends distally, culminating in a sharp lateral crest. In addition, a shallow fossa between this lateral crest and the lateral margin of deltopectoral crest. The setting of deltopectoral crest (*i.e.* presence of additional anterodistal ridge and the lateral crest) is also regarded as autapomorphic for *Tapuiasaurus* (see above).

Unfortunately, the distal end on all humeri assigned to *Tapuiasaurus* are very damaged, excepting the presented for the holotype, which preserves solely the ulnar condyle. The ulnar condyle is barely conserved, but apparently, it develops anteriorly. For the same reason, the width of distal end can not be assessed.

4.2.2.2.1.2. Ulnae

All ulnae are preserved within the holotype specimen (MZSP-PV 807). However, the right ulna is only preserved on its anterior side, wherein the posterior and the olecranon process are absent. On the other hand, the left ulna is complete and well preserved (Figure 45). The both ulnae has an elongated and slender aspect (Table 4.5-A), but its proximal end is strongly lateromedially expanded. The lateral diaphyseal margin is almost straight, while the medial is concave. The proximal end bears a broad and well-developed olecranon process, which possess a rugose rounded dorsal surface and develops above the anteromedial and anterolateral processes. The anteromedial process is strongly developed, exceeding the limit of the distal end. Differently, the anterolateral process is poorly developed, resembling a restricted lateral tuberosity.

The radial fossa is practically absent, limited to a shallow depression that is more evident close to the anteromedial process. Nearly to the distal end, the anterior face of the diaphysis exhibit a marked radial ridge. Differently, on posterior face of the diaphysis, the olecranon process is supported by a stout ridge that exceeds the diaphyseal mid-length, creating the characteristic triradiate pattern of the bone. In addition, posteromedially, the olecranon ridge with the anteromedial ridge surrounds a deep and excavated longitudinal fossa that extends into two thirds of the bone length. The distal end is medilaterally expanded, more conspicuously on the anterior view. In the posterior view, is possible to observe that the distal end is slightly twisted anteromedially. Likewise the anterior, the posterior face also presents a marked, but small, ridge close to the distal end.

4.2.2.2.1.3. Radius

A nearly complete left radius is present among the holotype remains (Figure 46). The right radius may is represented by a small fragment of a distal end. The radius is slender, anteroposteriorly flat and its extremities are expanded, in which give a sigmoid profile to the bone. However, although both ends are expanded, the distal is more developed than the proximal one and, while the medial margin are straight, the lateral is concave. The proximal end possess a flattened dorsal surface, and is marked by a prominent anteromedial process. The diaphysis is "D-shaped, and the convex posteromedial face is pierced by a continuous interosseous ridge along entire the proximodistal axis, which accompanies the sigmoid profile of the bone. Nearly the distal end expansion, a second ridge is present. The ulnar fossa is shallow and poor developed. The anteromedial side is almost featureless, displaying only a sharply ventral surface of the distal end.

4.2.2.2.1.4. Manus

Were recovered metacarpal remains from both manus of the MZSP-PV 807 individual. Nonetheless, only in the left manus the metacarpals are better preserved (Figure 47), whereas on the right one solely poorly preserved fragments were identified, such as the distal end of metacarpal-I and putative remains from the II and III. Among the conserved elements, the left manus kept the metacarpals interpreted here as I, II and IV. Despite the latter was found complete, the two firsts are broken on the mid-shaft, which does not allow identifying whether both ends are twisted relative to one another. The left metacarpal-III preserved a small fragment of proximal end, while the metacarpal-IV is absent.

The proximal end of left metacarpal-I is damaged, hampering the visualization of the characteristic "D-shaped" outline. The diaphysis exhibit in the posterolateral margin a pronounced ridge that extends mainly at the distal half. The distal end is rectangular in-shape on both metacarpal-I, and presents at the anteromedially surface a bevelled articular condyle. There, a small sub-rectangular proximal phalanx is present, as well as its correspondent ungual. The proximal phalanx displays a flat ventral and convex dorsal surfaces, and its proximal articulation is concave. The ungual are medially curved, and displays a reduced flexor tubercle in the ventromedial portion. The proximal end is flat and has an "8-shaped" outline. Lateral grooves are absent, and the ungual lacks mostly of the distal apex.

The putative metacarpal-II has extremities with equal widths and is sub-equal in length with the metacarpal-I. The proximal end is sub-circular to sub-ellipsoid in-shape, and posteromedially bowed. The lateral and medial margins on proximal half of diaphysis accompanies the contour of proximal end, while the distal end is expanded. Marks of tubercles or condyles are absent, limiting the evaluation that *Tapuiasaurus* had other manual phalanges. Although slightly compressed, the metacarpal-IV apparently exhibit a strongly lateromedially expanded proximal end and is slightly bowed in respect to the distal end. The anterolateral margin bears a developed crest, which surpasses the mid-height level. The diaphyseal transverse-section is sub-circular and the posteromedial margin is curve, almost concave.

4.2.2.2.2. Hindlimb

4.2.2.2.2.1. Femora

The both femora has been recovered with the holotype specimen (MZSP-PV 807) of *Tapuiasaurus*. The right element is almost complete, lacking parts of the proximal end (mostly of the lateral bulge, the greater trochanter and the femoral head), whereas the left femur (Figure 48) is badly conserved, preserving solely two thirds of the proximal portion and diaphysis. In addition, is known a complete left femur of an adult individual (MZSP-PV 1324), whose was designated as referred specimen of *Tapuiasaurus* (Figure 49). Based on measurements and estimates of all femora (Table 4.5-B), the Femoral Robustness Index (*sensu* Wilson & Upchurch 2003) of *Tapuiasaurus* is less than 0.28, regarding it as a gracile morphotype.

The femoral head on MZSP-PV 1324 is strongly dorsomedially turned, as well as appears in the left femur of MZSP-PV 807, which only preserves a portion of the medial side. The dorsal surface of MZSP-PV 1324 exhibit conspicuous rugosities, also bearing several small rounded pits. However, the greater trochanter is poor developed in respect to femoral head, giving to it a slender aspect. Although the diaphysis on all femoral remains are ellipsoid in-shape and retains the typical anteroposterior width lesser than to the mediolateral width (right femur: 7.3 cm x 17.7 cm; left femur: 7.6 cm x 17.8 respectively), the proximal end on both femora had a gracile profile compared to the mid-shaft proportions.

A well-developed lateral bulge is present, and accompanies the straight shape of lateral margin. On anterior surface, none of *Tapuiasaurus* femoral material presents sagittal interosseous ridges or grooves. On other hand, in posterior view of the right femur of MZSP-PV 807, is present a “U-shaped” welt above the level of fourth trochanter. The fourth trochanter is extremely reduced to small and thick rugose ridges, positioned posteromedially at close to the mid-height of the bone. Between the fourth trochanter and the medial margin is there a longitudinal fossa, which is shared by all femoral elements assigned to *Tapuiasaurus* and may correspond to an autapomorphic condition of this taxon.

