UNIVERSIDADE DE SÃO PAULO
FACULDADE DE FILOSOFIA, CIÊNCIAS E LETRAS DE RIBEIRÃO PRETO
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA COMPARADA

VERSÃO CORRIGIDA

Diversidade e evolução dos Titanossauros do Cretáceo Superior da Bacia Bauru

Diversity and evolution of the Titanosaurs from the Upper Cretaceous of the Bauru Basin

Julian Cristian Gonçalves da Silva Junior

Tese apresentada à Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo, como parte das exigências para obtenção do título de Doutor em Ciências, obtido no Programa de Pós-Graduação em Biologia Comparada

Ribeirão Preto - SP
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Orientador: Prof. Dr. Max Cardoso Langer

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2023

FICHA CATALOGRÁFICA

Silva Junior, Julian Cristian Gonçalves.
Taxonomy and Systematics of the Titanosaurs from the Upper Cretaceous of the Bauru Basin Ribeirão Preto, 2023.

p. 119: il; 30 cm

Doctorate Thesis, presented to the Biology Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto - USP. Area of concentration: Comparative Biology

Advisor: Langer, Max Cardoso

1. Sauropoda. 2. Titanosauria. 3. Phylogenetics. 4. Taxonomy. 5. Bauru Basin.

FOLHA DE APROVAÇÃO

Name: SILVA JUNIOR, Julian Cristian Gonçalves.

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AGRADECIMENTOS

Primeiramente, gostaria de agradecer minha esposa Tatiane, que esteve ao longo do caminho comigo, por todos estes anos, me dando suporte em cada etapa.

Gostaria de agradecer ao meu Orientador Max Langer, por toda a ajuda durante minha formação, pelas oportunidades únicas de trabalhos de campo e por todas as conversas sobre os mais aleatórios assuntos. Também preciso agradecer outras duas pessoas que foram essenciais para minha formação na paleontologia: Thiago Marinho e Agustín Martinelli. Ambos responsáveis por me ajudar nas primeiras etapas de minha carreira, e que se mostraram grandes parceiros até hoje.

Agradeço aos meus amigos da *República do Mário* (Fellipe, Silvio, Giovanne, Diego e Leandro) por todas as noites de pizzas e discussões. Agradeço aos meus primeiros amigos do Paleolab (Schumi, Wafa, Bete, Júlio, Gabriel F.) e aos novos amigos de laboratório, sem os quais a vida não teria sido tão divertida. Também agradeço a profa. Annie S. Hsiou pela contribuição na minha formação e trabalhos de campo.

Agradeço ao Programa de Pós-Graduação em Biologia Comparada pelo suporte para realização de meu Doutorado e a Fundação de Amparo à pesquisa do Estado de São Paulo (FAPESP) processo nº: 2018/21094-7, pelo suporte e financiamento desta pesquisa.

“Cuando despertó, el dinosaurio todavía estaba allí”

Augusto Monterosso.

SILVA JUNIOR, J. C. G. **Diversity and evolution of the Titanosaurs from the Upper Cretaceous of the Bauru Basin**. Ribeirão Preto, 2023. 119 f. Tese (Doutorado em Ciências). Programa de Pós-Graduação em Biologia Comparada. Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo.

RESUMO

Os titanossauros formam o clado mais abundante dentro de Sauropoda, representando também o grupo de dinossauros mais rico do Cretáceo do Brasil. Apesar do grande número de registros, as afinidades das espécies brasileiras ainda se encontram pouco resolvidas. Desta forma, os estudos conduzidos durante esta tese buscaram uma maior compreensão sobre os aspectos taxonômicos e sistemáticos destes animais. As contribuições foram divididas em quatro apêndices: o primeiro trata sobre a reavaliação de uma espécie de titanossauro do interior de São Paulo, antes inclusa no gênero tipicamente argentino *Aeolosaurus*. Após uma revisão das sinapomorfias do mesmo, um novo gênero – *Arrudatitan* – foi cunhado para receber esta espécie. A hipótese filogenética resultante deste estudo também foi usada para definir novos clados no *phylocode*. O apêndice 2 inclui a descrição de novos restos fósseis encontrados em Uberaba-MG, que levaram a reavaliação de duas outras espécies conhecidas na região: *Baurutitan britoi* e *Trigonosaurus pricei*. A informação resultante mostrou que o indivíduo atribuído como holótipo de *T. pricei* na verdade representava um espécime de *B. britoi*. Já o material atribuído como parátipo de *T. pricei* representa uma nova espécie, denominada neste artigo como *Caieiria allocaudata*. No apêndice 3, são descritos novos espécimes de dentes de titanossauro também da região de Uberaba, inclusive com a descrição do maior dente de titanossauro já encontrado no mundo. As informações deste manuscrito mostram que a região de Uberaba era capaz de suportar uma ampla fauna de titanossauros, desde animais juvenis até espécimes adultos gigantes. Por fim, o apêndice 4 apresenta alguns materiais que estão tombados no Museu dos Dinossauros em Uberaba, mas que ainda não foram formalmente descritos, seja pela a impossibilidade de atribuí-los a táxons já conhecidos ou pela ausência de características únicas que permitam a criação de novas espécies, mas que se mostram materiais com um importante valor comparativo e que também podem auxiliar pesquisas sobre titanossauros de outras regiões.

Palavras-chave: 1. Sauropoda. 2. Titanosauria. 3. Filogenética. 4. Taxonomia. 5. Bacia Bauru

SILVA JUNIOR, J. C. G. **Diversity and evolution of the Titanosaurs from the Upper Cretaceous of the Bauru Basin**. Ribeirão Preto, 2023. 119 f. Thesis (Doctorate). Graduate Program on Comparative Biology. Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo.

ABSTRACT

Titanosaurs form the most abundant clade within Sauropoda, also representing the richest group of dinosaurs from the Cretaceous of Brazil. Despite the large number of records, the affinities of the Brazilian species are still poorly resolved. Thus, the studies carried out during this thesis sought a greater understanding of the taxonomic and systematic aspects of these animals. The contributions were divided into four appendices: the first deals with the reassessment of a species of titanosaur from the interior of São Paulo, previously included in the typically Argentine genus *Aeolosaurus*. After a review of its synapomorphies, a new genus – *Arrudatitan* – was coined to receive this species. The phylogenetic hypothesis resulting from this study was also used to define new clades in the phylocode. Appendix 2 includes the description of new fossil remains found in Uberaba-MG, which led to the reassessment of two other known species in the region: *Baurutitan britoi* and *Trigonosaurus pricei*. The resulting information showed that the individual assigned as a holotype of *T. pricei* actually represented a specimen of *B. britoi*. The material assigned as paratype of *T. pricei* represents a new species, named in this paper as *Caieiria allocaudata*. In the appendix 3, new specimens of titanosaur teeth are described, also from the region of Uberaba, including the description of the largest titanosaur tooth ever found in the world. The information in this manuscript shows that the region of Uberaba was capable of supporting a wide fauna of titanosaurs, from juvenile animals to giant adult specimens. Finally, appendix 4 presents some materials that are listed in the Museum of Dinosaurs in Uberaba, but that have not yet been formally described, either because of the impossibility of assigning them to already known taxa or the absence of unique characteristics that allow the creation of new species, but which prove to be material with an important comparative value and which can also help research on titanosaurs from other regions.

Keywords: 1. Sauropoda. 2. Titanosauria. 3. Phylogenetics. 4. Taxonomy. 5. Bauru Basin.

SUMMARY

FOREWORD: thesis structure

This thesis is organized in two sections. The first section is called the thesis' integrative text and comprises a general introduction on the subject followed by a presentation of four appendices. The second section consists of four manuscripts referring to these appendices. Appendices 1 and 2 were published in scientific journals. Appendices 3 and 4 represent unpublished contributions. This thesis follows the structure provided in the resolution CoPGrNº6971 of November 3, 2014, from the Universidade de São Paulo.

SECTION 1:

Thesis integrative text

1. INTRODUCTION

1.1 Historical background

Sauropods comprises the largest terrestrial animals of all time and can be easily recognized by their unique body plan, with long necks and tails sustained by four columnar limbs. The first sauropod was described by the English naturalist Richard Owen (1804-1892) and named as *Cetiosaurus*. Owen did not recognize *Cetiosaurus* as a dinosaur at the time but as a giant sea creature, therefore the name meaning “whalelizard”.

The term Sauropoda was coined only a few years later, in 1878, by the American paleontologist Othniel Charles Marsh (1831-1899), and only included the then recently described *Camarasaurus* (Cope, 1877). Afterwards, sauropod remains were recovered from all around the globe, including few fossils from Antarctica (Cerda et al., 2012). Depending on the definition and inclusivity, these animals appear in the fossil record by the end of the Triassic or the beginning of the Jurassic (McPhee & Choiniere, 2017), reaching their peak of diversity between the Late Jurassic and Early Cretaceous (Pol et al., 2022).

Among the linages within Sauropoda, Titanosauria excels as the richest and more abundant. The first studied titanosaur, “*Titanosaurus indicus*”, was described by the English naturalist Richard Lydekker (1849-1915), based upon two caudal vertebrae unearthed from Cretaceous rocks of central India. Due to the poor preservation of the material, no characteristics could be found to keep its status as a valid taxon (Salgado, 2003). Titanosaurs probably originated during the Jurassic, reaching a cosmopolite distribution at the end of the Cretaceous (Wilson, 2006).

1.2 Diversity and evolutionary history

Titanosaurs can be distinguished from other sauropods by some unique anatomical traits, as for example: spongiform texture of presacral axial skeleton, trunk ribs with pneumatic cavities, and procoelic caudal vertebrae (Wilson & Sereno, 1998; Wilson, 2006) (**Fig. 1**). They represent the richest sauropod clade in South America, with more than fifty described species (de Jesus Faria et al., 2015; González Riga et al., 2019), as well as the most diverse dinosaur clade from the Brazilian Cretaceous (Bittencourt & Langer, 2011; Langer et al., 2022).

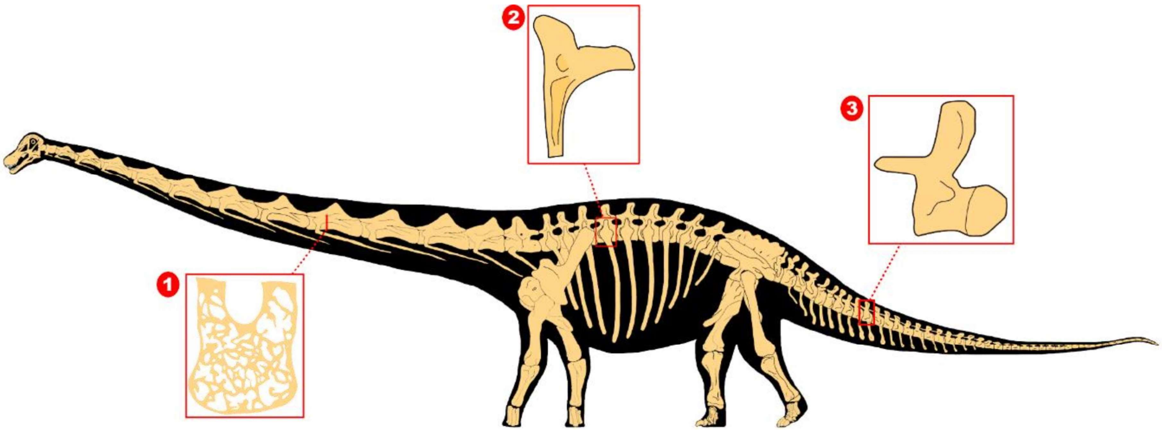

Figure 1. Simplified anatomical definitions of Titanosauria. 1, transversal slice of a cervical vertebra exemplifying the spongy inner structures; 2, internal (medial) view of a cervical rib highlighting a pneumatic cavity and 3, left lateral view of a procoelic caudal vertebra.

The first Brazilian record of a titanosaur comes from the early XX century, when the Brazilian naturalist Rodolfo Von Ihering (1883-1939) found some vertebrae during a well excavation. Von Ihering (1911) classified the remains as belonging to an "undetermined archosaur". These would be assigned to "*Titanosaurus*" later, by the German paleontologist Friedrich Von Huene (1875-1969; 1929). The description of a formal species would come after more than fifty years, when Arid & Vizzoto (1971) described a few fossils from São José do Rio Preto, naming *Antacrtosaurus brasiliensis*. Due to the poor condition of the specimens and lack Wof diagnostic features, the species is now considered a *nomen dubium* (Santucci & Bertini, 2006). Since then, a dozen of species were formally described from Cretaceous rocks of Brazil (**Table 1**).

The large number of species, mostly described upon fragmentary materials, hampers the proposal of evolutionary hypotheses encompassing titanosaurs (Salgado, 2003), resulting on conflicting phylogenetical arrangements. Yet, some consensus seems to be reached: Titanosaurs are now nested on a larger clade known as Titanosauriformes (e.g., Mannion et al., 2013; Poropat et al., 2016; Royo-Torres et al., 2017; González Riga et al., 2018) (**Fig. 2**), that also includes the cosmopolite and not very diverse Brachiosauridae and the Asian Euhelopodidae (Gorscak e O'connor, 2016; Poropat et al., 2016).

Table 1. List of Brazilian Titanosaurs.

Species	Reference	Locality	Geological context
Adamantisaurus mezzalirai	Santucci & Bertini, 2006	Flórida Paulista, São Paulo	Adamantina Formation, Late Cretaceous, Bauru Basin
Arrudatitan maximus	Santucci & Arruda-Campos, 2011	Monte Alto, São Paulo	Adamantina Formation, Late Cretaceous, Bauru Basin
Austroposeidon magnificus	Bandeira et al., 2016	Presidente Prudente, São Paulo	Presidente Prudente Formation, Late Cretaceous, Bauru Basin
Baurutitan britoi	Kellner et al., 2005	Uberaba, Minas Gerais	Serra da Galga Formation, Late Cretaceous, Bauru Basin
Brasilotitan nemophagus	Machado et al., 2013	Presidente Prudente, São Paulo	Presidente Prudente Formation, Late Cretaceous, Bauru Basin
Caieiria allocaudata	Silva Junior et al., 2022	Uberaba, Minas Gerais	Serra da Galga Formation, Late Cretaceous, Bauru Basin
Gondwanatitan faustoi	Kellner & Azevedo, 1999	Álvares Machado, São Paulo	Adamantina Formation, Late Cretaceous, Bauru Basin
Ibirania parva	Navarro et al., 2022	São José do Rio Preto, São Paulo	São José do Rio Preto Formation, Late Cretaceous, Bauru Basin
Maxakalisaurus topai	Kellner et al., 2006	Prata, Minas Gerais	Adamantina Formation, Late Cretaceous, Bauru Basin
Tapuisaurus macedoi	Zaher et al., 2011	Coração de Jesus, Minas Gerais	Quiricó Formation, Early Cretaceous, Sanfranscicana Basin
Triunfosaurus leonardii	Carvalho et al., 2017	Triunfo, Paraíba	Rio Piranhas Formation, Early Cretaceous, Triunfo Basin
Uberabatitan ribeiroi	Salgado & Carvalho, 2008	Uberaba, Minas Gerais	Serra da Galga Formation, Late Cretaceous, Bauru Basin

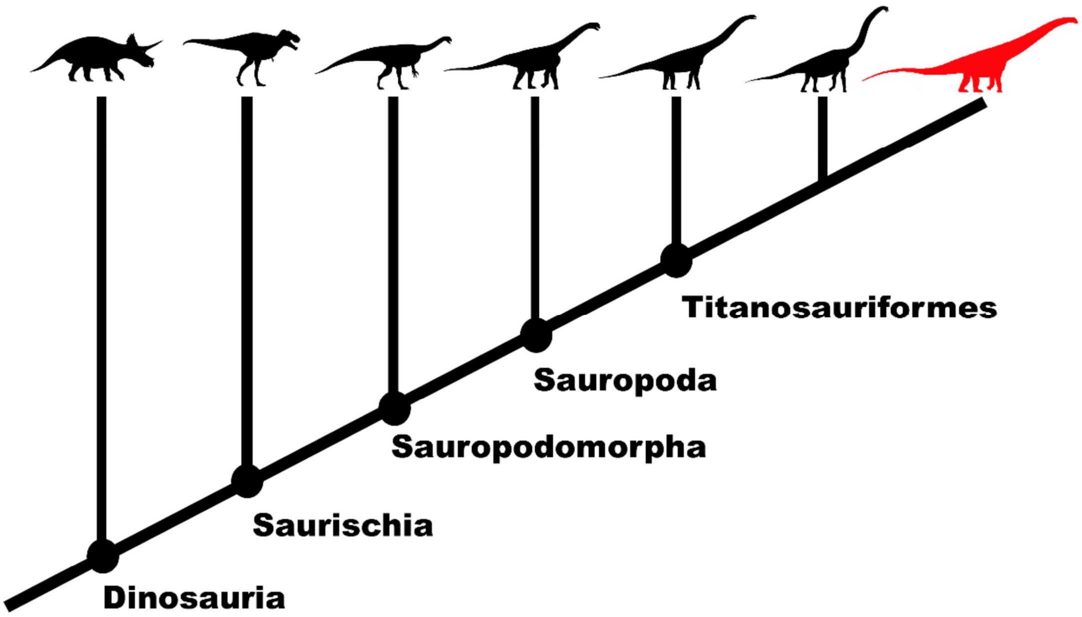

Figure 2. Simplified evolutionary arrangement of Dinosauria, with Titanosauria highlighted (in red).

1.3 Paleobiology

1.3.1 Pneumatization

Sauropods beard a complex respiratory system, quite similar to that of birds nowadays (Wedel, 2009). This pneumatic system is characterized by a network of diverticula and air-sacs that spread throughout their bodies, excavating some laminae and fossae on the axial skeleton and reducing the total weight of these animals, thus contributing to the achievement of immense sizes (Wilson, 1999; Wedel, 2003).

In some lineages, as in titanosauriforms and diplodocids, this pneumatic network can reach the distalmost portions of the skeleton, to the pelvic girdle and mid-posterior caudal vertebrae (Wedel et al., 2000; Wedel, 2003b; Salgado et al., 2006, Cerda et al., 2012b). This complex respiratory system could have also had metabolic impacts, acting as more efficient internal cooling mechanism (Sander & Clauss, 2008, Perry et al., 2009, 2011).

1.3.2 Gigantism

Another unique feature sauropods have is their large body sizes. Its origin was only possible due to a combination of different evolutionary novelties. Starting from the acquisition of a long neck, caused by both the increase of the total number of cervical vertebrae and their elongation (Sander, 2013; Sander et al., 2011). Such characteristic allowed a wider feed mobility, vertically and horizontally, reaching resources that were not available for other large herbivores at the time (Seymour, 2009; Taylor et al., 2011). The long necks were counterbalanced by a small and light head, decreasing the energetic cost to raise it (Taylor & Wedel, 2013; Preuschoft & Klein, 2013).

Another important feature of sauropods was the change from the ancestral bipedal to a graviportal quadrupedal stance (Apaldetti et al., 2018; Mcphee et al., 2018). Such unique posture allowed a reduction on the lateral tensions suffered during locomotion (Wilson & Carrano, 1999; Carrano, 2005), also providing a better gravitational support (Bonnan, 2003; Otero & Hutchinson, 2022). A quadrupedal stance was key for the acquisition of larger sizes and, hence, dominance of the sauropod fauna. It allowed a more consistent distribution of mass, providing better maneuverability that allowed the exploration of more topographicaly complex environments (Henderson, 2006; Mannion & Upchurch, 2010).

All these changes would result on lineages ever-increasing their body-sizes, especially during the Jurassic-Cretaceous, with the rise of the Neosauropoda (**Fig. 3**) (Bonaparte, 1986; Upchurch, 1995). This group included several species easily reaching more than 10t (tons) (Otero & Hutchinson, 2022). The clade also included Diplodocidae species reaching more than 30t (Paul, 2016; 2019; Campione & Evans, 2020), and finally the Titanosaurs, which encompasses the largest terrestrial animals, with species reaching more than 60t (e.g., Mazzetta et al., 2004; Campione, 2017; Carballido et al., 2017; Paul, 2019).

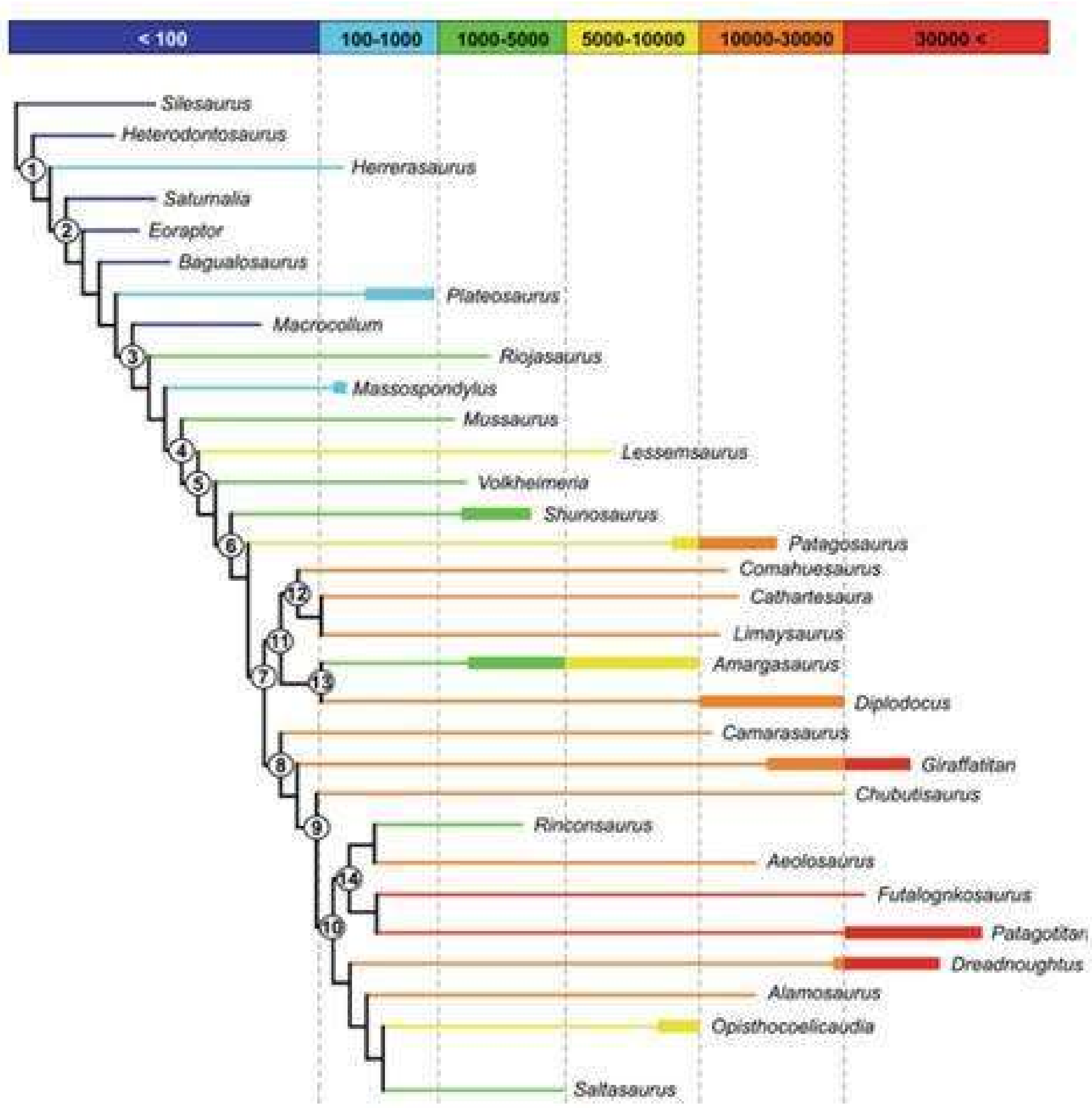

Figure 3. Phylogeny representing the evolution of corporal mass within Sauropodomorpha (after Otero & Hutchinson, 2022). Nodes = 1 = Dinosauria; 2 = Sauropodomorpha; 3 = Massopoda; 4 = Sauropodiformes; 5 = Sauropoda; 6 = Eusauropoda; 7 = Neusauropoda; 8 = Macronaria; 9 = Somphospondily; 10 = Titanosauria; 11 = Diplodocidea; 12 = Rebbachisauridae; 13 = Flagellicaudata; 14 = Colossosauria.

1.3.3 Osteoderms

Among sauropods, osteoderms were only recorded within titanosaurs. Although rarely preserved (Mannion, 2010), these elements were morphologically diverse, with records associated to this clade all over the world (e.g., Dodson et al., 1998; Gomani, 2005; Vidal et al., 2014; Fronimos, 2021). Several functions were proposed for the osteoderms, including protection, thermoregulation, or even as sexual and intraspecific display (Salgado, 2003b;

Cerda e Powell, 2010; Curry Rogers et al., 2011; Marinho e Iori, 2011). Currently, based upon the fact that osteoderms tend to hollow during the ontogeny, it has been proposed that their main function would be as a calcium reservoirs, replacing this mineral when lost during growth or pregnancy (Curry Rogers et al., 2011; Cerda et al., 2015; Vidal et al., 2017).

The defensive function of osteoderms in titanosaurs was proposed along with their first records, with the proposition that osteoderms composed a heavy dermal armor (i.e., Bonaparte & Powell, 1980; Sanz & Buscalioni, 1987). This idea has been challenged due to the absence of evidences that these elements were abundant enough in the skin and present in all species (D'emic, 2009; Curry Rogers, 2011). More recently, Silva Junior et al. (2021) found that osteoderms that did not suffer calcium lost could resist bite forces of possible predators, in simulated scenarios from an abelisaurid theropod and a baurusuchidae crocodiliform. This could benefit titanosaurs, especially on early ontogenetic stages, as juvenile could bare osteoderms proportionally larger and closer to one another, forming a more compact armor (Marinho, 2007; Marinho & Iori, 2011).

1.3.4 Nesting

The first sauropod eggs were found in southeast France in 1859 by the naturalist priest Jean-Jacques Pouech (1814-1892) and in south France ten years later by the geologist Philippe Matheron (1807-1899). At time, Pouech identified the eggs as belonging to a giant bird, whereas Matheron considered them as remains of a giant crocodile (Depéret, 1900). Only at the beginning of the XX century, these findings would be correctly identified as sauropod eggs, and attributed to titanosaurs (Joleaud, 1924; Buffetaut & Le Loeuff, 1994). In Brazil, the first of such eggs were collected by the paleontologist Llewellyn Ivor Price (1905-1980), during 1951, near Uberaba, Minas Gerais. This record, along with later ones from the same region, were identified as titanosaurs eggs (Magalhães Ribeiro, 2002; Grellet-Tiner & Zaher, 2008, Fiorelli et al., 2022).

These finds can provide resourceful data to better understand the nesting behavior of not only titanosaurs, but sauropods as a whole. The evidence of egg-clutching arranged in different levels suggests that the females would aggregate to lay their eggs in the same areas throughout different nesting seasons (Chiappe et al., 2015; Fiorelli et al., 2022). These eggs would then be burrowed or laid at the ground and then covered with sediments (Hechenleitner et al., 2015).

1.4 Final remarks

This short session glimpses onto the state of art of sauropod paleobiology, with emphasis on titanosaurs and including contributions made during the writing of this thesis (i.e., osteoderms = Silva Junior et al., 2021; nesting sites and behavior = Fiorelli et al., 2022). Focusing on the titanosaur fauna of the Brazilian Cretaceous, most of the research carried on the last years relate to the taxonomic status of different species, added of the description of new taxa or sparse remains. This first topic is explored in Appendices 1 and 2, whereas the latter – with the addition of specimens that can be useful for taxonomic considerations – is explored in Appendices 3 and 4.

2. OBJECTIVES AND OVERVIEW OF THE APPENDICES

The research presented in this thesis was conducted with two main objectives: (1) to expand the knowledge about Titanosauria via the study of novel specimens and the reassessment of previously known ones; and (2) to investigate the taxonomical richness of the titanosaur fauna of the Bauru Basin Cretaceous. In order to achieve these goals, an integrative suite of alpha-taxonomic revisions and cladistic methods were used. An overview and specific objectives of each contribution are presented below:

2.1 Appendix 1: the Brazilian Aeolosaurini

Appendix 1 presents the reassessment of fossils from the Late Cretaceous of the Adamantina Formation, along with a revision of the genus *Aeolosaurus*. A detailed revision of the diagnostic features of this genus is given, followed by the proposition of clade definitions for inner sauropod groups. This study aims to provide a better knowledge about possible taxa shared by Brazil and Argentina.

2.2 Appendix 2: the Uberaban chimaera

Appendix 2 presents the description of new fossil remains from the Late Cretaceous of the Serra da Galga Formation. These new fossils were associated to two species previously known from the region: *Baurutitan britoi* and *Trigonosaurus pricei*, led in to the revaluation of both and the proposition of a new genus and species, *Caieiria allocaudata*.

2.3 Appendix 3: some teeth diversity

Appendix 3 presents the description of different tooth morphotypes housed at the “Museu dos Dinossauros” collection, Uberaba, including the largest titanosaur tooth ever recorded. This contribution is relatively innovative, as no articles focusing only on titanosaur teeth from Brazil were ever published. It is expected that it contributes to a better understanding of paleobiological aspects of the local titanosaur fauna.

2.4 Appendix 4: dinosaurs in the attic

The final study (Appendix 4) contains the description of the titanosaur remains housed at the “Museu dos Dinossauros” that could not be attributed to previously known taxa, nor can be used to diagnose new species. Without a formal publication and proper figuration, these specimens are worth for anatomical comparisons.

3. CONCLUDING REMARKS, KEY FINDINGS AND FUTURE PERSPECTIVIES

The studies presented in Appendices (1-4) demonstrate the potential of the fossil record of Minas Gerais and São Paulo to better understand titanosaur evolution, shedding light on the evolutionary history of the group (Appendix 1), with the proposal of new species (Appendix 2) and insights into the paleobiology (Appendix 3) and richness (Appendix 4) of the local fauna. Taken together, it is expected that the key findings of this thesis (summarized below) could somehow enhance the titanosaur research.

Appendix 1: the Brazilian Aeolosaurini (published manuscript)

Some titanosaur remains unearthed from the Late Cretaceous Adamantina Formation near Monte Alto were first referred to the genus *Aeolosaurus* (Powell, 1978). This genus previously contained two species: *Ae. rionegrinus* and *Ae. colhuehuapensis* (Casal et al., 2007); and after its formal description, the Monte Alto titanosaur was also included in the genus, as *Ae. maximus* by Santucci & Arruda-Campos (2011).

In the same year, Martinelli et al. (2011) revised the materials previously assigned to the genus *Aeolosaurus*, and suggested that none of the Brazilian fossils, including *Ae. maximus*, could be unequivocally included in the Argentinean genus, but could be considered Aeolosaurini indet. Later, phylogenetic studies recovered *Ae. maximus* in disparate positions separated from the other *Aeolosaurus* spp. (Bandeira et al., 2016; Hechenleitner et al., 2020), strengthening the idea that is may not belong to the genus.

Finally, the taxon was revised, and based upon the lack of synapomorphic features of *Aeolosaurus*, a new genus, *Arrudatitan*, was created to accommodate the species. With the use of a large data matrix to determine the evolutionary relations of *Aeolosaurus*, the resulting topologies were used to propose phylogenetic definitions under the PhyloCode (Cantino & De Queiroz, 2020), for the successive clades including *Arrudatitan maximus*.

Appendix 2: the Uberabean chimaera (published manuscript)

Based upon a remarkably set of titanosaur remains unearthed by Price during the 1940's to 1960's, from rocks of the Late Cretaceous Serra da Galga Formation, near Uberaba, from a site he called "Ponto 1", two new species were erected: *Baurutitan britoi* (Kellner et al., 2005) and *Trigonosaurus pricei* (Campos et al., 2005). The holotype of the first includes the last sacral vertebra and an almost complete tail; whereas the latter represents one at the most complete titanosaur species know at the time, with the last cervical, complete trunk and the pelvis preserved. Additionally, Powell (1987) considered a set of ten vertebrae as possibly assigned to *Tr. pricei*. This association was first challenged by Campos & Kellner (1999), but later defined as the paratype of this species (Campos et al., 2005).

The description of new specimens from the same geological unit, but from a different site at BR-262 highway, called by Price as "Ponto 6", led to the taxonomical revision of these taxa. The BR-262 specimens share several anatomical traits with the cervical and trunk vertebrae of *Tr. pricei* and the caudal vertebrae of *B. britoi*. A detailed study of the new specimens indicated that they all belonged to a single individual, thus providing enough evidence that the "Ponto 1" taxa must belong to a single species, with nomenclatural priority given to *Baurutitan britoi*.

The BR-262 specimens also differed from the tail assigned to *Tr. pricei*, thus suggesting that it could represent a hitherto undescribed new species. After comparing the caudal tail anatomy to that of other titanosaurs, autapomorphic features were found, so that a new genus and species was erected: *Caieiria allocaudata*.

Appendix 3: some teeth diversity (unpublished manuscript)

The Uberaba region represents one of the most titanosaur-rich areas from the Brazilian Cretaceous. Unfortunately, such richness does not include teeth, as these elements are poorly represented in the region. So, aiming to provide better ground for future studies and comparisons including teeth, different morphotypes were identified and described. These morphotypes do not deviate from the overall teeth anatomy seen in other titanosaurs, and could not be referred to any specific taxa.

Among the studied specimen, some juvenile teeth were found, in the same site as adult ones. Also, a giant specimen was described, representing the largest titanosaur tooth ever recorded worldwide. This further confirms the idea that the paleoenvironment represented by the Cretaceous rocks in the Peirópolis region supported a distinct titanosaur fauna, including a nesting site (Fiorelli et al., 2022), juvenile specimens (Silva Junior et al., 2017), and fully grown giant individuals.

Appendix 4: the dinosaurs in the attic (unpublished manuscript)

Some of the material housed at “Museu dos Dinossauros” could not be assigned to any previously known taxon from the region, also not bearing any autapomorphic feature that justifies the creation of new species. Yet, they can provide important data for comparative studies. Thus, about thirty specimens were described and figured, and as such presented to the scientific community. Some specimens are particularly important. A few caudal vertebrae were previously referred to as an Aeolosaurini indet. and can be distinguished from all other Serra da Galga taxa (Martinelli et al., 2011). This could represent a hitherto unrecognized Aeolosaurini species, which could increase even more the titanosaurs taxonomic of that region.

