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Titanosauria of the Bauru Group: a summary of records and their importance for understanding the diversity of the clade in Brazil

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ABSTRACT. The present study provides a synthesis of the diversity and geographical distribution of Titanosauria (Dinosauria: Sauropoda) from Upper Cretaceous rocks of the Bauru Group in Brazil. There are currently ten valid species of titanosaurs described for the Bauru Group, some of which exhibit similarities to species found in Argentina. Among these species is the well-known clade Aeolosaurini, which is considered as endemic to South America. Members belonging to the Aeolosaurini clade remains have so far been found only in Argentina and Brazil. This faunal similarity helps in the interpretation of the paleogeographic distribution of these organisms, which reflects intense faunal interchange between these regions, thereby indicating a chrono-correlated geological age.

Keywords: Bauru Group, Fossil records, Sauropoda, Cretaceous.

RESUMEN. Titanosaurios del Grupo Bauru: un resumen de su registro e importancia para entender la diversidad de este clado en Brasil. El presente estudio presenta una síntesis de la diversidad y distribución geográfica de los dinosaurios saurópodos titanosaurios encontrados en las rocas del Cretácico Superior del Grupo Bauru, en Brasil. Actualmente existen diez especies de titanosaurios descritas para el Grupo Bauru, algunas de las cuales presentan similitudes con aquellas encontradas en Argentina. Entre estas especies se encuentra el conocido clado Aeolosaurini, considerado endémico de América del Sur. Hasta ahora, restos atribuibles este clado sólo se han encontrado en Argentina y Brasil. Esta afinidad faunística contribuye a la interpretación de la distribución paleogeográfica de estos organismos, la cual refleja un importante intercambio faunístico entre estas regiones, indicando por lo tanto una edad geológica correlacionable cronológicamente.

Palabras clave: Grupo Bauru, Registros fósiles, Sauropoda, Cretácico.

1. Introduction

The Bauru Group is an Upper Cretaceous succession of continental deposits in the Bauru Basin, in the states of Goiás, Minas Gerais, Mato Grosso do Sul, and São Paulo, Brazil (*e.g.,* Soares *et al*., 1980, 2020a,b; Fernandes and Coimbra, 1996) (Fig. 1). Divided in the Araçatuba, Adamantina, Uberaba, Marília and Serra da Galga formations, it is the main and richest geological group of this age in Brazil (*sensu* Batezelli, 2017; Soares *et al*., 2020a). The Bauru Group is a <480 m-thick clastic succession that mainly includes mudstones, sandstones, limestones, and conglomerates, genetically related to aeolian and fluvial-lacustrine processes (Fernandes and Ribeiro, 2015; Tcacenco-Manzano *et al*., 2024). The lithostratigraphic scheme of the Bauru Group has been greatly modified since its first descriptions, as evidenced by the works of Soares *et al*. (1980), Barcelos (1984, 1989, 1993), Fernandes and Coimbra (1996), Fernandes (1998), Batezelli (2003) and Basilici *et al*. (2012). Overall, the correlation and identification of the stratigraphic units of the Bauru Group has been difficult due to the apparent lack of precise radiometric dating, the marked lateral variation of its facies, and the varying nomenclature used over time.

The Bauru Group particularly crops out in the regions of Triângulo Mineiro (Minas Gerais State) and the western part of São Paulo State (Barcelos, 1984). Since the early 1900s, many theropod and titanosaur fossils have been discovered in the Bauru Group rocks. Over the last three decades, new titanosaur species have been described, shedding light into their faunal diversity, age, and paleobiogeography (Bertini *et al*., 1993; Santucci and Bertini, 2001, 2006; Candeiro *et al.,* 2006, 2024; Candeiro, 2010; Bittencourt and Langer, 2011; Motta-Gil and Candeiro, 2014; Brusatte *et al*., 2017). The phylogenetic relationships of Brazilian Cretaceous titanosaurs have been the subject of considerable interest as well. Recent studies on Titanosauria focused on traditional osteological comparisons (*e.g*., Gorscak *et al*., 2014) and cladistic analyses (*e.g*., Bandeira *et al.,* 2016; Gonzalez-Riga *et al*., 2016; Mannion *et al.,* 2019). It has been suggested that the Upper Cretaceous titanosaur fossils of southeastern Brazil would be related to contemporaneous titanosaurs found in Argentina and Madagascar.

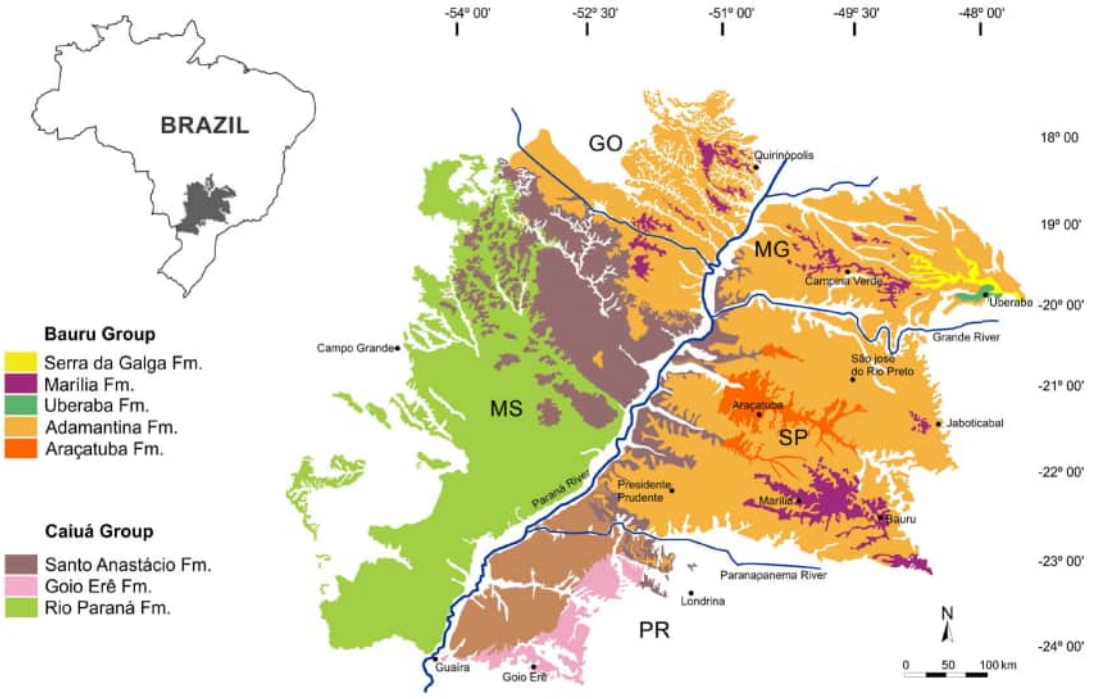

FIG. 1. Lithostratigraphic map of the Bauru Basin in southeastern Brazil (adapted from Fernandes and Ribeiro, 2015, and Soares *et al*., 2020a). **GO**: Goiás; **MG**: Minas Gerais; **MS**: Mato Grosso do Sul; **SP**: São Paulo; **PR**: Paraná.

As shown, the quality and abundance of the fossil record in the Bauru Group rocks is key for understanding the Upper Cretaceous fauna of South America, offering a more detailed view of their adaptations, speciation, and paleobiology (Vidal *et al*., 2024a,b). This study therefore aims to provide a comprehensive summary of the titanosaurian species found so far in southeastern Brazil, in addition to discussing their paleogeographic distributions along the region.

Institutional abbreviations. ANM: Agência Nacional de Mineração, Rio de Janeiro, Brazil; **CCCP**: Complexo Cultural e Científico de Peirópolis da Universidade Federal do Triângulo Mineiro, Uberaba, Brazil; **CPP:** Centro de Pesquisas Paleontológicas "Llewellyn Ivor Price" da Universidade Federal do Triângulo Mineiro, Uberaba, Brazil; **DGM:** Departamento de Geologia e Mineralogia da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **LPP:** Laboratório de Paleoecologia e Paleoicnologia do Departamento de Ecologia e Biologia Evolutiva da Universidade Federal de São Carlos, São Carlos, Brazil; **MCTer**: Museu de Ciências da Terra, Rio de Janeiro, Brazil; **MPM**: Museu de Paleontologia de Marília, Marília, Brazil; **MPMA**: Museu de Paleontologia "Professor Antônio Celso de Arruda Campos", Monte Alto, Brazil; **MN**: Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **MUGEO**: Museu Geológico Valdemar Lefèvre de São Paulo, São Paulo, Brazil.