The distal end is better preserved only in the right femur of MZSP-PV 807. It is transversely broader, showing well-developed condyles that extends to anterior portion of femur, mainly the tibial condyle. The tibial condyle is slightly bevelled dorsomedially and possesses a sub-equal dimension in relation to the fibular condyle. The intercondylar fossa is shallow and wide, few surpassing the condylar heights. The fibular condyle is barely preserved and very appressed to the epicondyle. This latter is damaged, but seems developed like a tuberosity on medial margin.

4.2.2.2.2.2. Fibula

Just the left fibula was preserved among holotype specimen materials. The bone lacks mostly of its proximal end, and the distal end is crushed. Nonetheless, the preserved diaphyseal shaft conserves several traits. The bone has a slender nature (Table 4.5-B), owning a general sigmoid shape in lateral view (Figure 50). The extremities are transversely flattened and more expanded than the diaphysis, but the distal one appears slightly more anteroposteriorly expanded than the proximal one. An incipient anterior crest in the proximal portion is present, however do not possible to ascertain whether forms an interlocking crus because the proximal end is not fully preserved.

The mid-shaft has a common “D-shaped” contour throughout most of its length, which the medial face is almost flat and facing a lateral convex portion. A well-developed lateral trochanter is present at anterolateral portion of the mid-shaft, extending obliquely anteroproximally to posterodistally. The *iliofibularis* scar is clearly visible as an interosseous ridge, pointed laterally in respect to the lateral trochanter and separated from the latter by a marked sulcus. Likewise, the *iliofibularis* scar extending obliquely through the lateral surface. On the medial side, the periosteum was partially eroded and lacks relevant characters, such as the astragalar facet.

4.2.2.2.2.3. Pes

The *Tapuiasaurus* holotype (MZSP-PV 807) includes an almost complete left pes, which preserves the five metatarsals, eight phalanges, being three of them unguals, and possibly lacking only the reduced phalanges IV-2 and V-2 (Figure 51). The left pes was recovered in close association, but not articulated, to the other hindlimb bone elements, such as the left tibia and fibula (Figure 26), but no tarsus bones have been found. Although the pes were disarticulated during the mechanical preparation, a cast was made *a priori* in order to recover the positions of each element. This cast, together with field seasons and preparation photos (Figure 52), demonstrates that all elements are articulated during the fossilization. The lengths and proximodistal axes orientations of the metatarsals differs radically, revealing a conspicuous entaxony in the pedal digits.

The digit one is strongly hypotrophied, in which the distal end apex of ungual I-2 do not reaches the distal limits of the unguals of digits two and three. It also is slightly directed medially than laterally, as well as the digit two. The digit two is the longest among the epipodial elements, surpassing the length of digit three, although it have sub-equal dimensions. Due the absence of the element IV-2, is not possible to assess the extent of the correspondent digit, however, yet it is possible to estimate that digit is, at least, a little less long than the previous one. The digit five lacks a large part of its proximal portion. Nevertheless, based on preserved portions, it dimensions appears approach to the length of the digit one.

The metatarsal-I exhibit a typical proximodistally short length, whose is nearly the half of the others metatarsals (Table 4.5-B), as well as it is medially deflected. The proximal end possesses a “D-shaped” profile with a convex surface that resembles restricted condyle. The dorsal surface is marked by a medial sulcus, which divides the metatarsal-I into lateral and medial portions. The lateral portion is barely preserved, whereas the medial portion preserves the periosteal bone and the “D-shaped” morphology, and both medial and lateral margins are slightly convex, as well as the ventral surface. As the proximal, the distal end, though damaged, features a convex articulation surface. The metatarsal-II fits ventrally to the metatarsal-I, in which the latter occupies approximately the half of dorsal surface of the metatarsal-II, at a medial depression.

The metatarsal-II is robust, dorsoventrally compressed and relatively longer than the third and fourth metatarsals. The proximal end is sub-rectangular in-shape and more lateromedially expanded than the distal portion, possessing a bipartite condylar type articulation that lacks marked rugosities. The shaft is ellipsoid in-shape, and shows a slightly sagittal ridge that to separate the medial depression, which holds the first metatarsal, of a second shallow and restricted depression on the lateral portion. The distal end is medially twisted, that keep the ellipsoid cross-sectional shape of the mid-shaft. Additionally, the distal end have a poor developed convex articulation, whose is ossified with the phalanx II-1.

The metatarsal-III is slender, with a sub-triangular to sub-oval transversal-section. Contrasting with the first and second metatarsals, just the proximal end have a convex articular surface, whereas the distal one possesses a concave articulation with the phalanx. The medial margin is slightly concave and bears an incipient medial process in the proximal end, whereas the lateral margin is straight. The metatarsal-IV is also slender with concave medial groove and straight lateral margins, but has an ellipsoid shape at transverse-section, and is little longer than the third metatarsal. The metatarsal-IV exhibit an expanded proximal end and both, proximal and distal ends, exhibit concave articulation surfaces. The metatarsal-V is broken and very damaged, mainly at proximal end, hampering major comparisons. Apparently, the margins are concaves, its mid cross-section is, likewise the fourth metatarsal, ellipsoid in-shape, and the distal end displays a flat articulation surface.

The phalanx I-1 is much reduced and the distal articulation have a medially developed hemispherical surface, due the lateral ginglymus is absent. The phalanx I-1 have convex (dorsally) and slightly concave (ventrally) surfaces, which possesses a set of vertical incipient ridges, which probably correspond to tendon scars. The remaining phalanges, except for the V-I, are ventrally flattened, dorsally convex and owning a medial ginglymus more developed rather than the lateral ones. In addition, all are remarkable ornamented on proximal and distal ends by rugosities. The phalanx II-1 differs from the III-1 and IV-1 because is less proximodistally developed, displays straight margins and articulates with the second metatarsal through a concave surface. In other hand, the III-1 and IV-1 phalanges exhibit concave medial, lateral and distal margins and the proximal end on both elements have convex condylar type articulations. The reduced phalanx IV-2 is not preserved. The phalanx V-1 is strongly reduced, more than the I-1, exhibiting a plate-like aspect, which the proximal, ventral and distal ends are slightly concave, raising the possibility of the existence of a phalanx V-II.

The unguals I-2 and II-2 are proximally broad and lateromedially compressed, which the second has a sub-equal length with the first. Except for the first ungual, the second and third have a strongly lateral deflection. Both have paired lateral grooves that do not reaches the ungual apex end, being the dorsal groove of I-2 more deeper. The ungual III-2, in contrast, bears an additional groove at each side of distal end, where both reaches close to the mid length of the bone. The proximal articulation surface has an irregular outline in the ungual I-2 and III-2, while is straight in the II-2. Additionally, the unguals I-2 and II-2 have developed flexor tubercles, medially and laterally, that approaches 70% of the ungual total length, being absent in the ungual III-2. Close to the apex end, the ungual I-2 displays a distinctive dorsolateral paired sulcus. The same sulcus is there on second and third unguals, but in greater numbers (four at least). Ventrally, in the anterior portion, the ungual I-2 and III-2 also possesses an irregular and elongated tuberosity that projects medially, forming a platform.