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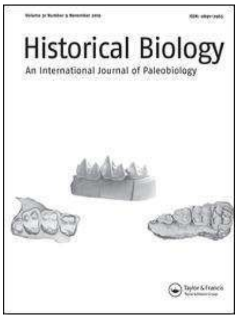
Appendix 1



Historical Biology

An International Journal of Paleobiology

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/ghbi20

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To cite this article: Julian C. G. Silva Junior, Agustín G. Martinelli, Fabiano V. Iori, Thiago S. Marinho, E. Martín Hechenleitner & Max C. Langer (2021): Reassessment of *Aeolosaurus maximus*, a titanosaur dinosaur from the Late Cretaceous of Southeastern Brazil, Historical Biology, DOI: 10.1080/08912963.2021.1920016

To link to this article: https://doi.org/10.1080/08912963.2021.1920016

HISTORICAL BIOLOGY
https://doi.org/10.1080/08912963.2021.1920016

ARTICLE

Reassessment of *Aeolosaurus maximus*, a titanosaur dinosaur from the Late Cretaceous of Southeastern Brazil

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ABSTRACT
Aeolosaurus is a late Cretaceous Titanosaur genus with two species discovered in Argentina and one in Brazil. Although the allocation of the Argentinean *Aeolosaurus* seems unequivocal, that is not the case for the Brazilian species *Aeolosaurus maximus* since several authors questioned its positioning into this genus, based on both anatomical and phylogenetic data. The revision of the diagnosis of *Ae. maximus*, with the proposition of a new autapomorphy, corroborates the anatomical uniqueness and our phylogenetic analysis stresses that the relation of *Ae. maximus* to the Argentinean *Aeolosaurus* is uncertain. Based upon that, we propose a new genus, *Arrudatitan*, to accommodate the Brazilian taxon.

ARTICLE HISTORY
Received 19 November 2020
Accepted 15 April 2021

KEYWORDS
Dinosauria; Titanosauria; Aeolosaurini; Late Cretaceous; South America

Introduction

Even though *Titanosauria* is the most diverse clade within Sauropoda, with several Cretaceous species described worldwide, the group is composed mainly of monospecific genera (Mannion and Calvo 2011; De Jesus Faria et al. 2015). One of the few exceptions is *Aeolosaurus*, erected by Powell (1986, 1987), which has three nominated species being two from Argentina and one from Brazil. The type species, *Ae. rionegrinus*, was proposed to include a partial skeleton (holotype MJG-R 01) discovered in the Late Cretaceous Angostura Colorada Formation, Casa de Piedra locality, Estancia Maquinchao, Río Negro, Argentina (Powell 1986, 1987). Powell (1987, p. 148) also described a sequence of 15 caudal vertebrae from the Campanian-Maastrichtian Los Alamitos Formation of Argentina as possibly referred to *Ae. rionegrinus*, but that assignment was questioned by Salgado and Coria (1993) and Salgado et al. (1997). Later, other remains discovered in northern Patagonia were ascribed to *Aeolosaurus* sp. (Salgado and Coria 1993; Salgado et al. 1997; Garcia and Salgado, 2013), coming from the roughly coeval Los Alamitos and Allen formations.

Casal et al. (2007) described a second *Aeolosaurus* species, *Ae. colhuehuapensis*, unearthed from the Campanian-Maastrichtian Bajo Barreal Formation, central Patagonia. Furthermore, in the last 20 years or so, there were several reports of *Aeolosaurus* sp. in the Upper Late Cretaceous rocks of southeastern and central Brazil, usually based upon incomplete and poorly preserved material (e.g., Bertini et al. 1999a; Bertini et al. 1999b, 2000; Candeiro 2006, 2010; Candeiro et al. 2006; Lopes and Buchmann 2008; Santucci and Bertini 2017). The referral of these specimens to *Aeolosaurus* was questioned by Martinelli et al. (2011), who instead considered them all as indeterminate *Aeolosaurini.*

In particular, one of the materials referred as *Aeolosaurus* sp. from the state of São Paulo consists of various axial and appendicular bones of a single individual (Bertini, 1999a) that was included in the review of the Brazilian material done by Martinelli et al. (2011; it was labelled at the time as MPMA/without number). Those authors concluded that this specimen lacks several diagnostic features of the genus and should be regarded as an indeterminate *Aeolosaurini.* In the same year, that specimen (then numbered as MPMA 12–0001/97) was designated as the holotype of a new species, *Aelosaurus maximus* Santucci and Arruda-Campos, 2011. The phylogenetic analysis that accompanied that proposal positioned *Ae. maximus* as the sister-taxon to *Ae. rionegrinus* plus *Ae. colhuehuapensis*, with the Brazilian *Gondwanatitan faustoi* as the sister taxon of that clade. However, more recent phylogenetic analyses placed *Ae. maximus* in disparate alternative positions (e.g., Bandeira et al. 2016; Filippi et al. 2019; Silva Junior et al. 2019; Hechenleitner et al. 2020). In this contribution, we revise the diagnosis and affinities of *Ae. maximus*, proposing a new genus to accommodate the species.

Institutional abbreviations: **CPPLIP**, Centro de Pesquisas Paleontológicas Llewellyn Ivor Price, Universidade Federal do Triângulo Mineiro, Uberaba, Brazil; **CRILAR**, Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja, Argentina; **IANIGLA-PV**, Instituto Argentino de Nivología, Glaciología y Ciencas Ambientales, Colección Paleovertebrados, Mendoza, Argentina; **MAU-Pv**, Paleontología de Vertebrados, Museo Municipal 'Argentino Urquiza', Rincón de los Sauces, Neuquén, Argentina; **MCT**, Museu de Ciências da Terra, Serviço Geológico do Brasil, Rio de Janeiro, Brazil; **MJG-R**, Museo Jorge Gerold, Ingeniero Jacobacci, Río Negro, Argentina; **MPM**, Museu

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Observations: Following article 6, recommendation 6.1A, from PhyloCode (Cantino and De Queiroz 2020), all clades established under this code are italicised.

Geological settings

The Bauru Basin (Figure 1) is a cratonic depression developed in the southeastern portion of the South American Plate during the Late Cretaceous (Fernandes and Ribeiro 2015). Sedimentation within the basin occurred under semi-arid to arid conditions, but the age of the deposits is a matter of intense debate (e.g., Batezelli and Ladeira 2016; Menegazzo et al. 2016). In particular, the Adamantina Formation had a complex nomenclatural history, being subdivided into different schemes in the literature (e.g., Soares et al. 1980; Fernandes and Coimbra 2000; Paula E Silva et al. 2005; Batezelli and Ladeira 2016; Menegazzo et al. 2016). As for its age, the most recent review suggested a Campanian assignment (Castro et al. 2018), but ages ranging from Cenomanian to Maastrichtian have been proposed (Gobbo-Rodrigues et al. 1999; Dias-Brito et al. 2001; Menegazzo et al. 2016), and different sites, with distinctive faunal components, may actually have different ages (Martinelli and Teixeira 2015; Martinelli et al. 2018).

The Monte Alto region is an important source of vertebrate fossils within the eastern border of the Bauru Basin, with dozens of catalogued digging sites referred to both the Adamantina and Marília formations, which yielded several species of turtles, crocodyliforms, and dinosaurs (e.g., Bertini et al. 2001; Carvalho et al. 2007; Andrade and Bertini 2008; Pinheiro et al. 2008; Santucci and Arruda-Campos 2011; Iori and Carvalho 2011; Iori and Garcia 2012; Méndez et al. 2014; Ferreira et al. 2018; Iori et al. 2018).

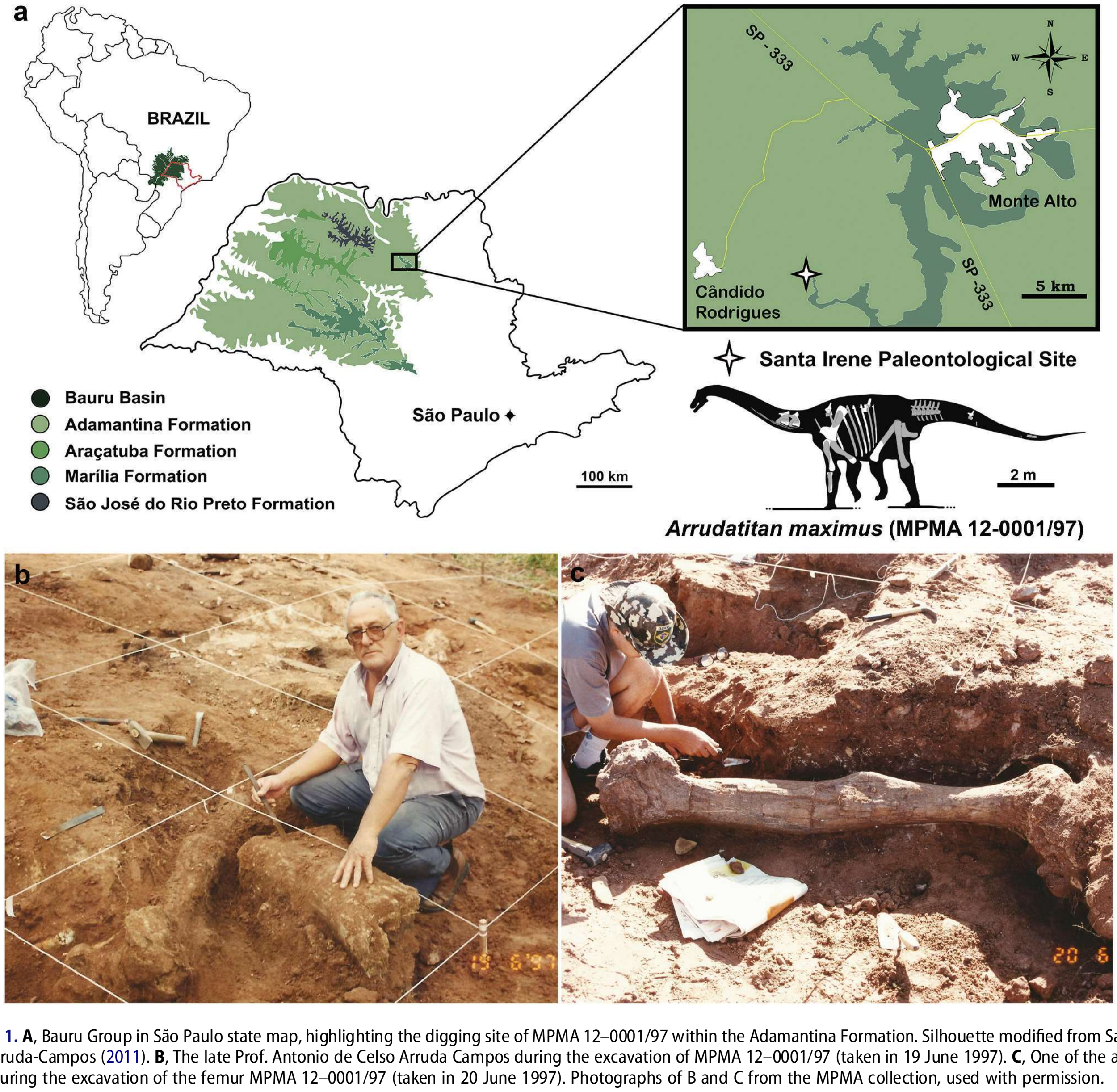

Figure 1. **A**, Bauru Group in São Paulo state map, highlighting the digging site of MPMA 12–0001/97 within the Adamantina Formation. Silhouette modified from Santucci and Arruda-Campos (2011). **B**, The late Prof. Antonio de Celso Arruda Campos during the excavation of MPMA 12–0001/97 (taken in 19 June 1997). **C**, One of the authors (FVI) during the excavation of the femur MPMA 12–0001/97 (taken in 20 June 1997). Photographs of B and C from the MPMA collection, used with permission.

The type-locality and holotype (MPMA 12–0001/97) of *Ae. maximus* were discovered during 1997 by Ademir Frare and Luiz Augusto dos Santos Frare in the 'Santa Irene' farm, a property located near the limits between Monte Alto and Cândido Rodrigues municipalities (Iori 2019; GPS = S21°19′44.3″/W 48°34′ 54.6″). Santucci and Arruda-Campos (2011) mentioned that the site is located about 12 km southwest of Monte Alto, but its position in their map (Santucci and Arruda-Campos 2011: Figure 1) is not correct. In fact, the outcrop is located further 9 km to northwest of the point marked at that map, within Cândido Rodrigues municipality. The specimen was unearthed during two excavation campaigns in 1997 and 1998, when most of the partially articulated skeleton was collected (see Santucci and Arruda-Campos 2011) associated with numerous isolated theropod and crocodyliform teeth (Tavares et al. 2011, 2014). The remains were removed from a massive, reddish sandstone layer, with local carbonatic cementation. According to Santucci and Arruda-Campos (2011), the skeleton has undergone little transport, and small theropod dinosaurs and crocodyliforms have fed on the carcase.

Taxonomy and affinities of *Aeolosaurus maximus*

Historical background

Along with the description of *Ae. rionegrinus*, Powell (1987) proposed several autapomorphies for the species, some of which were later suggested to represent synapomorphies of *Aeolosaurini* by Franco-Rosas et al. (2004). In the description of *Ae. colhuehuapensis*, Casal et al. (2007) proposed to diagnose the genus based on the presence of mid-caudal vertebrae with postzygapophyses located anterior to the anterior articular facet of the centrum and proximally opened haemal arches, with articular facets arranged on two planes. Later on, Santucci and Arruda-Campos (2011) employed two putative synapomorphies of *Aeolosaurus* to place MPMA 12–0001-97 in that genus: (1) well-developed posterior protuberance below the articular area on the anterior and middle haemal arches and (2) lateral bulge on the distal portion of the articular process of the mid-posterior haemal arches.

Based on the direct comparison between MPMA 12–0001-97 and the two Argentinean species of *Aeolosaurus*, Martinelli et al. (2011), stated that due to the absence of the synapomorphies proposed for the genus by Casal et al. (2007), MPMA 12–0001-97 could only be considered as an indeterminate *Aeolosaurini* as it bears a number of characteristics of this clade (i.e., antero-dorsal margin of caudal centrum anteriorly tilted, neural arch placed on the anterior half of the centrum, and neural spine anteriorly inclined and large prezygapophysis). In particular, the postzygapophyses of the caudal vertebrae of MPMA 12–0001-97 are not positioned anterior to the level of the anterior edge of the centrum. Notably, this trait is only seen in the Patagonian species of *Aeolosaurus* (Casal et al. 2007) and was never reported in other titanosaurs.

In the description of *Ae. maximus*, Santucci and Arruda-Campos (2011; see also França et al. 2016) used a modified version of the dataset of Wilson (2002) to evaluate its phylogenetic position. The taxon was recovered within *Aeolosaurini*, as sister taxon to the clade, including both Argentinean species of *Aeolosaurus*. Later, Bandeira et al. (2016) found *Ae. maximus* closer to *Rinconsauria* than to *Aeolosaurini*, whereas the analysis of a modified version of that matrix (Silva Junior et al. 2019) recovered *Ae. maximus* again as an *Aeolosaurini*, but not particularly close to the Argentinean *Aeolosaurus*. More recently, Carballido et al. (2017) and Filippi et al. (2019) recovered *Ae. maximus* as sister to *Overosaurus*, within *Rincosauria*, but these datasets did not include the Argentinean *Aeolosaurus*, nor *Gondwanatitan*. Lastly, a comprehensive phylogeny by Hechenleitner et al. (2020) obtained *Ae. maximus* as sister taxon of a clade including the Argentinean *Punatitan* and *Aeolosaurus*.

Uniqueness of Aeolosaurus maximus

Santucci and Arruda-Campos (2011) identified a set of unique traits of MPMA 12–0001-97. Some of these features are related to the peculiar laminae configurations seen in its vertebrae, which can be distinguished from those of all other titanosaurs. Firstly, according to Santucci and Arruda-Campos (2011), the posterior centrodiapophyseal lamina (pcdl) is at least 50% thicker (expanded both dorsoventrally and mediolaterally) than the postzygodiapophyseal lamina (podl) in the posterior cervical vertebrae. This condition differs from that of other titanosaurs, where pcdl and podl have similar dimensions, as is the case of *Overosaurus* (Coria et al. 2013; MAU-Pv-CO-439, Figure 2A) and some Bauru Group taxa, such as *Trigonosaurus* (Campos et al. 2005; MCT 1488-R, Figure 2) and *Brasilotitan* (Machado et al. 2013; MPM 125 R, Figure 5A). Santucci and Arruda-Campos (2011) identified the presence of intrapostzygapophyseal laminae (tpol) in the posterior trunk vertebrae of MPMA 12–0001-97 as autapomorphic. This condition is uncommon among titanosaurs, which normally have this lamina only in anterior and/or mid-trunk vertebrae as seen in *Petrobasaurus* (Filippi et al. 2011; MAU-Pv-PH-449/18, Figure 4G), *Mendozasaurus* (González Riga et al. 2018; IANIGLA-PV 066, Figure 6 C), and *Uberabatitan* (Silva Junior et al. 2019; CPPLIP-

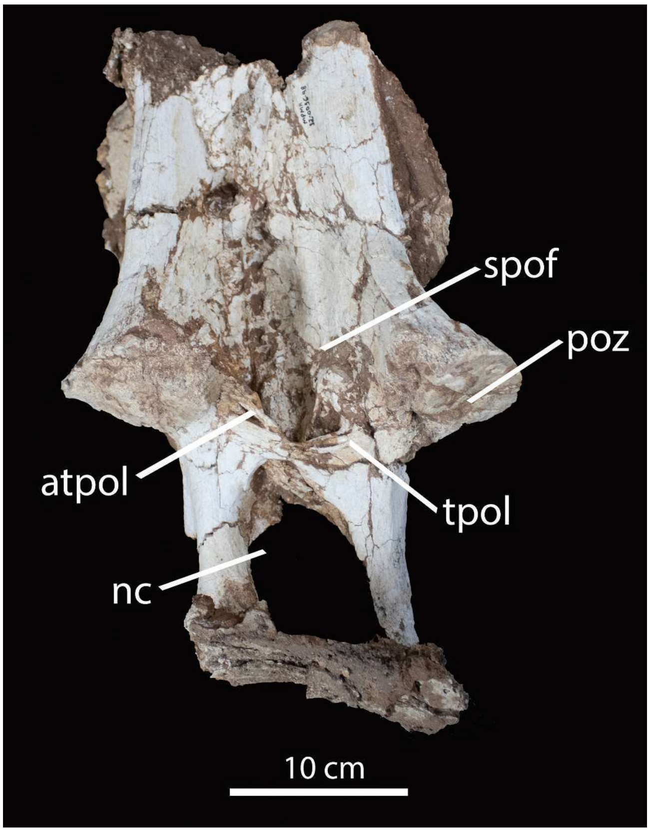

Figure 2. MPMA 12–0001-97. Posterior trunk vertebra in posterior view. Abbreviations: **atpol**: accessory intrapostzygapophyseal lamina; **nc**: neuralcanal; **poz**: postzygapophysis; **spof**: spinopostzygapophyseal fossa; **tpol**:intrapostzygapophyseal lamina.

1077, Figure 7A). Yet, given that this character is shared with other titanosaurs, such as *Narambuenatitan* (Filippi et al. 2011; MAU–Pv –N – 425, Figure 7B), *Dreadnoughtus* (Voegele et al. 2017; MPM-PV 1156–11, Figure 3G), and *Bravasaurus* (Hechenleitner et al. 2020; CRILAR-Pv 612, Figure 3F), it cannot be considered as unique to MPMA 12–0001-97.

As also mentioned by Santucci and Arruda-Campos (2011), MPMA 12–0001-97 has posterior trunk vertebrae with an oblique anterior centropostzygapophyseal lamina (acpol), which bifurcates from the proximal portion of the centropostzygapophyseal lamina (cpol). This pattern is indeed unknown in any other titanosaur, in which a single lamina (cpol) is responsible to connect the posterior portion of the neural arch to the postzygapophysis as seen in *Opisthocoelicaudia* (Borsuk-Białynicka 1977; ZPAL MgDI/48, Figure 3C), *Punatitan* (Hechenleitner et al. 2020; CRILAR-Pv 614, Figure 2D), and *Saltasaurus* (Powell 2003; PVL 4017–136, Figure 28). Although not discussed by Santucci and Arruda-Campos (2011), our comparative review shows that the posterior trunk vertebrae of *Ae. maximus* possess an accessory intrapostzygapophyseal lamina (atpol), creating two small lateral camerae on the

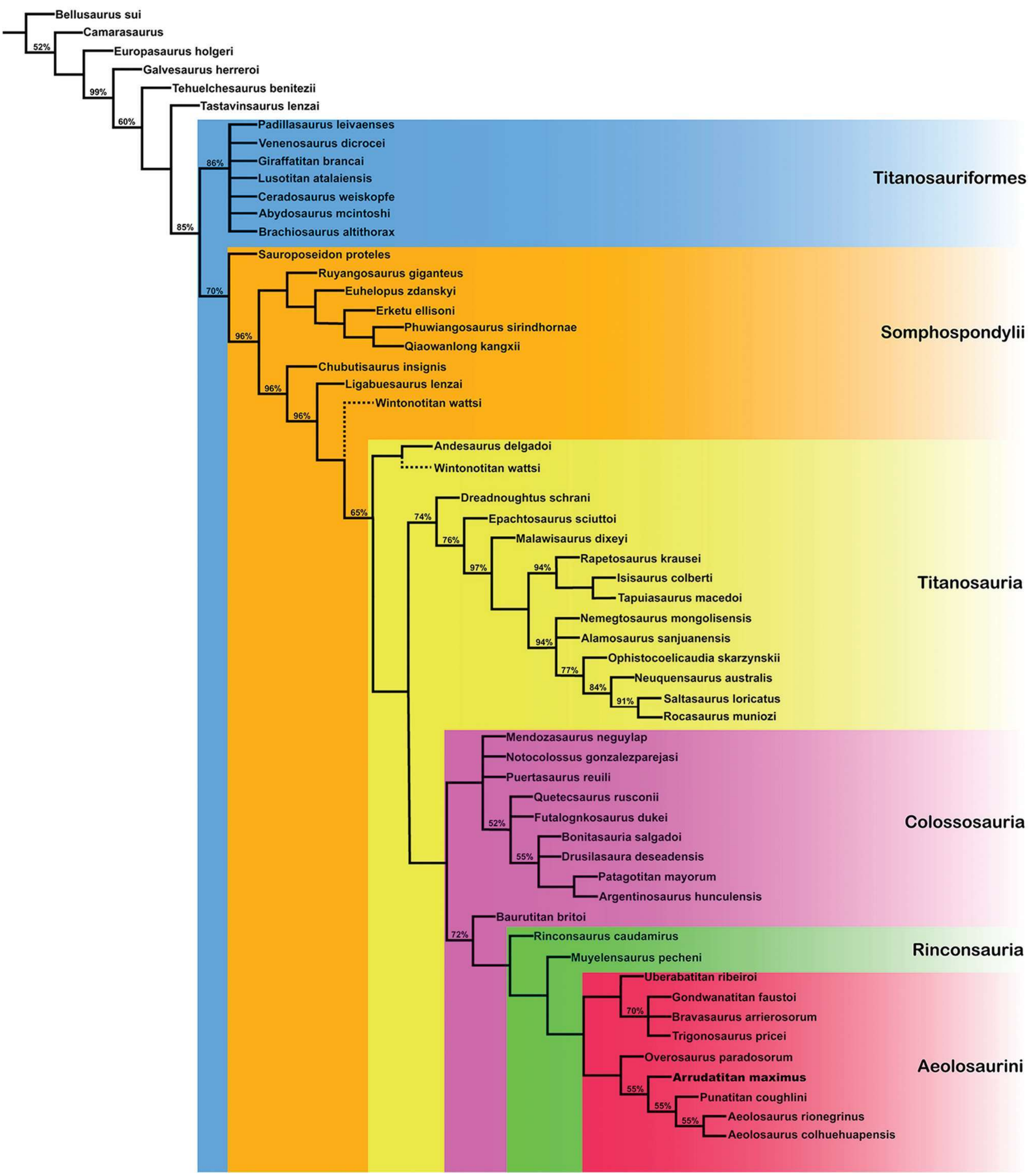

Figure 3. Simplified 50% majority-rule consensus of 3,680 MPTs based on Hechenleitner et al. (2020) plus modifications (see text).

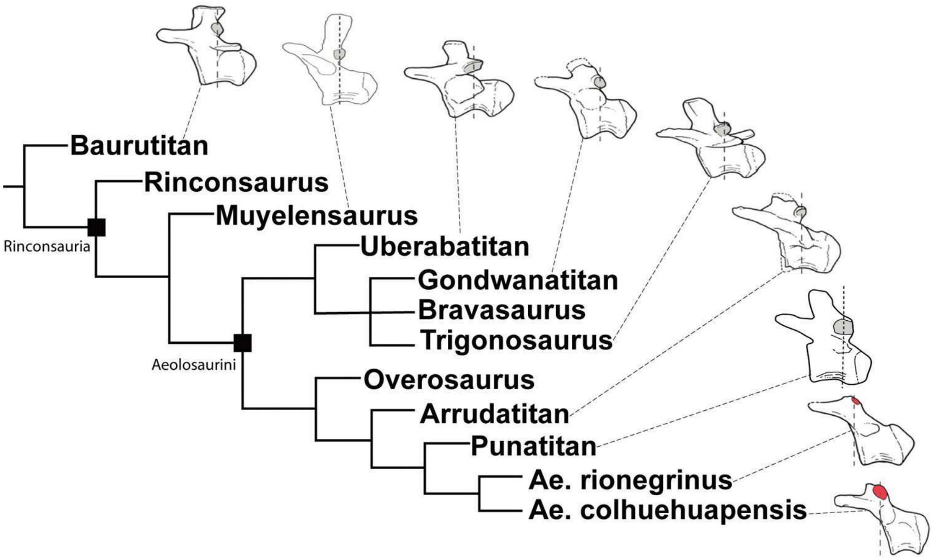

Figure 4. Comparison of the position of the postzygapophysis of posteriormost anterior to middle caudal vertebrae of *Aeolosaurini* and closely related taxa. Indicated only for taxa with those vertebrae preserved.

spinopostzygapophyseal fossa (Figure 2). Although the presence of accessory laminae is common in posterior trunk vertebrae of titanosaurs as seen in *Trigonosaurus* (Campos et al. 2005; MCT 1488-R, Figure 19) and *Dreadnoughtus* (Voegele et al. 2017; MPM-PV 1156–11, Figure 1E), they differ from the pattern found in *Ae. maximus* because in the later taxa the accessory laminae are associated with the diapophyseal lamination. Finally, titanosaurs usually possess plank-like shape trunk ribs (Wilson 2002), although this condition may vary as seen in *Uberabatitan* (Silva Junior et al. 2019; CPPLIP-923, Figure 13O), the rib shafts of which are concave on their medial portions. A different pattern was noted by Santucci and Arruda-Campos (2011) in *Ae. maximus*, in which the mid trunk ribs have well-developed anterior and posterior crests, creating a D-shaped cross section, as unique among titanosaurs.

The characters discussed above are indeed unique to *Ae. maximus* when compared with titanosaurs in general, including some *Aeolosaurini* as defined below (i.e., *Bravasaurus, Punatitan, Overosaurus, Trigonosaurus*, and *Uberabatitan*). Yet, the corresponding anatomical parts are not preserved in other *Aeolosaurini* such as *Ae. rionegrinus, Ae. colhuehuapensis*, and *Gondwanatitan*. Hence, as stated by Santucci and Arruda-Campos (2011), depending on further specimen recovered for these taxa and on the chosen phylogenetic arrangement, these characters may reveal to be synapomorphies of a given subset of *Aeolosaurini*, instead of autapomorphies of *Ae. maximus*.

Affinities of Aeolosaurus maximus *and its bearing on stratigraphic correlation*

In order to infer the relationships of *Ae. maximus*, we employed a modified version of the dataset of Hechenleitner et al. (2020), which was based on that provided by Carballido et al. (2020) and represents the most complete and up-to-date phylogenetic study of South American titanosaurs. Four characters (423–426) were added to the dataset (see supplementary material), which, respectively, correspond to characters 235, 238, 239, and 240 of Santucci and Arruda-Campos (2011). Furthermore, *Ae. colhuehuapensis* was added as a terminal unit and scored based on Casal et al. (2007). Summarising, the dataset analysed here (see Suppl. mater.) has 426 characters scored for 97 sauropodomorph terminals. The analysis was conducted in TNT 1.5 (Goloboff et al. 2016) with tree bisection and reconnection (TBR) as the branch swapping algorithm, hold established as 50, 5,000 replicates, and random seed as ‘0’.

The analysis resulted in 3,680 Most Parsimonious Trees (MPTs) of 1,496 steps. The strict consensus shows *Ae. maximus* forming a polytomy with *Overosaurus, Punatitan, Ae. rionegrinus*, and *Ae. colhuehuapensis*. In the 50% majority-rule consensus tree (Figure 2), *Ae. maximus* represents the sister taxon of the clade formed by *Punatitan* and *Ae. rionegrinus* + *Ae. colhuehuapensis*. The clade congregating these four taxa is supported by two synapomorphies: (1) posteriormost anterior and middle caudal vertebrae with neural spines directed anteriorly (Ch. 257), shared by *Ae. maximus* and *Punatitan*, and (2) middle caudal vertebrae with prezygapophysis longer than 50% of the centrum (Ch. 420), shared by all four taxa.

The clade composed by *Punatitan* and both Argentinean *Aeolosaurus* is supported by two synapomorphies: (1) groove in the ventral surface of anterior and middle caudal centra (Ch. 251), shared by *Punatitan* and *Ae. rionegrinus* – *Ae. maximus* lacks this grove –, and (2) prezygapophyses of middle caudal vertebrae oriented anterodorsally (Ch. 413), shared by all three taxa – whereas *Ae. maximus* presents prezygapophysis anteriorly oriented. *Ae. rionegrinus* and *Ae. colhuehuapensis* form a clade based on a single synapomorphy: postzygapophyses of posteriormost anterior and middle caudal vertebrae located anteriorly or at the level of the anterior border of the centrum (Ch. 424). As discussed above, this condition is unique to the Argentinean *Aeolosaurus* (Figure 4; Casal et al. 2007) and lacking in *Ae. maximus*, the anterior and middle caudal vertebrae of which have the postzygapophysis located at the level of the anterior half of the centrum.

The phylogenetic analyses presented here show that *Ae. maximus*, although related to *Aeolosaurini*, is not the sister-taxon to the clade formed by the Argentinean species of *Aeolosaurus*. This is not sufficient reason, according to the principles of Phylogenetic Nomenclature (Cantino and De Queiroz 2020), to replace the generic epithet of *Ae. maximus*. Yet, we believe this is the best option (see Systematic Palaeontology below) because the taxic approach in Palaeontology has been widely employed for stratigraphic correlation based on fossils. Such an approach may lead to erroneous assumptions if a given generic epithet is applied to species that do not form a clade but is otherwise interpreted as such. In the particular case of *Aeolosaurus*, the putative presence of that genus in the Bauru Basin, including *Ae. maximus*, has been used to propose a Campanian-Maastrichtian age for its bearing deposits (e.g., Bertin et al. 1999a; Bertini et al. 2000; Santucci and Bertini 2017) because such an age has been established for the *Aeolosaurus* records of Argentina (Powell 1987; Salgado and Coria 1993; Casal et al. 2007).

As defined here (Table 1), apart from *Ae. rionegrinus* and *Ae. colhuehuapensis, Aeolosaurini* includes Brazilian taxa from the Serra da Galga Formation, such as *Uberabatitan* and *Trigonosaurus*, which is almost consensually accepted as of Campanian-Maastrichtian age (see Soares et al. 2021), along with taxa from the more uncertainly dated Adamantina Formation, such as *Gondwanatitan* and *Ae. maximus*. As for the Argentinean taxa, *Overosaurus* was unearthed from the Bajo de la Carpa Formation (Filippi 2015), dated as Santonian (Hugo and Leanza 2001), whereas *Punantitan* and *Bravasaurus* come from the Cíenaga del Rio Huaco Formation, dated as Campaninan-Maastrichtian (Ciccioli et al. 2005; see also Hechenleitner et al. 2020: suppl. info.). Hence, all well-dated *Aeolosaurini* come from Santonian-Maastrichtian (i.e., a span of 20.3 million years) deposits. Therefore, even if *Ae. maximus* is not assigned to *Aeolosaurus*, its affinity to *Aeolosaurini* suggests a Santonian-Maastrichtian age for the Adamantina Formation.

Systematic palaeontology

Titanosauriformes Salgado et al. 1997
Somphospondyli Wilson and Sereno 1998
Titanosauria Bonaparte and Coria 1993
Colossosauria González Riga, Lamanna, Otero, Ortiz David, Kellner and Ibiricu, 2019
Rinconsauria Calvo et al. 2007
Aeolosaurini Franco-Rosas et al. 2004
Arrudatitan gen. nov.

Type-species: *Arrudatitan maximus* (Santucci and Arruda-Campos 2011)

Diagnosis: same as for the only known species.

Etymology: In honour of the late Prof. Antonio de Celso Arruda Campos, fossil collector, populariser of science, and first curator of the MPMA in Monte Alto.

Arrudatitan maximus (Santucci and Arruda-Campos 2011)
1999a *Aeolosaurus* sp. Bertini et al.
1999b *Aeolosaurus* sp. Bertini et al.
2001 *Aeolosaurus* sp. Santucci and Bertini
2011 *Aeolosaurini* indet. Martinelli et al.
2011 *Aeolosaurus maximus* Santucci and Arruda-Campos
2016 *Aeolosaurus maximus* Bandeira et al.
2016 *Aeolosaurus maximus* França et al.
2017 *Aeolosaurus maximus* Carballido et al.
2019 *Aeolosaurus maximus* Silva Junior et al.
2019 *Aeolosaurus maximus* Filippi et al.
2020 '*Aeolosaurus*' *maximus* Hechenleitner et al.

Holotype: MPMA 12–0001-97, two incomplete posterior cervical vertebrae, seven incomplete cervical ribs, a fragmentary anterior trunk centrum, a probable fragment of a middle trunk vertebra, a fragmentary posterior trunk vertebrae, several incomplete diapophysis of trunk vertebrae, 12 incomplete trunk rib, six articulated anterior caudal vertebrae, a mid-caudal centrum, two posterior caudal vertebrae, six anterior, one mid, and one posterior haemal arches, a probable fragmentary scapula, an incomplete right humerus, a probably fragmentary left humerus, a probably incomplete radius, incomplete right femur, left femur, left ischium, and several unidentified fragments.

Remarks: The above set of materials was assigned to the holotype of *Ar. maximus* based on topotypic principles (they were all found associated in the type-locality) and agreeing morphology. In order to further test if the elements could belong to more than one individual, we correlated two continuous variables using a linear regression on R environment (Development Core Team 2013): (1) the estimated total body lengths of four exceptionally well-preserved titanosaurs, *Rapetosaurus krausei* (Rogers and Forster 2001), *Alamosaurus sanjuanensis* (Tykoski and Fiorillo 2017), *Dreadnoughtus schrani* (Lacovara et al. 2014), and *Overosaurus paradasorum* (Coria et al. 2013) and, (2) the absolute size of a left femur and six anterior caudal vertebrae of *Ar. maximus* (the only elements complete enough to be measured), based on measurement of the same element in those titanosaurs. The vertebrae were measured based on the anteroposterior length of their centra and the femur on its proximodistal length. The estimates based on all elements indicate specimens measuring from 19 to 22 metres, within a confidence interval that intuitively suggests that they should belong to a single individual.

Diagnosis: Large-sized titanosaur sauropod with the following autapomorphies – new autapomorphy indicated with an asterisk (*); the others were proposed by Santucci and Arruda-Campos (2011): posterior cervical vertebrae with posterior centrodiapophyseal lamina (pcdl) at least 50% thicker than the postzygodiapophyseal lamina (podl); posterior trunk vertebrae with oblique anterior centropostzygapophyseal lamina (acpol) that bifurcates from the proximal portion of the centropostzygapophyseal lamina (acpol); accessory intrapostzygapophyseal lamina on the posterior trunk vertebrae, creating two small lateral camarae on the spinopostzygapophyseal fossa*; mid-trunk ribs with well-developed anterior and posterior crests with a D-shaped cross section.