2. Geological setting

The origin of the sedimentary deposits of the Bauru Basin is associated with thermal and lithostatic events from the outpouring of the basaltic lavas of the Serra Geral Formation. The cooling and contraction of these lava flows created a surface that favored the accommodation of sediments (Riccomini, 1997; Fernandes and Coimbra, 2000; Basilici *et al*., 2012). The stratigraphic succession of the Bauru Basin consists predominantly of very fine- to medium-sized sandstones. Conglomerate sandstones make up less than 5% of the total thickness of the succession, with fine layers of sandy clay streaked with sandstones constituting less than 2% (Riccomini, 1997; Fernandes and Coimbra 2000).

The evolution of the Bauru Basin has been well discussed by many researchers using different approaches; however, consensuses have yet to be reached, particularly in the interpretation of the different depositional processes of the basin. Soares *et al.* (1980) recognized four units from bottom to top: Caiuá Formation, Santo Anastácio Formation, Adamantina Formation, and Marília Formation. In the next decade, Fernandes and Coimbra (1994) reassessed the stratigraphic distribution of the Basin units and divided the sedimentary succession into two groups: Caiuá and Bauru (Fig. 1). The Caiuá Group is formed by the Rio Paraná, Goio Erê, and Santo Anastácio formations, while Bauru is formed by the Araçatuba, Adamantina, Uberaba, Marília, and Serra da Galga formations (Batezelli, 2015; Batezelli *et al*., 2019; Soares *et al*., 2020a). Sedimentary evidence suggests that the Bauru Group rocks were deposited in a distributive river system (Silva *et al*., 2016).

The Bauru Group rocks crop out irregularly in southern Goiás, Triângulo Mineiro, western São Paulo, and Mato Grosso do Sul. Among these rocks are those of the Araçatuba, Adamantina (which includes the Adamantina, Presidente Prudente, and São José do Rio Preto formations of Batezelli, 2017, and Langer *et al*., 2022), Uberaba, and Marília formations (*sensu* Batezelli, 2017). The Araçatuba Formation crops out in the states of São Paulo and Minas Gerais, and it was likely deposited in a swampy paleoenvironment (Zaher *et al*., 2006). The Adamantina Formation is the unit with the largest exposed coverage, cropping out in the states of Goiás, Mato Grosso do Sul, Minas Gerais, and São Paulo, and it is composed of fine-grained sandstones and pelites of fluvial-lacustrine origin (Barcelos, 1984). The Uberaba Formation is exposed exclusively in the state of Minas Gerais (Triângulo Mineiro), and its sandstones include abundant volcanic rock fragments from the Upper Paranaíba arc (Soares *et al*., 1980). The Uberaba rocks are associated with a braided fluvial depositional environment, chrono-correlated with the Adamantina Formation (Hasui, 1968; Fúlfaro and Barcelos, 1991; Fernandes and Coimbra, 1996, 2000; Ferreira Jr., 1996; Goldberg and Garcia, 2000). Finally, the Marília Formation rocks crop out in the states of Goiás, Mato Grosso do Sul, Minas Gerais, and São Paulo (Dal´Bó and Basilici, 2010). Soares *et al*. (1980) subdivided Marília into the Serra da Galga, Echaporã, and Ponte Alta members, while more recently Soares *et al*. (2020a) proposed the Serra da Galga Formation as part of the Bauru Group, which crops out in Minas Gerais exclusively.

The Bauru Group has provided one of the richest and most diverse assemblages of continental vertebrates from the Late Cretaceous of South America. Paleontological studies of vertebrate remains suggest that this group developed between the Campanian and the Maastrichtian (Batezelli, 2017; Langer *et al*., 2022). These ages are controversial though. For instance, while Gobbo-Rodrigues *et al*. (1999a,b) suggested a Campanian-Maastrichtian age for the Araçatuba and Adamantina formations, a Campanian age for the Uberaba Formation, and a Maastrichtian age for the Marília Formation, Dias-Brito *et al*. (2001) suggested a Turonian-Santonian age for the Adamantina Formation, a Coniacian-Santonian age for the Uberaba Formation, and a late Maastrichtian age for the Marília Formation. Langer *et al*. (2022) carried out a detailed work based on tetrapod faunas and suggested a Coniacian-Santonian age for the Araçatuba Formation, a Campanian-early Maastrichtian age for the Adamantina and Uberaba formations, and a Maastrichtian age for the Marília Formation. In this work, the stratigraphic and chronostratigraphic arrangement proposed by Batezelli (2017) and Langer *et al*. (2022) is followed.

3. Materials and Methods

This study is based on the following steps: 1) analysis of literature data; 2) compilation of species and ages formally described for the Bauru Group fossil record; and 3) comparison of dinosaur occurrences and geological features between the Bauru Group and contemporaneous Argentine formations.

The information on titanosaurian taxa provided here comes mostly from scientific literature sources and from the direct observation of the specimens. The taxonomic status of Titanosauria and its constituent species was based on Mannion *et al*. (2019). The systematics used here follows Mannion *et al.* (2019), where Neosauropoda includes the Diplodocoidea and Macronaria clades. Macronaria, in turn, includes Titanosauria within Titanosauriformes as a sister group of Brachiosauridae (Fig. 2).

4. Results

4.1. Sauropods from the Bauru Group

South America has yielded a large number of sauropod dinosaurs, many of which are assigned to Titanosauria (Salgado, 1999; Powell, 2003; Calvo *et al.,* 2007; Lacovara *et al.*, 2014). Currently, Brazil has 15 species of formally described sauropods, 10 of which are Titanosauria found in outcrops from the Bauru Group. These are described below:

1 ***Adamantisaurus mezzalirai*** Santucci and Bertini, 2006 (DGM 1490-R) is a species from the Adamantina Formation nearby Flórida Paulista town, in the state of São Paulo. The holotype comprises six articulated anterior caudal vertebrae (Fig. 3) and two hemapophyses that are housed at MUGEO.

Comments: Initially, Mezzalira (1959, 1966, 1989) classified the specimens as Titanosauridae indet., but Santucci and Bertini (2006) recognized it as a new species. According to these authors, *A. mezzalirai* shows similarities with other titanousaurids of the

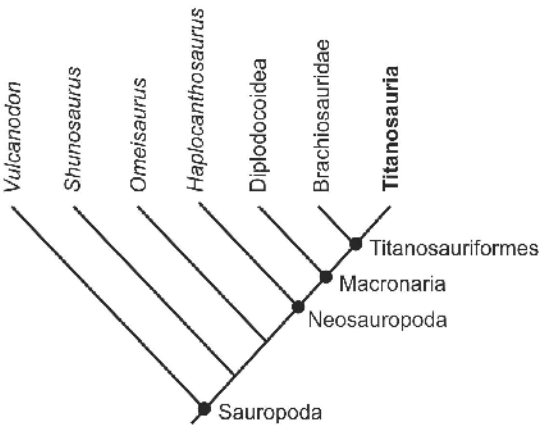

FIG. 2. Simplified sauropod cladogram (according to Mannion *et al*., 2019).

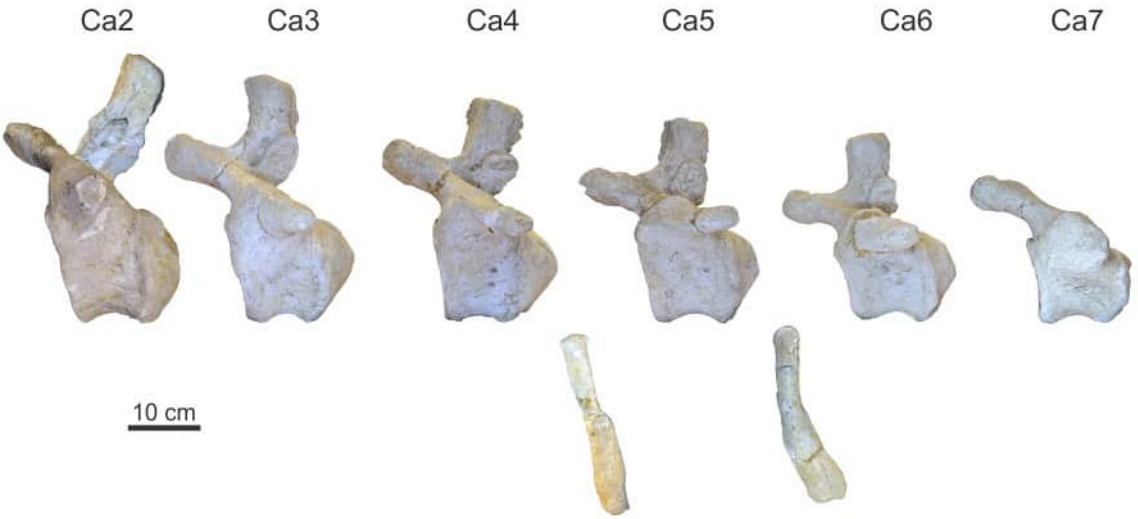

FIG. 3. *Adamantisaurus mezzalirai* (MUGEO 1282). Anterior caudal vertebrae and haemal arches in left lateral view (according to Vidal *et al.*, 2024b).