All unguals shares some features, such as sharp bifid apexes, whose is carved by an upturned sulcus. All unguals also are ornamented by several proximodistally horizontal lines, which indicates of a cornified coverage, being more conspicuous at proximal end, as a set of small lines distributed along dorsoventral axis. In addition, both unguals preserves putative marks of conjunctive tissues, such as a slightly “C-shaped” outline at its mid length, in which accompanies the extension of mediolateral compression present on proximal half of the unguals, and probably is related to the soft tissue cover.

4.3. Phylogenetic analysis

The phylogenetic analysis resulted in 2880 most parsimonious trees with 1637 steps in-length (CI=0.328, RI=0.708), which were found in all replicates. The strict consensus of the ingroup relationships is depicted in the Figure 53, and was acquired using the collapsing rule 3 of TNT (*i.e.* minimum length = 0). Bremer support values for the recovered groups in the consensus tree are given in each node. The complete Bremer analyses with all outgroups is presented in the volume II of this study (Chap. 6.4.), as well as the bootstrap support values for selected nodes (Chap. 6.5.) and a list of all apomorphies which supporting the nodes of the strict consensus (Chap. 6.3.).

The resampling analyses reveal that the branch support values for several nodes in Titanosauria are low, in which Bremer support values ranging between 1 and 3, and bootstrap frequencies not reaching values higher than 70 (*i.e.* statistically insignificant). The low values in resampling analyses are caused due the high degree of missing data and several rogue taxa within the sampling. Even so, the analysis recovered the main erected clades in titanosaurian taxonomy.

Titanosauria has its monophyly recovered in the all trees based on the following synapomorphies: (1) First caudal centrum with convex posterior articular surface (Char**.** 224: 0=>2); (2) Ischial blade not emanating distally to pubic peduncle (Char**.** 340: 0=>1); and (3) Presence of ischial tuberosity (Char**.** 347: 0=>1). Some trees has been also recovered another synapomorphy: dorsal vertebrae lacking middle single fossa projected through the midline of the neural spine (Char**.** 165: 0=>1).

Other major nodes (*i.e.* Lithostrotia and Eutitanosauria) were also recovered in strict consensus. All found trees supports Lithostrotia (Node 114) by six unambiguous synapomorphies: (1) Single neural spines of anterior dorsal vertebrae, in anterior or posterior view, displaying lateral margins dorsomedially inclined, that approach each other (Char. 158: 1=>3); (2) Middle and posterior dorsal neural spines strongly inclined, with an angle not bigger than 40 degrees (Char. 184: 1=>2); (3) Anterior caudal centra (excluding the first) turning from platycoelous to strongly procoelous articular face shape (Char. 230: 1=>3); (4) (Char. 259: 1=>0); (5) (Char. 260: 0=>1); (6) (Char. 412: 0=>2). In addition, some trees have been showed the flat or slightly convex transversely ventral surface of cervical centra (Char. 123: 1 => 0) as synapomorphy of that group.

On the other hand, Eutitanosauria (Node 121), considered here as the clade composed by the most recent common ancestor of *Mendozasaurus neguyelap* Gonzalez Riga 2003, *Trigonosaurus pricei* Campos *et al.* 2005, *Saltasaurus loricatus* Bonaparte & Powell 1980 and all of its descendants (Table 3.2), is supported by the follow five synapomorphies: (1) Middle and posterior dorsal vertebrae, bearing an accessory spinodiapophyseal lamina (Char. 197: 0=>1); (2) Dorsal margin of the coracoids reaching or surpassing the level of dorsal margin of the scapular expansion in lateral view (Char. 288: 1=>0); (3) Presence of a ridge on the ventral surface of the sternal plate (Char. 295: 0=>1); (4) Manual digits two and three lacking phalanges (Char. 323: 1=>3); (5) Absence of phalanges on metatarsal V (Char. 417: 1=>2).

Seven less inclusive clades were identified (see chap. 6.3.): Andesauroidea (*sensu* Salgado 2003), supported solely by one synapomorphy; Lognkosauria, also sharing only one synapomorphy; Rinconsauria (two synapomorphies); Saltasauridae (five synapomorphies); and Saltasaurini (two synapomorphies). The remaining two clades represents new unrecognized groups, here provisionally named Trigonosaurinae and Tapuiasaurinae (see above for the phylogenetic definitions).

Trigonosaurinae is supported through osteological analysis by the autapomorphic combination of 11 characters, while phylogenetics that recovered three additional synapomorphies: (1) Cervical vertebrae exhibiting stout epipophysis, as pillar-like shape (2) expansions above postzygapophyses (Chars. 127: 0=>1 and 129: 0=>1); (3) Anterior caudal centra bearing small foramen-like pneumatophores (Char. 231: 0=>2).

Tapuiasaurinae represents the clade formed by *Tapuiasaurus* plus *Yongjinglong* + the Prata titanosaur, and forms the sister-group of *Rapetosaurus* + *Isisaurus*. The monophyly of Tapuiasaurinae is sustained in all trees by 11 synapomorphies which four of them were previously identified through osteology (Chars. 157: 0=>1; 188: 0=>1; 408: 1=>2; 409: 2=>4). The other seven apomorphies were recovered in the strict consensus: (1) Middle to posterior dorsal vertebrae neural spines possessing subparallel lateral margins in anterior or posterior view (Char. 159: 1=>0); (2) Convex transversely mid to posterior dorsal centra (Char. 177: 1=>0); (3) Neural arch pedicel sub-equal to the centrum height (Char. 203: 0=>1); (4) Humeral deltopectoral crest markedly expanded distally (Char. 301: 0=>1); (5) Humeral lateral margin almost straight until the proximal third of the total length of the bone (Char. 306: 1=>2); (6) Distal condyle orientation of radius beveled approximately 20º, proximolaterally relative to long axis of shaft (Char. 314: 0=>1); (7) Femoral fourth trochanter reduced to ridges (Char. 352: 2=>1).

The clade formed by *Yongjinglong* + Prata titanosaur (Node 116) is supported by the presence in mid and posterior dorsal vertebrae of a weakly developed hyposphene, mainly as a laminar rim (Char. 179: 3=>2), and a single TPOL supporting the hyposphene or postzygapophysis from below (Char. 181: 0=>1).