Phylogenetic definitions

The hierarchical patterns expressed in the 'Systematic Palaeontology' of *Ar. maximus* as inferred from its position in the phylogeny of Figure 3, invites the proposal of phylogenetic definitions under the renewed aftermath of the PhyloCode (Cantino and De Queiroz 2020) and Phylonyms (De Queiroz et al. 2020). Accordingly, for future systematised use, Table 1 provides definitions for the successively more inclusive clades that include *Ar. maximus: Aeolosaurini, Rinconsauria, Colossosauria, Titanosauria, Somphospondyli*, and *Titanosauriformes*. In the particular case of *Titanosauria*, a polytomy encompassing *Andesaurus, Wintonotitan*, and a large clade including *Colossosauria* and Lognkosauria, hampers the precise identification of the name-bearing clade. This problem was graphically avoided in Figure 3 by pruning *Wintonotitan* from the original consensus tree and indicating the two possible positions it takes in the whole set of MPTs.

Conclusions

A revised diagnosis, with the proposition of a new autapomorphy, strengthens the validity of *Ae. maximus*. A phylogenetic analysis

Table 1. Phylogenetic definitions of clade names used in this study.

Clade name and registration	Phylogenetic definition, reference phylogeny, and composition
Titanosauriformes **L. Salgado, R. Coria and J. Calvo, 1997** [this work], converted clade name **Registration Number**: 438	**Phylogenetic definition**: The least inclusive clade containing *Giraffatitan* (originally *Brachiosaurus*) *brancai* Janensch 1914, and *Saltasaurus loricatus* Bonaparte and Powell 1980. This is a minimum clade definition. **Reference phylogeny**: Phylogenetic hypothesis depicted in Figure 2 of this work. **Composition**: based on the reference phylogeny, *Titanosauriformes* includes Brachiosauridae and *Somphospondylii*.
Somphospondylii **J. Wilson & P.** Sereno 1998 [this work], converted clade name **Registration Number**: 436	**Phylogenetic definition**: The largest clade containing *Saltasaurus loricatus* Bonaparte and Powell 1980, but not *Giraffatitan* (originally *Brachiosaurus*) *brancai* Janensch 1914. This is a maximum clade definition. **Reference phylogeny**: Phylogenetic hypothesis depicted in Figure 2 of this work. **Composition**: based on the reference phylogeny, *Somphospondylii* includes *Titanosauria, Chubutisaurus insignis, Ligabuesaurus lenzai, Wintonotitan wattsi*, and a clade including *Erketu ellisoni, Phuwiangosaurus sirindhornae, Qiaowanglong kangxii*, and *Tastavinsaurus sanzi*.
Titanosauria **J. F. Bonaparte and R. Coria, 1993** [this work], converted clade name **Registration Number**: 435	**Phylogenetic definition**: The least inclusive clade containing *Andesaurus delgadoi* Calvo and Bonaparte 1991, and *Saltasaurus loricatus* Bonaparte and Powell 1980. This is a minimum clade definition. **Reference phylogeny**: Phylogenetic hypothesis depicted in Figure 2 of this work. **Composition**: based on the reference phylogeny, *Titanosauria* includes *Andesaurus delgadoi, Colossosauria¸ Dreadnoughtus schrani, Epachtosaurus sciuttoi* and Lithostrotia.
Colossosauria **González Riga, Lamanna, Otero, Ortiz David, Kellner and Ibiricu, 2019** [this work], converted clade name **Registration number**: 551	**Phylogenetic definition**: The largest clade containing *Mendozarasaurus neguyelap* González Riga, 2003, but not *Saltasaurus loricatus* Bonaparte and Powell 1980 or *Epachthosaurus sciuttoi* Powell 1990. This is a maximum clade definition. **Reference phylogeny**: Phylogenetic hypothesis depicted in Figure 2 of this work. **Composition**: based on the reference phylogeny, *Colossosauria* includes Lognkosauria, *Baurutitan britoi*, and *Rinconsauria*.
Rinconsauria **J. Calvo, B. González-Riga and J. Porfiri, 2007** [this work], converted clade name **Registration Number**: 434.	**Phylogenetic definition**: The least inclusive clade containing *Rinconsaurus caudamirus* Calvo & González-Riga, 2003, and *Muyelensaurus pecheni* Calvo, González-Riga & Porfiri, 2007. This is a minimum clade definition. **Reference phylogeny**: Phylogenetic hypothesis depicted in Figure 2 of this work. **Composition**: based on the reference phylogeny, *Rinconsauria* includes *Aeolosaurini, Muyelensaurus pecheni*, and *Rinconsaurus caudamirus*.
Aeolosaurini **A. Franco-Rosas, L. Salgado and I. Carvalho, 2004** [this work], converted clade name **Registration Number**: 433.	**Phylogenetic definition**: The least inclusive clade containing *Aeolosaurus rionegrinus* Powell 1987, and *Gondwanatitan faustoi* Kellner and Azevedo 1999. This is a minimum clade definition. **Reference phylogeny**: Phylogenetic hypothesis depicted in Figure 2 of this work. **Composition**: based on the reference phylogeny, *Aeolosaurini* includes *Aeolosaurus rionegrinus, Aeolosaurus colhuehuapensis, Arrudatitan maximus, Bravasaurus arrierosorum, Gondwanatitan faustoi, Punantitan coughlini, Overososaurus paradasorum, Trigonosaurus pricei*, and *Uberabatitan ribeiroi*.

stresses that, although related to *Aeolosaurini*, its sister taxon relationship to the Argentinean *Aeolosaurus* is uncertain, and perhaps even the less probable option, given that this position is occupied by *Punatitan* in the majority rule consensus tree. As such, we opted to establish a new genus, *Arrudatitan*, to accommodate *Ae. maximus* as *Ar. maximus*. Otherwise, keeping *Ar. maximus* in *Aeolosaurus* could lead taxic-approach-based macroevolutionary studies to erroneous conclusions. The postzygapophyses placed anteriorly or just at the level of the anterior border of the centrum in posteriormost anterior and middle caudal vertebrae remains as a feature only recovered in the two Argentinean species, *Ae. rionegrinus* and *Ae. colhuehuapensis*, not seen in any other related taxa (e.g., *Arrudatitan, Punatitan, Overosaurus, Trigonosaurus*), that is useful to bolster previous proposals to diagnose the genus *Aeolosaurus* (Casal et al. 2007; Martinelli et al. 2011) and thus to exclude other related *Aeolosaurini* form of the genus.

Acknowledgments

The authors thank Sandra Aparecida Simionato Tavares (MPMA), Diógenes de Almeida Campos (MCT), Rodrigo Machado (MCT), and to the Complexo Cultural e Científico de Peirópolis, Universidade Federal do Triângulo Mineiro staff (CPPLIP) for providing access to their respective collections. This work was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) [grant to J.C.G.S.J, process number 2018/21094-7], Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG) [APQ-02194-15] and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Fundação de Amparo à Pesquisa do Estado de Minas Gerais [APQ-02194-15]; Fundação de Amparo à Pesquisa do Estado de São Paulo [2018/21094-7].

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Appendix 2

New specimens of *Baurutitan britoi* and a taxonomic reassessment of the titanosaur dinosaur fauna (Sauropoda) from the Serra da Galga Formation (Late Cretaceous) of Brazil

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ABSTRACT

The description of new titanosaur specimens unearthed from deposits of the Serra da Galga Formation (Bauru Group, Late Cretaceous) at the BR-262 site, near Peirópolis (Uberaba, Minas Gerais State, Brazil), sheds light on the taxonomy of two taxa previously known from the same area and geological unit: *Baurutitan britoi* and *Trigonosaurus pricei*. A comparative revision indicates that *T. pricei* represents a junior synonym of *Ba. britoi*, and that the BR-262 specimens belong to that latter species. The information provided by the new specimens also revealed that the paratype of *T. pricei* (MCT 1719-R), a caudal vertebral series, actually represents a new taxon, named here as *Caieiria allocaudata* gen. et sp. nov.

Submitted 13 April 2022
Accepted 12 October 2022
Published 15 November 2022

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Academic editor
Emanuel Tschopp

Additional Information and Declarations can be found on page 39

DOI **10.7717/peerj.14333**

Subjects Evolutionary Studies, Paleontology, Taxonomy, Zoology
Keywords Titanosaur, Sauropoda, Late Cretaceous, Brazil, Reassement

INTRODUCTION

Titanosauria currently represents the most species-rich dinosaur clade in the Brazilian Cretaceous (*Bittencourt & Langer, 2011*; *Ghilardi et al., 2016*; *Carvalho et al., 2017*; *Bandeira et al., 2018*), with numerous records coming from the Serra da Galga Formation (Bauru Group, Bauru Basin) in the surroundings of Uberaba, Minas Gerais State (*Candeiro et al., 2006*; *Martinelli & Teixeira, 2015*). Field work carried-out in that area, from the late 1940's to the 1960's, by the Brazilian paleontologist Llewellyn Ivor Price, were especially productive (*Campos & Kellner, 1999*), followed by systemic excavations conducted by the Centro de Pesquisas Paleontológicas Llewellyn Ivor Price (CPPLIP) and Museu dos Dinossauros since the beginning of the 1990s.

How to cite this article Silva Junior JCG, Martinelli AG, Marinho TS, da Silva JI, Langer MC. 2022. New specimens of *Baurutitan britoi* and a taxonomic reassessment of the titanosaur dinosaur fauna (Sauropoda) from the Serra da Galga Formation (Late Cretaceous) of Brazil. **PeerJ 10:e14333 DOI 10.7717/peerj.14333**

Price was responsible for unearthing a remarkable set of titanosaur remains from the quarry known as "Caieira", a site he called "Ponto 1", located less than 2 km from the town of Peirópolis and about 20 km east of Uberaba. The material was later assigned to supposedly individual specimens known as Series A, B, and C (*Powell, 1987*, *2003*; *Bertini, 1993*; *Campos & Kellner, 1999*). Series A (MCT 1487-R) consists of 12 cervical and three anterior trunk vertebrae. It was only partially described by *Powell (1987*, *2003)* and until recently remained unassigned to any particular taxon. *Silva Junior et al. (2019)* suggested its referral to *Uberabatitan ribeiroi*, another species from the Serra da Galga Formation, the holotype of which was unearthed from the "BR-050 Km 153" locality, about 40 km from "Caieira".

Series B (MCT 1488-R) is one of the best-preserved titanosaurs recorded in the area, consisting of five cervical and ten trunk vertebrae, the sacrum, and one ilium. *Powell (1987)* considered a set of 10 caudal vertebrae (MCT 1719-R) as possibly articulated, and assigned it to Series B. This association was questioned by *Campos & Kellner (1999*, p. 22); according to whom: "Price separated the caudal vertebrae of Series B from the pelvis and, as far as known, never regarded them as belonging to the same individual". However, in proposing a new species, *Trigonosaurus pricei*, based on MCT 1488-R, *Campos et al. (2005)* assigned the caudal sequence MCT 1719-R as its paratype. In support of the referral of MCT 1719-R tail vertebrae to *T. pricei*, *Campos et al. (2005*, p. 3) stated that: "their size is compatible with the sacral elements and therefore we cannot preclude the possibility that they belong to the same individual represented by MCT 1488-R, as has been apparently assumed by Price". It is, therefore, controversial whether or not Price associated MCT 1719-R with MCT 1488-R.

Finally, Series C (MCT 1490-R) consists of the last sacral and eighteen caudal vertebrae with 15 articulated chevrons. This specimen represents the holotype of *Baurutitan britoi*, as proposed by *Kellner, Campos & Trotta (2005)*. Owing to the completeness of the sequence and the presence of the first caudal vertebra, *Ba. britoi* has been used in studies focusing on titanosaur tail musculature and anatomy (*e.g.*, *Gallina & Otero, 2009*; *Ibiricu, Lamanna & Lacovara, 2014*).

Another site in which Price had been working was "Point 6" or "Rodovia", located about 1.5 km east of Peirópolis, in the northern slope of BR-262 highway (Fig. 1). Field work during the 1980s and 1990s resulted in the recovery of titanosaur bones, including cervical, trunk, and caudal vertebrae, plus appendicular elements, all in close association. A preliminary report by *Martinelli et al. (2014)* indicated that the trunk vertebrae resemble those of *T. pricei*, whereas the caudal vertebrae resemble those of *Ba. britoi*. Here we provide a full anatomical description of all titanosaur specimens collected at "Rodovia", which are housed at CPPLIP. This led to a taxonomic revision of both *T. pricei* and *Ba. britoi*, as well as to the reassessment of MCT 1719-R.

Geological settings

The "Rodovia" quarry (here termed as BR-262 site) is located about 1.5 km southeast of Price's "Ponto 1" (Fig. 2) as part of a series of outcrops located along the Veadinho Hills (*i.e.*, "Serra do Veadinho"; *Campos & Kellner, 1999*; *Martinelli et al., 2015*). The sandstone

Escavação ao lado da estrada Uberaba-Araxá: região atrai cientistas desde 1945

QUARTA-FEIRA O ESTADO DE S. PAULO 10 DE AGOSTO DE 1988

Cientistas iniciam caça ao dinossauro

WILSON MARIN

UBERABA — Está decretada a caça ao dinossauro no Brasil. O distrito de Peirópolis, a 19 quilômetros de Uberaba, é a base científica de uma expedição que iniciou na semana passada a busca de fósseis escondidos em depósitos geológicos há milhões de anos. O chefe de Paleontologia do Departamento Nacional da Produção Mineral (DNPM), Diógenes de Almeida Campos, há vários anos sonda o local e agora comanda um grupo de pesquisadores que está procurando o primeiro esqueleto completo de um dinossauro brasileiro.

O sítio arqueológico escolhido pela equipe do DNPM faz parte da Formação Bauru, uma área de 104 mil quilômetros quadrados, que abrange metade do Estado de São Paulo (regiões de Presidente Prudente, Araçatuba, Marília, Bauru, Ribeirão Preto e São José do Rio Preto), o Sul de Goiás, parte do Mato Grosso e do Mato Grosso do Sul, Extremo Oeste de Minas Gerais (Triângulo Mineiro) e Noroeste do Paraná.

Essa região, cortada ao meio pela bacia do rio Paraná, é constituída de arenitos e contém rochas formadas no cretáceo superior, período da era mesozóica entre 66,4 milhões e 97,5 milhões de anos atrás, quando os répteis gigantes desapareceram da Terra. Nesse vale desconhecido, os cientistas estão à procura de um rastro que ajude a desvendar os enigmas que cercam o tema no mundo inteiro.

Fósseis ajudam a desvendar passado

Base de Peirópolis: começam as escavações em depósitos geológicos que escondem fósseis há milhões de anos

Pesquisa reconstitui tipo de vida

Escavação ao lado da estrada Uberaba-Araxá: região atrai cientistas desde 1945

Vegetal marinho abre a evolução

Diógenes: estuda evolução

Ossos vão para museu

Figure 1 **(A) "Rodovia" quarry in 2012 (photo by AGM).** (B and C) News article depicting the field works in 1988 (from the archives of Beethoven Teixeira).

Full-size DOI: 10.7717/peerj.14333/fig-1

layers exposed at the site are equivalent to the most fossiliferous levels of "Ponto 1" (*Campos & Kellner, 1999*; *Martinelli et al., 2015*, *2019*; *Soares et al., 2021*) and correspond to the Serra da Galga Formation, Bauru Group, with a Maastrichtian age (*Fernandes & Ribeiro, 2015*; *Martinelli et al., 2019*; *Soares et al., 2020*, *2021*). The detailed geological setting of the Serra da Galga Formation at the Veadinho Hills was described by *Soares et al. (2020*, *2021)*. The holotypes of *T. pricei* and *Ba. britoi*, the referred specimen MCT 1719-R, and the new material here described were unearthed at the base of their respective outcrops from structureless medium- and fine-grained sandstone, which are part of a distributive fluvial system with overall direction of flow to the NNW, developed under the influence of a semiarid climate regime (*Soares et al., 2020*, *2021*).

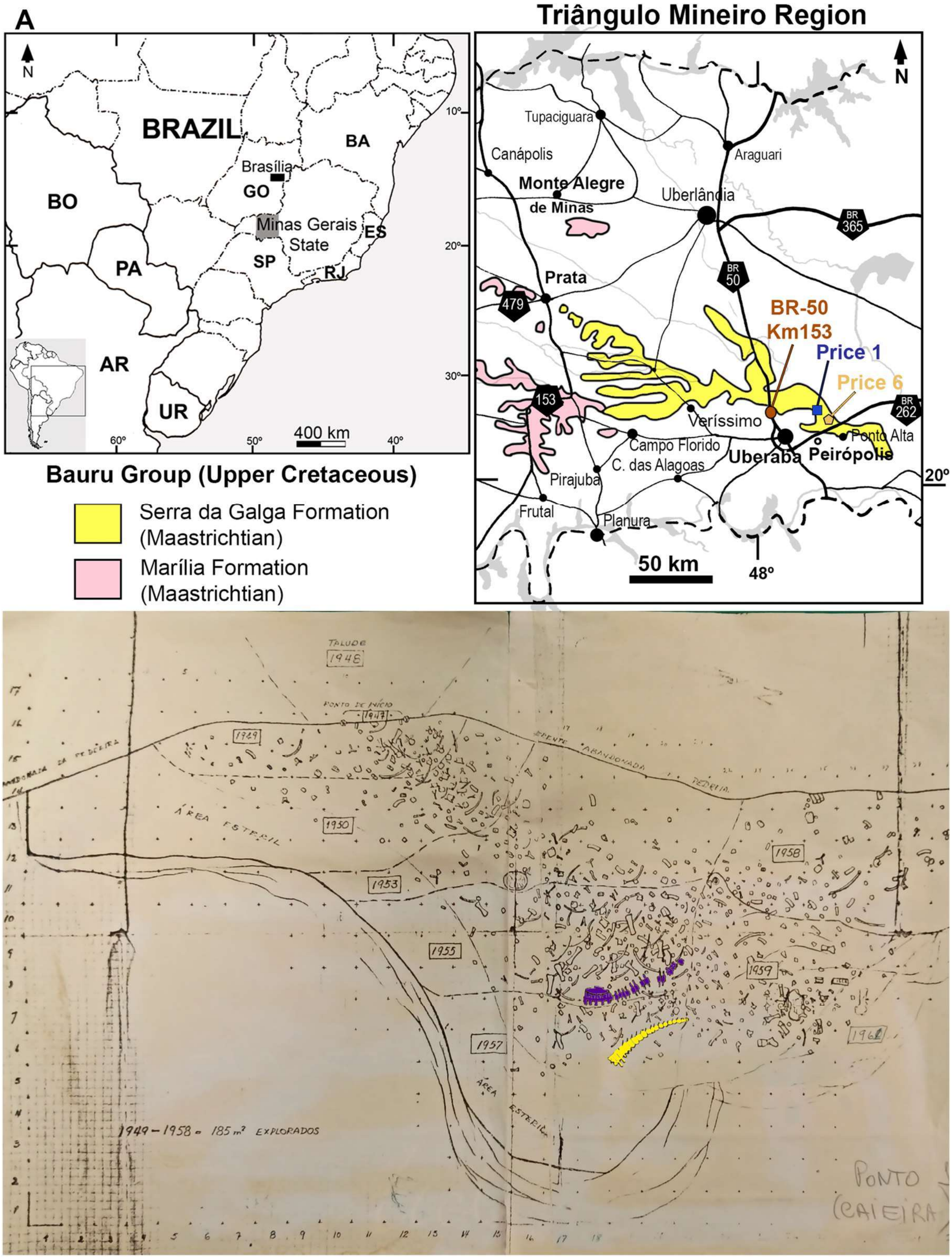

Figure 2 **(A) Map of the Bauru Basin detailing the Uberaba region. (B) Map of "Ponto 1" quarry made by Price, detailing positions of Series B (Purple) and C (Yellow).** It is noteworthy that MCT 1719-R cannot be located on the map (From the archives of CPPLIP).

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MATERIALS AND METHODS

The specimen described here, as well as those used for comparisons, belong to public collections and were examined with the explicit permission of appropriate curators and/or collection managers. We followed all Brazilian regulations for fossil collection.

We employ the nomenclature proposed by *Wilson (1999*, *2012)* and *Wilson et al. (2011)* to describe the laminae and fossae of titanosaur vertebrae. For muscle-related structures we follow *Borsuk-Białynicka (1977)* and *Voegele et al. (2020*, *2021)*.

Following article 6, recommendation 6.1A, from the PhyloCode (*Cantino & De Queiroz, 2020*), all clades established under that code are italicized.

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Phylogenetic analysis

In order to assess the phylogenetic position of the species revised here, we performed a couple of phylogenetic analyses using a modified version of the *Silva Junior et al. (2022)* dataset, which is itself modified from *Hechenleitner et al. (2020)* (Files S2 and S3), with the addition of MCT 1719-R and the BR-262 specimens as new operational taxonomic units (OTUs). For a second iteration, the BR-262 specimens coding was combined with *Baurutitan britoi* and *Trigonosaurus pricei* as a single OTU, with both states kept for polymorphic characters. The analyses were conducted in TNT 1.5 (*Goloboff & Catalano, 2016*) with equal weighting of characters and tree bisection and reconnection (TBR) as the branch swapping algorithm, hold established as 50, 5,000 replicates, and random seeds as '0'. A total of 24 characters were considered as ordered (14, 61, 100, 102, 109, 115, 127, 132, 135, 136, 167, 180, 196, 257, 260, 277, 278, 279, 280, 300, 304, 347, 353, 355). The data scores are detailed in File S1.

DESCRIPTION

Aside from a disproportionally large humerus (CPPLIP-263), all other BR-262 remains are compatible in size so they could represent a single individual. Moreover, we found no *a priori* anatomical differences among the elements indicating the presence of more than one taxon in the quarry. A direct comparison to the *U. ribeiroi* bonebed (*Salgado & De Souza Carvalho, 2008*; *Silva Junior et al., 2019*) can be useful. Even with the presence of individuals of different sizes and ontogenetic stages, the specimens of *U. ribeiroi* share several anatomical traits, such as the laminar patterns of the cervical vertebrae, a low degree of pneumatization in the trunk vertebrae, caudal neural spines that vary from vertically oriented to only slightly inclined anteriorly, and chevrons with dorsally open haemal canals and mediolaterally flattened distal processes. An equivalent congruent anatomy is seen within the BR-262 specimens. The middle cervical vertebrae share a robust postzygodiapophyseal lamina and a low neural spine, whereas the trunk vertebrae are highly pneumatized and bear posteriorly inclined neural spines. Posteriorly inclined neural spines are also present in all caudal vertebrae and the chevrons share dorsally closed haemal canals and robust proximal processes.

Axial skeleton

Cervical vertebrae. Four sauropod cervical vertebrae (CPPLIP-035, CPPLIP-039, CPPLIP-040 and CPPLIP-049) were recovered from BR-262 site. Based on traits such as the width of neural canals and height of neural spines, the four elements were assigned to their respective regions of the neck.

CPPLIP-035 and 039 (middle cervical vertebrae; Fig. 3). These two vertebrae possess a similar anatomy, but have different states of preservation. CPPLIP-039 lacks its anterior half, the distal portion of the neural spine, and all laminae from the left side. CPPLIP-035 lacks the parapophyses and diapophyses, with the postzygapophyses and laminae slightly better preserved on the right side.

The centra are anteroposteriorly elongated and dorsoventrally shallow. CPPLIP-035 has an aEI (average elongation index; *Chure et al., 2010*) of 3.4. The anterior margins of the condyles lie at the same anteroposterior level as those of the prezygapophyses. The cotyles are wider than deep, circular in posterior view, and extend as posteriorly as the interpostzygapophyseal laminae. Ventrolateral ridges form thin laminae that project laterally from the ventral margins of the centra. The ventral surfaces of the centra are slightly concave in both lateral and anterior views. The pneumatic fossae are deep, extending from the posterior portion of the condyles to the dorsal contact between the postzygodiapophyseal and the posterior centrodiapophyseal laminae.

In lateral view, the prezygapophyses extend anterodorsally, with the articular facets positioned immediately dorsal to the condyles, facing medially. They connect posteromedially with the interprezygapophyseal laminae, which extend until the anterior margin of the neural canal. The spinoprezygapophyseal laminae delimit the spinoprezygapophyseal fossa laterally, the spinodiapophyseal fossae dorsally, and reach the distal tip of the neural spines. The neural spines are triangular in lateral view, displaced posteriorly and each possess a 'bulbous', *i.e.*, mediolaterally expanded, apex. They are anteriorly limited by the spinoprezygapophyseal fossae, which are shallow and perforated by small depressions, and laterally delimitated by accessory laminae in CPPLIP-035. The spinopostzygapophyseal laminae are not preserved.

The diapophyses and parapophyses are poorly preserved and lay posterior to the condyles. The diapophyses are connected to the centra *via* the posterior centrodiapophyseal laminae, situated below the spinodiapophyseal fossae, and connected to the prezygapophyses by the prezygodiapophyseal laminae. They reach posteriorly the contact between the postzygodiapophyseal and posterior centrodiapophyseal laminae.

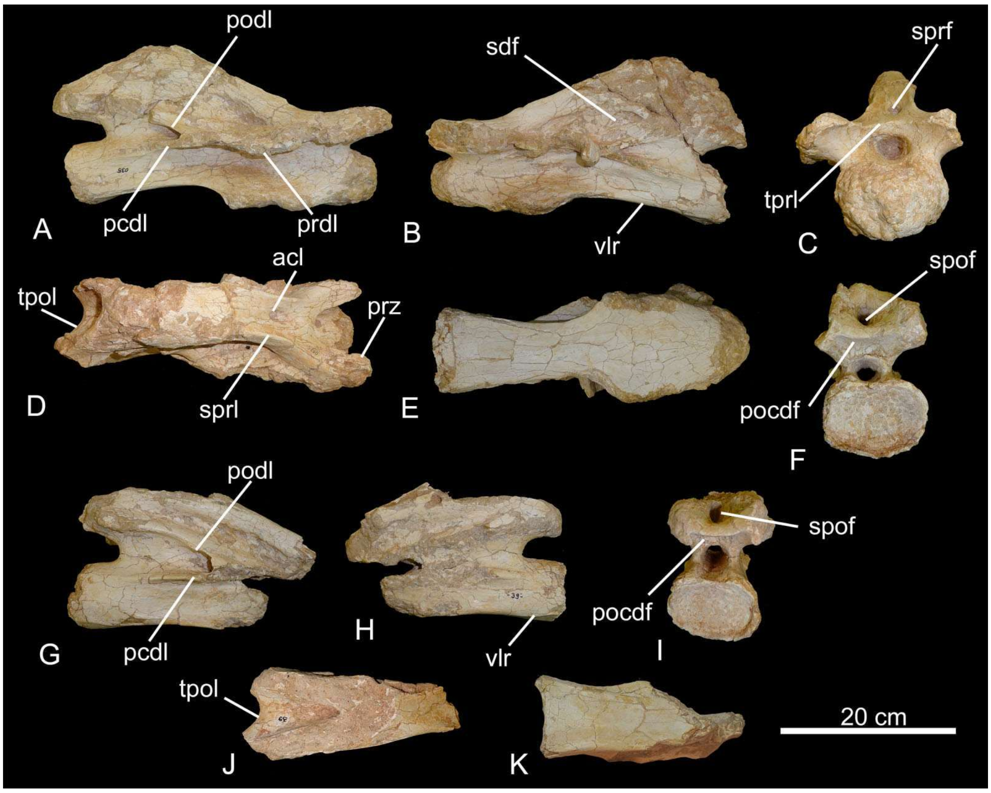

Figure 3 **Middle cervical vertebrae of the BR-262 specimens.** CPPLIP-035 in (A) right lateral; (B) left lateral; (C) anterior; (D) dorsal; (E) ventral and (F) posterior views. CPPLIP-039 in (G) right lateral; (H) left lateral; (I) posterior; (J) dorsal and (K) ventral views. Abbreviations: acl, accessory lamina; pcdl, posterior centrodiapophyseal lamina; pocdf, postzygapophyseal centrodiapophyseal fossa; podl, postzygodiapophyseal lamina; prdl, prezygodiapophyseal lamina; sdf, spinodiapophyseal fossa; spof, spinopostzygapophyseal fossa; sprl, spinoprezygapophyseal lamina; tpol, interpostzygapophyseal lamina; tprl, interprezygapophyseal lamina; vlr, ventrolateral ridge. Full-size DOI: 10.7717/peerj.14333/fig-3

The postzygapophyses are not preserved, but were connected to one another *via* the interpostzygapophyseal laminae, which have almost the same breadth as the neural canal, and separate the spinopostzygapophyseal fossa from the postzygapophyseal centrodiapophyseal fossae. Each of the former fossae is also pierced by a large depression, which is not surrounded by accessory laminae.

CPPLIP-040 and 049 (posterior cervical vertebrae, Fig. 4). These two vertebrae possess similar anatomy and preservation, with only their anteriormost portions and prezygapophyses preserved.

On the anterior portion of the centra that are preserved, shallow pneumatic fossae are visible and the lateral surfaces are slightly concave anteroposteriorly. The prezygapophyses do not overhang the centrum, and extend anterodorsally, with the articular facets facing mediodorsally. The prezygapophyses are connected posteromedially by the interprezygapophyseal lamina, which extends anteriorly in CPPLIP-040. In CPPLIP-049, only small anterior portions of the spinoprezygapophyseal laminae are preserved, whereas larger portions are preserved in CPPLIP-040.

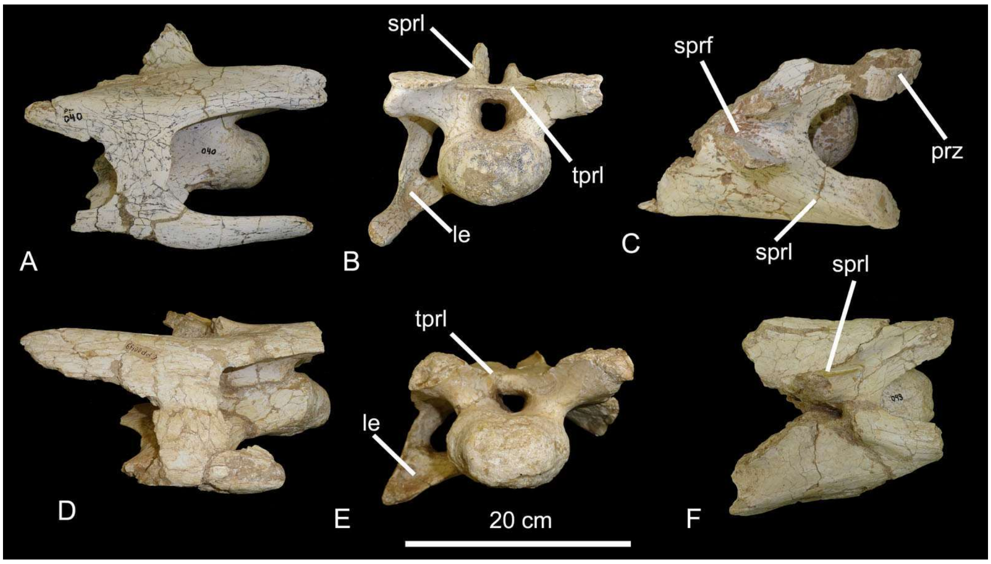

Figure 4 **Posterior cervical vertebrae of the BR-262 specimens.** CPPLIP-040 in (A) right lateral; (B) anterior and (C) dorsal views. CPPLIP-049 in (D) right lateral; (E) anterior and (F) dorsal views. Abbreviations: eprl, epipophyseal-prezygapophyseal laminae; le, longitudinal excavation; prz, prezygapophyses; sprl, spinoprezygapophyseal lamina; tprl, interprezygapophyseal lamina.
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The spinoprezygapophyseal laminae delimit deep spinoprezygapophyseal fossae laterally. Laterally, diapophyses and parapophyses are preserved only on the right side. The diapophyses lay posterior to the condyles and the parapophyses are short and slightly bent downwards, with shallow excavations dorsally.

Cervical ribs. Two partially preserved, isolated cervical ribs (CPPLIP-014 and CPPLIP-109; Fig. 5) were recovered from BR-262. They are gracile elements, mainly corresponding to mediolaterally flattened laminae, each with a shallow dorsal concavity on the proximal portion. CPPLIP-109 has several small foramina on its most anterior portion. The tuberculum of CPPLIP-014 forms a thin lamina, whereas that of CPPLIP-109 is more robust, but both project dorsoventrally. Their capitula are not preserved.

Trunk vertebrae. Eight sauropod trunk elements were recovered from BR-262: seven complete vertebrae (CPPLIP-036, CPPLIP-037, CPPLIP-043, CPPLIP-103, CPPLIP-110, CPPLIP-111 and CPPLIP-458) and a posterior neural spine (CPPLIP-043). The location of the eight elements along the trunk was identified based on the development of the pre- and postzygapophyses and the position of parapophyses and diapophyses.

CPPLIP-036 and 110 (anterior trunk vertebrae, Fig. 6). These two vertebrae possess similar anatomy and preservation, both lacking the distal tips of the neural spines. The condyles are robust, expanding anteroposteriorly for one third the length of the respective centra. CPPLIP-110 possesses a rounded cotyle, whereas that of CPPLIP-036 is dorsoventrally expanded. The lateral and ventral surfaces of the centra are slightly concave anteroposteriorly. The pneumatic fossae are deep, reaching the medial portion of the

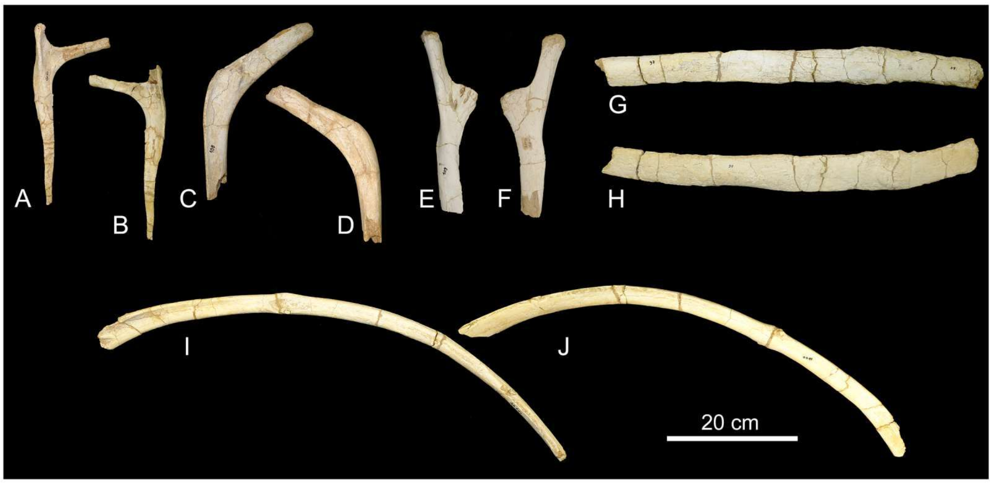

Figure 5 **Cervical and trunk ribs of the BR-262 specimens.** CPPLIP-014 (cervical rib) in (A) lateral and (B) medial views. CPPLIP-108 (trunk rib) in (C) anterior and (D) posterior views. CPPLIP-109 (trunk rib) in (E) lateral and (F) medial views. CPPLIP-097 (trunk rib) in (G) dorsal and (H) ventral views. CPPLIP-044 (trunk rib) in (I) anterior and (J) posterior views.