Bauru Group (DGM 'Series B' from Peirópolis) and with the genus *Aeolosaurus* from Argentina in presenting postzygapophyses with concave articular facets. In addition, it shares with the DGM 'Series B' the presence of laterally expanded, robust, and short neural spines.

2 *Arrudatitan maximus* (Santucci and de Arruda-Campos, 2011; Silva Junior *et al*., 2022) (MPMA 12-0001-97) was discovered in the Santa Irene outcrop, Adamantina Formation, close to the Monte Alto town, in the state of São Paulo. The holotype consists of: two incomplete distal cervical vertebrae, seven incomplete cervical ribs, a fragmented anterior dorsal vertebral body, a possible fragment of a middle dorsal vertebra, a fragmented posterior dorsal vertebra, several incomplete diapophyses of dorsal vertebrae, twelve incomplete dorsal ribs, one middle caudal vertebral body, two posterior caudal vertebrae, six articulated anterior caudal vertebrae, seven haemal arches, two mid-caudal vertebrae (Fig. 4), a possible fragment of scapula, incomplete right humerus and femur, a fragmented left humerus, an incomplete radius, the left femur and ischium, and several unidentified fragments. This material is housed at MPMA.

Comments: *A. maximus* was described by Santucci and de Arruda-Campos (2011), who considered it as belonging to the genus *Aelosaurus* because it shared many synapomorphies with *Aeolosaurus rionegrinus* Powell, 1987 and *Aeolosaurus colhuehuapensis* Casal *et al*., 2007. Thus, they named it as *Aeolosaurus maximus*. Santucci and de Arruda-Campos (2011) pointed out that although *A. maximus* was included in *Aeolosaurus*, this species exhibited more basal characteristics of Titanosauria, such as a more robust vertebral body. Some years later, Silva Junior *et al*. (2021) redescribed *A. maximus* and considered it as a different taxon from the genus *Aeolosaurus* and removed it from the clade, calling it *Arrudatian maximus*, where the specific epithet was in honor of Professor Antonio Celso de Arruda Campos. Although the authors considered *Arrudatitan* closer to *Rinconsaurus*, the phylogenetic relationships of the clade remain uncertain (Bandeira *et al*., 2016; Navarro *et al*., 2022).

3 *Austroposeidon magnificus* Bandeira *et al*., 2016 (MCT 1628-R) was discovered in the Adamantina Formation rocks, nearby Presidente Prudente city, in the state of São Paulo. The holotype comprises two incomplete cervical vertebrae (Fig. 5), a cervical rib, a dorsal vertebra, seven fragments of dorsal vertebrae, and one fragment of a sacral vertebra.

Comments: *Austroposeidon* is estimated to have measured about 25 meters long in total body length (Bandeira *et al.,* 2016), making it one of the largest dinosaurs ever found in Brazil. All vertebral elements

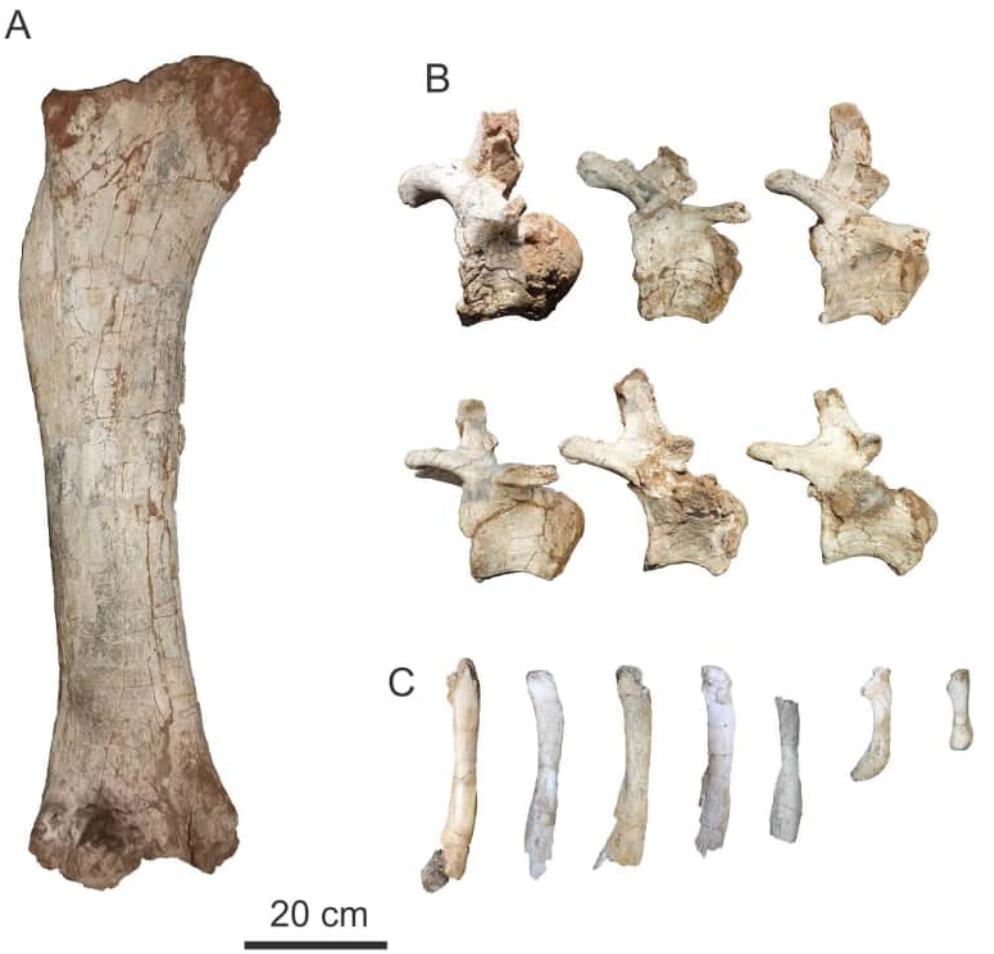

FIG. 4. *Arrudatitan maximus*. **A.** Femur in posterior view. **B.** Anterior caudal vertebrae Ca4 to Ca9 in left lateral view. **C.** Haemal arches in lateral view.

of this specimen were considered as belonging to the same individual and are housed at MCTer. Bandeira *et al*. (2016), Silva *et al*. (2019) and Navarro *et al*. (2022) positioned *Austroposeidon* as the sister taxon to Lognkosauria based on analyses of the cervical and dorsal vertebrae.

4 *Baurutitan britoi* Kellner *et al*., 2005 (MCT 1490-R) was collected from rocks of the Serra da Galga Formation (*sensu* Soares *et al.*, 2020a) in a quarry known as "Caieira", located in the private property Fazenda São Luís, Serra do Veadinho, nearby the rural district of Peirópolis, Uberaba municipality, Minas Gerais State (Kellner *et al*., 2005; Soares *et al*., 2020a,b). The holotype includes the last sacral vertebra followed by a sequence of eighteen anterior and middle caudal vertebrae and fifteen haemal arches (currently only thirteen units) (Fig. 6). This specimen is housed at MCTer.

Comments: According to Kellner *et al.* (2005), one of the main characteristics of *Baurutitan britoi* is that the caudal vertebrae exhibit a dorsal tuberosity, and, in anterior view, its vertebral bodies are rectangular-shaped. Silva Junior *et al*. (2022), based on a review on the caudal vertebral region of BR-262 from the Marília Formation, allocated *Baurutitan* within the Aeolosaurini clade that is well known from the Bauru Group and widely distributed in the Late Cretaceous of Argentina.