Besides the osteological examination, the phylogenetic analysis also recovered the follow autapomorphies in *Tapuiasaurus*: (1) teeth with marginal denticles on both carinae edges (Char. 114: 2=>0), (2) Ventral surface of cervical centra transversely concave (Char. 123: 0=>1), (3) Middle and posterior dorsal neural arches retaining the PCPL (Char. 193: 1=>0), (4) Middle caudal centra with platycoelous and slightly procoelous articular face shapes (Char. 251: 3=>1, 2), (5) Posterior caudal centra with slightly procoelous articular shape (Char. 260: 3=>2), (6) Reduced epicondyle on femoral distal end (Char. 350: 0=>1).

5 - Discussion

5.1. Comparative osteology and diagnostic features of *Tapuiasaurus*

Tapuiasaurus represents one of the first and mostly complete “true” titanosaurians known from the earliest Cretaceous until now (Zaher *et al.* 2011, Wilson *et al.* 2016), given several Asian sauropods from the same age have controversial phylogenetic placements, in which those taxa fluctuate its position as titanosaurs or non-titanosaur somphospondylians (see Mannion *et al.* 2013, Averianov & Sues 2017). Although crucial, this period of titanosaur evolution remains unclear since occurrences from this age are rare and the limited anatomical sampling are composed by highly fragmentary specimens (*e.g.* Upchurch *et al.* 2015, Ghilardi *et al.* 2016, McPhee *et al.* 2016, Averianov & Skutschas 2017, Carvalho *et al.* 2017, Averianov & Efimov 2018). In contrast, *Tapuiasaurus* becomes a key-taxon for polarization of transformation series because its holotype (MZSP-PV 807) preserves important anatomical modules (*e.g.* skull and mandibles, cervical, dorsal and caudal vertebrae, fore and hindlimbs) which are poorly or non-sampled in several taxa.

Regarding *Tapuiasaurus* cervical series, one of the most essential elements found are the proatlases, since this bone is known only in another titanosaur until now (Berman & Jain 1982). Hence, major comparisons with other related taxa are hampered. Comparisons with outgroups, such as diplodocoids, display that this structure possesses discrepant morphologies in very close related taxa. An example can be seen in the diplodocines *Kaateodocus* and *Galeamopus* (Tschopp *et al.* 2015), which the first exhibits broader and anteroposteriorly shortened proatlases, while the second exhibit a narrow elongated shape. *Tapuiasaurus* and *Galeamopus* shares a similar proatlas morphology, which posterior tips of those tappers toward distally. Nevertheless, due the reasons commented above, it can not be assumed that this pattern represent an autapomorphy, as well as if other titanosaurs share the same morphology, until new taxa with this structure are identified.

The Atlas of *Tapuiasaurus* differs substantially from to the condition presented by other titanosauriforms, such as *Giraffatitan* (Janensch 1950), *Erketu* (Ksepka & Norell 2006), *Futalognkosaurus* (Calvo *et al.* 2007c) and *Rapetosaurus* (Curry Rogers 2009) because in these taxa the atlantal intercentrum has a tall dorsoventral height and its neurapophyses lacks incipient zygapophyses or transversely expanded distal ends. The atlantal intercentrum of *Tapuiasaurus* resembles, mainly in the posterior view, to the condition present in *Mongolosaurus* which has a slightly procoelous shape and the articular rib surfaces are there on beveled ventral projections, but its neurapophyses are almost absent, hindering other comparisons (Mannion 2011). Neurapophysis in *Tapuiasaurus* are more similar to the displayed by an isolated atlas of undetermined titanosaur from Peirópolis (CPPLIP-247; Martinelli *et al.* 2015) that shares distal ends with wing-like shapes, but differs from this in intercentrum morphology.

Axial anatomy of *Tapuiasaurus* is quite similar in some aspects to that observed in other titanosaurs. The axial intercentrum displays cylindrical parapophyses that are posterolaterally projected, like *Mongolosaurus* and the unnamed titanosaur from India (Wilson & Mohabey 2006, Mannion 2013). However, contrasts with them on the development of a mid ventral keel, which is weakly developed in *Tapuiasaurus*. Diapophyses on axial neural arch bears a projected posterior process as in *Bonitasaura* (Gallina & Apesteguía 2015) and *Uberabatitan* (Mumbuca specimen MCT 1487-R of Powell 2003), differing from these only in neural spine shape.

Neural spines of anterior and mid cervical vertebrae of *Tapuiasaurus* displays in lateral view a remarkable step on anterior edge. This feature is distributed along the cervical series of several taxa, such as *Mongolosaurus*, *Mnyamawamtuka, Malawisaurus* and *Trigonosaurus* (Campos *et al.* 2005, Mannion 2013, Gorscak 2016, Gorscak & O'Connor 2019). Furthermore, its middle cervical neural spines also display lateral bulges as in *Trigonosaurus*, *Overosaurus* and the Mumbuca titanosaur, but less pronounced than in these taxa (Powell 2003, Campos *et al.* 2005, Salgado & Coria 2013).

Incipient epipophyseal-prezygapophyseal laminae (EPRL) are present as in *Uberabatitan* and *Brasilotitan* (Wilson 2012), occurring in *Tapuiasaurus* from the axis until to the most posterior preserved mid cervical. The pattern exhibited by these Brazilian taxa unlike to the showed by Early Cretaceous somphosphondylians, such as *Phuwaingosaurus* (Suteethorn *et al.* 2009) and *Erketu* (Ksepka & Norell 2006), that bears prong-like epipophysis, or *Euhelopus* which that laminae is sharply and well-developed dividing the SPDF along the anteroposterior axis into two fossa (Wilson & Upchurch 2009, Wilson 2012).

Anterior and mid cervical vertebrae of *Tapuiasaurus* are distinguished by a set of characters which are not found in any other titanosaur at this time. For example, some elements exhibit posterolateral tubercles on the spinodiapophyseal fossa (SPDF), which are associated with a sulcus that crosses each spinopostzygapophyseal laminae (SPOL). This morphology can be associated to ligaments marks that were attached to the posterolateral tubercles present in this fossa, as present in some sauropods such as *Apatosaurus* (Taylor & Wedel 2013).

Another distinctive feature of *Tapuiasaurus* cervical vertebrae is the postzygapophyseal laminae (PODL) that connects to the posterior centrodiapophyseal lamina (PCDL) posteriorly in respect to the diapophyseal process. These laminae forms a thick posterior diapophyseal laminae that differs to the observed in *Rapetosaurus* and *Uberabatitan*, which the contact of these laminae is there anteriorly to diapophyseal process and the EPRL appears ventrally to the PODL, respectively (Curry Rogers 2009, Silva Junior *et al.* 2019).

The neural spine on the mid to posterior cervical vertebrae is tall and slightly posteriorly projected as in *Rapetosaurus*, *Isisaurus* and *Dreadnoughtus* (Jain & Bandyopadhyay 1997, Curry Rogers 2009, Lacovara *et al.* 2014). However, the morphology present in *Tapuiasaurus* diverge from all other titanosaurians by owning medial spinopostzygapophyseal laminae (mSPOL) which is sharp and well developed.