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centra and extending from the posterior portion of the condyles to the anterior margin of the cotyles.

On the anterior surfaces, the prezygapophyses extend anterodorsally with their articular facets facing mediodorsally. In CPPLIP-110, they surpass the posterior margin of the condyle, whereas those of CPPLIP-036 are positioned immediately above it. The prezygapophyses are posteromedially connected to the anterior margins of the neural spines by the spinoprezygapophyseal lamina. In CPPLIP-036, the left prezygoparapophyseal lamina delimits a small centroprezygapophyseal fossa dorsally.

The spinoprezygapophyseal laminae of CPPLIP-110 extend subparallel to the prespinal lamina and are separated from it by the spinoprezygapophyseal fossae. The spinoprezygapophyseal laminae also delimit shallow prezygapophyseal spinodiapophyseal fossae medially. In CPPLIP-036, the spinoprezygapophyseal lamina is absent, so the prezygapophyseal spinodiapophyseal fossa is bound laterally by the spinodiapophyseal lamina. In both vertebrae, the spinodiapophyseal laminae connect the diapophyses dorsolaterally to the neural spines and delimit the postzygapophyseal spinodiapophyseal fossae anteriorly.

The neural spines are dorsoventrally short, with triangular outlines in anterior/posterior views. Along their posterolateral edges, the spinopostzygapophyseal laminae extend to the postzygapophyses. Those are wide with oval shaped articular facets that face ventrolaterally. The postzygapophyses are connected anteroventrally to the postspinal laminae in CPPLIP-110 and directly to the base of the neural spine in CPPLIP-036; both are limited ventrally by the dorsal portion of the centropostzygapophyseal fossa. The postzygapophyses are connected ventrally to the centra *via* the centropostzygapophyseal laminae. Those laminae limit laterally the centropostzygapophyseal fossa.

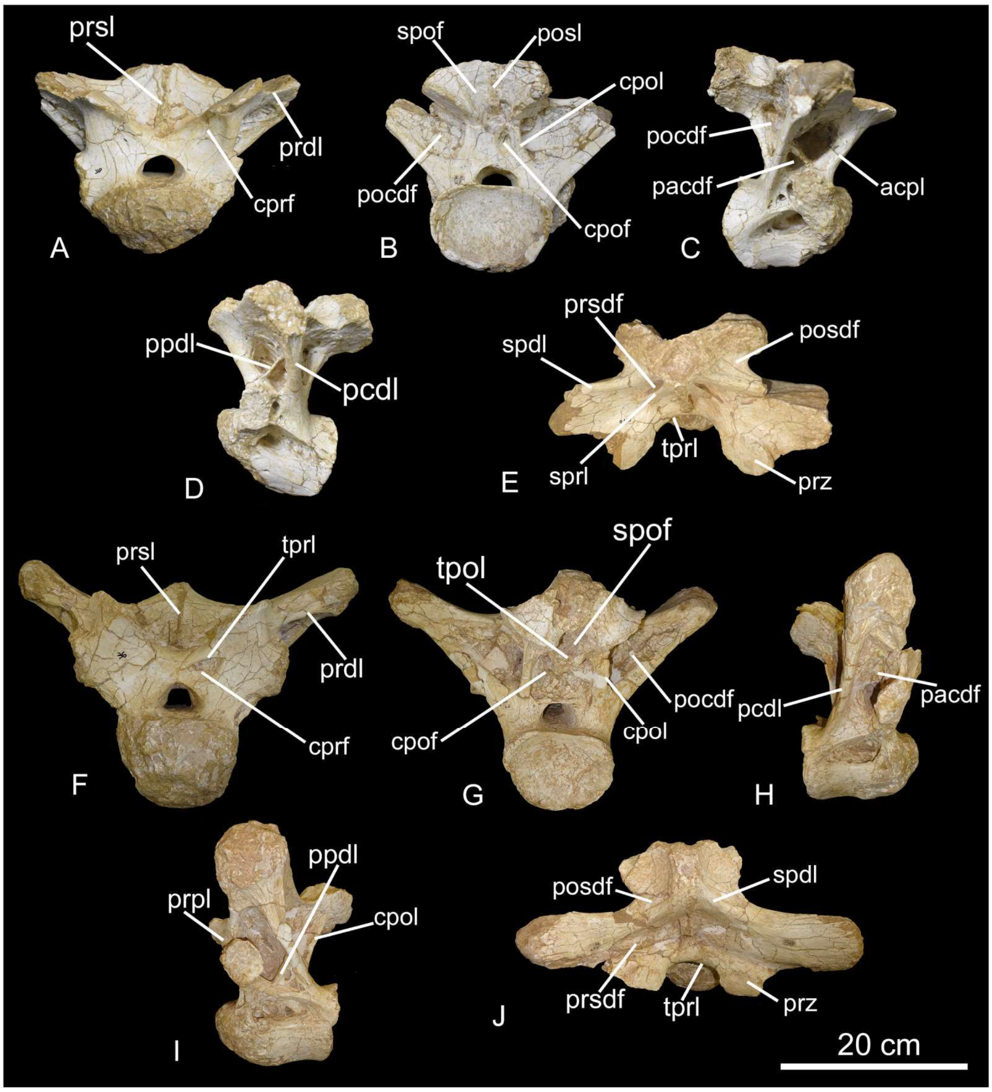

Figure 6 **Anterior trunk vertebrae of the BR-262 specimens.** CPPLIP-110 in (A) anterior; (B) posterior; (C) right lateral; (D) left lateral and (E) dorsal views. CPPLIP-036 in (F) anterior; (G) posterior; (H) right lateral; (I) left lateral and (J) dorsal views. Abbreviations: acpl, anterior centroparapophyseal lamina; cdf, centrodiapophyseal fossa; cpof, centropostzygapophyseal fossa; cpol, centropostzygapophyseal lamina; cprf, centroprezygapophyseal fossa; pacdf, parapophyseal centrodiapophyseal fossa; pcdl, posterior centrodiapophyseal lamina; pocdf, postzygapophyseal centrodiapophyseal fossa; ppdl, paradiapophyseal lamina; posdf, postzygapophyseal spinodiapophyseal fossa; prpl, prezygoparapophyseal lamina; prsdf, prezygapophyseal spinodiapophyseal fossa; prsl, prespinal lamina; prz, prezygapophysis; spdl, spinodiapophyseal lamina; spof, spinopostzygapophyseal fossa; sprl, spinoprezygapophyseal lamina; tpol, interpostzygapophyseal lamina; tprl, interprezygapophyseal lamina.

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In CPPLIP-110, as seen only below the right postzygapophyses, that fossa corresponds to a small perforation, whereas they are larger in CPPLIP-036, with almost half the cotyle height. The centropostzygapophyseal laminae also limit the postzygapophyseal centrodiapophyseal fossae medially.

On the lateral surfaces, the diapophyses are connected medioposteriorly to the neural spines by the spinodiapophyseal laminae. The parapophyses of CPPLIP-110 are placed immediately above the posterior margin of the condyle, whereas those of CPPLIP-036 delimit the parapophyseal centrodiapophyseal fossae anteriorly. In CPPLIP-110, the parapophyseal centrodiapophyseal fossa is deep and divided in anterior and posterior portions by a thin paradiapophyseal lamina. The parapophyseal centrodiapophyseal fossae are bordered posteriorly by the posterior centrodiapophyseal laminae, which lie on the posterodorsal margins of the pneumatic fossae, and anteriorly by the prezygoparapophyseal laminae, which lie on the ventral margins of the parapophyses. The latter possess large rounded articular facets, which border dorsally the parapophyseal centrodiapophyseal fossae.

CPPLIP-036 possesses a slightly different laminar pattern. The parapophyseal centrodiapophyseal fossa is larger, with the posterior portions limited anterodorsally by thin accessory laminae. The centroparapophyseal fossae are limited anterodorsally by short paradiapophyseal laminae, which connect the diapophyses to the parapophyses. The latter also possess large rounded articular facets, but are positioned much more dorsally than those of CPPLIP-110. The parapophyses are also connected to the centrum *via* the anterior centroparapophyseal laminae and posteriorly by the posterior centroparapophyseal laminae.

CPPLIP-103 and CPPLIP-111 (middle trunk vertebrae, Figs. 7 and 8A–8E). CPPLIP-103 lacks the apex of the neural spine and the left parapophysis and diapophysis, whereas CPPLIP-111 preserves only the centrum, the most proximal portion of the neural arch, and the left parapophysis.

The condyles are robust and dorsoventrally expanded. The cotyle of CPPLIP-103 has a rounded shape, whereas that of CPPLIP-111 is dorsoventrally expanded. The lateral surfaces of the centra are more concave anteroposteriorly than those of the most anterior trunk vertebrae, whereas the ventral surfaces are also slightly anteroposteriorly concave in lateral view. The pneumatic fossae are deep and pierced by pneumatic foramina, extending from the posterior portion of the condyles to posterior centrodiapophyseal laminae. These foramina are inserted in concavities and the right pneumatic fossa of CPPLIP-111 is divided in anterior and posterior portions by a thin vertical lamina.

On the anterior surface, the prezygapophyses extend anteriorly, with their articular facets in CPPLIP-103 positioned immediately above the condyle, facing dorsomedially. The prezygapophyses are connected to the anterior margin of the neural spines posteromedially by the spinoprezygapophyseal lamina. On both vertebrae, small centroprezygapophyseal fossae are visible, delimited medially by an accessory vertical lamina and dorsally by the interprezygapophyseal lamina.

On the lateral surfaces, the diapophyses are connected posterodorsally to the postzygapophyses *via* the postzygodiapophyseal laminae. The diapophyses are connected to the centra anteroventrally by the anterior centrodiapophyseal laminae and posteroventrally by the posterior centrodiapophyseal laminae. The anterior centrodiapophyseal laminae posteriorly delimit deep parapophyseal centrodiapophyseal fossae, which are bordered anteriorly by the anterior centroparapophyseal laminae.

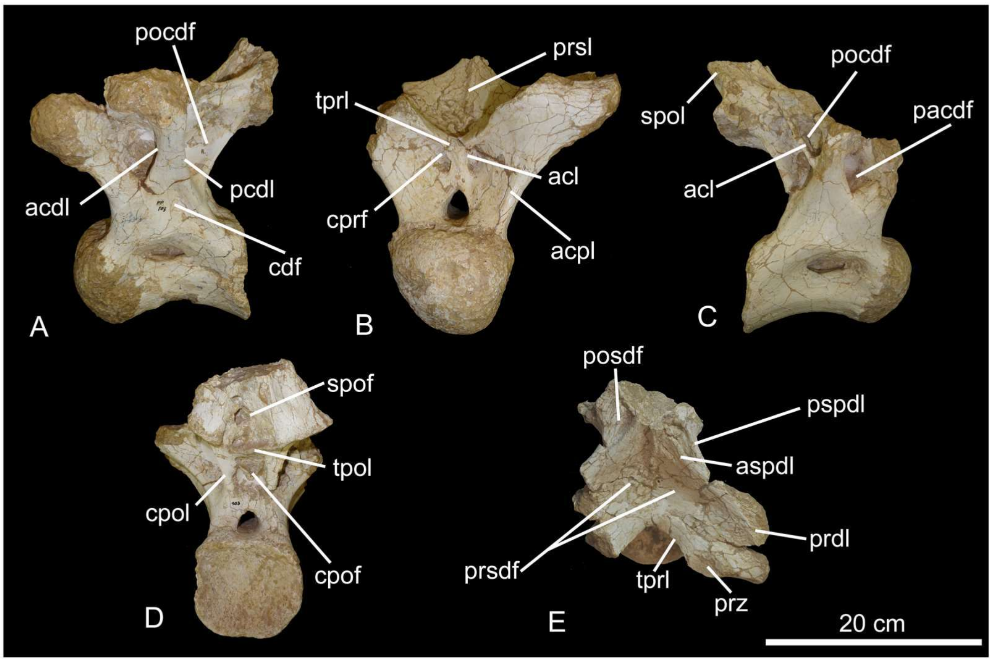

Figure 7 Middle trunk vertebrae of the BR-262 specimens. CPPLIP-103 in (A) left lateral; (B) anterior; (C) right lateral; (D) posterior and (E) dorsal views. Abbreviations: acl, accessory lamina; acpl, anterior centroparapophyseal lamina; aspdl, anterior ramus of the spinodiapophyseal lamina; cdf, centrodiapophyseal fossa; cpof, centropostzygapophyseal fossa; cpol, centropostzygapophyseal lamina; cprf, centroprezygapophyseal fossa; pacdf, parapophyseal centrodiapophyseal fossa; pcdl, posterior centrodiapophyseal lamina; pocdf, postzygapophyseal centrodiapophyseal fossa; posdf, postzygapophyseal spinodiapophyseal fossa; poz, postzygapophyses; prpl, prezygoparapophyseal lamina; prsdf, prezygapophyseal spinodiapophyseal fossa; pspdl, posterior ramus of the spinodiapophyseal lamina; prdl, prezygodiapophyseal lamina, prsl, prespinal lamina; spof, spinopostzygapophyseal fossa; sprl, spinoprezygapophyseal lamina; sprf, spinoprezygapophyseal fossa; tpol, interpostzygapophyseal lamina; tprl, interprezygapophyseal lamina. Full-size DOI: 10.7717/peerj.14333/fig-7

The spinodiapophyseal laminae present on CPPLIP-103 are divided into an anterior and a posterior portion, extending laterally from the apex of the neural spine and delimiting a shallow fossa between them. Both anterior and posterior portions of the spinodiapophyseal laminae connect the neural spines to the diapophyses and are separated by shallow postzygapophyseal spinodiapophyseal fossae. In lateral view, the neural spine of CPPLIP-103 angles posterodorsally, surpassing the cotyle. The spinopostzygapophyseal laminae limit the neural spines posteriorly, and extend to the postzygapophyses, which are wide, oval in shape, and their articular facets face ventrolaterally. The postzygapophyses are limited medially by deep spinopostzygapophyseal fossae and connected ventrally to the centra *via* centropostzygapophyseal laminae. Those laminae delimit deep centropostzygapophyseal fossae laterally and the postzygapophyseal centrodiapophyseal fossae anteriorly.

CPPLIP-037 (middle trunk vertebra, Figs. 8F–8J). This vertebra lacks the apex of the neural spine and both parapophyses and diapophyses. The condyle is short and do not surpass the prezygapophyses anteriorly. The cotyle is subcircular in posterior view and

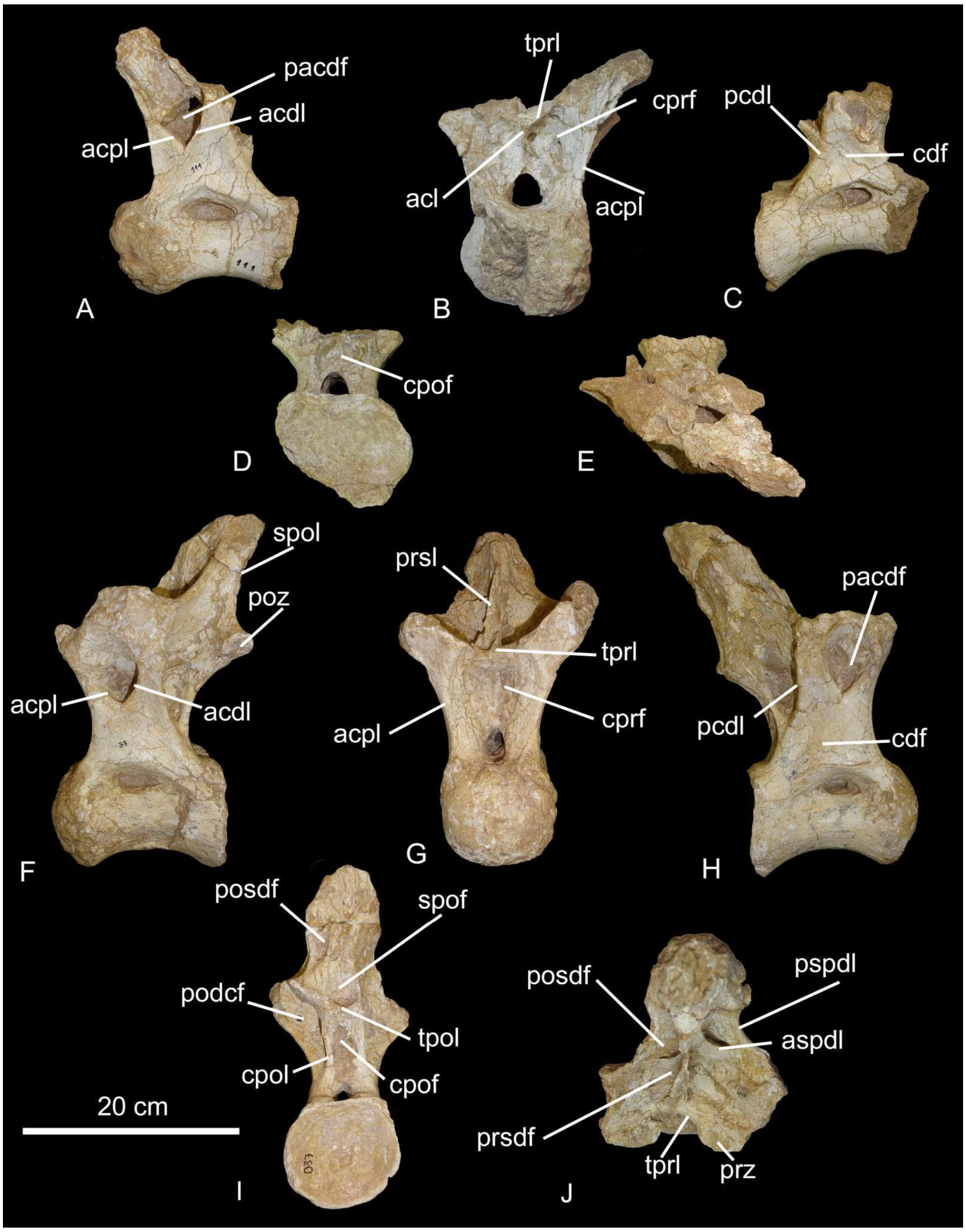

Figure 8 Middle trunk vertebrae of the BR-262 specimens. CPPLIP-111 in (A) left lateral; (B) anterior; (C) right lateral; (D) posterior and (E) dorsal views. CPPLIP-037 in (F) left lateral; (G) anterior; (H) right lateral; (I) posterior and (J) dorsal views. Abbreviations: acl, accessory lamina; acdl, anterior centrodiapophyseal lamina; acpl, anterior centroparapophyseal lamina; aspdl, anterior spinodiapophyseal lamina; cdf, centrodiapophyseal fossa; cpof, centropostzygapophyseal fossa; cpol, centropostzygapophyseal lamina; cprf, centroprezygapophyseal fossa; pacdf, parapophyseal centrodiapophyseal fossa; pcdl, posterior centrodiapophyseal lamina; pcpl, posterior centroparapophyseal lamina; pocdf, postzygapophyseal centrodiapophyseal fossa; pocdfl, postzygapophyseal centrodiapophyseal fossa lamina; posdf, postzygapophyseal spinodiapophyseal fossa; poz, postzygapophyses; prsdf, prezygapophyseal spinodiapophyseal fossa; pspdl, posterior spinodiapophyseal lamina; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; tpol, interpostzygapophyseal lamina; tprl, interprezygapophyseal lamina. Full-size DOI: 10.7717/peerj.14333/fig-8

extends posteriorly beyond the postzygapophyses. The pneumatic fossae are deep and located on the dorsal margin of the centrum. On the anterior surface, the prezygapophyses extend anteromedially. Their facets face dorsomedially and are mediolaterally expanded. The prezygapophyses are connected to the anterior margin of the neural spine *via* the interprezygapophyseal lamina. This lamina delimits dorsally the deep centroprezygapophyseal fossa. In lateral view, the neural spine leans posterodorsally, reaching the posterior margin of the cotyle. The neural spine is limited posteriorly by the spinopostzygapophyseal laminae, which extend subparallel to the posterior ramus of the spinodiapophyseal laminae, creating small postzygapophyseal spinodiapophyseal fossae, only visible on the left side. Both laminae reach the postzygapophyses dorsally.

Only the left postzygapophysis is preserved. It has an oval shape and its facet faces ventrolaterally. It would be connected to the other postzygapophysis by the interpostzygapophyseal lamina, which also delimits ventrally the spinopostzygapophyseal fossa. The postzygapophysis is connected ventrally to the centrum by the centropostzygapophyseal lamina. This lamina limits the centropostzygapophyseal fossa laterally and posteromedially the postzygapophyseal centrodiapophyseal fossa. On the lateral surfaces, the diapophyses are connected ventrolaterally to the centrum by the posterior centrodiapophyseal laminae, which extend to the posterior margin of the centrum. The diapophyses limit dorsally the parapophyseal centrodiapophyseal fossa, which are also limited anteriorly by the anterior centroparapophyseal laminae and posteriorly by the anterior centrodiapophyseal lamina.

CPPLIP-458 (posterior trunk vertebra, Figs. 9A–9E). This vertebra is well-preserved, only lacking the diapophyses and parapophyses. The condyle projects anteriorly and is less convex than those of more anterior vertebrae. The cotyle is transversely expanded and its posterior margin lies below the postzygapophyses. The pneumatic fossae are located on the dorsal margin of the centrum. The left one is deeper than the right, with a small depression on its anterodorsal margin. On the anterior surface, only the right prezygapophysis is preserved; its articular facet faces dorsomedially and is mediolaterally expanded. The interprezygapophyseal laminae limits the centroprezygapophyseal fossae dorsally, which are separated in the center by a vertical accessory lamina. The prezygapophyses are connected ventrally to the centrum by the centroprezygapophyseal lamina, which also limit laterally the centroprezygapophyseal fossae.

The neural spine has a triangular shape in lateral view, with a 'bulbous' apex, *i.e*., it is expanded transversely. It is connected to the diapophyses by the spinodiapophyseal laminae, which are divided dorsally in anterior and posterior rami, both of which limit the spinodiapophyseal lamina fossae. Each anterior spinodiapophyseal lamina—assuming the presence of this lamina instead of a spinoprezygapophyseal lamina, as seen on the anterior elements—extends parallel to the robust prespinal lamina and is separated from it by the spinoprezygapophyseal fossa. The neural spine is connected posteroventrally to the postzygapophyses by spinopostzygapophyseal laminae. These laminae extend parallel to the postspinal lamina and are separated from it by the spinopostzygapophyseal fossae. The postzygapophyses are wide, with rounded facets that face ventrolaterally, and which are connected to one another by a short interpostzygapophyseal lamina—which also

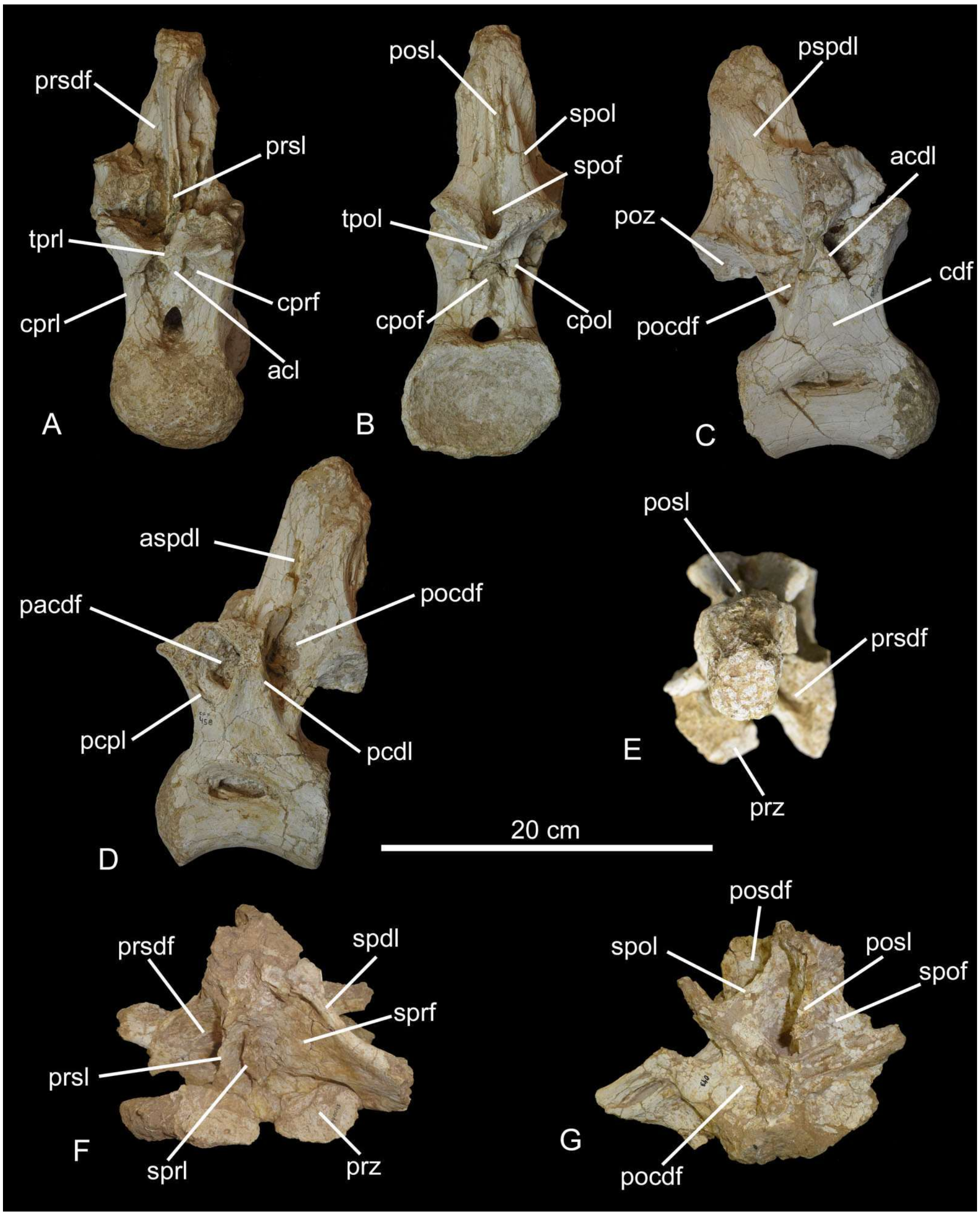

Figure 9 **Posterior trunk vertebrae of the BR-262 specimens.** CPPLIP-458 in (A) anterior; (B) posterior; (C) right lateral; (D) left lateral and (E) dorsal views. CPPLIP-043 in (F) dorsal and (G) posteroventral views. Abbreviations: acl, accessory lamina; acdl, anterior centrodiapophyseal lamina; aspdl, anterior spinodiapophyseal lamina; cdf, centrodiapophyseal fossa; cpof, centropostzygapophyseal fossa; cpol, centropostzygapophyseal lamina; cprf, centroprezygapophyseal fossa; pacdf, parapophyseal centrodiapophyseal fossa; pcdl, posterior centrodiapophyseal lamina; pcpl, posterior centroparapophyseal lamina; pocdf, postzygapophyseal centrodiapophyseal fossa; prsdf, prezygapophyseal spinodiapophyseal fossa; pspdl, posterior spinodiapophyseal lamina; prsl, prespinal lamina; prz, prezygapophysis; spdl, spinodiapophyseal lamina; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; tpol, interpostzygapophyseal lamina; tprl, interprezygapophyseal lamina.

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delimits the centropostzygapophyseal fossa dorsally—and to the centrum by the centropostzygapophyseal laminae. Such laminae also limit the postzygapophyseal centrodiapophyseal fossae posteriorly. On the lateral surface, the posterior centrodiapophyseal lamina extends posteroventrally from the diapophysis to the posterior margin of the neural arch, and limit the postzygapophyseal centrodiapophyseal fossa anteriorly. A small parapophyseal centrodiapophyseal fossa is visible in lateral view, which is limited anteriorly by the posterior centroparapophyseal lamina and posteriorly by the centrodiapophyseal lamina.

CPPLIP-043 (posterior trunk neural arch fragment, Fig. 9). The prezygapophyses are displaced laterally, with wide articular facets facing dorsally, and connected to one another by a short interprezygapophyseal lamina. The spinodiapophyseal laminae extend laterally from the neural spine to the diapophyses. They limit a deep spinoprezygapophyseal fossa anteriorly, which is only present on the right side of the neural arch and limited medially by the spinoprezygapophyseal lamina. The latter also limits laterally a shallow prezygapophyseal spinodiapophyseal fossae anteriorly, which are divided in half by robust prespinal laminae. The neural spine is connected posterolaterally to the postzygapophyses by the spinopostzygapophyseal laminae, which also limit the postzygapophyseal centrodiapophyseal fossae posteriorly. The postzygapophyses are poorly preserved, lacking the articular facets. They limit the spinopostzygapophyseal fossae ventrally, which is separated on two portions by the postspinal lamina. The postzygapophyses also limit mediodorsally the postzygapophyseal centrodiapophyseal fossa.

Trunk ribs. Three isolated sauropod trunk rib fragments (Fig. 5) have been recovered from BR-262 locality: CPLIP-044, 097, and 108. The first two are distal fragments, composed mainly of a thin and flattened, laminar bone. CPPLIP-108 represents a proximal portion, with a shallow longitudinal groove on its anterior face.

Caudal vertebrae. Ten sauropod caudal vertebrae (CPPLIP-045, 046, 047, 061, 091, 093, 094, 095, 096, 102) were recovered from BR-262. Based on comparisons with more complete caudal series such as those of *Baurutitan britoi* (*Kellner, Campos & Trotta, 2005*), *Dreadnoughtus schrani* (*Lacovara et al., 2014*), and *Rapetosaurus krausei* (*Curry Rogers, 2009*), we identified the elements as one anterior, four middle, and five posterior caudal vertebrae.

CPPLIP-102 (anterior caudal vertebra, Fig. 10). The lateral and ventral surfaces of the centrum are slightly anteroposteriorly concave. The centrum has an aEI of 0.7. The condyle is strongly convex, corresponding to almost half of the remaining length of the centrum. The cotyle is shallow and with a sub-oval outline. The neural spine is transversely expanded in its distal half, creating an ellipse-like format in dorsal view, and leans gently posteriorly. It is connected to the prezygapophyses by short spinoprezygapophyseal laminae. Such laminae extend parallel to a robust prespinal lamina and are separated from it by a shallow spinoprezygapophyseal fossa. The prezygapophyses project anteriorly and are connected to the transverse processes *via* the prezygodiapophyseal laminae. The transverse processes are laterally projected, with their most distal portions leaning posteriorly, surpassing the posterior margin of the condyle. On the posterior surface, the postzygapophyses are connected to the neural spine by the spinopostzygapophyseal

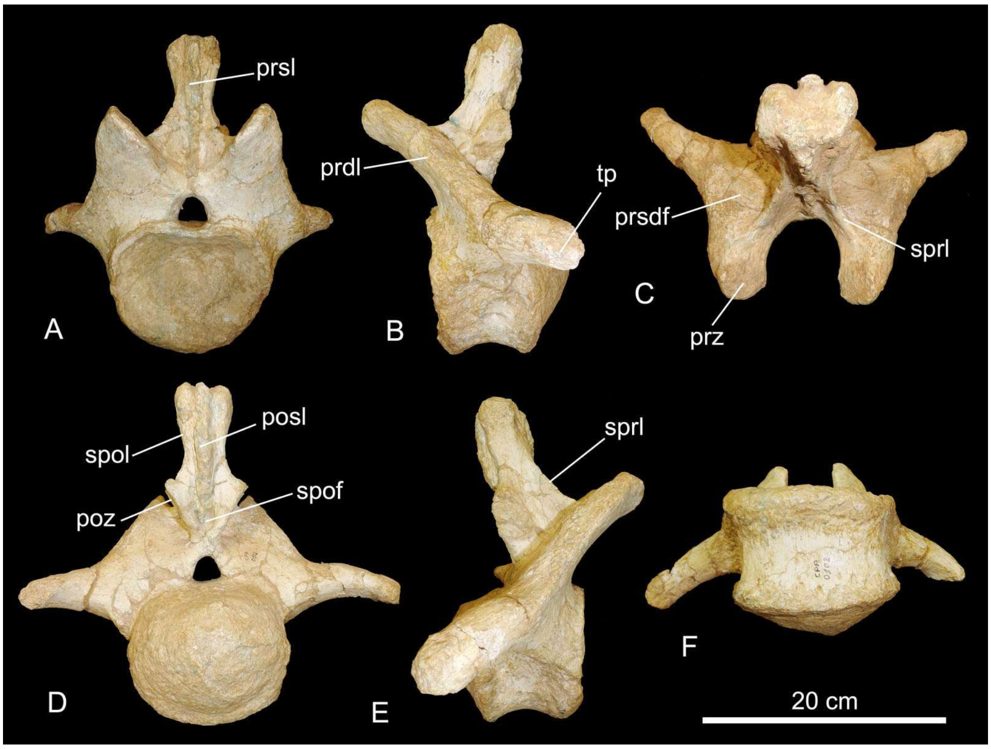

Figure 10 Most anterior caudal vertebra of the BR-262 specimens. CPPLIP-102 in (A) anterior; (B) left lateral; (C) dorsal; (D) posterior; (E) right lateral and (F) ventral views. Abbreviations: posl, postspinal lamina; poz, postzygapophyses; prdl, prezygodiapophyseal lamina; prsdf, prezygapophyseal spinodiapophyseal fossa; prsl, prespinal lamina; prz, prezygapophyses; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; tp, transverse process. Full-size DOI: 10.7717/peerj.14333/fig-10

laminae, which have their most distal portions mediolaterally expanded, creating a 'bulbous' outline in posterior view. Such laminae extend parallel to a robust postspinal lamina, which contacts ventrally a small interpostzygapophyseal lamina. The postzygapophyses are wide, with articular facets that are dorsoventrally expanded and face ventrolaterally.

CPPLIP-046, 047, and 061 (middle caudal vertebrae, Fig. 11). These vertebrae possess a similar anatomy. All structures are preserved in CPPLIP-047 and 061, except the distalmost portion of the neural spines and the most distal portions of the transverse processes, whereas only the proximal portions of the transverse processes are preserved in CPPLIP-046. CPPLIP-046 and 047 have their lateral and ventral surfaces slightly concave anteroposteriorly. CPPLIP-061 has slightly anteroposteriorly concave lateral surfaces, whereas its ventral surface is strongly anteroposteriorly concave, with the condyle dorsoventrally taller than the cotyle. Posterior chevron facets are visible on both CPPLIP-046 and CPPLIP-061, but were not preserved on CPPLIP-047. They project ventrolaterally from the distal portion of the condyles and have triangular shapes in dorsal view.