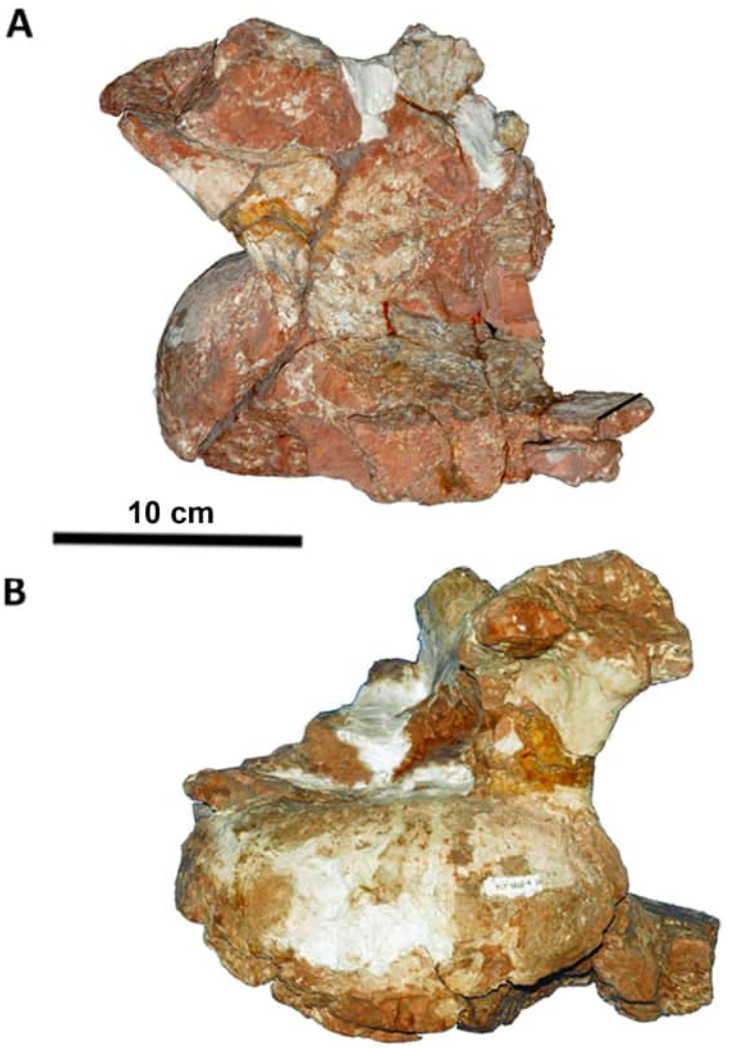

FIG. 5. Cervical vertebra (Cv 12) of *Austroposeidon magnificus* in (**A**) left lateral and (**B**) anterior views.

The majority of titanosaur fossils reported from the Serra da Galga Formation are small in size and are interpreted as small- to medium-sized sauropods. For example, the total body length of *Trigonosaurus*, *Baurutitan*, the sacrum MCT 1536, and the specimen BR-262 are estimated between 9 to 13 meters long (Campos *et al*., 2005; Kellner *et al*., 2005; Silva Junior *et al*., 2022). Except *Uberabatitan*, which could reach 26 meters long (Silva Junior *et al*., 2019), the sauropod fossil materials from this region represent a paleofauna composed mostly of small- to medium-sized sauropods.

5 *Brasilotitan nemophagus* Machado *et al*., 2013 (MPM 125R), was discovered in the Adamantina Formation rocks, nearby the Presidente Prudente city, in the state of São Paulo. The holotype consists of a right dentary (MN 7371-V) housed at MN (Fig. 7A), as well as two cervical vertebrae (Fig. 7B), three incomplete sacral vertebrae (Fig. 7C), a fragment of the ilium, fragments of the ischium, and several other fragmentary elements that are housed at MPM.

Comments: In the mandible of *Brasilotitan nemophagus*, it is possible to observe that the

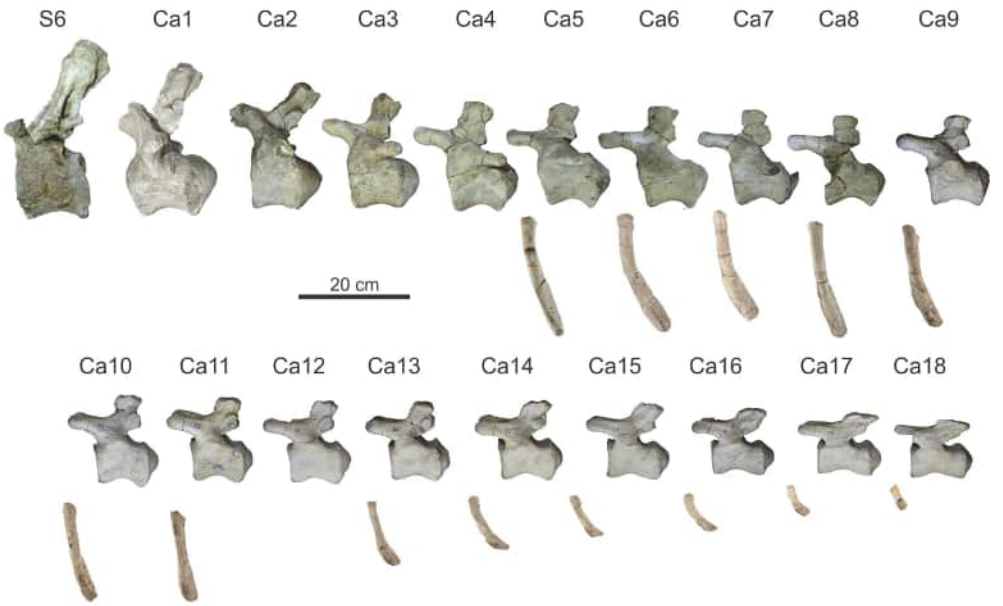

FIG. 6. *Baurutitan britoi*. Caudal vertebrae (S6, Ca1 to Ca18) and haemal arches in left lateral view (according to Vidal *et al.*, 2024b).

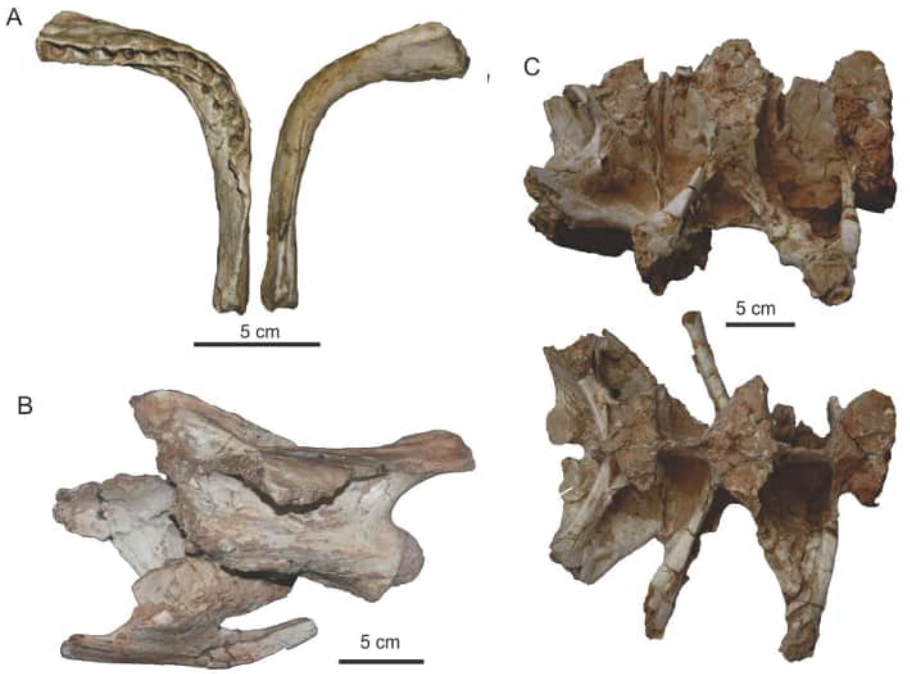

FIG. 7. Materials of *Brasilotitan nemophagus*. **A**. Right dentary in dorsal and ventral views. **B**. Posterior cervical vertebrae in ventrolateral view. **C**. Sequence of sacral vertebrae in left lateral and dorsal views (Machado *et al*., 2013).

symphyseal region of the dentary is L-shaped and slightly twisted medially, which is a unique characteristic for Titanosauria (Machado *et al.,* 2013). The dentary of *Brasilotitan* has a sequence of three dental rows that shows that while the first tooth was being used and worn down, two others were being formed to eventually replace the functional one (Machado *et al.,* 2013). For Machado *et al*. (2013) the morphology of the *Brasilostitan* maxilla shares characters with *Antarctosaurus* and *Bonitasaura* from the Late Cretaceous of northern Argentine Patagonia, so the Brazilian material provides little-known anatomical data on the jaw of Gondwanan titanosaurids. The phylogenetic analysis of this species places it as a sister taxon to *Uberabatitan* reported from the Marília Formation in Peirópolis (Machado *et al*. 2013).