Posterior cervical neural arch of *Tapuiasaurus* displays lateral and medial spinoprezygapophyseal laminae (lSPRL and mSPRL) and an expanded neural spine, which the lateral expansion is formed by the lateral spinoprezygapophyseal laminae (lSPRL) as in the early titanosaurian *Ligabuesaurus* (Bonaparte *et al.* 2006) and in lithostrotian *Malawisaurus* (Gomani 2005, Gorscak 2016). Expanded neural spines were known in several taxa, however, differ in their origin and format. The expansion present in lognkosaurians, such as *Mendozasaurus* and *Futalognkosaurus*, are formed by additional laminae (SPDL?) along the vertical axis and bears strongly lateral development (Calvo *et al.* 2007c, González Riga *et al.* 2018). In turn, some taxa as *Bonitasaura*, *Shingopana*, and the Big Bend specimen associated to *Alamosaurus*, shares lateral bulbous expansions that are formed by the SPOL (Gallina 2011, Gorscak *et al.* 2017, Tykoski & Fiorillo 2017).

Tapuiasaurus differs from all of them because the expanded neural spine is strongly slanted posteriorly and the medial spinoprezygapophyseal lamina exhibits an additional medial ramus, which are marked by small fossae between the two branches, a condition not seen in other titanosaurians. Nonetheless, many of the cervical features seen in *Tapuiasaurus,* due to preservation biases, cannot be assessed in other tapuiasaurines such as *Yongjinglong* (Li *et al.* 2014), precluding major evaluations whether some of these features are synapomorphic for that group.

Dorsal vertebrae in *Tapuiasaurus*, and tapuiasaurines as well, are characterized by possessing almost flat anterior surface with paired and restrict centroprezygapophyseal fossa (CPRF) between the centroprezygapophyseal laminae, forming two distinct rami (lCPRL and mCPRL). This condition is too observed in other titanosaurians, such as "*Aeolosaurus*" *maximus*, *Maxakalisaurus* and *Uberabatitan* (CPPLIP-494), differing from the pattern shared by *Opisthocoelicaudia*, *Dreadnoughtus* and *Epachthosaurus* which has single and enlarged CPRL that forms lateral pedicels in CPRF (Borsuk Bialynicka 1977, Martínez *et al.* 2004, Lacovara *et al.* 2014), and from *Muyelensaurus* and *Trigonosaurus* which the CPRF is divided by the ventral bulge of TPRL and/or by a vTPRL above the neural canal (Calvo *et al.* 2007b). However, in tapuiasaurines, the CPRL are splited at the mid-height, in which the lateral ramus is merged with the anterior centroparapophyseal lamina (ACPL) and contacts ventrally to prezygapophyses, while the medial ramus connects with the dTPRL.

Tapuiasaurines shares a set of distinctive characters on mid and posterior dorsal vertebrae that contrasts it from other lithostrotians, such as laterally compressed and slightly opisthocoelous centra, pneumatophores near to the neurocentral joint, the retaining of anterior centrodiapophyseal laminae (ACDL) in posterior elements, posterior centrodiapophyseal laminae (PCDL) not bifurcated ventrally, accessory spinodiapophyseal laminae (aSPDL) absent on almost elements (which occurs asymmetrically on *Tapuiasaurus* posterior dorsal), reduction to absence of postspinal lamina (POSL) and aliform processes limited to a prominent lateral protuberances. In addition, *Yongjinglong* and the Prata titanosaur shares a marked laminar hyposphenal ridge (vTPOL) below to postzygapophyses. *Tapuiasaurus* dorsal vertebrae differs from them by holding a medial prezygodiapophyseal laminae (PRDL) that contacts anterodistally to the spinodiapophyseal laminae (SPDL), a condition not found in other titanosaurs.

Fragmentary caudal remains are known in *Tapuiasaurus* and reveals a noteworthy morphology. The most-anterior middle element bears a remarkable platycoelous articulation shape as in *Wintonotitan, Malawisaurus*, *Rukwatitan*, *Triunfosaurus* and *Mnyamawamtuka* (Gomani 2005, Gorscak *et al.* 2014, Poropat *et al.* 2014, Carvalho *et al.* 2017, Gorscak & O'Connor 2019), whereas the most-posterior mid caudal centra has a slightly procoelous type articulation. Moreover, the preserved centra of distal segment displays a procoelous type articulation. The association of platycoely-procoely in caudal vertebrae plus distal procoely has been regarded as autapomorphic to *Malarguesaurus* (González Riga *et al.* 2009). However, other titanosauriforms sharing similar settings, such as *Cedarosaurus, Gobititan* and *Tastavinsaurus* (Tidwell *et al.* 1999, You *et al.* 2003, Canudo *et al.* 2008), which may correspond to a synapomorphy uniting these three taxa. In this case, the condition presented by *Tapuiasaurus* would be homoplastic, but it should be noted that the distal tail portions in titanosaurians still represents a poorly sampled anatomical module.

Contrasting with axial morphology, which exhibit a mixture of apomorphic (*e.g.* single neural spines, absence of hyposphene-hypantrum) and plesiomorphic (*e.g.* platycoelous mid caudal centra) lithostrotian characters, the appendicular *Tapuiasaurus* anatomy is more conservative, retaining several plesiomorphies in mesopodial, metapodial and epipodial elements. On both recovered *Tapuiasaurus* humeri the proximal end is well expanded, but not so broadly as in *Quetecsaurus, Notocolossus* and *Shingopana* (González Riga & David Ortiz 2014, González Riga *et al.* 2016, Gorscak *et al.* 2017). Additionally, the humeral head of all specimens of *Tapuiasaurus* bears an anteroproximal tuberosity at the medial corner of deltopectoral fossa and the same morphology of deltopectoral crest, which supports the allocation of the second specimen into this genus. Due MZSP-PV 831 has been recovered in the type-site it is designated as topotype specimen of *Tapuiasaurus macedoi*.

The deltopectoral crest is medially deflected, as in the *nomen dubium* taxon "*Antarctosaurus brasiliensis*", in the Prata titanosaur, *Malawisaurus, Paralititan* and *Jainosaurus* (Arid & Vizotto 1971, Smith *et al.* 2001, Wilson *et al.* 2009, Wilson *et al.* 2011b, Gorscak *et al.* 2017), as well as shares with *Jainosaurus* a bulge posterolaterally located in respect to the deltopectoral crest. Nevertheless, the humerus of *Tapuiasaurus* presents an autapomorphic setting, such as deltopectoral crest with flat and rugose anterior surface that exhibits sharp anterior and lateral crests. In addition, a shallow fossa is present between the lateral and posterior margins.