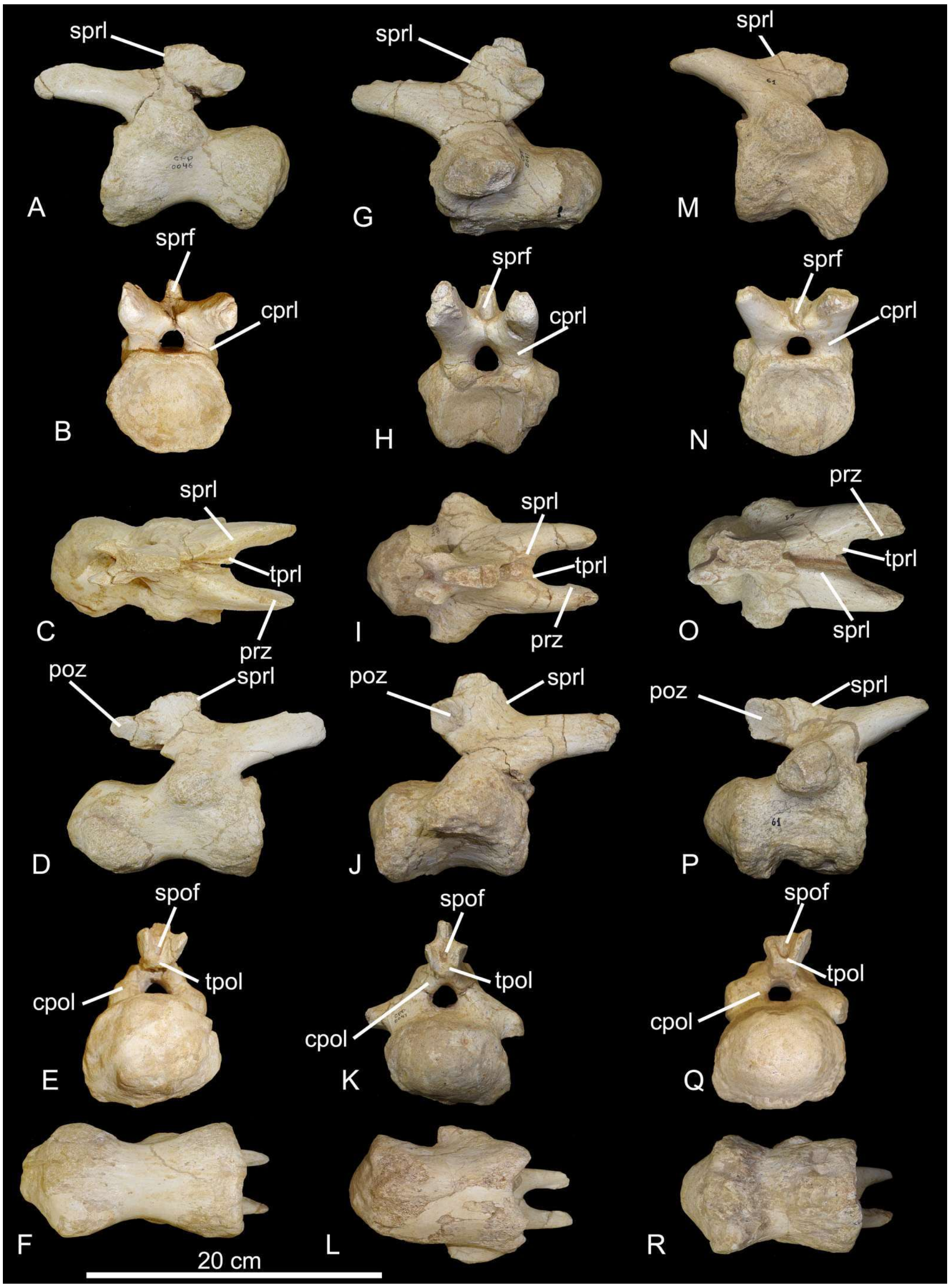

Figure 11 Middle caudal vertebrae of the BR-262 specimens. CPPLIP-046 in (A) left lateral; (D) anterior; (G) dorsal; (J) right lateral; (M) posterior and (P) ventral views. CPPLIP-047 in (B) left lateral; (E) anterior; (H) dorsal; (K) right lateral; (N) posterior and (Q) ventral views. CPPLIP-061 in (C) left lateral; (F) anterior; (I) dorsal; (L) right lateral; (O) posterior and (R) ventral views. Abbreviations: cpol, centropostzygapophyseal lamina; cprl, centroprezygapophyseal lamina; poz, postzygapophyses; prz, prezygapophyses; spol, spinopostzygapophyseal lamina; sprf, spinoprezygapophyseal fossa; sprl, spinoprezygapophyseal lamina; tprl, interprezygapophyseal; tpol, interpostzygapophyseal lamina.

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The centra possess an aEI of 1.2 (CPPLIP-046), 1.1 (CPPLIP-047) and 0.9 (CPPLIP-061). The condyles are robust, projecting posterior to the postzygapophyses. That of CPPLIP-047 is dorsoventrally compressed, whereas those of CPPLIP-046 and 061 have rounded outlines. The cotyle of CPPLIP-046 is transversely compressed, whereas those of CPPLIP-047 and 061 have rounded outlines, all with well-defined margins. The neural spines are connected to the pre- and postzygapophyses *via* the spinoprezygapophyseal and spinopostzygapophyseal laminae, respectively. The transverse processes are poorly preserved and located anteriorly, near the cotyles. That of CPPLIP-047 is more robust, *i.e.*, expanded dorsoventrally and projecting posteriorly.

The prezygapophyses are long (almost half the respective centrum length) and dorsoventrally flattened, their articular facets facing medially. They are connected to their counterparts by thin interprezygapophyseal laminae and to the neural spines by the spinoprezygapophyseal laminae, which extend until the apex of the neural spines, where they limit shallow spinoprezygapophyseal fossae. The prezygapophyses are posteriorly connected to the centra *via* centroprezygapophyseal laminae, which extend until the dorsal margins of the cotyles. The postzygapophyses are short, separated by thin interpostzygapophyseal laminae, with wide articular facets facing laterally. They are connected to the neural spines by the spinopostzygapophyseal laminae, which laterally delimit shallow spinopostzygapophyseal fossae. The postzygapophyses are connected to the centra—ventrally in CPPLIP-047 and anteroventrally in CPPLIP-046 and 061—*via* the centropostzygapophyseal laminae, which extend until the dorsal margin of the neural canals.

CPPLIP-096 (middle caudal vertebra, Fig. 12A). This vertebra lacks the distalmost portions of the neural spine and postzygapophyses. The ventral and lateral surfaces of the centrum are slightly concave anteroposteriorly, the former has four points for the chevron articulation, two below the condyle and two below the cotyle. The centrum has an aEI of 1.7. The condyle is strongly expanded anteroposteriorly, extends beyond the postzygapophyses and has a small slit extending ventrodorsally. The cotyle is shallow, with a rounded outline and well-defined margins. The neural spine is lateromedially narrow and connected to the pre- and postzygapophyses *via* the spinoprezygapophyseal and spinopostzygapophyseal laminae, respectively. Due to its more posterior position along the tail, the vertebra has transverse processes composed only by small lateral projections.

The prezygapophyses are long with the articular facets facing medially. They are connected posteriorly to the neural spine by the spinoprezygapophyseal laminae, which laterally limit shallow spinoprezygapophyseal fossae. The prezygapophyses are connected posteriorly to the centrum by the centroprezygapophyseal laminae, which extend anteriorly towards the cotyle. The postzygapophyses are connected to the neural spine by the spinopostzygapophyseal laminae, which laterally delimit shallow spinopostzygapophyseal fossae. They are connected to the centrum by the centropostzygapophyseal laminae, which extend until the dorsal margin of the neural canal.

CPPLIP-091, CPPLIP-094, and CPPLIP-095 (posterior caudal vertebrae, Fig. 12). These vertebrae are quite similar, with all structures preserved, except for the neural spine and the

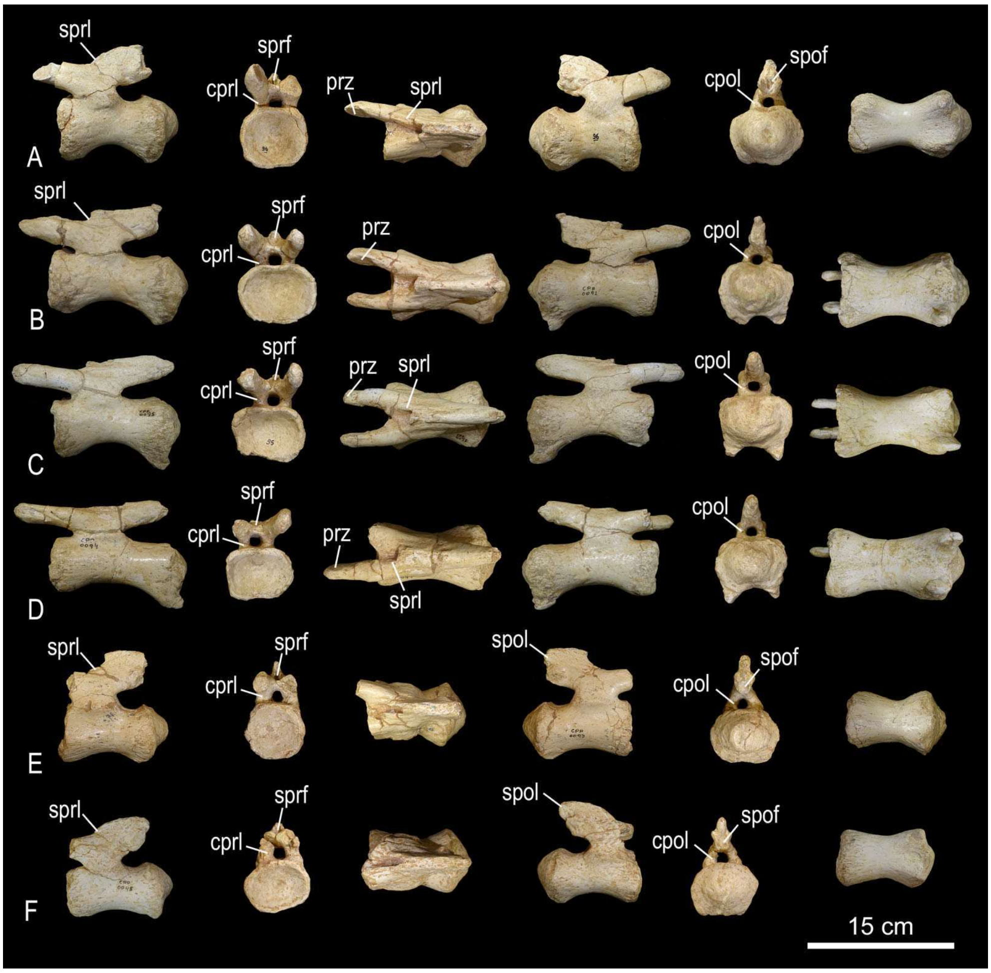

Figure 12 Middle and posterior caudal vertebrae of the BR-262 specimens. (A) CPPLIP-096 in left lateral; anterior; dorsal; right lateral; posterior and ventral views. (B) CPPLIP-091 in left lateral; anterior; dorsal; right lateral; posterior and ventral views. (C) CPPLIP-095 in left lateral; anterior; dorsal; right lateral; posterior and ventral views. (D) CPPLIP-094 in left lateral; anterior; dorsal; right lateral; posterior and ventral views. (E) CPPLIP-093 in left lateral; anterior; dorsal; right lateral; posterior and ventral views. (F) CPPLIP-045 in left lateral; anterior; dorsal; right lateral; posterior and ventral views. Abbreviations: cpol, centropostzygapophyseal lamina; cprl, centroprezygapophyseal lamina; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprf, spinoprezygapophyseal fossa; sprl, spinoprezygapophyseal lamina. Full-size DOI: 10.7717/peerj.14333/fig-12

right prezygapophysis of CPPLIP-094. Their centra have convex lateral and ventral surfaces. CPPLIP-094 and 095 bear two processes below their condyles, which are remains of fused chevrons. The condyles extend posteriorly and are surrounded laterally by concave margins. The cotyles are deep, with rounded outlines and well-defined margins. Only the most proximal portion of the neural spine is preserved in CPPLIP-091. It is laterally narrow and connected to the pre- and postzygapophyses by the spinoprezygapo- and spinopostzygapophyseal laminae, respectively. The centra possess aEIs of 1.8 (CPPLIP-091), 1.9 (CPPLIP-094) and 1.6 (CPPLIP-095).

The prezygapophyses are long, with convex lateral margins. Their articular facets, only preserved on the right side of CPPLIP-091, are anteroposteriorly expanded and face medially. The spinoprezygapophyseal laminae laterally delimit shallow spinoprezygapophyseal fossae. The prezygapophyses are posteroventrally connected to the centra by the centroprezygapophyseal laminae, which extend until the lateral margins of the neural canals. The postzygapophyses are short, lack well preserved articular facets, and are connected posteroventrally to the centra by the centropostzygapophyseal laminae.

CPPLIP-093 and 045 (posterior caudal vertebrae, Fig. 12). These two vertebrae are the only articulated elements found at 'Rodovia' site. Their lateral and ventral surfaces are anteroposteriorly concave. The latter have two points for the articulation of the chevrons, below the condyles. The centrum aEI is 1.5 for CPPLIP-045 and 1.6 for CPPLIP-045. The condyles are slightly projected posteriorly and are surrounded by concave margins. CPPLIP-093 possess a small depression on the center of the condyle, whereas CPPLIP-045 has a small slit projecting dorsoventrally. The cotyles are shallow with rounded outlines. Only the most proximal portion of the neural spines are preserved. They are transversely narrow and connected to the prezygapophyses by the spinoprezygapophyseal laminae, which limit laterally shallow spinoprezygapophyseal fossae. The prezygapophyses are posteroventrally connected to the centra by the centroprezygapophyseal laminae, which extend until the dorsal margin of the neural canals. The postzygapophyses are short, with rounded articular facets that face laterally, and also form the lateral limits of shallow spinopostzygapophyseal fossae. They are anteroventrally connected to the centra by short centropostzygapophyseal laminae, which extend until the dorsal margin of the neural canals.

Chevrons. Nine sauropod chevrons were recovered from the BR-262 site, seven from the anterior and two from the posterior portions of the tail.

CPPLIP-055, 056, 098, 099, 112, and 188 (anterior chevrons, Fig. 13). The haemal canals are dorsally open. The articular facets are composed of single surfaces, without divisions, and those from CPPLIP-055 and 098 are posteriorly inclined. The preserved distal rami of the chevrons represent almost two thirds of their total length. They are transversely flattened and some of the elements possess an anteriorly projected crest (CPPLIP-056 and CPPLIP-059), whereas the others bear a small depression (CPPLIP-055, CPPLIP-098, CPPLIP-099 and CPPLIP-112). On their posterior surfaces all elements possess a posteriorly projected crest.

CPPLIP-057 and 100 (posterior chevrons, Fig. 13). Only their proximal rami are preserved. Each of the elements has a small crest projecting anterolaterally and bear a dorsally open haemal canal. The articular facets are poorly preserved, but are undivided.

Appendicular skeleton

Titanosaur appendicular remains recovered from BR-262 site include: right pectoral girdle (scapula, coracoid) and sternal plate, right and left humeri, possible right metacarpal I, right and left ischia, and possible left metatarsals III and IV.

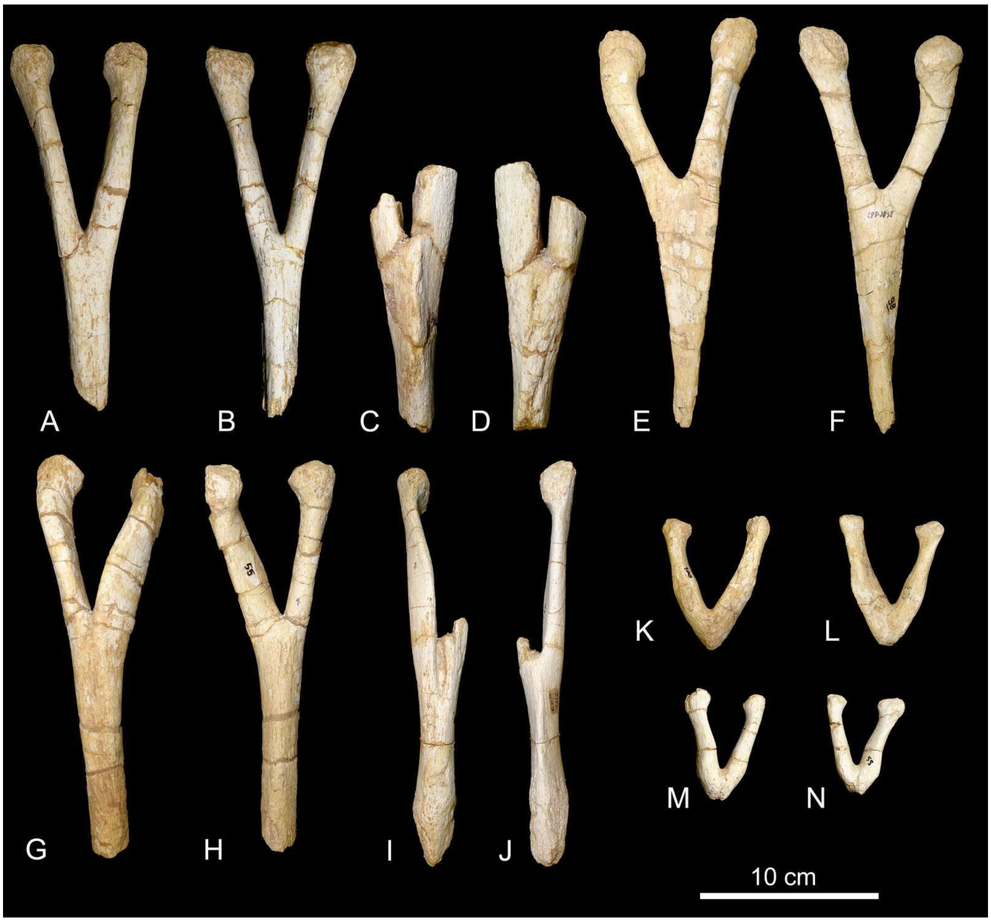

Figure 13 Anterior and posterior chevrons of the BR-262 specimens. CPPLIP-099 (anterior chevron) in (A) anterior and (B) posterior views. CPPLIP-056 (anterior chevron) in (C) anterior and (D) posterior views. CPPLIP-098 (anterior chevron) in (E) anterior and (F) posterior views. CPPLIP-055 (anterior chevron) in (G) anterior and (H) posterior views. CPPLIP-112 (anterior chevron) in (I) anterior and (J) posterior views. CPPLIP-100 (posterior chevron) in (K) anterior and (L) posterior views. CPPLIP-055 (posterior chevron) in (M) anterior and (N) posterior views.

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Pectoral girdle. CPPLIP-038 (right scapula, Fig. 14). The scapula is described here with the long axis of the blade oriented horizontally and its external surface facing laterally. The lateral surface of the acromion plate is slightly anteroposteriorly concave and limited posteriorly by a robust acromial ridge, which represents the insertion of *M. deltoideus clavicularis*. The scapular glenoid is laterally deflected and expands ventrally, with a subtriangular outline when seen in lateral/medial view. Its ventralmost portion acts as the insertion for *M. triceps*. The glenoid medially bounds a small mediolaterally oriented crest, which is the insertion for *M. scapulohumeralis posterior*. The scapular blade extends posteriorly as a flat lamina, with a subrectangular cross section and a subsquared posterior end. It has a small ridge on the lateral surface where *M. serratus superficialis* was inserted. On its dorsal surface, the scapula is limited laterally and medially by a pair of anteroposteriorly extending crests.

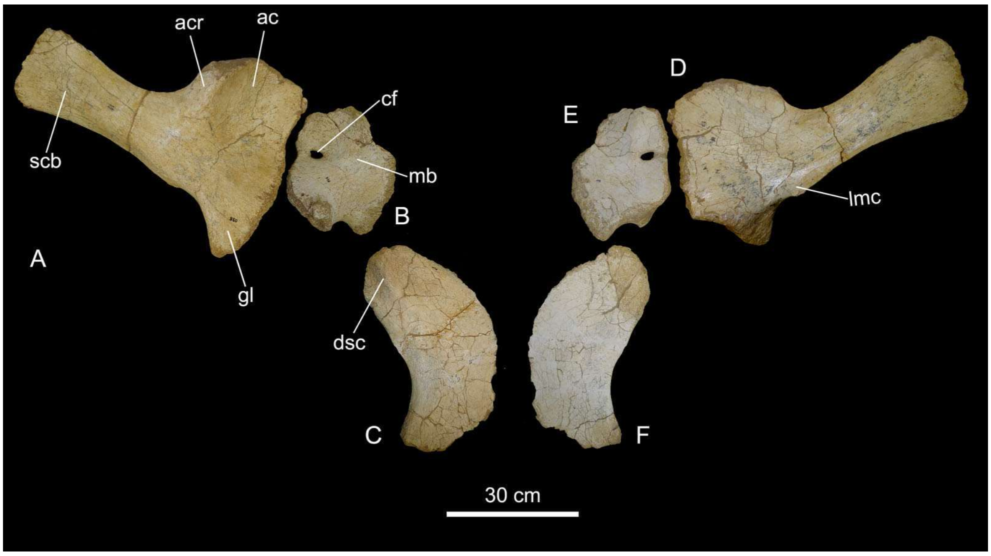

Figure 14 **Scapular girdle and sternal plate of the BR-262 specimens.** CPPLIP-038 (right scapula) in (A) lateral and (D) medial views. CPPLIP-140 (right coracoid) in (B) lateral and (E) medial views. CPPLIP-138 (right sternal plate) in (C) ventral and (F) dorsal views. Abbreviations: ac, acromion; acr, acromial ridge; cf, coracoid foramen; dsc, dorsoventrally projected crest; lmc, lateromedially projected crest; mb, medial bulge; scb, scapular blade. Full-size DOI: 10.7717/peerj.14333/fig-14

CPPLIP-140 (right coracoid, Fig. 14). The bone is poorly preserved and has a rounded outline when seen in medial/lateral view. Although not complete, the dorsal margin of the coracoid is at about the same level as that of the scapula, with a small medial projection. The medial face is slightly concave on its more proximal portion. The glenoid fossa is well preserved and strongly excavated with a mediolaterally-expanded lateral margin. Anterior to that, a marked bulge represents the insertion of *M. coracobrachialis brevis*. The coracoid foramen is located on the posterior portion of the bone, near the scapular articulation. Anteroventral to the coracoid foramen, a convex surface acts as the insertion for the *M. biceps*.

CPPLIP-138 (right sternal plate, Fig. 14). The sternal plate is a flat, laminar bone, expanded lateromedially on both anterior and posterior ends, creating the typical kidney-shape common in titanosaurs (*Salgado, Coria & Calvo, 1997*). The medial margin is convex, whereas the lateral is concave. Its ventral surface bears a small anteroposteriorly oriented crest that bounds a lateral concavity.

Forelimb (Fig. 15). CPPLIP-008 (right humerus) and 007 (proximal portion of left humerus) are likely paired, whereas CPPLIP-263 (proximal portion of left humerus) is a much larger element. Because it cannot be assigned to the same specimen as the other BR-262 remains, it is not described here. The humeri are gracile elements (ECC (eccentricity index) for CPPLIP-008: 1.2), with similar anatomy that are described together, with the differences cited when necessary. The deltopectoral crest projects anteriorly from the lateral margin of the proximal portion of the bone and is slightly medially deflected. It extends distally until half the length of the bone, with its mediolateral thickness almost doubling towards its distal end. Its lateral surface marks the insertion for *M. scapular*

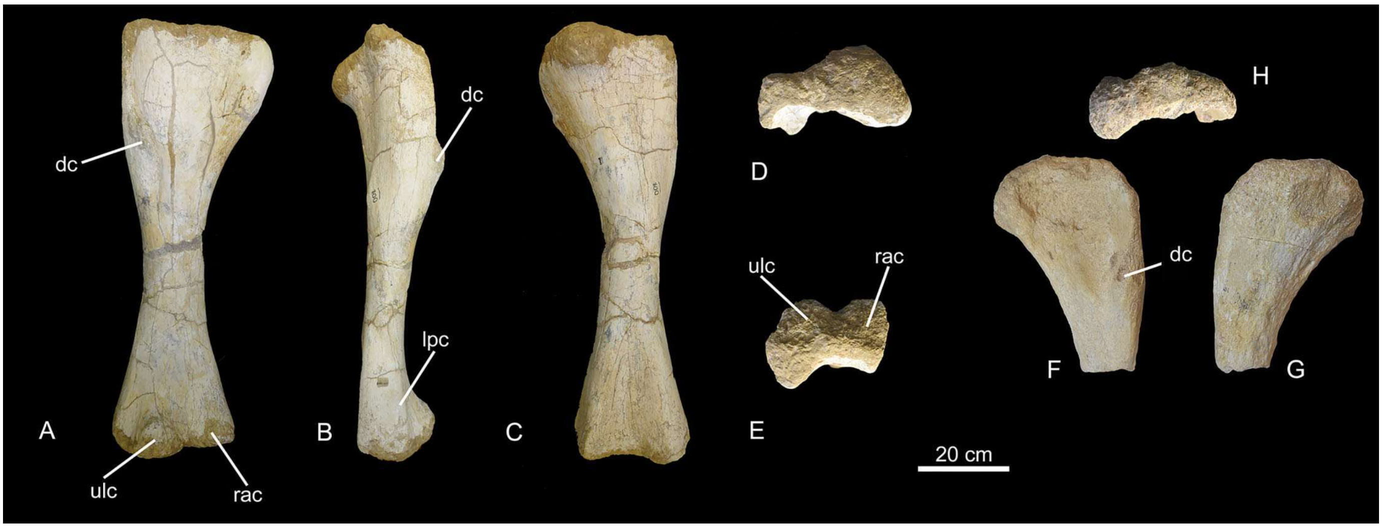

Figure 15 Humeri of the BR-262 specimens. CPPLIP-008 (right humerus) in (A) anterior; (B) lateral; (C) posterior; (D) proximal and (E) distal views. CPPLIP-007 (left humerus) in (F) anterior; (G) posterior and (H) proximal views. Abbreviations: dc, deltapectoral crest; lpc, laterally projected crest; rac, radial condyle; ulc, ulnar condyle. Full-size DOI: 10.7717/peerj.14333/fig-15

deltoid, whereas its proximal margin received *M. pectoralis*. Proximally on the posterior surface of the humeral head, a concavity extends mediolaterally, representing the insertion of *M. coracobrachialis brevis*. The medial border of the head expands anteriorly, forming a bulge, which represents the insertion for *M. supracoracoideus*.

At mid-shaft, the humerus has a sub-circular cross-section, slightly compressed anteroposteriorly. In the distal portion, the radial and ulnar condyles are pronounced. The former is anteriorly expanded, limited both medially and laterally by shallow fossae, creating a triangular outline in anterior view. Its anterior surface is slightly concave, without divisions. The lateral fossa separates the ulnar condyle from a laterally projecting crest. The first represents the insertion of both *Mm. extensor carpi radialis* and *extensor digitalis communis*, whereas the last received *M. extensor carpi ulnaris*. The radial condyle is more robust, expanded both proximodistally and lateromedially. Its anterior surface represents the insertion for *M. corobrachialis longus*. On the posterior surface of the distal third of the bone there is a deep supracondylar fossa bound by both medial and lateral ridges.

CPPLIP-010 (right metacarpal I, Fig. 16). Both proximal and distal surfaces of the bone are slightly convex. The first is heavily anteroposteriorly compressed and bears a small posterior projection, whereas the distal surface is subtriangular in distal view. The anterior (external) surface is flat. Distally, the shaft becomes concave laterally and the posterior surface bears a proximodistally oriented crest along the mid-shaft. On the lateral surface, another crest extends longitudinally along the bone. Medially, there is a small concavity where *M. extensor carpi radialis* inserted.

Pelvic girdle. CPPLIP-069 and 042 (right and left ischia, Fig. 17). CPPLIP-069 is complete and well-preserved, whereas CPPLIP-042 has only the proximal portion preserved. The ischium is a gracile element with a strongly concave posterodorsal margin.

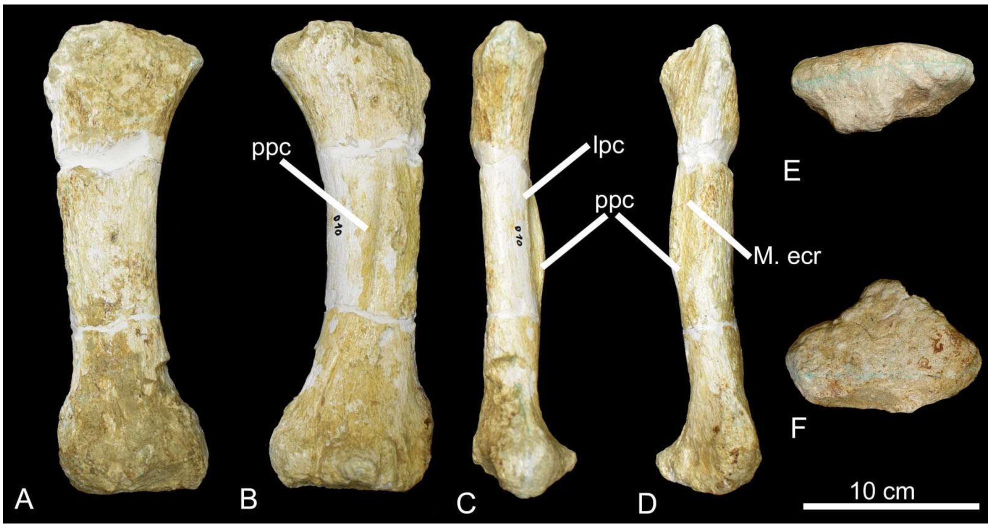

Figure 16 **Metacarpal of the BR-262 specimens.** CPPLIP-010 (Metacarpal I) in (A) anterior (external); (B) posterior (internal); (C) lateral; (D) medial; (E) proximal and (F) distal views. Abbreviations: lpc, laterally projected crest; M. ecr, insertion for the *M. extensor* carpi radialis; ppc, posteriorly projected crest. Full-size DOI: 10.7717/peerj.14333/fig-16

The contribution to the acetabular margin is *via* a thin, concave lamina. Anterodorsally, the bone expands lateromedially, forming a robust iliac peduncle, that has a rectangular outline in lateral/medial views. The lateral surface bears a lateral protuberance, which represents the attachment of the ischial head of *M. flexor tibialis*. On the anteroventral margin, the bone thickens, forming the pubic articulation. Posterior to that, the ventral margin is formed by a thin lamina. The medial surface of the ischium is mainly flat, with its proximal portion slightly bulged medially, close to the pubic articulation.

Hindlimb. CPPLIP-011 and 054 (left metatarsals II and III, Fig. 18). The position of the metatarsals can be inferred based on the shape of the proximal and distal articular surfaces, compared to those of complete pedes, such as those of the “La Invernada” titanosaur (MUCPv-1533) and *Rapetosaurus krausei* (*Riga, Calvo & Porfiri, 2008*; *Curry Rogers, 2009*). The proximal ends are lateromedially expanded. CPPLIP-011 has a robust, lateromedially expanded shaft, whereas CPPLIP-054 is a slender element, both having slightly concave ventral margins. Proximally, small concave surfaces indicate where the metatarsals would articulate with the lateral ones. The distal surfaces are dorsoventrally expanded and have rounded distal outlines.

DISCUSSION

Comparisons with the Serra da Galga Formation titanosaurs

In an attempt to identify the BR-262 (“Rodovia” site) specimens, we compared them with the three titanosaur nominal species known for the Serra da Galga Formation, based on the holotypes of *T. pricei* and *Ba. britoi*, and the holotype and referred specimens of *U. ribeiroi* (*Salgado & De Souza Carvalho, 2008*; *Silva Junior et al., 2019*).

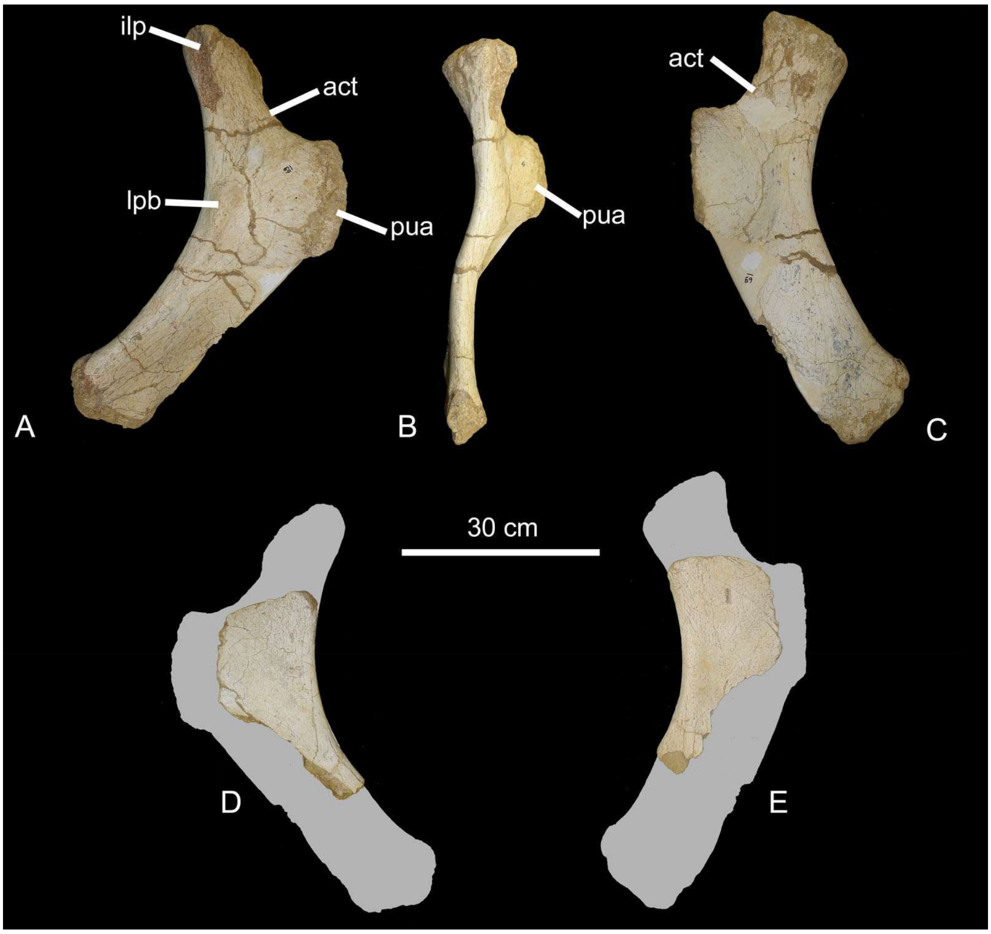

Figure 17 **Ischia of the BR-262 specimens.** CPPLIP-069 (right ischium) in (A) lateral; (B) dorsal and (C) medial views. CPPLIP-042 (left ischium) in (D) lateral and (E) medial views. Abbreviations: act, acetabulum; lpb, lateral protuberance; ilp, iliac peduncle; pua, pubic articulation.
Full-size DOI: 10.7717/peerj.14333/fig-17

Uberabatitan ribeiroi—The BR-262 cervical vertebrae share a number of anatomical features with those of *U. ribeiroi*, such as a ventrolateral crest on the ventral surface of the centra and a neural spine with a bulbous apex (*Silva Junior et al., 2019*, fig. 4A), but lack the low (dorsoventrally compressed) neural spine apex of *U. ribeiroi*. The BR-262 cervical vertebrae also lack the unique laminar pattern of *U. ribeiroi*, in which the epipophyseal-prezygapophyseal lamina is composed of a zygapophyseal and a diapophyseal portion (*Silva Junior et al., 2019*, fig. 4A). Instead, the BR-262 cervical vertebrae (CPPLIP-035, CPPLIP-039; Fig. 3) possess a robust, dorsoventrally expanded postzygodiapophyseal lamina. The anterior BR-262 trunk vertebrae (*i.e.*, CPPLIP-110 and CPPLIP-036) show a higher degree of pneumatization compared to those of *U. ribeiroi*. They have pneumatic fossae perforated by several small foramina (CPPLIP-036; Fig. 6) and a deep centroparapophyseal fossa, with accessory laminae (CPPLIP-110, 036; Fig. 6). Instead, *U. ribeiroi* trunk vertebrae have deep pneumatic fossae and centroparapophyseal fossae, but no foramina or accessory laminae (*Silva Junior et al., 2019*, fig. 7A).