6 *Gondwanatitan faustoi* Kellner and Azevedo, 1999 (MN 4111-V) was discovered in rocks of the Adamantina Formation in the Álvares Machado city, in the state of São Paulo. The holotype comprises two partial cervical vertebrae, seven dorsal vertebrae, six sacral vertebrae, twenty-four caudal vertebrae (some articulated), four unidentified vertebrae, the proximal portion of the left scapula, the left ilium incomplete, the middle portion of both pubes, ischia and humeri (both incomplete), a tibia, many rib fragments, and other unidentified osseous fragments. All material is assigned as belonging to the same individual (Fig. 8).

Comments: The material was identified as "*Titanosaurus*" sp. (currently not considered) by Powell (1986) in a first basic analysis that identified Titanosauria characteristics in this specimen. It was later reviewed by Kellner and Azevedo (1999) who described it as a new taxon, *Gondwanatitan faustoi*. According to Santucci and Bertini (2001), *G. faustoi* shares some specific characteristics with the genus *Aeolosaurus*, such as neural spines anteriorly projected, neural arches positioned in the anterior portion of the vertebral body, and prezygapophyses that are relatively longer than in other titanosaurs. Santucci and Bertini (2001) therefore proposed that the taxon should be classified within the genus *Aeolosaurus* and thus renamed as *Aeolosaurus faustoi*. The material was housed at MN, although it was destroyed during a fire in 2018.

7 *Maxakalisaurus topai* Kellner *et al*., 2006 (MN 5013-V) was collected from the Adamantina Formation near the municipalities of Prata and Campina Verde, in the state of Minas Gerais. The holotype (Fig. 9) consists of an incomplete maxilla, seven dorsal vertebrae, a neural arch and a vertebral body of the sacrum, several ribs and haemal arches, portions of both scapulae, both external plates, the distal portion of the ischium, both humeri, some metacarpals, a fragment of fibula, an osteoderm, and indeterminate incomplete remains.

Comments: *Maxakalisaurus topai* was the fifth Brazilian titanosaur species to be described. The analysis of the material reveals tooth marks, which suggest that some subaerial exposure occurred such that some bones were attacked by opportunistic predators. This species is housed at MN (Kellner *et al*., 2006). França *et al*. (2016) described a partial

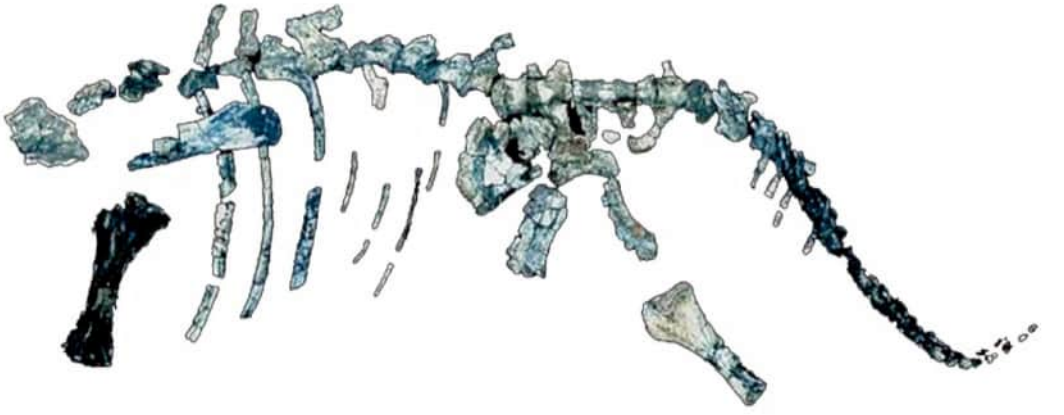

FIG. 8. Skeleton of *Gondwanatitan faustoi* (adapted from Kellner and Campos, 2000). Not to scale. No higher resolution available.

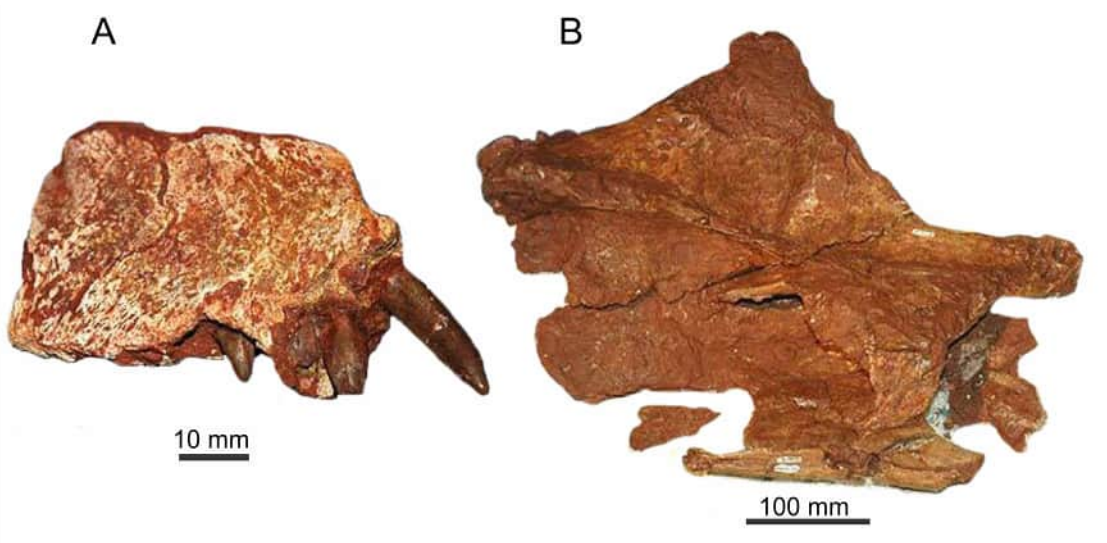

FIG. 9. *Maxakalisaurus topai*. Lateral views of (**A**) maxilla, and (**B**) cervical vertebra (according to Kellner *et al*., 2006). No higher resolution available.

right dentary, including five isolated teeth, that was collected from the *M. topai* holotype area. Based on a phylogenetic analysis, this taxon was positioned within the Aeolosaurini tribe (França *et al*., 2016).

8 *Trigonosaurus pricei* Campos *et al*., 2005 (MCT 1488-R as holotype and MCT 1719-R as paratype) was discovered in the rocks of the Serra da Galga Formation and recovered from a quarry known as "Caieira", located in the private property Fazenda São Luís, Serra do Veadinho, near the rural district of Peirópolis, Uberaba municipality, Minas Gerais State. The holotype comprises several elements of the axial skeleton: cervical, dorsal and caudal vertebrae, and sacrum with the left ilium (Fig. 10). This species is housed at MCTer.

Comments: *Trigonosaurus* is one of the few Brazilian dinosaurs whose material includes cervical, dorsal, and caudal vertebrae and the sacrum. This large number of elements from the axial skeleton makes *Trigonosaurus* one of the most representative and best known titanosaurian species of South America. There are few well-preserved titanosaur sacra in Brazil. Three sacra are housed at MCTer and one of them is assigned to *Trigonosaurus.*

This genus was a small sauropod compared to other titanosaurs (Powell, 2003; Campos *et al.,* 2005; Kellner *et al.,* 2005). It was originally allocated to Titanosauria by Campos *et al*. (2005), as *Trigonosaurus* shares some similarities with *Aeolosaurus* and *Gondwanatitan* (Aeolosaurini). Silva Junior *et al*. (2022) synonymized it with *Baurutitan ribeiroi*. According to these authors, the holotype materials attributed to *Trigonosaurus* belong to the genus *Baurutitan*. As *Baurutitan* is the oldest name, *Trigonosaurus* would therefore be an invalid taxon. In addition, the caudal vertebrae (MCT 1719-R), which were originally also interpreted as *Trigonosaurus*, were assigned by Silva Junior *et al*. (2022) to the new genus and species *Caieiria allocaudata* (not considered in this contribution; see below) based on a series of anatomical features and on the fact that the caudal series is not directly associated with the *Trigonosaurus* holotype.