Mesopodial bones of *Tapuiasaurus* has the most conservatives comparing with the general titanosaurian morphology. Although the ulna is gracile and elongated, your proximal end is triradiate and very-expanded transversally, bearing strongly developed olecranon process as in other titanosaurs, such as saltasaurids, *Argyrosaurus*, *Elaltitan*, *Yongjinglong* and the putative early titanosaur *Haestasaurus* (Mannion & Otero 2011, Li *et al.* 2014, Upchurch *et al.* 2015). The radius has an expanded distal end as in almost titanosaurians and *Haestasaurus* (Upchurch *et al.* 2015), differing from non-titanosaur somphospondylians, such as *Angolatitan* (Mateus *et al.* 2011) which the radius exhibit non-expanded distal end. Likewise, the proximal end bears a prominent anteromedial process, like *Jainosaurus* (Wilson *et al.* 2011).

Left manus remains of *Tapuiasaurus* reveals a slightly metacarpus asymmetry, which decreasing in size from metacarpal-I towards metacarpal-V. Differently from that presented by *Andesaurus* and *Argyrosaurus* (Apesteguía 2005, Mannion & Calvo 2011, Mannion & Otero 2011), metacarpal-I is straight and its distal end exhibit an anterior a tubercle. In this structure, articulates a phalange and ungual, representing one of the few titanosaurs with this preserved region (Table 5.1.). Given the absence of complete titanosaur manus the understanding of when phalangeal loss occurs in the group still unclear. *Tapuiasaurus* indicates that early lithostrotians had retained manual phalanges, at least, only in the metacarpal-I, contrary to late taxa as *Diamantinasaurus* that possess a manus with a 2-2-2-2-2 phalangeal formula, or *Opisthocoelicaudia*, which has ossified reduced phalanges (Poropat *et al.* 2015).

Hindlimb of *Tapuiasaurus* shows a typical lithostrotian anatomy, with a lateromedially expanded diaphysis and medially projected femoral head. The fourth trochanter is marked by a sagittal groove, dividing it into two small ridges and is placed nearly to the proximal third of the total femur length. This latter condition is similar to the observed in *Bonitasaura, Patagotitan* and *Rapetosaurus* (Curry Rogers 2009, Gallina & Apesteguía 2015, Carballido *et al.* 2017). Otherwise, several titanosaurs displays a fourth trochanter close to the diaphyseal mid-height, being even some more below in *Opisthocoelicaudia* (Carballido *et al.* 2017). Although both femora of *Tapuiasaurus* specimens are poorly preserved, an epicondyle also can be observed as in *"Aeolosaurus" maximus*. It differs from the extremely pronounced shape present in *Patagotitan*, as well as the poorly developed epicondyles seen in *Adamantisaurus, Dreadnoughtus*, *Opisthocoelicaudia* and saltasaurines (Lacovara *et al.* 2014, Carballido *et al.* 2017).

In the same way of the manus, records of titanosaur pedes are equally scarce (Table 5.2.). The occurrence of a well-preserved left pes in *Tapuiasaurus* bring new information about the evolution of this body region in Sauropoda as whole. The recovered elements represents a nearly complete left pes, which exhibit a combination of plesiomorphies and apomorphies. *Tapuiasaurus* exhibit a conspicuously entaxony, which entire 1st digit has the half size in relation to the metatarsus I to IV, being sub equal in size with the 5th digit. This condition is giving due the very reduced phalanx I-1, whose presents less than the half breadth rather the others phalanges, as in *Opisthocoelicaudia, Epachthosaurus* and La Invernada titanosaur (MUCPv-1533). However, differ in shape with these taxa because they had I-1 pedal phalanx with flat articulations, while *Tapuiasaurus* hold hemispherical or "ball-shaped" surface on distal articulation (Borsuk Bialynicka 1977, Martínez *et al.* 2004, González Riga *et al.* 2008).

Metatarsal-II compose the tallest element, unlike to the mostly titanosaurians, such as *Opisthocoelicaudia, Notocolossus*, and *Alamosaurus* which the metatarsal-III is greater than the others (Borsuk Bialynicka 1977, D'Emic *et al.* 2013, González Riga *et al.* 2016). Despite some elements have been not preserved (IV-2 and V-2), the preserved parts possesses enough features that allow to infer that *Tapuiasaurus* displays a 2-2-2-2-2 formula, leading a high phalangeal count (10) that differs from several lithostrotians, such as *Mendozasaurus* and *Notocolossus* (8), or to the highly apomorphic condition present in *Opisthocoelicaudia* and *Alamosaurus* (7). The phalanges IV-1 and V-1 bears marked articulations on distal surfaces. The pattern observed in *Tapuiasaurus* is identical to the present in *Gobititan*, which also shows a disk-like morphology in phalanx V-1 that articulates with a strongly reduced and spherical V-II phalanx (You *et al.* 2003). Additionally, *Gobititan* shares the same caudal setting of *Tapuiasaurus*, which means that this taxon may also represent a Tapuiasaurinae member.

5.2. Phylogenetic relationships of *Tapuiasaurus* and biogeographic implications

Since its description, *Tapuiasaurus* was present in several phylogenetic studies (Figure 54). Nonetheless, given the fact that its postcranial skeleton has not been fully described and figured until now, as well as due the paucity of scored terminals with cranial data, most of the recovered relationships inferences were biased by incompleteness data. The phylogenetic position of *Tapuiasaurus* among these titanosaurian relationships analyses are conflicting (Table 5.3).

This taxon has long been considered as an advanced titanosaurian (*e.g.* Zaher *et al.* 2011, Carballido *et al.* 2012, Gorscak *et al.* 2014, Lacovara *et al.* 2014, Bandeira *et al.* 2016, Martínez *et al.* 2016, Tykoski & Fiorillo 2016) due its apomorphic skull, in which most of the hypotheses it appears as sister-group of *Isisaurus* and/or *Rapetosaurus*. In addition, only few other previous works have recovered *Tapuiasaurus* within other Early Cretaceous titanosaurs (Poropat *et al.* 2015, Wilson *et al.* 2016, Gorscak *et al.* 2017, Sallam *et al.* 2018).

As already discussed by Wilson *et al.* (2016), the achievement of the understanding of *Tapuiasaurus* relationships is essential for comprehension about trends and the timing of cladogenetic events in early titanosaurian history. Nevertheless, the absence of well-sampled anatomical modules of other several taxa, with a good anatomical overlapping as well, still hinders robust phylogenetic inferences. Although the resulting topology presented here showed low support measures, the scoring and analysis of postcranial skeleton data of *Tapuiasaurus* allowed for the first time a better investigation scenario.

The strict consensus of 2880 most parsimonious trees (Figure 53) recovered the monophyly of the main most (*i.e.* Lithostrotia, Eutitanosauria, Saltasauridae) and less (*i.e.* Rinconsauria, Lognkosauria, Saltasaurini) inclusive recognized Titanosauria clades. Other two minor groups, identified *a priori* by osteology, has also been recovered. The first, named here Trigonosaurinae, consist in an endemic clade of Brazilian titanosaurians from the Late Cretaceous (Coniacian-Maastrichtian) Bauru Basin (Dias Brito *et al.* 2001).