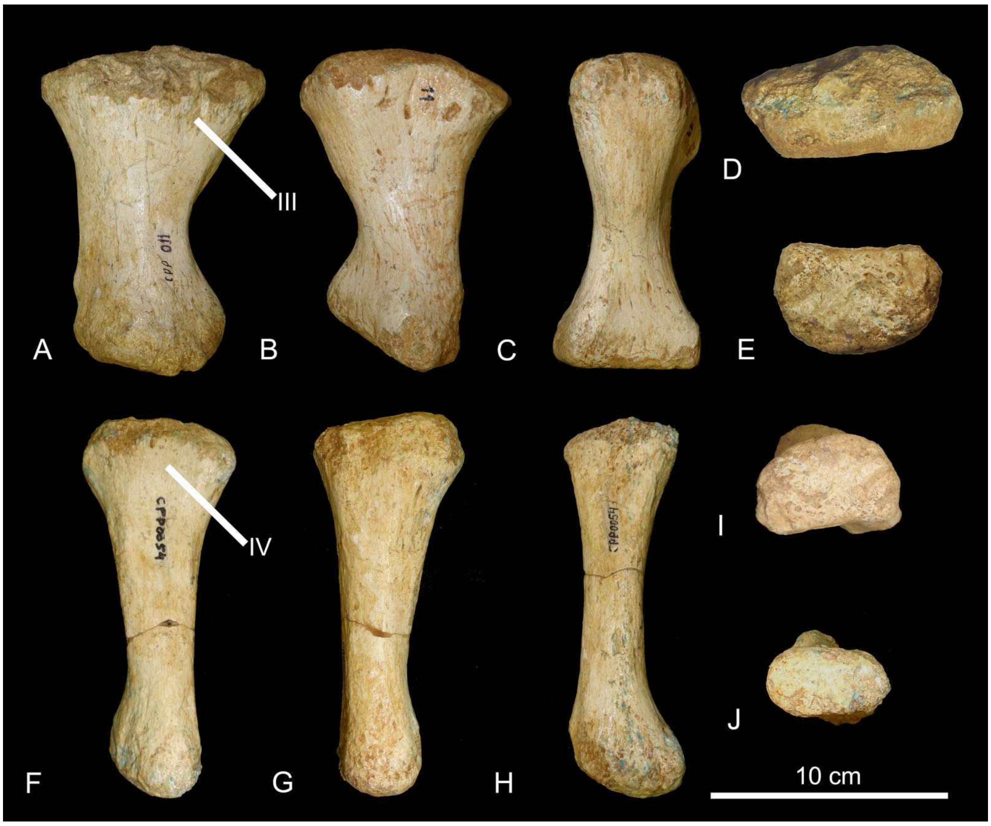

Figure 18 Metatarsals of the BR-262 specimens. CPPLIP-011 (left metatarsal II) in (A) medial; (B) lateral; (C) plantar; (D) proximal and (E) distal views. CPPLIP-054 (left metatarsal III) in (F) medial; (G) lateral and (H) plantar; (I) proximal and (J) distal views. Abbreviations: III, articulation with metatarsal III; IV, articulation with metatarsal IV. Full-size DOI: 10.7717/peerj.14333/fig-18

The BR-262 caudal vertebrae (*e.g*., CPPLIP-102; Fig. 10) also differ from those of *U. ribeiroi* (*Silva Junior et al., 2019*, fig. 9) by lacking strongly excavated lateral surfaces of the centrum and the tubercle on the proximal portion of the transverse processes. The preserved neural spines of the BR-262 tail vertebrae are strongly inclined posteriorly, also differing from those of *U. ribeiroi*, the neural spines of which vary from vertically oriented to only slightly inclined anteriorly (*Silva Junior et al., 2019*, figs. 9–12).

Both anterior and posterior chevrons of the BR-262 specimens differ from those of *U. ribeiroi*. Its anterior chevrons possess more robust proximal rami (Fig. 13), whereas those of *U. ribeiroi* are mediolaterally flattened (*Silva Junior et al., 2019*, fig. 14A–14D). The distal rami of *U. ribeiroi* chevrons are also strongly mediolaterally flattened, forming a robust anteriorly projected crest. Only the proximal rami of the posterior chevrons are preserved in the BR-262 specimens (Fig. 13). Those share with *U. ribeiroi* the presence of a laterally projected crest, but this crest is more robust in the latter taxon (*Silva Junior et al., 2019*, fig. 14E). In addition, *U. ribeiroi* possesses haemal canals with a wider dorsal opening than those of the BR-262 specimens.

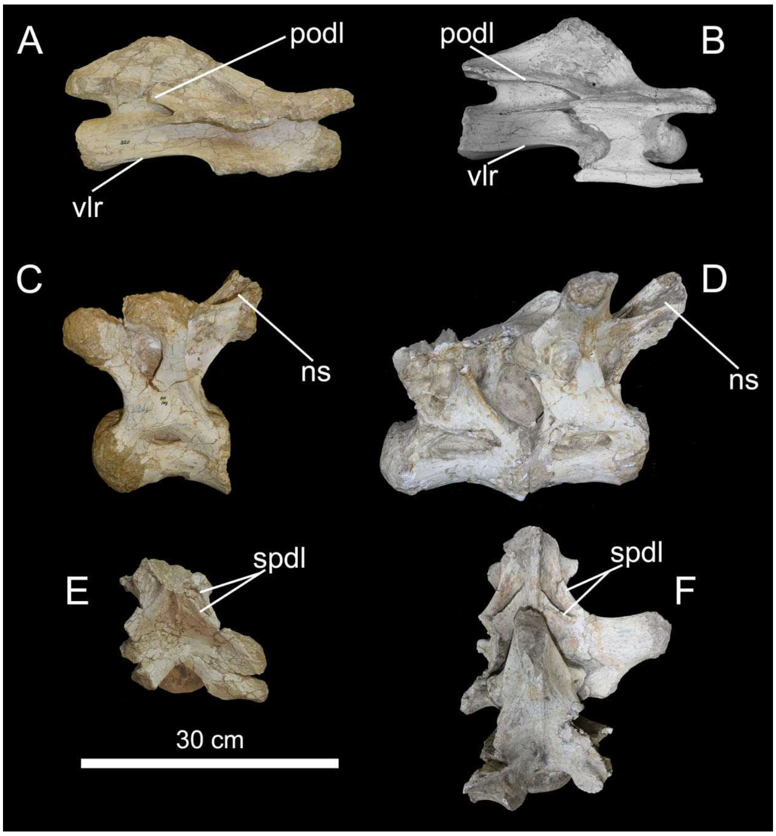

Figure 19 Axial elements of MCT 1488-R and BR-262. (A) Right lateral view of CPPLIP-035. (B) Possible 9th cervical vertebrae of *T. pricei*, left (reversed) lateral view. CPPLIP-103 in (C) left lateral, and (E) dorsal, views. 4th and 5th trunk vertebrae of *T. pricei* in (D) left lateral, and (F) dorsal, views. Abbreviations: ns, neural spine; podl, postzygodiapophyseal lamina; vlr, ventrolateral ridge; spdl, anterior and posterior spinodiapophyseal laminae. Full-size DOI: 10.7717/peerj.14333/fig-19

Trigonosaurus pricei (MCT 1488-R)—The BR-262 cervical vertebrae share similarities with those from the middle-posterior part of the *T. pricei* neck, including a ventrolateral crest and a low neural spine with a bulbous apex, although this apex is located more posteriorly in relation to the centrum than in *T. pricei*. In addition, the mid-posterior cervical vertebrae of *T. pricei* have dorsoventrally expanded postzygodiapophyseal laminae.

The trunk vertebrae from BR-262 are quite similar to those of *T. pricei*, so that they can be directly compared to the different trunk regions of the latter. CPPLIP-036 and 110 are compatible with the most anterior trunk vertebrae of *T. pricei*. They share large pneumatic fossae—with almost half of the centrum height—and deep postzygapophyseal spinodiapophyseal fossae that extend anteroventrally and are delimited by robust spinodiapophyseal laminae (Fig. 6). CPPLIP-103 and 111 are similar to the middle trunk vertebrae of *T. pricei*. They share neural spines with a strong posterior inclination, so they surpass the margin of the cotyle (CPPLIP-103; Fig. 19), a condition that was tentatively proposed as autapomorphic for *T. pricei* (Campos et al., 2005, fig. 15). Further, their

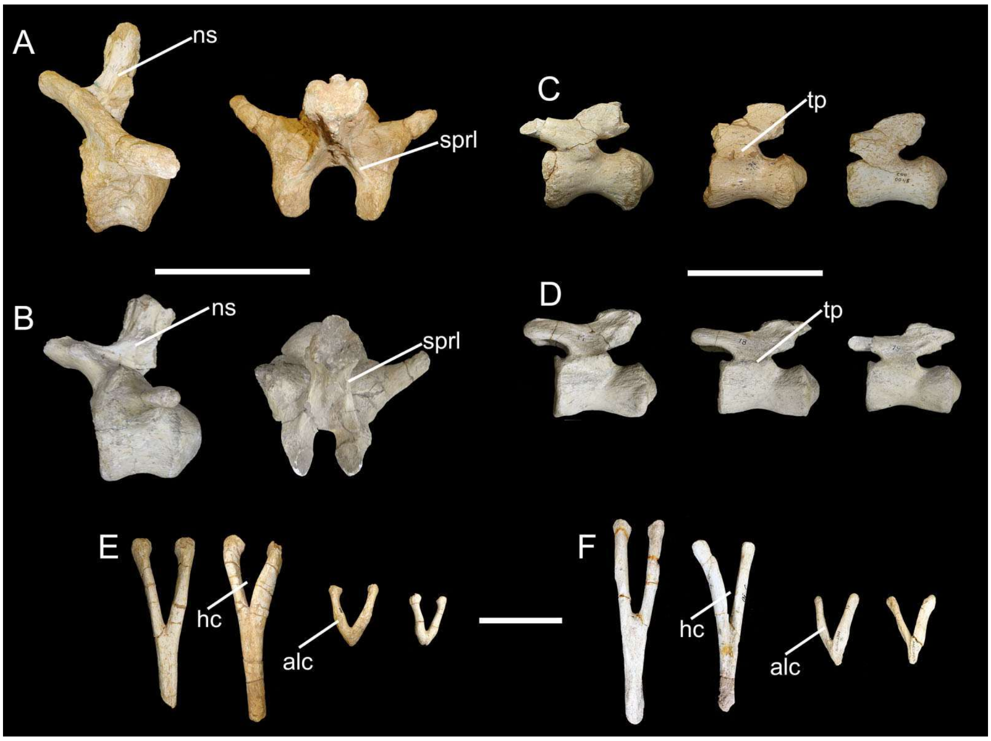

Figure 20 **Caudal elements of *Baurutitan britoi* and BR-262 specimens.** (A) Anterior caudal vertebra of BR-262 specimens in left lateral and dorsal views. (B) Anterior caudal vertebra of *B. britoi* in left lateral and dorsal views. (C) Mid-posterior caudal vertebrae of BR-262 specimens in left lateral views. (D) Mid-posterior caudal vertebrae of *B. britoi* in left lateral views. (E) Chevrons of BR-262 specimens in anterior view. (F) Chevrons of *B. britoi* in anterior view. Abbreviations: alc, anterolateral projecting crest; hc, haemal canal; ns, neural spines; sprl, spinoprezygapophyseal lamina; tp, transverse process. Scale for anterior vertebrae: 20 cm; scale for mid-posterior vertebrae: 15 cm; scale for chevrons: 10 cm.

Full-size DOI: 10.7717/peerj.14333/fig-20

spinodiapophyseal laminae are divided into anterior and posterior portions (CPPLIP-103, Fig. 19; *Campos et al., 2005*, fig. 18). As for CPPLIP-037 and 458, they are comparable to the most posterior trunk vertebrae of *T. pricei*, sharing pneumatic fossae restricted to the dorsal portion of the centra, ventrally delimiting large centrodiapophyseal fossae (Figs. 8 and 9; *Campos et al., 2005*, fig. 19). On the other hand, the BR-262 specimens lack the postzygodiapophyseal lamina that laterally connects the postzygapophyses with the diapophyses, which was tentatively proposed as an autapomorphy for *T. pricei* (*Campos et al., 2005*).

Baurutitan britoi (MCT 1490-R)—The BR-262 caudal series is quite similar to that of MCT 1490-R. Although the exact position of CPPLIP-102 cannot be defined, it is similar to the most anterior elements of *Ba. britoi*. The 2nd and 3rd caudal vertebrae of *Ba. britoi* possess aEIs of 0.6 and 0.7, respectively, similar to the 0.7 value of CPPLIP-102. They also share neural spines that are posteriorly inclined and slightly curved forwards (Fig. 20; *Kellner, Campos & Trotta, 2005*, fig. 16), though the neural spines of *Ba. britoi* are displaced more posteriorly in the centra. The prezygapophyses of CPPLIP-102 are also located more laterally than those of *Ba. britoi*.

CPPLIP-046, 047, and 061 are similar to the middle caudal vertebrae of *Ba. britoi*, though their positions cannot be precisely defined. They share non deeply excavated centra and posteriorly inclined neural spines, characters also present in more posterior caudal vertebrae. CPPLIP-093 and 045 seem to be from a more posterior portion of the tail than that preserved in *Ba. britoi* (Fig. 20; *Kellner, Campos & Trotta, 2005*, fig. 22), so that they are not directly comparable.

The chevrons of the BR-262 specimens (Fig. 13) are also similar to those of *Ba. britoi*. They share dorsally open haemal canals in both anterior and posterior elements. *Baurutitan britoi* also shows proximal rami with laterally projected crests, although this feature is asymmetrically distributed, present in just one of the sides of one of the most posterior chevrons (*Kellner, Campos & Trotta, 2005*, figs. 26 and 27). A similar laterally projected crest is visible on both right sides of CPPLIP-100 and 055 (Fig. 20), although less prominent on the latter specimens.

In sum, although the BR-262 titanosaur specimens can be differentiated from those referred to *U. ribeiroi*, only very minor differences exist compared to the holotypes of *T. pricei* and *Ba. britoi*. This is further evidenced by the presence of either autapomorphies or unique sets of features of both *Ba. britoi* and *T. pricei*, which are also present in the BR-262 material, as highlighted below.

Campos et al. (2005) identified a set of traits in the cervical vertebrae of MCT 1488-R as autapomorphies of *T. pricei*, including elongated mid-cervical vertebrae, with low neural spines and concave ventral margins. The latter two traits are also seen in the preserved BR-262 cervical elements (Fig. 3). The 9th cervical vertebra of *T. pricei* (*Campos et al., 2005*, figs. 8–10) and a slightly more anterior cervical vertebra from BR-262 (CPPLIP-035) have both aEIs of 3.4. Here, we also identified a new feature shared uniquely by MCT 1488-R and the BR-262 cervical vertebrae (Fig. 19), namely a robust (*i.e.*, dorsoventrally expanded) postzygodiapophyseal lamina. This differs from the condition present in other titanosaurs, in which both the posterior centrodiapophyseal and the postzygodiapophyseal laminae have similar proportions, as seen in *Futalognkosaurus dukei* (*Calvo, González Riga & Porfiri, 2007*; fig. 2), *Rinconsaurus caudamirus* (*Calvo & González Riga, 2003*; Plate 2), and *Rapetosaurus krausei* (*Curry Rogers, 2009*; fig. 9).

Campos et al. (2005) also proposed autapomorphic features for the trunk vertebrae of *T. pricei* (MCT 1488-R): *i.e.*, elongated mid-trunk vertebrae, with strongly posteriorly inclined neural spines, and trunk vertebrae 9–10 with incipient postzygodiapophyseal laminae. The anteroposterior length (excluding the condylar ball) to cotyle height ratio in the mid-trunk vertebrae of MCT 1488-R is ~1.3, whereas a lower value (~1.0) is seen in BR-262 specimens. Regarding the neural spines, those of MCT 1488-R form an angle of ~55° to the centrum. Strongly posteriorly inclined neural spines are also seen in BR-262 trunk vertebrae (CPPLIP-103; Fig. 19), but poor preservation precludes a precise measurement of the angle. The vertebrae identified as most posterior of the BR-262 specimens lack such incipient postzygodiapophyseal laminae.

Kellner, Campos & Trotta (2005) identified a couple of features in the holotype of *Ba. britoi* (MCT 1490-R) as potential autapomorphies of that species: *i.e.*, strongly pointed and laterally directed process intercepting the spinoprezygapophyseal lamina on the first caudal vertebra and anterolaterally directed spinoprezygapophyseal laminae. A first caudal vertebra cannot be unambiguously identified in the BR-262 specimens, hampering the assessment of the former character, whereas the spinoprezygapophyseal laminae (CPPLIP-102; Fig. 20) are more laterally located in their neural spines than in those of MCT 1490-R.

Reassessment of *Baurutitan britoi* and *Trigonosaurus pricei*

The taxonomic status of *T. pricei* and *Ba. britoi* has to be analyzed based on some basic premises: 1—Although both species possess one overlapping element, the last sacral vertebra, it disallows any meaningful comparison; 2—The holotypes of both species are anatomically compatible with BR-262 specimens; 3—The BR-262 caudal vertebrae differ from those of MCT 1719-R (paratype of *T. pricei*; see below). Further, there is no *prima facie* evidence that the caudal series MCT 1719-R belongs to *T. pricei*—their association was first rejected by *Campos & Kellner (1999)* and then accepted based on sparse evidence by *Campos et al. (2005)*—so two taxonomic scenarios are possible. If the tail MCT 1719-R were assigned to *T. pricei*, then *T. pricei* and *Ba. britoi* could be distinguished based solely on their different caudal vertebrae and the BR-262 material would be assigned to *Ba. britoi* based on the caudal vertebral anatomy, even if its cervical and trunk vertebrae are totally compatible with those of *T. pricei*. On the other hand, if MCT 1719-R is not *a priori* assigned to *T. pricei*, the matching anatomy of the BR-262 specimens to the holotypes of both *T. pricei* (MCT 1488-R) and *Ba. britoi* (MCT 1490-R) indicates that those two taxa are not taxonomically disparate. In this case, the caudal series MCT 1719-R would represent a hitherto undescribed new species, because it is not compatible with either MCT 1490-R or the BR-262 specimens, (see below). We consider the latter arrangement, which results in the synonymization of *T. pricei* and *Ba. britoi* better justified, so that these two species are not differentiated only based on characters found in a specimen ambiguously associated to *T. pricei*.

Trigonosaurus pricei and *Ba. britoi* were both first published in the same volume, but nomenclatural priority is given to *Ba. britoi*, because it was proposed some pages ahead (p. 529) of *T. pricei* (p. 565). So, if considered synonyms, as suggested here, *Ba. britoi* is the name to be adopted. Likewise, the set of BR-262 specimens is also referred to *Ba. britoi*, the systematic paleontology of which is given below.

Systematic paleontology

Dinosauria Owen, 1842; *Langer et al., 2020*
Sauropodomorpha Huene, 1932; *Fabbri et al., 2020*
Titanosauriformes Salgado, Coria & Calvo, 1997, *Silva Junior et al., 2022*
Titanosauria Bonaparte & Coria, 1993, *Silva Junior et al., 2022*
Baurutitan britoi Kellner, Campos & Trotta, 2005
Syn. Trigonosaurus pricei Campos et al., 2005 (a complete list of synonyms is provided on the supplementary)

Type-species: *Baurutitan britoi Kellner, Campos & Trotta, 2005*

Holotype: MCT 1490-R (Series C): last sacral vertebra articulated with a sequence of eighteen caudal vertebrae.

Referred specimens: MCT 1488-R (Series B; holotype of *T. pricei*): five cervical and 10 trunk vertebrae; sacrum and ilium. Forty-four specimens, possibly constituting a single individual, recovered from BR-262 locality, including: CPPLIP-035 (middle cervical vertebrae), CPPLIP-039 (middle cervical vertebrae), CPPLIP-040 (posterior cervical vertebrae), CPPLIP-049 (posterior cervical vertebrae), CPPLIP-014 (cervical rib), CPPLIP-110 (anterior trunk vertebra), CPPLIP-036 (anterior trunk vertebra), CPPLIP-103 (middle trunk vertebra), CPPLIP-111 (middle trunk vertebra), CPPLIP-037 (middle trunk vertebrae), CPPLIP-458 (middle trunk vertebrae), CPPLIP-43 (posterior trunk neural spine), CPPLIP-044 (trunk rib fragment), CPPLIP-097 (trunk rib fragment), CPPLIP-108 (trunk rib fragment), CPPLIP-109 (trunk rib fragment), CPPLIP-102 (anterior caudal vertebra), CPPLIP-046 (middle caudal vertebra), CPPLIP-047 (middle caudal vertebra), CPPLIP-061 (middle caudal vertebra), CPPLIP-096 (middle caudal vertebra), CPPLIP-091 (posterior caudal vertebra), CPPLIP-093 (middle caudal vertebra), CPPLIP-094 (posterior caudal vertebra), CPPLIP-095 (posterior caudal vertebra), CPPLIP-045 (posterior caudal vertebra), CPPLIP-055 (anterior chevron), CPPLIP-056 (anterior chevron), CPPLIP-098 (anterior chevron), CPPLIP-099 (anterior chevron), CPPLIP-112 (anterior chevron), CPPLIP-188 (anterior chevron), CPPLIP-057 (posterior chevron), CPPLIP-100 (posterior chevron), CPPLIP-038 (right scapula), CPPLIP-140 (right coracoid), CPPLIP-138 (right sternal plate), CPPLIP-007 (fragment of left humerus), CPPLIP-008 (right humerus), CPPLIP-010 (right metacarpal I), CPPLIP-042 (left ischium fragment), CPPLIP-069 (right ischium), CPPLIP-011 (left metatarsal II), CPPLIP-054 (left metatarsal III).

Type-locality and horizon: MCT 1490-R was collected from the Serra da Galga Formation (*Soares et al., 2021*), in the site known as "Caieira", "Quarry 1", or "Ponto 1 do Price", Serra do Veadinho area, near Peirópolis, Uberaba-MG (*Campos & Kellner, 1999*; *Martinelli & Teixeira, 2015*).

Revised diagnosis: titanosaur diagnosed based on a set of autapomorphic features, *i.e.*: expanded postzygodiapophyseal laminae on mid-posterior cervical vertebrae (newly proposed here) and first caudal vertebra with strongly pointed and laterally directed processes intercepting the spinoprezygapophyseal lamina (*Kellner, Campos & Trotta, 2005*).

Reassessment of MCT 1719-R

The redefinition of the specimens referred to *Ba. britoi* implies that MCT 1719-R cannot be associated to that taxon, as these caudal vertebrae clearly differ from those of MCT 1490-R and the BR-262 specimens. As discussed above, the BR-262 caudal neural spines lean posteriorly, as also seen in *Ba. britoi* (*Kellner, Campos & Trotta, 2005*, figs. 8, 12, 16 and 19), but not in MCT 1719-R, the spines of which lean gently anteriorly or stand nearly vertical (Figs. 21, 22). MCT 1719-R also lacks another trait shared between *Ba. britoi* and the BR-262 specimens: transverse processes that turn into a lateral ridge on the middle of

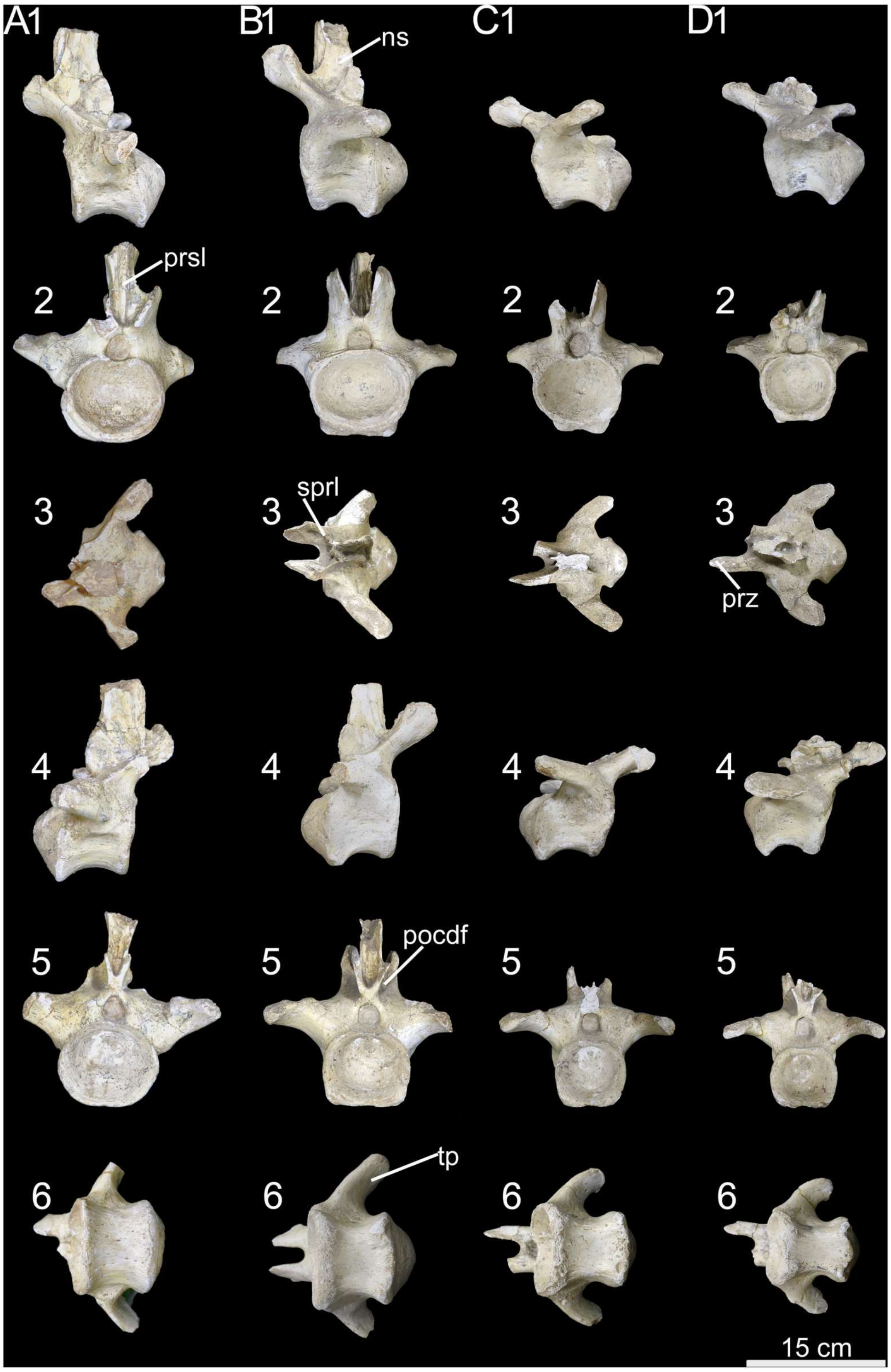

Figure 21 Anterior caudal vertebrae of *Caieiria allocaudata* (MCT 1719-R). In (1) left lateral; (2) anterior; (3) dorsal; (4) right lateral; (5) posterior and (6) ventral views. Abbreviations: ns, neural spine; pocdf, postzygapophyseal centrodiapophyseal fossa prz, prezygapophyses; sprl, spinoprezygapophyseal lamina; tp, transverse process. Full-size DOI: 10.7717/peerj.14333/fig-21

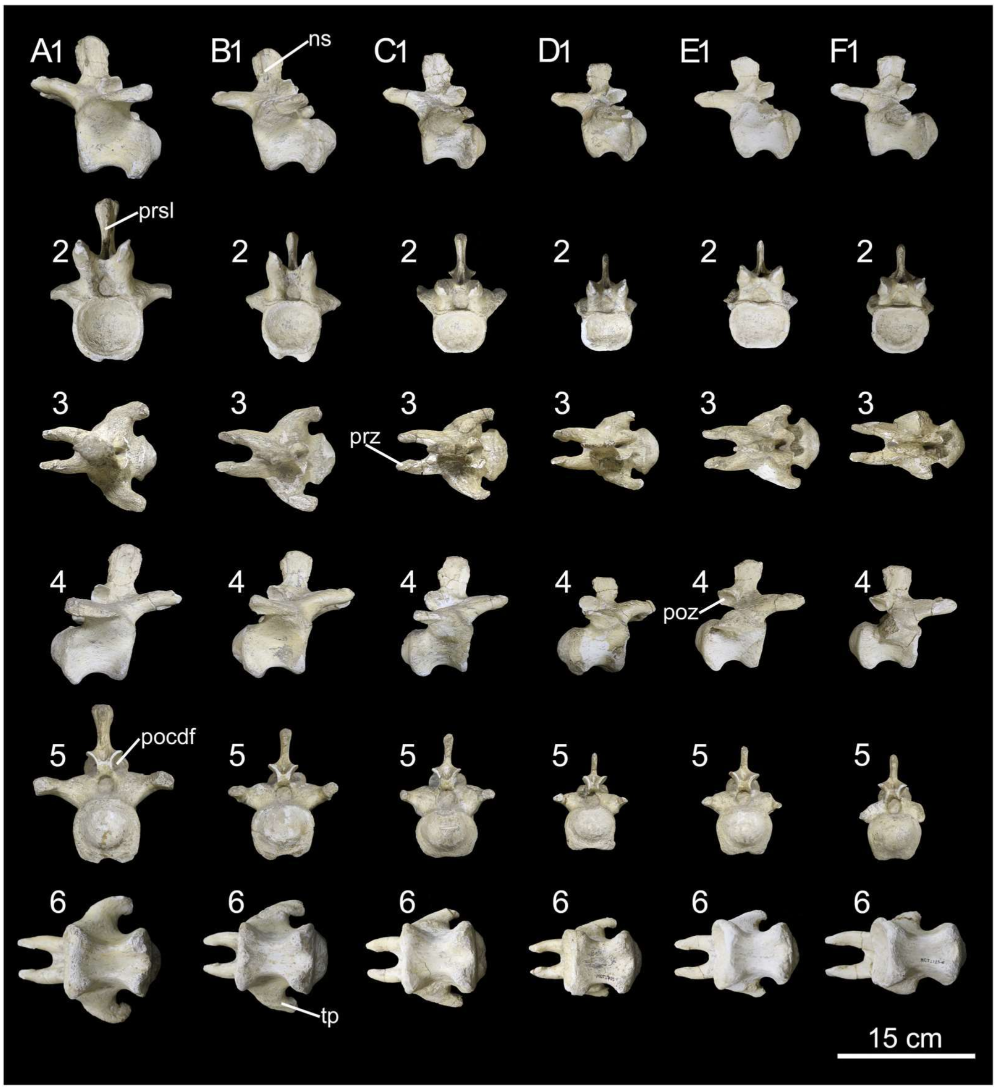

Figure 22 **Middle caudal vertebrae of *Caieiria allocaudata*.** In (1) left lateral; (2) anterior; (3) dorsal; (4) right lateral; (5) posterior and (6) ventral views. Abbreviations: ns, neural spine; pocdf, postzygapophyseal centrodiapophyseal fossa; poz, postzygapophyses; prz, prezygapophyses; prsl, prespinal lamina; tp, transverse process. Full-size DOI: 10.7717/peerj.14333/fig-22

the series. Below, we further revise the features of MCT 1719-R that Campos et al. (2005) used to diagnose *T. pricei*.

Campos et al. (2005) proposed that the centra of the anterior tail vertebrae possess thin ventral margins that broaden towards the top and transverse processes with pronounced dorsal depressions, two in the anterior (2–5) and one in the middle caudal vertebrae. The 2nd caudal vertebra possesses a deep muscular scar on its lateral face, followed by centra with lateral faces more deeply excavated than those at a similar serial position in *Gondwanatitan faustoi* (Kellner & Azevedo, 1999; fig. 6), *Panamericansaurus schroederi* (Porfiri & Calvo, 2010; fig. 3), and *U. ribeiroi* (Silva Junior et al., 2022; fig. 10). Also, anteriorly extended caudal prezygapophyses, with wide (dorsoventrally expanded) articular faces, are unique to MCT 1719-R among titanosaurs from the Serra da Galga Formation. These are about 70% the centrum length in middle caudal vertebrae, a proportion similar to that found on some *Aeolosaurini*, such as *Aeolosaurus rionegrinus* (72%; Powell, 1987) and *Arrudatitan maximus* (76%; Santucci & Arruda-Campos, 2011). The latter also shares wide articular facets (Santucci & Arruda-Campos, 2011; fig. 4) with MCT 1719-R, as well as with *Punatitan coughlini* (Hechenleitner et al., 2020).

As mentioned by Campos et al. (2005), MCT 1719-R has articular surfaces for the haemal arches that are strongly developed from the third caudal vertebra until the last preserved element (20th caudal vertebra). Although suggested as a unique feature of MCT 1719-R, a similar condition is present in *Rocasaurus muniozi* (Salgado & Azpilicueta, 2000; figs. 6 and 8) and *U. ribeiroi* (Silva Junior et al., 2022; fig. 10). Finally, the presence of well-developed transverse processes along the anterior and middle (1–20) caudal vertebrae was also proposed as unique to MCT 1719-R (Campos et al., 2005). In fact, some other titanosaurs—*e.g.*, *Ar. maximus* (Santucci & Arruda-Campos, 2011; fig. 4) and *U. ribeiroi* (Silva Junior et al., 2022; fig. 9)—possess transverse processes as long as those of MCT 1719-R (Figs. 21 and 22), almost reaching the posterior margin of the condyles, although less developed in more posterior vertebrae. Yet, those of MCT 1719-R are unique because they are strongly expanded dorsoventrally, to almost half the centrum height, including those of middle caudal vertebrae. As for the persistence of the transverse processes minimally until the twentieth caudal vertebra; this feature is also present in *Overosaurus paradosorum* (Coria et al., 2013; fig. 6) and *P. coughlini* (Hechenleitner et al., 2020; fig. 2).