However, recent anatomical and biomechanical analyses (Vidal *et al*., 2024a) indicate that *Trigonosaurus* and *Baurutitan* are distinct taxa due to a number of distinctive anatomical features, for example, the last sacral vertebra (S6) of *Baurutitan* (MCT 1490-R) is concave and the first caudal vertebrae (Ca1) is biconvex, while in *Trigonosaurus* (MCT 1488-R) the S6 is convex and, therefore, a concave first caudal would be necessary. These authors also highlight that MCT 1719-R probably belong to the genus *Trigonosaurus* (as proposed by Powell, 1987 and Campos *et al*., 2005) due to a series of shared characteristics between the last sacral vertebra (S6 of MCT 1488-R) and the first anterior caudal (MCT 1719-R) such as: the last sacral presents

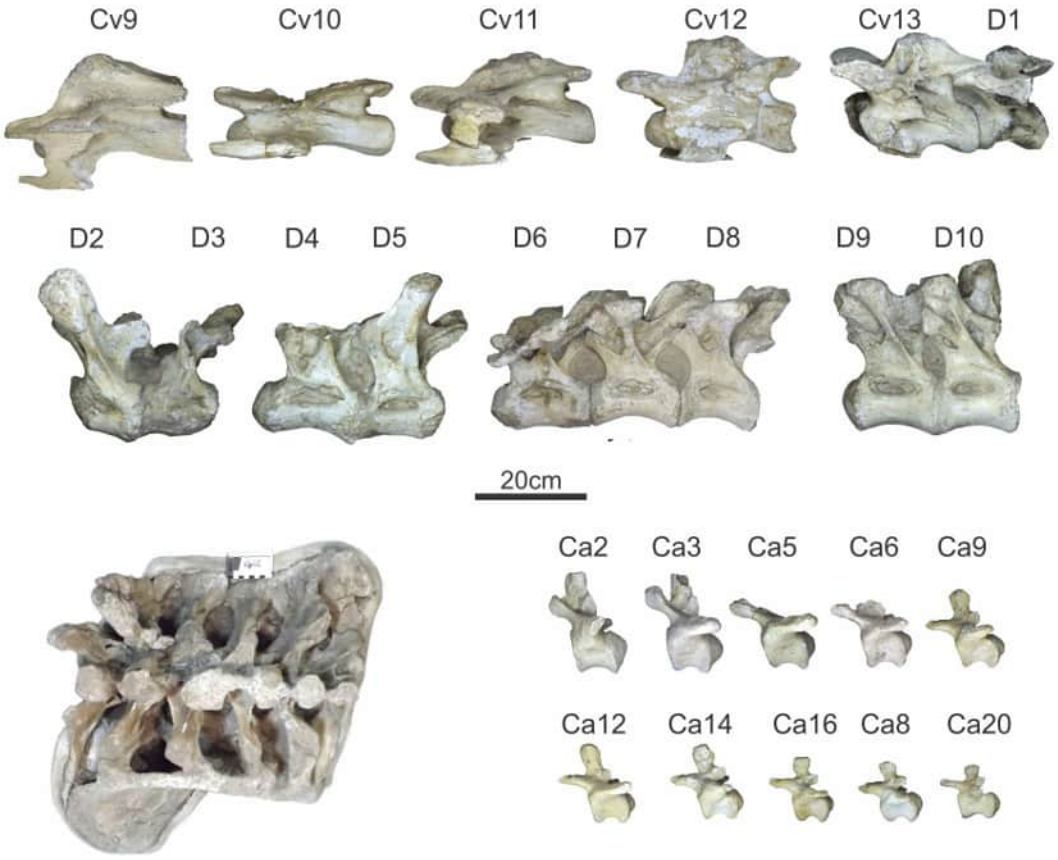

FIG. 10. *Trigonosaurus pricei*. Cervical, dorsal and caudal vertebrae in left lateral view, and sacrum and left ilium in dorsal view (according to Vidal *et al.*, 2024a).

transverse processes directed caudolaterally, much larger dorsoventrally than anteroposteriorly, and deflected posteriorly, such as in the anterior caudal of MCT 1719-R; the neural spines of the anterior caudal vertebrae of MCT 1719-R have the same direction as MCT 1488-R, which are directed more anteriorly than in MCT 1490-R, which are directed more posteriorly (which are divergent from MCT 1488-R); and the general morphology of the last sacral vertebra and the second and the third caudal vertebrae are essentially the same. According to the Vidal *et al*. (2024a), this convergence of characteristics suggests that these specimens might belong to the same species. This makes *C. allocaudata* an uncertain taxon and future phylogenetic analyses can help to better understand the relationships between these specimens and corroborate or refute these hypotheses.

9 *Uberabatitan ribeiroi* (Salgado and Carvalho, 2008) (série - A, CPP-UrHo) was collected from the rocks of the Serra da Galga Formation, in the municipality of Uberaba, in the state of Minas Gerais. The holotype is represented by three sequences of incomplete vertebral elements (A, B, and C) (Fig. 11), containing more than sixty bones. The A vertebral series is the most complete one. The material is housed at CCCP.

Comments: In the verified materials of *Uberabatitan ribeiroi*, three ribs belong to different sizes and ages. One of the main characteristics of the *U. ribeiroi* model is the presence of elements that integrate the anterior and posterior limbs. Silva Junior *et al*. (2019) carried out a detailed review of *U. ribeiroi*, as well as of new materials collected from the holotype area, and presented phylogenetic analyses placing the species in Aeolosaurini.

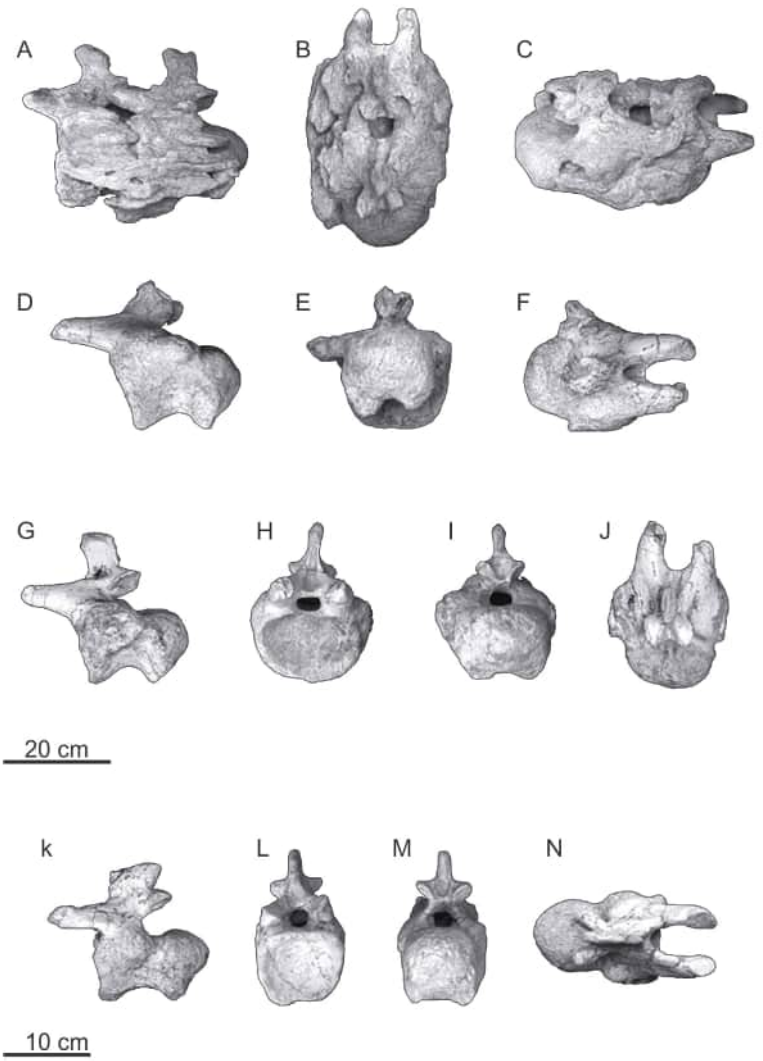

FIG. 11. *Uberabatitan ribeiroi*, mid-caudal vertebrae (according to Salgado and Carvalho, 2008). A-C (CPP-1020-UrB) in left lateral (**A**), dorsal (**B**) and dorsolateral (**C**) views. D-F (CPP-1018-UrB) in left lateral (**D**), posterior (**E**) and dorsal (**F**) views. G-J (CPP-1019-Ub) in left lateral (**G**), anterior (**H**), posterior (**I**) and dorsal (**J**) views. K-N (CPP-1017-UrHo) in left lateral (**K**), anterior (**L**), posterior (**M**) and dorsal (**N**) views. Scale bars: A-J 20 cm, K-N 10 cm. No higher resolution available.