Tapuiasaurus, *Yongjinglong* and the unnamed titanosaur from Prata municipality, compose the second group, which is named here as Tapuiasaurinae. This group may represent one of the first lithostrotian irradiations across the world, given that its representatives were already widespread in the first part of the Lower Cretaceous. *Tapuiasaurus* comes from the Barremian-Aptian Quiricó Formation of Brazil, while *Yongjinglong* come from the Valanginian-Albian Hekou Group, China (Li *et al.* 2014, Dai *et al.* 2015). The third representative, the Prata titanosaur, comes from Late Cretaceous deposits (Santonian-Campanian) of Adamantina Formation (Bauru Basin), Brazil.

This unusual widespread grouping raise some discussions about the timing and origin-centre of first lithostrotians (Figure 55), as well as the role of tapuiasaurines in titanosaurian evolutionary history. The earlier age of *Yongjinglong*, in respect to the others lithostrotians, evidences of an origin, at least of this clade, on Asian continent.

In this scenario, the first lithostrotians would have dispersed to southern continents through Europe still in the Early Cretaceous, being corroborated by the occurrence of coeval putative lithostrotians, such as *Daxiatitan,* in coeval deposits of China, and true-titanosaurs in the Hauterivian of Russia, such as *Volgatitan* (Averianov & Efimov 2018), and in the Hauterivian-Barremian of South America, such as *Triunfosaurus* (Carvalho *et al.* 2017). Additionally, given the extensive ghost-lineage between *Yongjinglong* and other tapuiasaurines, the Prata titanosaur becomes a relictual taxon of this group.

In turn, an alternative hypothesis would be that the titanosaurs originated in Europe, at some point in the Jurassic-Cretaceous boundary, having subsequently dispersed in two distinct directions, one heading to Asia and one moving towards the Gondwana. Occurrences of putative early titanosaurians in the Wealden Supergroup (Upchurch *et al.* 2011, 2015), such as *Haestasaurus* (Berriasian) and *Eucamerotus* (Barremian) can offer support this scenario. Similarly to the first view, titanosaurians would have arrived into South America and Africa prior to the Aptian interval based, beyond *Triunfosaurus*, on the problematic record of *Algoasaurus*, which comes from the Valanginian-Hauterivian Kirkwood Formation of South Africa (McPhee *et al.* 2016, Carvalho *et al.* 2017). This second hypothesis also provides a basis for explaining some of the vicariant patterns displayed by the group (see below), due the isolation of continental landmasses in Late Cretaceous (Figure 55-C).

In addition, Tapuiasaurinae forms a monophyletic group with the clade composed by the latest Cretaceous taxa *Rapetosaurus* and *Isisaurus*, corroborating with an early dispersion in the group, given these taxa are temporarily and geographically distant from tapuiasaurines. However, the recovered phylogenetic inference shows that the early lithostrotians are represented by a set of Aptian-Albian taxa from Africa, such as *Malawisaurus*, *Mnyamawamtuka* and *Rukwatitan* (Gorscak 2016), which does not support the presented biogeographic scenarios, as well as the position of *Rapetosaurus* and *Isisaurus* would be skewed due to anatomical sampling is composed by few taxa with cranial data (*Tapuiasaurus, Rapetosaurus* and *Nemegtosaurus*), creating and differential branch-attraction. Nonetheless, a trade-off between morphological and stratigraphic concordance is difficult to resolve (Wilson *et al.* 2016), due the poor sampling anatomical record and by the scarcity of deposits of determined ages.

5.3. Patterns in early titanosaur diversification

Osteological comparisons of *Tapuiasaurus* with other titanosaurians, as well as their relationships recovered through phylogenetic analysis, reveals that the acquisition of some typical titanosaur characters (*e.g.* caudal procoely) were not gradually, occurring on different timings and groups along its evolutionary history. As cited anteriorly, the scarcity of Early Cretaceous titanosaurs with well-sampled anatomical modules and relevant anatomical overlapping hampers the major patterns which leading early titanosaur diversification.

The strict consensus topology presented here suggest that first titanosaurians, such as *Ligabuesaurus* (Bonaparte *et al.* 2006), are characterized by possessing the distinctive single and laterally expanded neural spines on posterior cervical vertebrae. However, other early titanosaurs such as *Andesaurus* and *Rukwatitan* lacks all or mostly of cervical series, not allowing to evaluate if they already had this condition, or displayed the bifid neural spines shape like others somphospondylians, such as *Phuwiangosaurus* (also regarded as a basal titanosaur in previous studies), and the recently described titanosaurian *Kaijutitan* (Upchurch 1995, Suteethorn *et al.* 2009, Filippi *et al.* 2019).

This condition is also shared both by early, such as *Malawisaurus* and *Tapuiasaurus*, and late lithostrotians, such as *Bonitasaura* and lognkosaurians. However, the laminas in which these expansions develop diverges radically: some expansions are formed by lSPRL (*Ligabuesaurus, Malawisaurus* and *Tapuiasaurus*) or the SPOL (*Bonitasaura*, *Quetecsaurus*), while some lognkosaurs as *Mendozasaurus* exhibit an accessory lamina, probably the SPDL. This indicates a homoplastic pattern along evolution of this character, marked by several convergence events.

Previously regarded as a plesiomorphy retained by the early titanosaurians, hyposphene-hypantrum articulations also seems homoplastic in titanosaur evolution, given this condition appears in multiple taxa not intimately related, such as the early titanosaur *Andesaurus,* the lognkosaurian-like forms *Patagotitan*, *Argentinosaurus*, and the ‘saltasauroid’ eutitanosaurian *Epachthosaurus* (Bonaparte & Coria 1993, Martínez *et al.* 2004, Carballido *et al.* 2017). This feature would be associated with a size increase, which was attained by the group on gigantism episodes occurred during the Albian-Cenomanian time-interval (±100 My).

A long-dated titanosaurian synapomorphy is the procoelous condition of caudal vertebrae. Bonaparte and Coria (1993) first divided the titanosaurs into two groups: a most basal, which besides retains hyposphene-hypantrum complex in dorsal vertebrae, the procoely on caudal vertebrae occurs only in the most anterior elements (‘andesaurids’); and a derived group that lacks extra articulations and bears fully procoelous caudal series (‘titanosaurids’). Nonetheless, the evolution of caudal vertebrae morphology in sauropods and the development of shape types has a confusing history, marked by reversions and convergences. Several non-titanosaurian sauropod lineages displays procoelous anterior caudal vertebrae, such as mamenchisaurids, turiasaurs, dicraeosaurids and diplodocines (Bonaparte *et al.* 2000, Royo Torres *et al.* 2017, Mannion *et al.* 2019).