Our comparative review has shown the presence of yet another unique feature of MCT 1719-R: the presence of deep postzygapophyseal-centrodiapophyseal fossae, expanding anteromedially on the dorsal margin of the neural arch (Figs. 21, 22). This condition differs from that of other titanosaurs, in which this fossa is present but does not expand medially, as for instance in *Ba. britoi* (Fig. 20D: Kellner, Campos & Trotta, 2005; fig. 18), *U. ribeiroi* (Silva Junior et al., 2019; fig. 9), and the BR-262 specimens. A well-developed postzygapophyseal-centrodiapophyseal fossa is also present in *Adamantisaurus mezzalirai* (Santucci & Bertini, 2006; plate 1), but restricted to the most anterior vertebrae and not as deep as in MCT 1719-R. Deep postzygapophyseal-centrodiapophyseal fossae are also present in *Narambuenatitan palomoi* (Filippi, García & Garrido, 2011; fig. 8) and *Mendozasaurus neguyelap* (González Riga et al., 2018; fig. 9), although these are dorsoventrally expanded in the former, reaching the neural canal, and limited medially by a centropostzygapophyseal lamina in the latter.

In conclusion, the uniqueness of MCT 1719-R among Bauru Group and other South American titanosaurs, including the presence of autapomorphic features (see below), warrants the proposition of a new taxon to accommodate the specimen.

Systematic paleontology

Dinosauria Owen, 1842; Langer et al., 2020
Sauropodomorpha Huene, 1932; Fabbri et al., 2020
Titanosauriformes Salgado, Coria & Calvo, 1997, Silva Junior et al., 2022

Titanosauria *Bonaparte & Coria, 1993*, *Silva Junior et al., 2022*
Caieiria allocaudata gen. et sp. nov.

Etymology: The generic name derives from "Caieira", the site where the type-specimen was unearthed. The specific name employs the word *allos* (Greek for strange) and cauda (Latin for tail), in reference to the unique anatomy of the animal's tail vertebrae.

Holotype: MCT 1719-R, 10 anterior to middle caudal vertebrae.

Type-locality and horizon: MCT 1719-R was collected in the site known as "Caieira", or "Quarry 1", Serra do Veadinho area, near Peirópolis, Minas Gerais, Brazil (*Campos & Kellner, 1999*). The bearing sandstones belong to the Serra da Galga Formation, Bauru Group (*Martinelli et al., 2019*; *Soares et al., 2020*, *2021*).

Diagnosis: *Caieiria allocaudata* can be distinguished from *Baurutitan britoi, Uberabatitan ribeiroi*, and *Gondwanatitan faustoi* by the presence of caudal vertebrae with robust and dorsoventrally expanded transverse processes, almost half the centrum height (modified from *Campos et al., 2005*), and anterior caudal vertebrae with a deep postzygapophyseal centrodiapophyseal fossa (newly proposed here).

Phylogenetic analysis

For the first iteration we added the BR-262 specimens, plus the holotypes of *Ba. britoi*, *T. pricei*, and *C. allocaudata* to the matrix. This resulted in 1,620 most parsimonious trees (MPTs) of 1,504 steps. The strict consensus tree (Fig. 23B) shows *Gondwanatitan faustoi*, the BR-262 specimens, plus the holotypes of *Ba. britoi* and *T. pricei*, within a polytomy along with a clade including *C. allocaudata* and *Bravasaurus arrierosorum*. In the entire set of MPTs, four possible arrangements for this polytomy were found, as seen in Fig. 23C. *Caieira allocaudata* and *Br. arrierosorum* form a minimal clade in all alternative arrangements, sister to either *G. faustoi* or to a clade congregating the other Serra da Galga Formation titanosaurs. Alternatively, *G. faustoi* was recovered either within or as sister-taxon to the specimens assigned here to *Ba. britoi*.

The second iteration was performed with the coding of the BR-262 specimens and the holotypes of *Ba. britoi* and *T. pricei* combined. This resulted in 1,500 MPTs of 1,502 steps. The strict consensus tree (Fig. 23A) shows *Ba. britoi* in a polytomy with *G. faustoi* and a clade including *C. allocaudata* and *Br. arrierosorum*. The clade congregating these four taxa is supported by a single synapomorphy: middle to posterior trunk vertebrae with pneumatic fossae located on the dorsal margin of the centra (Ch. 189), as seen in *Ba. britoi* and *Br. arrierosorum*. The clade composed of *C. allocaudata* and *Br. arrierosorum* is also united by a single synapomorphy: posteriormost anterior and middle caudal vertebrae with vertical neural spines (Ch. 257).

With additional specimens (MCT 1488-R and BR-262), the phylogenetic results confirm the position of *Ba. britoi* as an *Aeolosaurini*, as proposed by *Hechenleitner et al. (2020)* and *Silva Junior et al. (2022)*. Previously, *Ba. britoi* was recovered either as a *Lithostrostia* indet. (*Carballido et al., 2017*; *Filippi, Salgado & Garrido, 2019*) or as a Saltasaurinae-like taxon (*e.g.*, *Santucci & Arruda-Campos, 2011*; *França et al., 2016*;

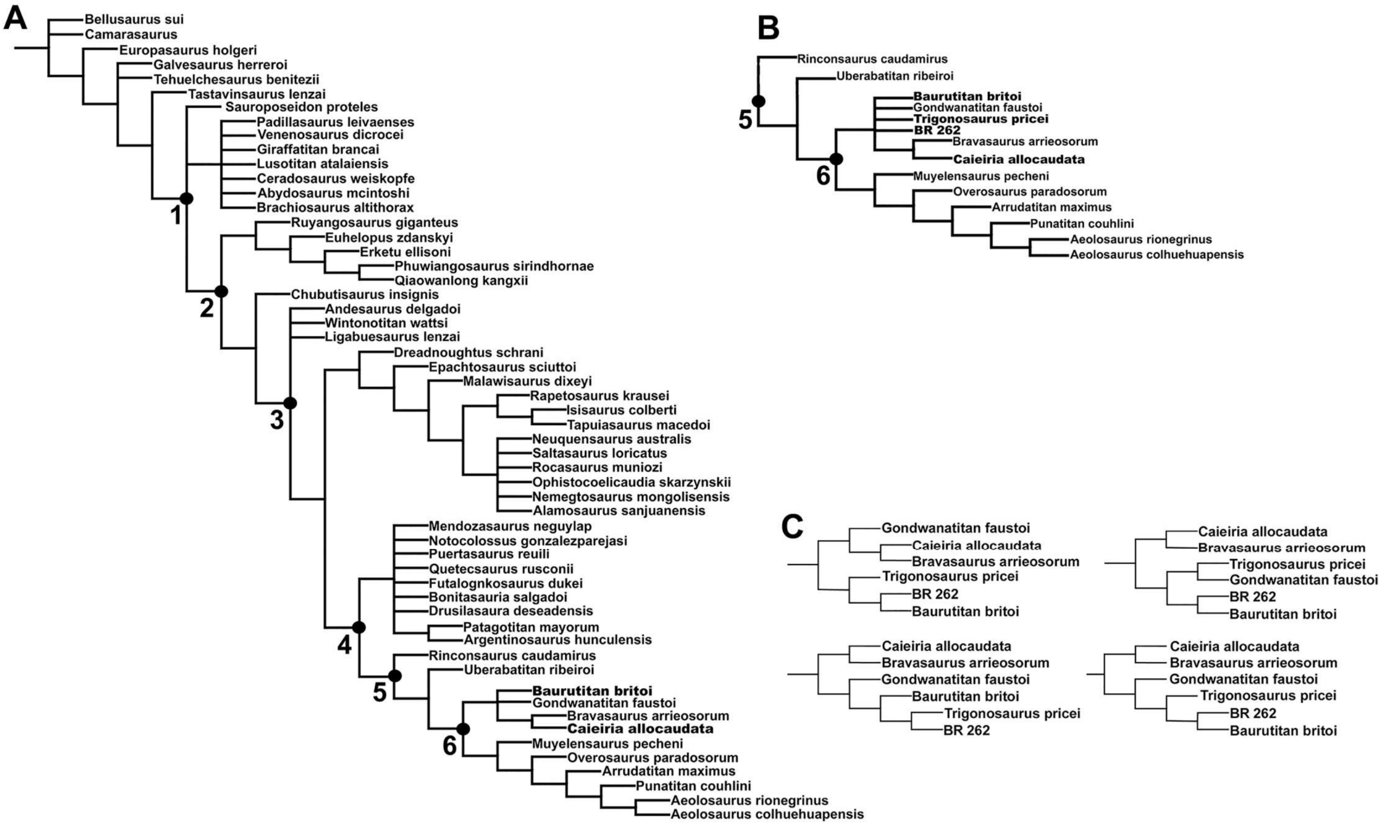

Figure 23 Phylogenetic results. (A) Strict consensus of the 1,500 MPTs found in the second iteration; (B) simplified strict consensus of the 1,620 MPTs found in the first iteration. (C) Alternative arrangements for the Serra da Galga Specimens and *G. faustoi* on Iteration I. Nodes: 1, Titanosauriformes; 2, Somphospondylii; 3, Titanosauria; 4, Colossosauria; 5, Rinconsauria; 6, Aeolosaurini.

Full-size DOI: 10.7717/peerj.14333/fig-23

Gorscak et al., 2017; *Carballido et al., 2020*). As for the now defunct *T. pricei*, besides its recent association to *Aeolosaurini* (*Hechenleitner et al., 2020*; *Silva Junior et al., 2022*), it has been previously recovered in disparate positions within *Lithostrotia* (*e.g.*, *Bandeira et al., 2016*; *Martínez et al., 2016*; *Gorscak & O'Connor, 2019*).

The affinity of *C. allocaudata* also to *Aeolosaurini* reinforces that this clade dominated the Late Cretaceous sauropod fauna of the Bauru Basin. This is the case not only of the Serra da Galga Formation, with *Ba. britoi*, *U. ribeiroi*, and *C. allocaudata*, but also of the Adamantina Formation, with *Ar. maximus* and *G. faustoi* (*Santucci & Arruda-Campos, 2011*; *Silva Junior et al., 2022*).

Comparisons to closely related taxa

Apart from the uniqueness of *Ba. britoi* and *C. allocaudata* established here on anatomical/phylogenetic grounds, both taxa also differ from the closely related *G. faustoi* and *Br. arrierosorum*. *Baurutitan britoi* and *G. faustoi* differ because the latter possesses trunk vertebrae with short condyles that are more ventrally displaced, surpassing the ventral margin of the centra (*Kellner & Azevedo, 1999*; fig. 7), and a humerus that is less mediolaterally expanded and slightly more medially curved (*Kellner & Azevedo, 1999*;

fig. 20) than that of *Ba. britoi*. *Baurutitan britoi* and *C. allocaudata* caudal vertebrae differ from those of *G. faustoi* because the latter have neural arches located on the anterior margin of the centra, with long prezygapophyses that exceed the centrum length (*Kellner & Azevedo, 1999*; Figs. 11 and 12).

Baurutitan britoi differs from *Br. arrierosorum* because the middle posterior cervical vertebrae of the latter lack ventrolateral crests projecting from the centra. Middle caudal vertebrae of *Ba. britoi* differ from those of *Br. arrierosorum*, because the latter lacks posteriorly inclined neural spines. Also, those of *Br. arrierosorum* differ from the condition in *C. allocaudata* in the absence of laterally excavated centrum surfaces and in having condyles with posteriorly projected articular surfaces (*Hechenleitner et al., 2020*; figs. 3h, 3i).

Baurutitan britoi has middle cervical vertebrae with neural spines that are lower than those of *Muyelensaurus pecheni* (*Calvo et al., 2007*; fig. 5) and *Overosaurus paradosorum* (*Coria et al., 2013*; fig. 2). Also, its trunk vertebrae lack both the ventral crest present in the latter taxon (*Coria et al., 2013*; fig. 3) and the anteroposteriorly compressed neural spine present in *Punatitan coughlini* (*Hechenleitner et al., 2020*; fig. 2). The caudal vertebrae of *Ba. Britoi* can be differentiated from those of *Aeolosaurus* spp. And *Arrudatitan maximus*, because they lack the anteriorly located neural arch present in the former (*Powell, 1987*; fig. 1. and *Casal et al., 2007*; fig. 2) and the elongated prezygapophyses with expanded facets of the latter taxon (*Santucci & Arruda-Campos, 2011*; fig. 4). Also, *Ba. Britoi* lacks the strongly posteriorly inclined caudal neural spines present in *M. pecheni* (*Calvo et al., 2007*; figs. 9, 10) and the crest on the ventral surface of the caudal vertebrae of *O. paradasorum* (*Coria et al., 2013*; fig. 6).

The caudal vertebrae of *C. allocaudata* lack the anteriorly located neural arch present in *Aeolosaurus* spp. (*Powell, 1987*; figs. 1. And *Casal et al., 2007*; fig. 2), and the anteriorly inclined neural spines present in both *Ar. maximus* (*Santucci & Arruda-Campos, 2011*; fig. 4) and *P. coughlini* (*Hechenleitner et al., 2020*; fig. 2). *Caieiria allocaudata* also lacks the dorsoventrally expanded neural spines of *M. pecheni* (*Calvo, González Riga & Porfiri, 2007*; figs. 9, 10) and the ventral crest on the caudal vertebrae of *O. paradasorum* (*Coria et al., 2013*; fig. 6).

CONCLUSIONS

The description of the titanosaur material unearthed at BR-262 site (Serra da Galga Formation, Bauru Group) shows that it shares several traits with two species previously known from this area and geological unit: *Ba. britoi* and *T. pricei*. A taxonomic revision indicates that *T. pricei* is a junior synonym of *Ba. britoi*, and that the BR-262 specimens belong to that latter species. Our taxonomic revision also revealed that the paratype of *T. pricei* (MCT 1719-R), a caudal vertebral series, actually represents a different species, named here as *Caieiria allocaudata*.

ACKNOWLEDGEMENTS

We thank Beethoven Teixeira and the staff of Museu dos Dinossauros (CCCP-UFTM) for their help during the development of this study. Particularly, BT participated in the excavations at BR-262 (as well as one of the authors, JIS), providing us with relevant information regarding those specimens. We thank Rafael Costa da Silva (MCT) for collection access. We also thank Dr. Díez Díaz, Dr. Poropat, Dr. Mannion and Dr. Tschopp for comments that greatly improved the strength of this article.

INSTITUTIONAL ABBREVIATIONS

CPPLIP	Centro de Pesquisas Paleontológicas Llewellyn Ivor Price, Universidade Federal do Triângulo Mineiro, Uberaba, Brazil
MCT	Museu de Ciências da Terra, Serviço Geológico do Brasil, Rio de Janeiro, Brazil
MUCPv	Museo de Geología y Paleontología Universidad, Nacional del Comahue, Argentina

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

This work was supported by Fundação de Amparo a Pesquisa do Estado de São Paulo (FAPESP) (Grant to J.C.G.S.J, Process Number 2018/21094-7; M.C.L, Process Number 2020/07997-4). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:
Fundação de Amparo a Pesquisa do Estado de São Paulo (FAPESP): 2018/21094-7 and 2020/07997-4.

Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Julian C. G. Silva Junior conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Agustín G. Martinelli conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Thiago S. Marinho conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- João Ismael da Silva conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.

- Max C. Langer conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The table of measurements, referred specimens, coding and the data matrix are available in the Supplemental Files.

New Species Registration

The following information was supplied regarding the registration of a newly described species:

Publication LSID: urn:lsid:zoobank.org:pub:28423C0B-A3E2-4ABF-8751-2E3A8FA98D4A

Caieiria allocaudata LSID: urn:lsid:zoobank.org:act:7E981FB6-6165-4851-B65A-C3C588FD9021

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.14333#supplemental-information.

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Appendix 3

The titanosaurian (Dinosauria, Sauropoda) teeth record from the Late Cretaceous of the Serra da Galga Formation (Bauru Basin, Southeast Brazil)

The Serra da Galga Formation (Bauru Basin) excels as the richest titanosaur bearing deposits in the Late Cretaceous of Brazil, with remains varying from eggs and juveniles (Fiorelli et al., 2022; Silva Junior et al., 2017) to fully grown specimens (Kellner et al., 2005; Salgado and Carvalho, 2008; Silva Junior et al., 2022). This richness, though, does not include titanosaurian teeth, as these elements are poorly represented on the region, with just a few specimens housed at the Centro de Pesquisas Paleontológicas Llewellyn Ivor Price/Museu dos Dinossauros and some collected from previous field work carried-out on that region (Kellner, 1996). Even with the high replacement tooth rate of sauropods, especially on titanosaurs (D'Emic et al., 2013; Kosch et al., 2014), the Serra da Galga preservation bias tends to select larger specimens (Martinelli et al., 2019), hampering the preservation of such elements.

Amongst the specimens found on the region and those from the collection, three distinct morphotypes (after Marinho and Martinelli, 2013) could be identified, as also the presence of few elements that point to juvenile individuals. One particular specimen stands out as the single largest titanosaurian tooth ever recorded. Thus, this contribution aims to help understand the richness of the titanosaur fauna of the Late Cretaceous of the Bauru Basin, as well as provide a better data for comparison with other similar findings.

Institutional abbreviations – **CPPLIP**, Centro de Pesquisas Paleontológicas Llewellyn Ivor Price, Universidade Federal do Triângulo Mineiro, Uberaba, Brazil; **MML-Pv**, Museo Municipal Lamarque, colección de paleovertebrados, Río Negro, Argentina.

MATERIALS AND METHODS

The specimens described here come from a series of outcrops located in the Uberaba region, Brazil (**Fig. 1**). CPPLIP-1166 and CPPLIP-1337 come from the BR-050 Km. 153 (*Uberabatitan*'s site; Salgado and Carvalho, 2009); CPPLIP-1458 from a few meters away of the previous site, though at a lower level, at the BR-050 Km. 153.5 (Martinelli and Teixeira, 2015) or Km. 24 (Bertini et al., 1993) and CPPLIP-214 from the Price's "Ponto 1" site (Campos and Kellner, 1999; Martinelli and Teixeira, 2015). The sandstone layers exposed correspond to the Serra da Galga Formation, Bauru Group, with a Maastrichtian age (Fernandes and Ribeiro, 2015; Martinelli et al., 2019; Soares et al., 2020, 2021).

The teeth possess the typical “chisel-like” morphology (Calvo, 1994; Chure et al., 2010; Mocho et al., 2017) present on derived titanosaurs. They were previously divided on three distinct morphotypes by Marinho and Martinelli (2013), which were modified here as: (1) robust teeth with a rounded transversal section, crown apex tapered than the base and without mesial and distal edges; (2) teeth with an elliptical transversal section due to labiolingual compression, acute mesial and distal edges, crown apex tapered than the base, slight curved both mesiodistally and labiolingually; (3) teeth slender than the previous morphotypes, circular transversal section, without mesial and distal edges. The double wear facets are inferred to belong to upper whereas the single ones to lower teeth (Wilson et al., 2016).

DISCUSSION

Morphotype 1. CPPLIP-1166 (**Fig. 2A**). The representative tooth is poorly preserved, lacking most of its enamel on the lingual face and a lateral portion of it on its labial one. The enamel is strongly ornamented with ridges and grooves extending perpendicularly to the main axis. The apicobasal axis is gently curved labially. The transverse section of the crown base is subcircular whereas the apical region is labiolingually compressed. Both mesial and distal facets are marked by a weak carinae. The tooth tapers apically creating a convex end. A chisel-shaped apical wear facet occupies almost half of the crown, with diagonal scratches.

Morphotype 2. CPPLIP-1458 (**Fig. 2B**). The representative tooth is poorly preserved, lacking most of its root. The enamel is smooth, with a parallels scratch marks visible. It has a subcircular cross section, been slightly labiolingually compressed towards its apex due to heavy wearing. The apex is apically tapered, creating an acute ending. The tooth possesses a wear facet on its labial face restricted to the most apical sections, whereas the lingual one covers almost the entire tooth crown, creating a chisel-shaped wear surface. Parallel scratch marks are also visible on the wear facets.

Morphotype 3. CPPLIP-214 (**Fig. 2C**). This representative specimen is also poorly preserved, with most of its root missing. The enamel is smooth, with few scratch marks extending parallel to the main axis. The apicobasal axis is gently curved labially. The tooth is strongly labiolingually compressed, with the carinae creating acute mesial and distal edges. It tapers apically creating an acute end. The wear facet is restricted to the most apical portion of the crown on the lingual face, with barely visible parallel scratch marks.

Juvenile teeth. CPPLIP-1337 (**Fig. 2D**). This specimen is considered to had belonged to a juvenile specimen due to its small size and weaker wear marks. The tooth lacks its root and the enamel is wrinkled as in CPPLIP-1166, but lacking the deep perpendicular grooves and scratch marks. It has a subcircular cross section, with the apicobasal axis gently curved labially. CPPLIP-1337 possess wear facets on the lingual and labial faces, both restricted to the apex of the tooth. Those wear facets show presence of shallow scratch marks.

The teeth from the Serra da Galga Formation do not deviate from the overall morphology of other titanosaurs and cannot be assessed to any specific taxa. Both morphotypes 1 and 3 resembles those of *Nemegtosaurus* (Wilson, 2005) – as this species possess teeth with both rounded and transversal sections – but a comparison with this taxon is not feasible as there is no osteological remains preserved in the Uberaba region that resembles it. The morphotype 2 seems to be the most common, as it is similar to other species as *Bonitasauria* (Gallina and Apesteguía, 2011), *Pitenkusaurus* (Filippi and Garrido, 2008), *Maxakalisaurus* (Kellner et al., 2006) and *Tapuiasaurus* (Wilson et al., 2016).

The difference on microwear of enamel and wear facets can be an indicative of feed habits, niche partition and even ontogenetic stages (Calvo, 1994; Fiorello, 1998; Sereno et al., 2007). All the studied teeth lack pits on both surfaces, what is an indicative of a diet with a scarcity of grit or hard vegetables that could mark those surfaces (Fiorillo, 1998; García, 2013) – contrasting with the feed mechanisms common on other titanosaurs (García and Cerda, 2010; Díez Díaz et al., 2013) – and suggesting that a similar diet was shared by all the analyzed specimens. It has been shown that some sauropods could pass through a diet change during their ontogeny, based on the differentiation of wear marks (Fiorillo, 1991, 1998). The absence of pits also in CPPLIP-1337, however, does not suggest any noticeable niche partition when compared with the adult specimens.

Another specimen recovered from the *Uberabatitan*'s site, CPPLIP-1166, represents the largest titanosaur tooth ever recorded. It is about 11% larger than MML-Pv 1030 (García, 2013), a tooth unearthed from the Upper Cretaceous of the Allen Formation, Argentina. In the discussion of its paper, García (2013) pointed that as all titanosaurs found on that Formation were relatively small, e.g., *Bonatitan, Rocasausaus* and *Aeolosaurus* (Martinelli and Forasiepi, 2004; Salgado and Azpilicueta, 2000 and Salgado and Coria, 1993), this tooth must have pertained to a large-toothed specimen or with a disproportionally large head.

With the previous data available from the Serra da Galga Formation, herein we suggest a different interpretation for the giant tooth found. It has been recorded in the Uberaba region the presence of giant specimens of *Uberabatitan*, with estimated sizes reaching up to 26m length (Silva Junior et al., 2019). Thus, it is possible that CPPLIP-1166 belonged to a giant individual rather than a titanosaur with a larger head. Unfortunately, all other giant species, such as *Argentinosaurus, Dreadnoughtus* and *Patagotitan* (Bonaparte and Coria, 1993; Lacovara et al., 2014; Carballido et al., 2017) lack preserved teeth, hampering a direct comparison to them.

The new data provided by the identification of teeth with distinct morphologies and ontogenetic stages, albeit brief, can provide a better understand to the titanosaur fauna of the region. It shows that the Serra da Galga Formation environment was conducive to bear a distinct fauna of titanosaurs, as also offer support starting from a nesting site to the development of juveniles to fully grown giant specimens.

ACKNOWLEDGMENTS

We would like to thank the Centro de Pesquisas Paleontológicas Llewellyn Ivor Price, Universidade Federal do Triângulo Mineiro, for providing the specimens studied here. This work was financed by FAPESP (XXX).

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Specimen	Crown length	pmmw	mmw	mlw	SI
CPPLIP-214	2,87	3,41	0,85	0,56	3,2
CPPLIP-1166	6,2	7,32	1,34	1,18	4,77
CPPLIP-1337	2,39	2,39	0,59	0,48	4,05
CPPLIP-1458	4,38	4,7	0,6	0,76	7,3

Table 1. Measurements (cm) of titanosaur teeth from the Serra da Galga Formation. Abbreviations: **mmw:** maximum mesiodistal width; **mlw:** maximum labiolingual width; **ppmw:** preserved maximum mesiodistal width; **SI:** slender index (after Upchurh, 1998).

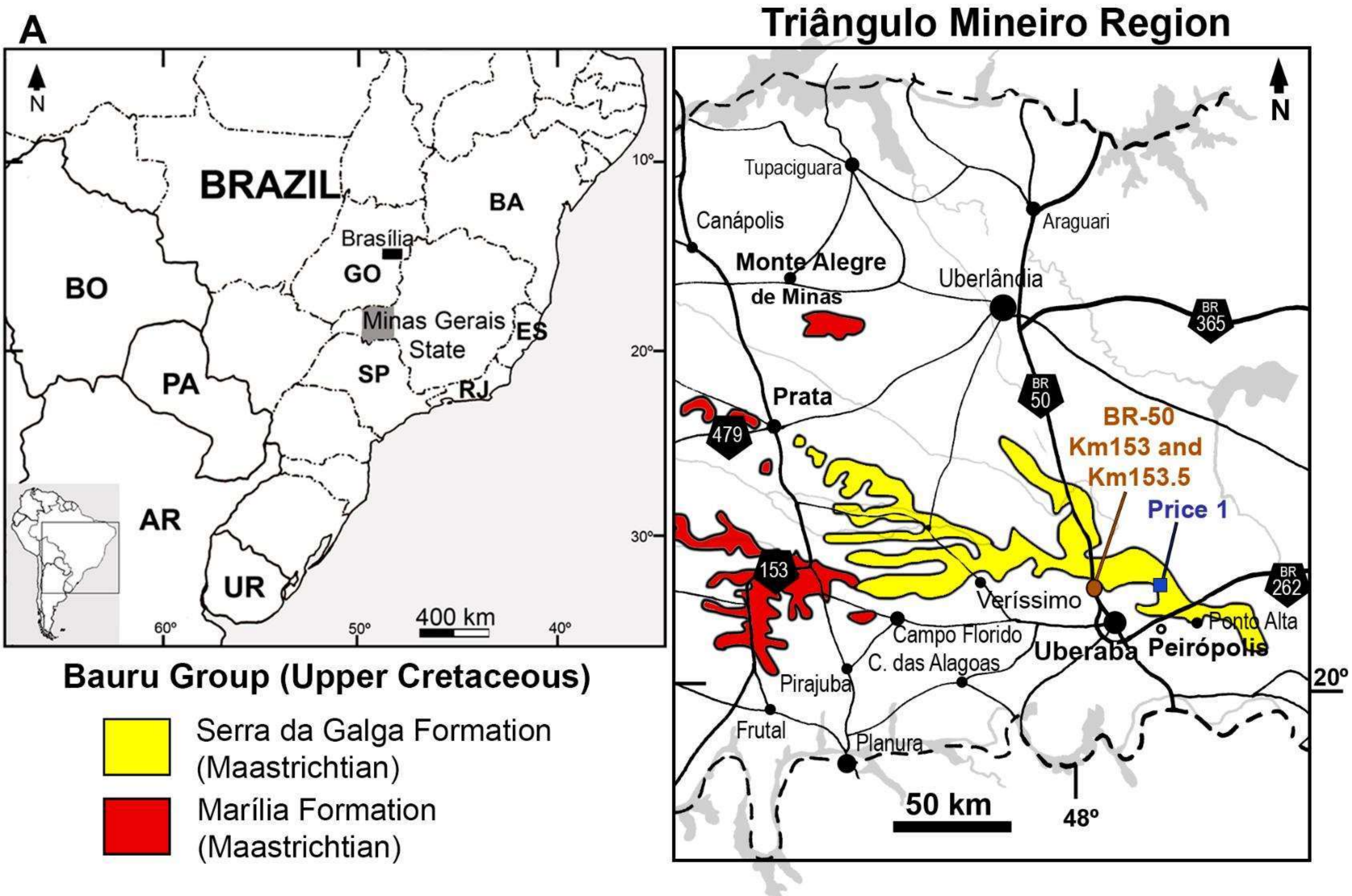

Figure 1. Map of the Bauru Basin detailing the Uberaba region with selected outcrops highlighted (modified from Silva Junior et al., 2022).

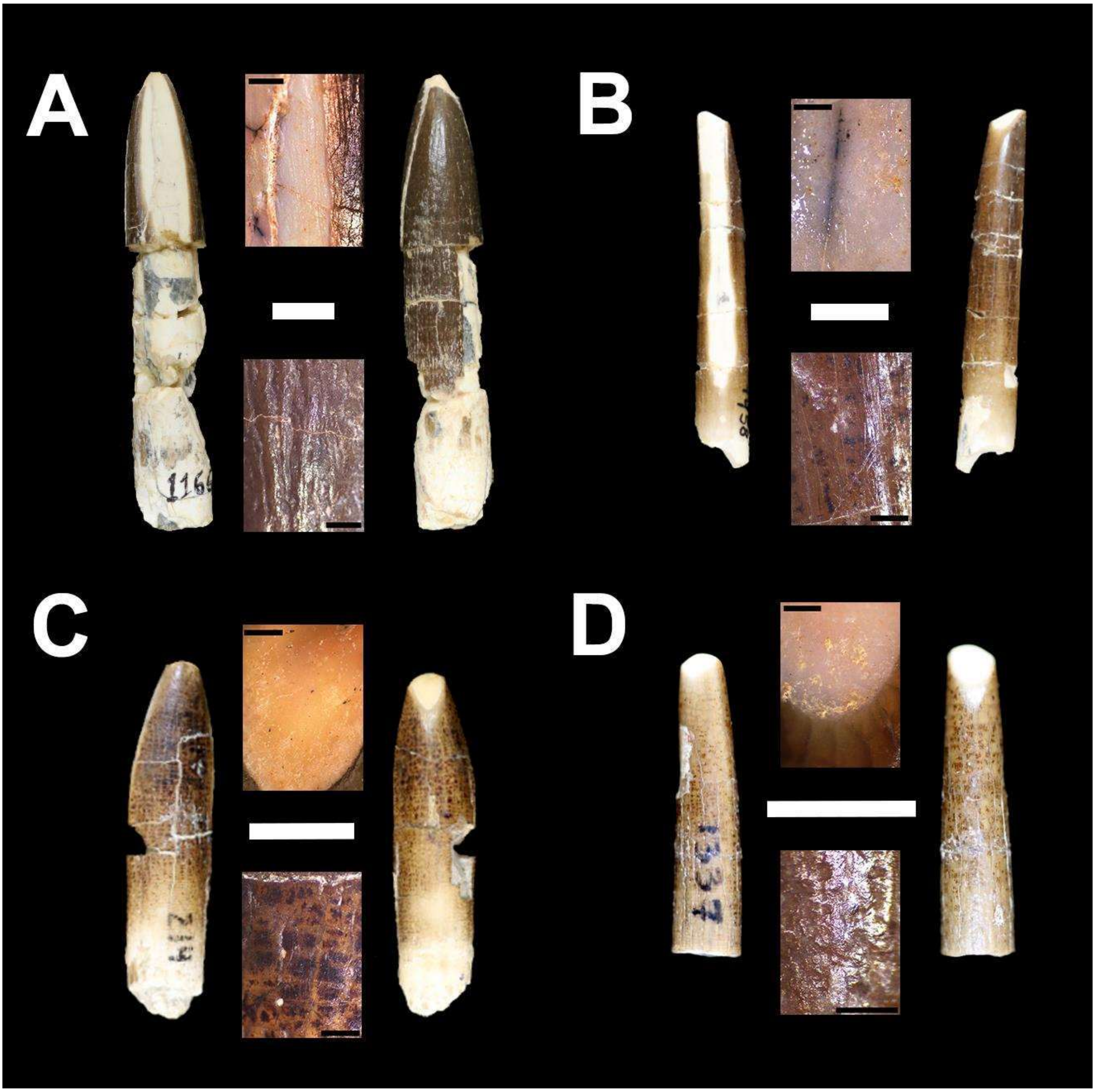

Figure 2. Representative teeth of the different morphotypes from the Serra da Galga Formation. **A,** CPPLIP-1166 in lingual and labial views, with wear facets and enamel magnified; **B,** CPPLIP-1458 in lingual and labial views, with wear facets and enamel magnified; **C,** CPPLIP-214 in lingual and labial views, with wear facets and enamel magnified and **D,** juvenile teeth CPPLIP-1337 in lingual and labial views, with wear facets and enamel magnified. All scales equal 1 cm for external and 0,5 mm for magnified views.

Appendix 4

INVENTORY OF THE TITANOSAURS REMAINS HOUSED AT THE MUSEU DOS DINOSSAUROS – UBERABA, BRAZIL

INTRODUCCION

The Uberaba region, in Minas Gerais, is a hotspot for digging Cretaceous tetrapods in Brazil, with numerous fossils reported along nearly a century. The area was first explored by the Brazilian paleontologist Llewellyn Ivor Price (1905-1980), who collected hundreds of specimens along more than thirty years (Cassab & Melo, 2016), now housed at the Museu de Ciências de Terra, Rio de Janeiro.

Since 1989, fossils collected around Uberaba started to be kept in the area, waiting for the building of a museum. This happened three years later, with the opening of the "Museu dos Dinossauros" (Ribeiro & Carvalho, 2007; Ribeiro et al., 2011). The museum crew continued to conduct field-works to the outcrops previously explored by Price, increasing the number of specimens in its collection. Almost ten years after its foundation, the "Museu dos Dinossauros" was integrated into the Universidade Federal do Triângulo Mineiro, as part of a larger complex called "Centro de Pesquisas Paleontológicas Llwellyn Ivor Price – CPPLIP".

Currently, the CPPLIP collection houses more than 1,800 specimens, gathered from all around Brazil, whereas the regional findings are mostly represented by titanosaur remains, a dinosaur group especially abundant in the area. Four species were formally described, *Baurutitan britoi* (Kellner et al., 2005), *Trigonosaurus pricei* (Campos et al., 2005), *Uberabatitan ribeiroi* (Salgado & Carvalho, 2008), and *Caieiria allocaudata* (Silva Junior et al., 2022), the second of which has been recently synonymized to the first (Silva Junior et al., 2022).

Most of the titanosaur specimens housed at "Museu dos Dinossauros" corresponds to isolated remains. They do not bear autapomorphic/diagnostic features of the known species, but may still serve as resourceful comparative materials. Thus, this contribution aims to described and figure all titanosaur remains housed at the CPPLIP that were not already published elsewhere, which can help future research about this group of dinosaurs.

GEOLOGICAL CONTEXT

All fossil remains described here were unearthed from four different localities in the Uberaba region, Minas Gerais. The most productive sites are those called by Price as "*Ponto 1*" and

"*Ponto 2*", which are located less than 0,5 km from one another and less than 2 km north of "Museu dos Dinossauros", in Peirópolis (Campos & Kellner, 1999; Martinelli & Teixeira, 2015). Other remains have been marked as coming from "*Ponte Alta*", which is a town located about 12 km west of Peirópolis. Finally, few other remains were collected on different points along "*Rodovia*", a name used in reference to BR-262 highway, which connects Uberaba to Ponte Alta, via Peirópolis. All these sites expose sandstone layers from the Maastrichtian Serra da Galga Formation, Bauru Group (Soares et al., 2020, 2021).