10 ***Ibirania parva*** (Navarro *et al*., 2022) (LPP-PV-0200 and LPP-PV-0043). This titanosaur was reported from the early Campanian in the Adamantina Formation at Ibirá Municipality, in the state of São Paulo. The holotype consists of disarticulated postcranial remains of a single individual (Fig. 12), including: a moderately preserved posterior dorsal vertebra, a partial anterior and posterior caudal central, a partial neural arch of a mid-caudal vertebra, fragmentary radius and ulna (LPP-PV-0202; Fig. 12), a distal portion of a metacarpal, and a nearly complete metatarsal. This species is housed at LPP.

Comments: Navarro *et al.* (2022) argued that *Ibirania* was a dwarf species (characteristic of nanism) due to its small size for a sauropod (around 5.7 meters in length). Histological analysis showed that the studied specimens were adults, meaning their small size was not due to immaturity. According to Navarro *et al*. (2022), *Ibirania* was a derived member of the Saltasaurinae, a clade known to encompass some

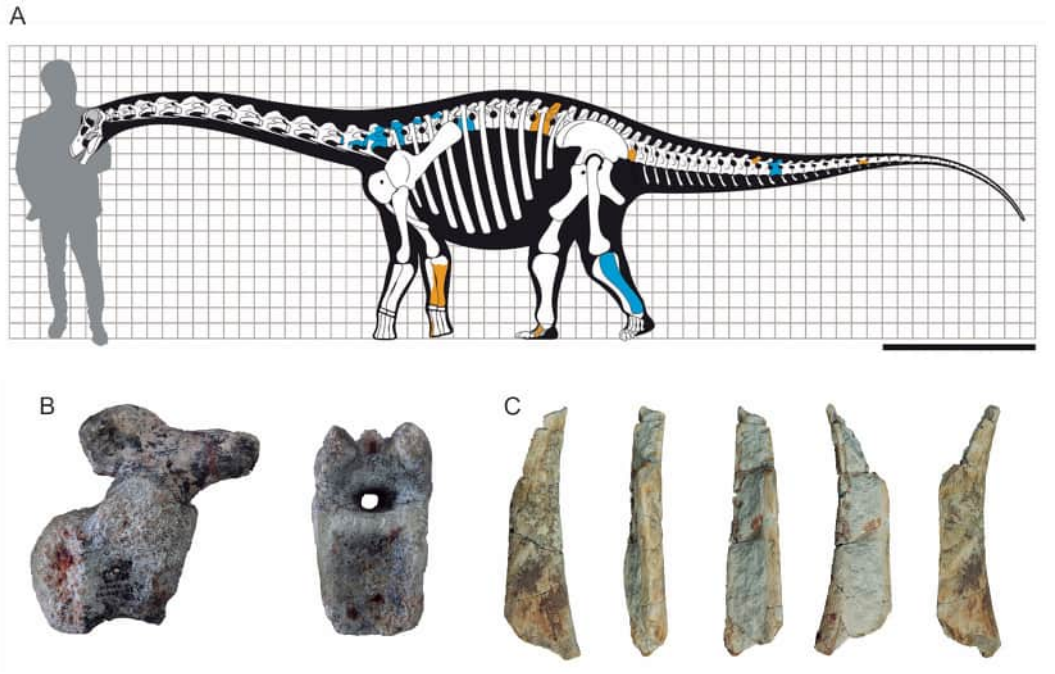

FIG. 12. **A.** *Ibirania parva* reconstruction. **B.** Middle caudal vertebra (MPMA 08-0060-07). **C.** Views of partial right ulna (LPP-PV-0202). According to Navarro *et al*. (2022).

of the smallest titanosaurs. This Brazilian species is sister taxon to the clade formed by saltasaurines *Bonatitan* and *Rocasaurus* from the Late Cretaceous of north Patagonia, Argentina.

4.2. Paleogeography of the titanosaurs from the Bauru Group

The Bauru Group has provided the most significant records of Brazilian dinosaurs (Kellner and Campos, 2000); for example, *Baurutitan* and *Trigonosaurus* were instrumental in the morphological determination of sauropod vertebral sequences (Powell, 1987). Beyond their taxonomic importance, the study of the sauropods of the Bauru Group has provided significant insights into paleobiology and biomechanics, allowing for a greater general understanding of titanosaur body morphology, feeding strategies, and tail shape patterns (Vidal *et al*., 2021, 2024a,b). This new knowledge enabled the grouping and differentiation of organisms through morphological comparisons. To illustrate this point, Vidal *et al*. (2021) proposed a tail morphology for *Arrudatitan maximus*, suggesting that the Aeolosaurini clade found in both Brazil and Argentina had a more curved anterior tail portion, resulting in a lower, more ground-proximal sigmoidal tail shape. Subsequently, Vidal *et al*. (2024b) observed these characteristics in *Baurutitan* and *Adamantisaurus*, which helped clarify the degree of kinship between these species. All these discoveries contributed significantly to understanding titanosaur evolution in this part of Gondwana.

The dinosaur remains described here are commonly found in the states of Minas Gerais and western São Paulo (Table 1), from rocks known for their rich fossiliferous content (Candeiro *et al*., 2008; Bittencourt and Langer, 2011). Seven species of titanosaurs were collected in the Adamantina Formation rocks whereas three species were reported from the Serra da Galga Formation (Table 1). From these records it is possible to define four regions with distinctive paleogeographic distribution. This distribution relates to the climatic and paleogeographic context of Gondwana. In fact, the first half of the Cretaceous was characterized by global warming, followed by cooling during the second half of that period, with fluctuations between more or less warm temperatures during the Maastrichtian (*e.g*., Barron and Washington, 1982; Goldberg and Garcia, 2000). The Bauru Group sediments, in particular, were

TABLE 1. RECORDS OF TITANOSAURID SAUROPODS FROM THE ADAMANTINA AND SERRA DA GALGA FORMATIONS, IN THE BAURU GROUP.

Species	Adamantina Formation (Campanian-Maastrichtian)	Serra da Galga Formation (Maastrichtian)
Adamantisaurus mezzalirai	X	-
Arrudatitan maximus	X	-
Austroposeidon magnificus	X	-
Baurutitan britoi	-	X
Brasilotitan nemophagus	X	-
Gondwanatitan faustoi	X	-
Maxakalisaurus topai	X	-
Trigonosaurus pricei	-	X
Uberabatitan ribeiroi	-	X
Ibirania parva	X	-

deposited under a semi-arid to arid climate with marked seasonality, in which dry periods alternated with periods of intense rainfall. An increase in aridity is indicated by the succession of the Adamantina (Campanian-Maastrichtian) to the Serra da Galga (Maastrichtian) formations (Soares *et al*., 2020a). Seasonality not only affected sedimentation, but also the life cycles of these dinosaurs; for example, the lakes underwent surface variations according to the amount of precipitation (Goldberg and Garcia, 2000). These conditions had a direct influence on the diagenetic processes of the fossils found. The fossiliferous sites in the study area are part of fluvial deposits that are vertically and laterally associated with lake deposits (Goldberg and Garcia, 2000). The presence of water may have contributed to the preservation of the large number of sauropod species reported for the Bauru Group. In drier seasons, the animals that died perhaps left their remains exposed on the plains, and in the rainy season these could have been dragged along with the river sediments to the places where the fossil-diagenetic processes would take place.