Immediate titanosaur sister-taxa, like *Chubutisaurus*, are characterized by possessing platycoelous anterior caudal associated to amphyplatyan mid and posterior caudal vertebrae (Carballido *et al.* 2011). On the other hand, first titanosaurians differ substantially from one another, given some taxa such as the Early Cretaceous *Mnyamawamtuka* has retained the plesiomorphic condition, while *Andesaurus* displays procoelous anterior caudal vertebrae (Mannion & Calvo 2011, Gorscak & O’Connor 2019). Other Early Cretaceous lithostrotians as *Malawisaurus* and *Rukwatitan* also exhibit the same morphology and this pattern persists along the group evolution, since basal lithostrotians with platycoelous/amphyplatyan caudal vertebrae are recorded until the Late Cretaceous (Santonian-Maastrichtian), such as *Traukutitan* and *Paludititan* (Gomani 2005, Csiki et al. 2010, Juarez Vallieri & Calvo 2011, Gorscak 2016).

On other early lithostrotian, in turn, the procoely appears in different caudal segments with discrepant developments. *Tapuiasaurus* shares with *Gobititan*, *Malarguesaurus* and *Cedarosaurus* the association of platycoelous plus slightly procoelous mid-centra, towards the most distal vertebrae has fully procoelous centra (You *et al.* 2003, Gonzalez Riga *et al.* 2009). Nonetheless, *Rapetosaurus* and *Isisaurus* (sister group of tapuiasaurines) displays fully procoelous caudal series (Curry Rogers 2009, Jain & Bandyopadhyay 1997).

In Eutitanosauria, procoely seems more uniform only in the Saltasauridae related taxa, which also shares the first caudal (or last sacral) bearing a biconvex type articulation whereas the most distal segment is marked by owning caudal centra also with biconvex articulations (Huene 1929, Powell 1992). It should be noted that few analyses have recovered the monophyly of titanosaurs that have this condition (*e.g.* Gorscak *et al.* 2017).

The close saltasaur related *Opisthocoelicaudia*, alongside this highly autapomorphic opisthocoely in the caudal series, displays anterior dorsal (and probably cervical) bifid neural spines that could correspond to a reversal condition or a plesiomorphy retained by this taxon. This pattern leading some authors suggest a more basal position for this taxon (*e.g.* Upchurch 1995, Salgado et al. 1997, Sanz et al. 1999, Santucci 2002), which also was supported by phylogenetic analyses.

Similarly to saltasaurines, rinconsaurians and trigonosaurines possess fully procoelous caudal vertebrae, excepting on a small sector of distal part of the series that has an intercalation of amphicoelous-biconvex and/or an amphicoelous-opisthocoelous-biconvex shaped centra between the remaining procoelous elements (Calvo & González Riga 2003). Lognkosauria and associated taxa, in contrast, exhibit a heterogeneous caudal centrum shape pattern, which some taxa as *Mendozasaurus* displays anterior procoelous plus slightly procoelous to platycoelous mid caudal centra, while other forms, such as *Patagotitan* and *Quetecsaurus*, has fully procoelous caudal series.

Titanosaur appendicular anatomy shows more conservative and gradual patterns in respect to the axial series morphology. This factor could be associated with a graviportal instance marked by several body-sizes trends, such gigantism (Huene 1929, Bonaparte & Coria 1993, Lü *et al.* 2009, Lacovara *et al.* 2014, González Riga *et al.* 2016, Carballido *et al.* 2017) and nanism (Nopcsa 1930, Stein et al. 2010, Company, 2011, Díez Díaz *et al.* 2013, 2018) episodes, as well as with a wide-gauge locomotion (Wilson & Carrano 1999), while the axial is related to physiological (*e.g.* Wedel 2003a, 2003b, 2005) and biomechanical issues (*e.g.* Salgado *et al.* 2006).

Along its evolution, titanosaur forelimbs displayed a progressive robustness increase, exemplified by an expansion of proximal end of the humerus, which the dorsal outline turn from a bowed to a straight outline and, allied to this, the diaphyseal transversal section reaches a strongly development in lateromedial width. Likewise, mesopodial and metapodial bones (radii, ulnae and metacarpus) shows stout shapes with expanded ends.

In contrast, the evolution of manus morphology in Titanosauria still poorly known. Besides *Tapuiasaurus* only other two taxa has been found with phalanges, the Albian-Cenomanian *Diamantinasaurus* and *Savannasaurus* (Poropat et al. 2015, 2017), while the remaining titanosaurs with preserved metacarpus lacks manual phalanges (see Table 5.1.).

Due the absence of other Early Cretaceous taxa with well-preserved manus, there is a gap, which makes impossible to assess whether the phalangeal loss/retention occurred gradually or evolved several times in the group, given *Tapuiasaurus* exhibit less phalangeal elements than to the other sampled titanosaurs.

Femoral anatomy also exhibits an increase in shaft width (*i.e.* transversely elongate and anteroposteriorly compressed shape), as well as a remarkable development of femoral head, which is strongly deflected inwards (Salgado et al. 1997, Wilson & Carrano 1999). This pattern is associated with a specialization of the graviportal condition shared by almost sauropods. In all titanosauriforms, the medially deflected femoral head develops a lateral bulge (see Chap. 1.1.). In turn, advanced titanosaurians, such as saltasaurids, also displays offset distal femoral condyles that serve to direct the medially femur shaft, creating an angle between proximal end and the vertical axis of the diaphysis (Wilson & Carrano 1999). These features would have contributed to a wide-gauge instance, being shared by all titanosaurs.

Lastly, titanosaur pedal anatomy has a decrease phalanx pattern which ranges from the metatarsal-V towards II, as in almost sauropods (see Table 5.2.), although the phalangeal count in the metatarsal-III and V varies substantially. Early titanosaurians as *Tapuiasaurus* and *Gobititan* exhibit the plesiomorphic condition present in basal Sauropoda, retaining two elements in fifth digit, although the remain ones bears the same arrangement that other lithostrotians, such as *Mendozasaurus* and *Notocolossus,* differing from titanosauriforms such as *Tastavinsaurus* that shows solely one phalanx in the fifth digit. In turn, *Epachthosaurus* lacks a phalanx in the last metatarsal as almost late titanosaurs, but bears an additional element in third digit as present in *Camarasaurus* and the turiasaurian *Mierasaurus*. This uncommon setting would can be linked to reproduction strategies, such as different nesting behaviour (Vila et al. 2010).

Thus, is clear that *Tapuiasaurus* represents early-appearing lithostrotian that possess derived features shared with later-appearing taxa, as suggested by Wilson *et al.* (2016). Through the postcranial osteology and analysis carried, *Tapuiasaurus* is diagnosed by a series of axial and appendicular autapomorphies (see above), as well as by a unique combination of characters that reveals among early titanosaurians a mosaic acquisition of plesiomorphic and apomorphic features.

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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