The overall arid paleoenvironment of the Bauru Group was not only due to global climatic conditions, but also to the existence of geographic barriers that contributed to the formation of a dry microclimate. The Serra do Mar in the southwest, the Arco de Ponta Grossa in the south-southeast, and the Alto do Paranaíba in the northeast (Barcelos and Bertini, 1990; Goldberg and Garcia, 2000), all acted as barriers to the entry of humid winds, which ascended and dried when reaching the highlands. Humidity was restricted to the mountains, favoring the development of coniferous forests (Lima *et al*., 1986; Goldberg and Garcia, 2000), while dry winds contributed to increasing the aridity as they passed through the plains. On the other hand, the frequency of rainy periods suggested from the Adamantina Formation strata and the subsequent fluvial reworking provided the dinosaurs with favorable conditions for life and for the establishment of their nests, even in the face of more arid conditions (Goldberg and Garcia, 2000). Thus, the titanosaurs were configured in a diverse fauna, something well illustrated in the different species found, particularly in the Adamantina Formation.

During the Maastrichtian, the general climatic conditions became more arid in the Bauru Basin area, and seasonality was marked by longer dry intervals, interrupted by periods of very heavy rain. In regions closer to the headwaters of the river systems, the preservation of paleosol profiles was not favored, which may be a determining factor for the records found in the formations of this period. The presence of these river systems may have influenced the places that were more propitious for titanosaurs to live due to the presence of water and food (such as in the Uberaba municipality, where a representative number of records was recognized), as well as which regions might have served as migratory routes for these animals (Goldberg and Garcia, 2000).

During the dry seasons, the fauna was likely concentrated around the lakes and close to the vegetated areas, which helped to guarantee the survival of the

large herbivores. Subsequently, animals killed during this period were disarticulated, both by subaerial exposure and by scavengers. After a long period of drought, rain would restart the cycle, refilling the lakes and covering the plains with vegetation again. As rain was more frequent in the surrounding highlands than within the basin itself, the contribution of groundwater allowed the continued growth of vegetation despite the generally arid conditions (Goldberg and Garcia, 2000).

From a regional perspective, the presence of *Arrudatitan* (Aeolosaurini) and *Ibirania* (Saltasaurinae) in the Bauru Group establishes a connection with some fossiliferous sites in Argentina, such as in the Angostura Colorada, Allen, and Los Alamitos formations (Salgado and Coria, 1993; Salgado *et al*., 1997; Garrido, 2010; González-Riga *et al*., 2019). According to Salgado *et al*. (1997), these localities have records of closely related species. The latter provides paleogeographic information on the distribution of Titanosauria and suggests faunal exchange between southeastern Brazil and the Argentine Río Negro Province (Santucci and Bertini, 2001; Lopes and Buchmann, 2008; González-Riga *et al*., 2019).

Together, all the above suggests that seasonality and geographic features present during the Late Cretaceous in Brazil were the main factors in controlling the life cycle of these herbivorous dinosaurs, as well as their possible migration routes. This also contributes to how the fossil record is currently interpreted, since fossil preservation can be affected by climatic conditions. The regions with the highest number of records collected (Adamantina and Serra da Galga formations) probably represent areas where environmental conditions were more favorable for the thriving of titanosaurs and their preservation as fossils (Fig. 13).

5. Concluding remarks

The record of titanosaurian sauropods of the Bauru Group is considered one of the most representative of South America. In addition to their paleobiogeographic significance, these specimens have also provided key information on the paleoecological, taphonomic, and paleobiological aspects of titanosaurians. The new taxonomic arrangements for the sauropods of the Adamantina and Serra da Galga formations are consistent with the Late Cretaceous ages of these rocks. Based on faunal comparisons to well-studied Argentine sites, *Arrudatitan* and *Ibirania* have been used as an indicator to assign Campanian-Maastrichtian ages to the Adamantina Formation (Bertini *et al.*, 1999; Santucci and Bertini 2001; Bandeira *et al.*, 2016; Navarro *et al.,* 2022). However, according to Martinelli *et al.* (2011) and Filippi *et al.* (2013), there is no sufficient evidence of *Arrudatitan* in the Bauru Group for a conclusive temporal correlation. In addition, some specimens that were once identified as *Arrudatitan* (Santucci and Bertini, 2001; Franco-Rosas *et al.* 2004; Marinho and Candeiro, 2005; Lopes and Buchmann, 2008; Santucci and de Arruda-Campos, 2011) were later assigned to the more general Titanosauria (Martinelli *et al.,* 2011) and Aeolosaurini indet. (Martinelli *et al.*, 2011; Filippi *et al.*, 2013). Considering the age of the rocks where the Aeolosaurini and Saltasaurinae groups are reported in Argentina (Coniacian-Maastrichtian; Filippi *et al.*, 2013), it is possible to suggest that the deposition of the Adamantina and Marília formations occurred in this same time interval. Furthermore, Machado *et al*. (2013) observed that *Brasilotitan nemophagus* (Adamantina Formation) is likely closely related to *Antarctosaurus wichmannianus* (Campanian, Argentina) and *Bonitasaura salgadoi* (Santonian, Argentina), and these phylogenetic relationships may also suggest that at least part of the Adamantina Formation may have been deposited during the late Santonian.

The sauropods reported from the Adamantina Formation belong to the Titanosauria clade and show a wide morphological diversity within the group. The group diagnosis is mainly based on the morphological characteristics of the anterior caudal vertebrae. However, as discussed in this study, many specimens are fragmentary or non-diagnostic and were also poorly described or erroneously assigned to other clades. Thus, we suggest that many Titanosauria fossils from the Bauru Group need a thorough revision so that the diversity of the group in Brazil can be refined. On the other hand, given the variety of diagnostic elements of the taxa, it is possible to recognize that Titanosauria was a very diverse and distributed group in Brazil and elsewhere. Furthermore, the known diversity of titanosaurs is related to regions where there has been more investment in research and fossil prospection, which suggests that knowledge about this group could be even greater with more fieldwork.

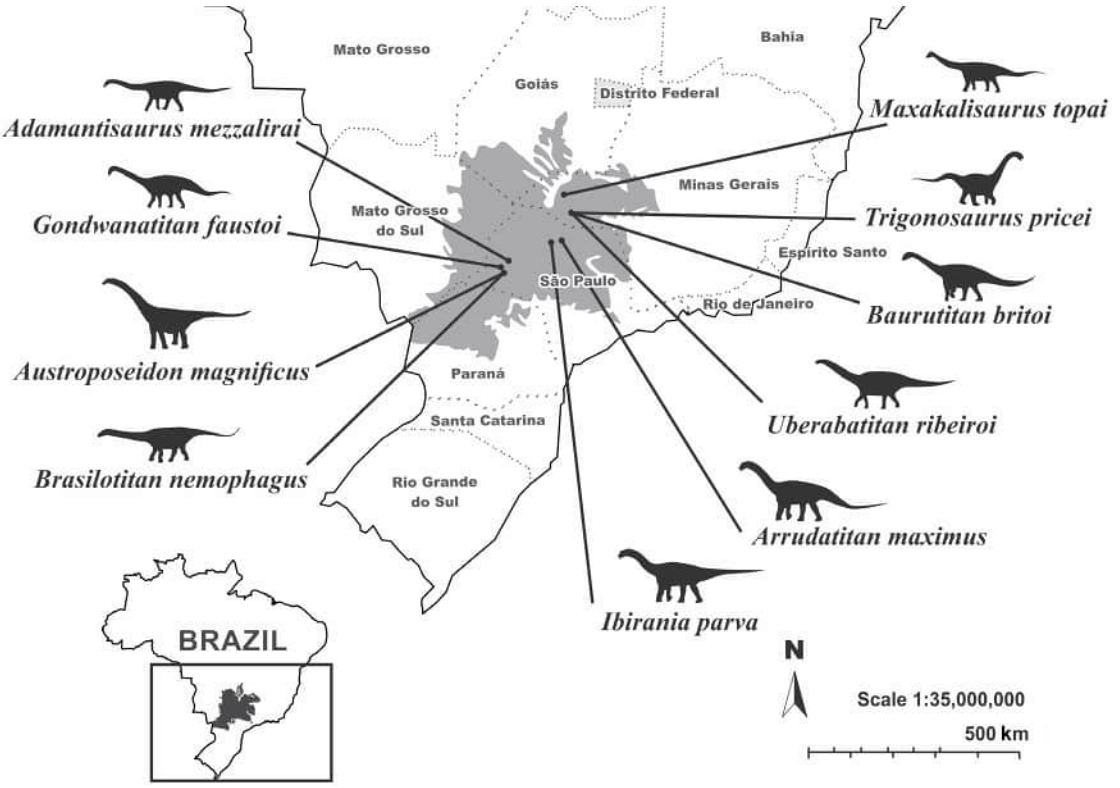

FIG. 13. Map of the localities in the Bauru Basin where the sauropod dinosaurs were collected.

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