DESCRIPTION

Here we employ the nomenclature proposed by Wilson (1999, 2012) and Wilson et al. (2011) to describe laminae and fossae of the titanosaur vertebrae. For muscle-related structures, we follow Borsuk-Białynicka (1977), Otero & Vizcaíno (2008), and Voegele et al. (2020, 2021).

Axial Skeleton

Cervical vertebrae. Four isolated sauropod cervical vertebrae are housed at "Museu dos Dinossauros". Their respective positions along the neck were defined based on traits such as the width of neural canal and height of neural spine.

CPPLIP-234 (middle cervical vertebra, **FIG. 3A**). This vertebra lacks the left postzygapophysis and both transverse processes and prezygapophyses. The centrum is anteroposteriorly elongated, with a 3.58 aEI (average elongation index; Chure et al., 2010). The condyle is dorsoventrally compressed, with its dorsal margins surpassing that of the cotyle. The latter is wider than deep, subcircular in posterior view, and lies at the same anteroposterior level as the postzygapophyses. Its ventral surface is slightly concave in both lateral and anterior views. Pneumatic fossae are deep, extending from the posterior portion of the condyle to the dorsal contact between the postzygodiapophyseal and the posterior centrodiapophyseal laminae, almost reaching the cotyle.

The neural spine is triangular in lateral view, slightly displaced anteriorly, and with a 'bulbous', i.e., mediolaterally expanded, apex. It is connected anteriorly to the prezygapophyses by the spinoprezygapophyseal lamina. This lamina bounds a deep spinodiapophyseal fossa dorsally and a small spinoprezygapophyseal fossa medially. The latter bounds the intraprezygapophyseal lamina dorsally, which has the same lateromedial width as the neural canal. The diapophyses and parapophyses are missing, but the first would be connected to the to the centrum via the posterior centrodiapophyseal laminae, set below the spinodiapophyseal fossae, and to the prezygapophyses by the prezygodiapophyseal laminae.

Only the right postzygapophysis is preserved, with the articular facet mediolaterally expanded and facing ventrally. It is connected anterodorsally to the neural spine via the spinopostzygapophyseal lamina, and to the diapophysis via the postzygodiapophyseal lamina. These laminae bear a peculiar bulbous expansion on their posteriormost portions. The postzygapophyses are connected to one another by the intrapostzygapophyseal lamina, which is lateromedially wider than the neural canal, and dorsally bounds a shallow postzygapophyseal centrodiapophyseal fossa.

CPPLIP-258 (posterior cervical vertebra, **FIG. 3B**). This vertebra lacks the right post- and both prezygapophyses, as well as the distal portion of the neural spine the right diapophysis and parapophysis. The centrum is heavily dorsoventrally compressed, with an aEI of 1.19 and the ventral margins of both condyle and cotyle lying at the same dorsoventral level. The ventral surface is slightly concave anteroposteriorly. Pneumatic fossae are deep, with rounded margins and extending from the posterior margin of the condyle to the distal portion of the posterior centrodiapophyseal lamina. The latter bounds a parapophyseal centrodiapophyseal fossa dorsally, which has almost the same depth and length as the pneumatic fossa.

The neural spine is connected anteriorly to the prezygapophyses by the spinoprezygapophyseal laminae, which is only preserved on the left side, laterally bounding a deep spinoprezygapophyseal fossa. The prezygapophyses, although absent, would be connected by the intraprezygapophyseal lamina, which is lateromedially wider than the neural canal. Laterally, diapophyses and parapophyses are preserved only on the right side. The parapophysis is short and slightly bent downwards, with shallow dorsal excavations. The diapophysis lays posterior to the condyle and is connected anteromedially to the centrum via the prezygodiapophyseal lamina and posteromedially via the posterior centrodiapophyseal lamina.

Only the left postzygapophysis is preserved. It would be connected to its rigth counterpart by a thin intrapostzygapophyseal lamina, which is lateromedially shorter than the neural canal. The articular facet is anteroposteriorly expanded and faces ventrally. It is connected to the neural spine by the spinopostzygapophyseal lamina medially and by the lamina intrapostzygapophyseal posteromedially, which bounds a deep spinopostzygapophyseal fossa. The postzygapophyses are connected to the centrum via the centropostzygapophyseal laminae, which anteromedially bond deep postzygapophyseal centrodiapophyseal fossae.

CPPLIP-1457 (posterior cervical vertebra, **FIG. 3C**). This vertebra is poorly preserved, lacking the neural spine and the distal portions of the diapophyses and parapophyses. The centrum is anteroposteriorlly elongated, with an 1.53 aEI. The condyle is slightly dorsoventrally compressed, with the dorsal margin at the same dorsoventral level as that of the cotyle, which has a rounded posterior outline. A crest extends anteroposteriorlly along the ventral surface of the centrum, separating small depressions located posterior to the condyle. The pneumatic fossa is deep, with rounded margins and extending from the posterior portion of the condyle to the anterior margin of the cotyle.

The prezygapophyses project beyond the condyle, connected to one another by the intraprezygapophyseal lamina – which has the same lateromedial breath as the neural canal – and medioposteriorly to the neural spine by the spinoprezygapophyseal lamina. The articular facets are lateromedially expanded, with half the condyle width, and face mediodorsally. The diapophyses and parapophyses are poorly preserved, the latter curve slightly upwards and have a shallow concavity on the dorsal margin of each. The diapophyses are connected to the centrum anteromedially by the anterior centroparapophyseal, and medioposteriorly the posterior centrodiapophyseal laminae. These laminae dorsally bound a deep centrodiapophyseal fossa, which is divided on anterior and posterior portions by the anterior centrodiapophyseal lamina.

Caudal vertebrae. Numerous caudal vertebrae are housed at "Museu dos Dinossauros". Their respective positions along the tail were defined based on comparisons with more complete caudal series such as those of *B. britoi* (Kellner, Campos & Trotta, 2005), *Dreadnoughtus schrani* (Lacovara et al., 2014), and *Rapetosaurus krausei* (Curry Rogers, 2009).

CPPLIP-1130 (middle caudal vertebra, **FIG. 4A**). This vertebra lacks the prezygapophyses. The lateral and ventral surfaces are anteroposteriorly concave and the centrum has an 1.74 aEI. The condyle is slightly convex, with chevron articular facets extending ventrally from its most posterior margin. The cotyle is shallow and a rounded anterior outline. The neural spine is strongly displaced posteriorly and connected to the zygapophyses via the spinoprezygapophyseal and spinopostzygapophyseal laminae. The postzygapophyses are ventrally connected to the centrum by the centropostzygapophyseal laminae and have dorsoventrally compressed facets that face medially.

CPPLIP-248, 899, and 1175 (middle caudal vertebrae, **FIG. 4B-D**). This set was found associated, and based on agreeing morphology and size are inferred to belong to a single individual. CPPLIP-248 was previously assigned to *Aeolosaurus* sp. by Santucci & Arruda-Campos (2011), but Martinelli et al. (2011) considered it as an *Aeolosaurini* indet., as it lacks diagnostic features of this genus (Casal et al., 2007). We corroborate the latter classification here.

CPPLIP-248 lacks the of the neural spine and the most distal portion of the transverse processes; CPPLIP-899 lacks the neural spine, both postzygapophyses and transverse processes, and right prezygapophysis; only the centrum is preserved in CPPLIP-1175. Their aEIs are 1.53 and 1.5 for CPPLIP-248 and 899, respectively. The lateral surfaces of the centra are strongly anteroposteriorly concave, and CPPLIP-1175 has the left one pierced by a small foramen. The ventral surfaces are excavated, forming shallow septa between the posterior articular facets for the chevron. Only such articular facets are preserved in CPPLIP-248 and 1175, whereas the anterior ones are also preserved in CPPLIP-899. The condyles are robust, with that of CPPLIP-1175 possessing a small depression on its center. The cotyles are deep, with a rounded anterior outline.

The neural spine of CPPLIP-248 is connected to the pre- and postzygapophyses via the spinoprezygapophyseal and spinopostzygapophyseal laminae, respectively. The former bounds a shallow spinoprezygapophyseal fossa laterally. The transverse processes are poorly preserved and located anteriorly, close to the cotyles. The prezygapophyses are long, with almost the same length as the centrum; they curve downwards and have medially facing facets. The postzygapophyses are short, directly connected to one another medially and with facing laterally broad articular facets. The postzygapophyses are anteroventrally connected to the centra via the centropostzygapophyseal laminae, which extend until the dorsal margin of the neural canal.

CPPLIP-393 and 394 (posterior caudal vertebrae, **FIG. 5A-B**). These elements were found articulated with those of FIG. 5C-J and figured by Santucci and Bertini (2001) with no further anatomical information. They cannot be attributed to any specific taxon within the Serra da Galga Formation, but can be assigned to *Titanosauria*, based upon the presence of procoelic articulations (sensu Wilson and Sereno, 1998).

The vertebrae possess a similar anatomy, both lacking the distalmost portion of the neural spines. Their centra have slightly anteroposteriorly concave lateral and ventral surfaces, with the posterior chevron facets projecting ventrally. CPPLIP-393 and 394 have aEIs of 1.57 and 1.56, respectively. The condyles are robust, projecting posterior to the postzygapophysis, whereas the cotyles have rounded outlines with well-defined margins. The transverse processes are short, posteriorly projected and located anterior to the postzygapophyses. The neural spines are connected anteriorly to the prezygapophyses via the spinoprezygapophyseal laminae, which laterally bound shallow spinoprezygapophyseal fossae, and posteriorly to the postzygapophyses by short spinopostzygapophyseal laminae.

The prezygapophyses are posteroventrally connected to the centra by the centroprezygapophyseal laminae, which extend until the dorsal margin of the neural canals and have dorsoventrally expanded facets that face mediodorsally. The postzygapophyses are short, with rounded articular facets that face ventrolaterally, also forming the lateral limits of shallow spinopostzygapophyseal fossae. They are anteroventrally connected to the centra by short centropostzygapophyseal laminae, which extend until the dorsal margin of the neural canals.

CPPLIP-170, 395, 396, 397, 398, 399, 400 and 401 (posterior caudal vertebrae, **FIG. 5C-J**). All these elements share similar anatomy and preservation, lacking the distalmost portions of the neural spines. Their aEIs are available in Table 1. The centra have the lateral and ventral surfaces slightly concave anteroposteriorly and become more anteroposteriorly elongated starting from CPPLIP-400. The centrum of CPPLIP-398 is biconcave, whereas that of CPPLIP-397 is biconvex. The chevron articular facets project ventrally and are present until CPPLIP-399. There is evidence that the chevrons of CPPLIP-398 were fused to the centrum. The condyles of CPPLIP-395 and 396 project posterior to the postzygapophyses, whereas those of the subsequent vertebrae are set at the same anteroposterior level. All vertebrae – except CPPLIP-399 and 401 – possess a small concavity in the center of the condyle, although its absence on those two elements could be due to preservation. The cotyles are shallow, with well-defined margins and a rounded outline.

On the lateral surfaces, the neural spines are anteriorly connected to the prezygapophyses via the spinoprezygapophyseal laminae, which also delimit shallow spinoprezygapophyseal fossae. These spines are present until the last preserved element, connected posteriorly to the postzygapophyses via the spinopostzygapophyseal laminae. The prezygapophyses are long, with medially facing articular facets that become gradually ventrolaterally to dorsomedially compressed in the most posterior vertebrae. They are posteroventrally connected to the centra by short centroprezygapophyseal laminae, which extend until the lateral margin of the neural canals. The postzygapophyses are short, with laterally facing articular facets, and anteroventrally connected to the centra via short centropostzygapophyseal laminae.

Appendicular Skeleton

Pectoral girdle (**FIG. 6**). CPPLIP-444 (left scapula). The scapula is described here with its long axis oriented horizontally and the external surface facing laterally. The lateral surface of the acromial plate is slightly anteroposteriorly concave and bound posteriorly by a robust acromial ridge, which has a triangular lateral outline and receive *M. deltoideus claviculares*. The glenoid is deflected laterally and its ventral end gives rise to a small crest that extends posteriorly along the medial surface of the bone, receiving *M. triceps*. The scapular blade extends posteriorly as a flat lamina, with a subrectangular cross section and a subsquared posterior end. It bears a ridge on the lateral surface that receives *M. serratus superficialis*. The dorsal margin of the scapula is slightly concave and a protuberance project laterally from the dorsal portion of the acromion.

Forelimb. CPPLIP-119 (left humerus, **FIG. 7A**), 877 (right humerus, **FIG. 7B**), 408 (right humerus, **FIG. 7C**) and 1174 (right humerus, **FIG. 7D**). The humeri are gracile elements with the following ECC (eccentricity index): CPPLIP-119 = 1.1, 877 = 1.08, 408 = 1.26, 1174 = 1.45. CPPLIP-119 lacks the medial margin of the humeral head and CPPLIP-877 its most proximal portion, whereas CPPLIP-408 and 1174 are fully preserved. The deltopectoral crest projects anteriorly from the lateral margin of the proximal portion of the humeri. They are slightly medially deflected and extend distally until half the length of the bones. On the posterior surface of the humeral head, a lateromedially concave area receives *M. coracobrachialis brevis*. The medial margin of the head expands anteriorly, creating a subrectangular outline in CPPLIP-408 and 1175, which is much thinner in CPPLIP-877.

The humeri have sub-circular mid-shaft cross-sections, but slightly lateromedially compressed. In the distal portion, the radial and ulnar condyles are separated by a shallow fossa. The former is anteroposteriorly projected and slightly deflected medially, with a triangular anterior outline. The ulnar condyle is less pronounced and projects anteriorly; laterally bound by a small fossa that separates it from a laterally projected crest. The posterior surface of the distal third of the humerus bears a supracondylar fossa. It extends dorsoventrally, medially and laterally bound by ridges, which are more pronounced in CPPLIP-119 and 877.

Hindlimb. CPPLIP-653 (left femur, **FIG. 8A**) and 881 (left femur, **FIG. 8B**). Both femora are robust and have similar anatomy and preservation; with CPPLIP-881 lacking the fibular condyle. In anterior/posterior view, the femoral head it is slightly beveled medially and projects proximally, surpassing the level of the great trochanter. The anterior surface of the shaft is almost flat, with a concavity extending proximodistally on the distal half. This is bound laterally by a proximodistally expanded crest, which is more pronounced in CPPLIP-653. Lateral to that, the fourth trochanter expands as a small lamina from the first half of the shaft. It is more posteriorly projected in CPPLIP-653, but less pronounced and barely visible in posterior view in CPPLIP-881.

The posterior surface of the shaft is laterally bound by a bulge that extends distally from the femora head, and is more laterally projected in CPPLIP-881. Medial to the bulge, a proximodistally extending depression is also deeper in CPPLIP-881. Medial to this depression, the trochanteric shelfs extend proximodistally, reaching distally the proximalmost tip of the fourth trochanter in CPPLIP-881. At mid-shaft, the femur has a sub-circular cross section. Distally, the tibial and fibular condyles are pronounced, with the first just slightly lateromedially broader than the former in CPPLIP-653. The condyles are separated by a shallow fossa and project posteriorly to the femoral heads.

CPPLIP-493 (right tibia, **FIG. 9A**). The medial margin of the shaft is flat with both proximal and distal ends anteroposteriorly expanded, the former bearing a squared lateral/medial outline. On the lateral surface, the tibia possesses a protuberance at the proximal portion, matching the fibular articulation. The proximal articulation is mainly a single bulge, slightly concave in dorsal view, where it articulates with the femur. The cnemial crest projects anteriorly and its mid-session is laterally deflected. Laterally, between the cnemial crest and the tibial protuberance, a deep depression extends proximodistally, congregating most of the hindlimb musculature (*i.e., Mm ambiens, femorotibialis internus* and *externus*, *iliotibialis* and *popliteus*). Distally, the lateral surface of the shaft becomes slightly concave anteroposteriorly. The distal end of the tibia is poorly preserved, with the articulation with the astragalus, the lateral and medial malleoli missing.

CPPLIP-262 (left fibula, **FIG. 9B)** and 403 (right fibula, **FIG. 9C**). These elements show a similar anatomy and preservation; CPPLIP-262 lacking the posterior margin of its proximal end. The proximal portion of the fibula is anteroposteriorly expanded and has a rugose proximal articular facet. On the lateral surface, the lateral trochanter forms a large protuberance in CPPLIP-403, but is mediolaterally compressed in CPPLIP-262, with a small concavity on its central portion. The medial surface of the fibula is flat and the fibular knob has a triangular medial outline. CPPLIP-262 has a rounded distal outline, whereas that of CPPLIP-403 is subtriangular. Both surfaces are rugose and concave.

CONCLUSIONS

Some titanosaurs of the Serra da Galga Formation are known based on very incomplete skeletons. This is the case of “Series A” (Powell, 1986, 2003), known by a complete neck and anterior trunk vertebrae, and of *C. allocaudata*, known only by a portion of its tail. Hence, pending on the identification of further anatomical parts of such forms, the remains housed at CPPLIP and described here may help to complement the knowledge on parts of their anatomy.

Among those, the Aeolosaurini indet. CPPLIP-248 is particularly important. All three titanosaur nominal species from the Serra da Galga Formation (i.e., *B. britoi*, *U. ribeiroi*, and *C. allocaudata*) can be differentiated from this specimen based on the anatomy of their preserved antero-to-mid caudal vertebrae (Martinelli et al., 2011). Hence, it may represent a hitherto unrecognized Aeolosaurini, a clade that already congregates most titanosaurs from the Bauru Group (*e.g.,* Hechenleitner et al., 2020; Silva Junior et al., 2022; Navarro et al., 2022).

Finally, the "Museu dos Dinossauros" and all the research conducted at CPPLIP highlights the importance of these institutions for the advancement of Paleontology. Specially in this case, when systemic diggings are carried out and new fossil specimens are constantly unearthed.

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Figure 1. Historical pictures of the Peirópolis region. **A,** the deactivated train station before was turned on the museum; **B,** vision of the museum and titanosaur sculpture; **C,** The Caiera quarry, also known as "Ponto 1" and **D,** former museum exhibition (from the archives of AGM).

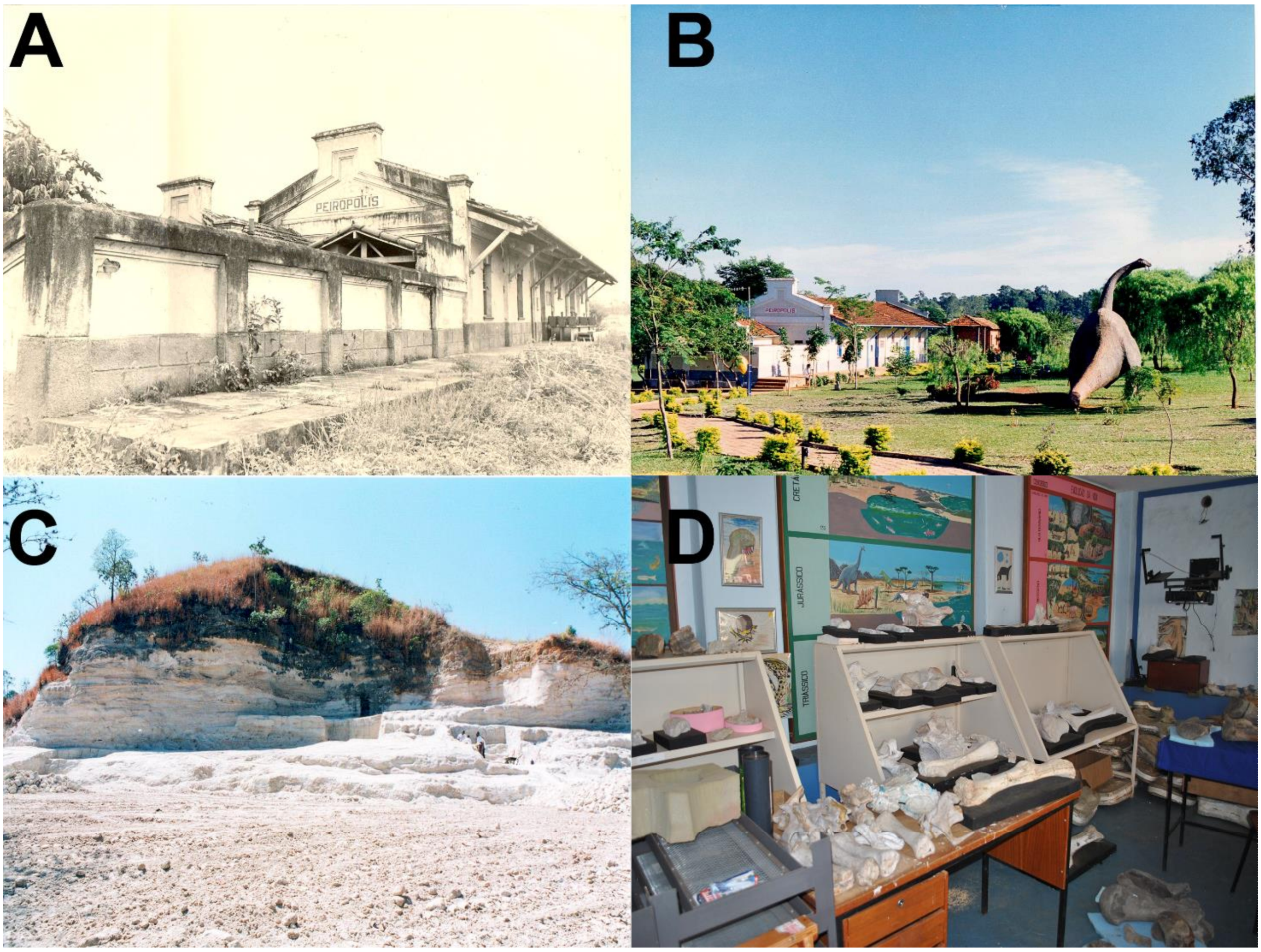

Figure 2. Map of the Uberaba region indicating different outcrops (Modified from Silva Junior et al., 2022).

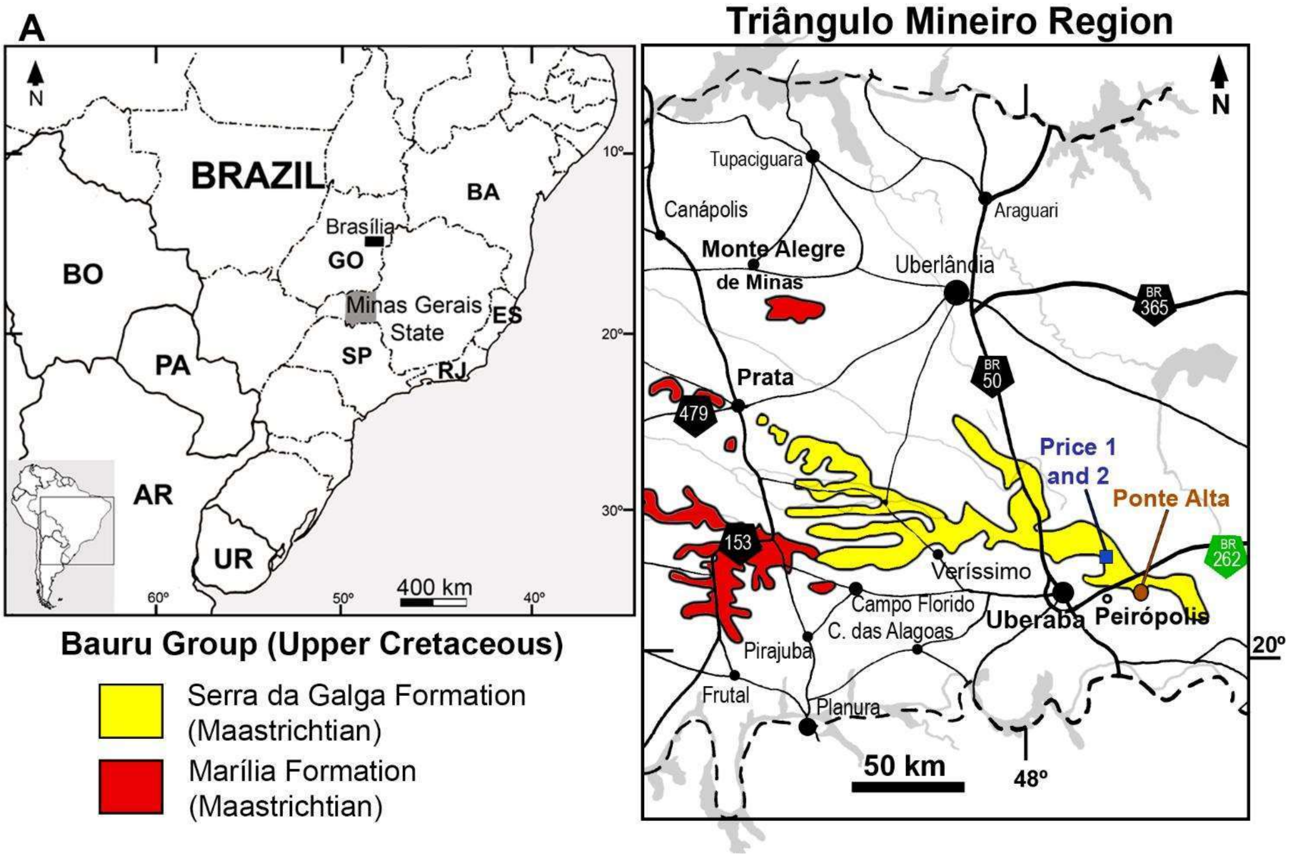

Figure 3. Cervical vertebrae. **A,** CPPLIP-234 in 1, left lateral; 2, right lateral; 3, anterior; 4, posterior; 5, dorsal and 6, ventral views. **B,** CPPLIP-258 in 1, left lateral; 2, right lateral; 3, ventral; 4, posterior and 5, anterior views. **C,** CPPLIP-1457 in 1, left lateral; 2, right lateral; 3, ventral; 4, posterior and 5, anterior views. Abbreviations: **adcl:** anterior centrodiapophyseal lamina; **acpl:** anterior centroparapophyseal lamina; **pacdf:** parapophyseal centrodiapophyseal fossa; **pcdl:** posterior centrodiapophyseal lamina; **spof:** spinopostzygapophyseal fossa; **sprl:** spinoprezygapophyseal lamina; **sprf:** spinoprezygapophyseal fossa; **tpol:** interpostzygapophyseal lamina; **tprl:** interprezygapophyseal lamina.

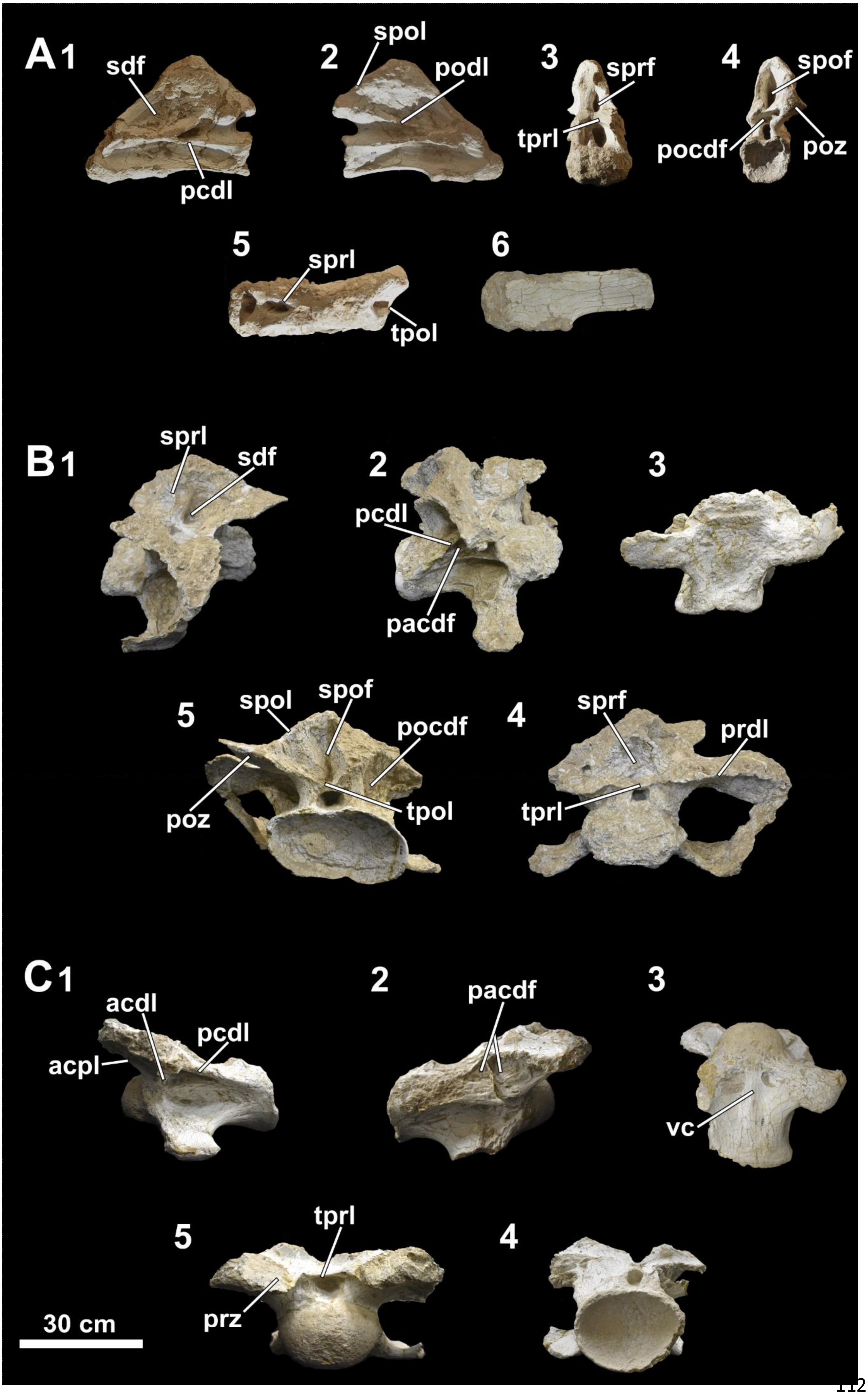
A1
sdf
pcdl
2
spol
podl
3
sprf
tprl
4
spof
pocdf
poz
5
sprl
tpol
6
B1
sprl
sdf
2
pcdl
pacdf
3
5
spol
spof
pocdf
poz
tpol
4
sprf
prdl
tprl
C1
acdl
pcdl
acpl
2
pacdf
3
vc
5
tprl
prz
4
30 cm

Figure 4. Caudal vertebrae. **A,** CPPLIP-1130 in 1, left lateral; 2, anterior; 3, dorsal; 4, right lateral; 5, posterior and 6, ventral views. **B,** CPPLIP-1175 in 1, left lateral; 2, anterior; 3, dorsal; 4, right lateral; 5, posterior and 6, ventral views. **C,** CPPLIP-899 in 1, left lateral; 2, anterior; 3, dorsal; 4, right lateral; 5, posterior and 6, ventral views. **D,** CPPLIP-248 in in 1, left lateral; 2, anterior; 3, dorsal; 4, right lateral; 5, posterior and 6, ventral views. Abbreviations: **cprl:** centroprezygapophyseal lamina; **cpol:** centropostzygapophyseal lamina; **poz:** postzygapophyses; **spol:** spinopostzygapophyseal lamina; **sprl:** spinoprezygapophyseal lamina; **sprf:** spinoprezygapophyseal fossa.

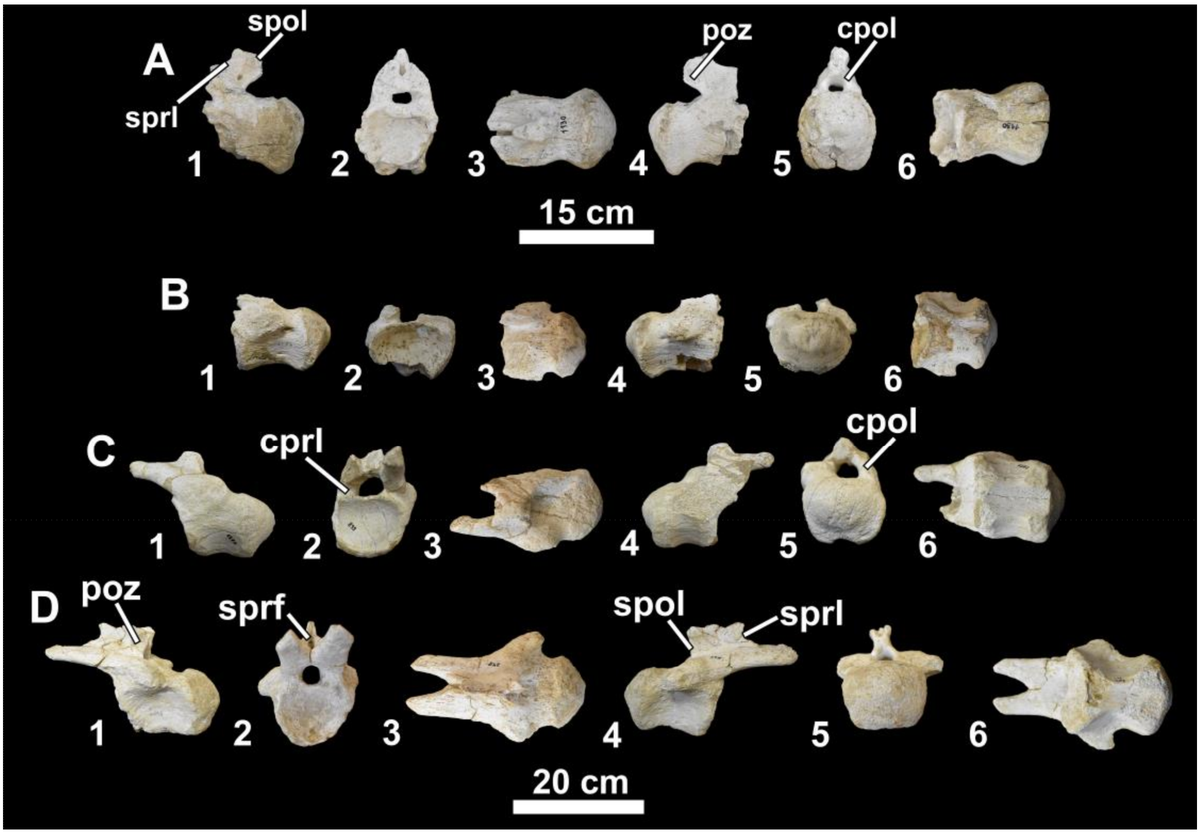

Figure 5. Caudal vertebrae. **A,** CPPLIP-394; **B,** CPPLIP-393; **C,** CPPLIP-395; **D,** CPPLIP-396; **E,** CPPLIP-400; **F,** CPPLIP-398; **G,** CPPLIP-401; **H,** CPPLIP-399; **I,** CPPLIP-170 and **J,** CPPLIP-401 in left lateral, anterior, dorsal, right lateral, posterior and ventral views. Abbreviations: **cprl:** centroprezygapophyseal lamina; **cpol:** centropostzygapophyseal lamina; **spol:** spinopostzygapophyseal lamina; **sprl:** spinoprezygapophyseal lamina; **sprf:** spinoprezygapophyseal fossa.

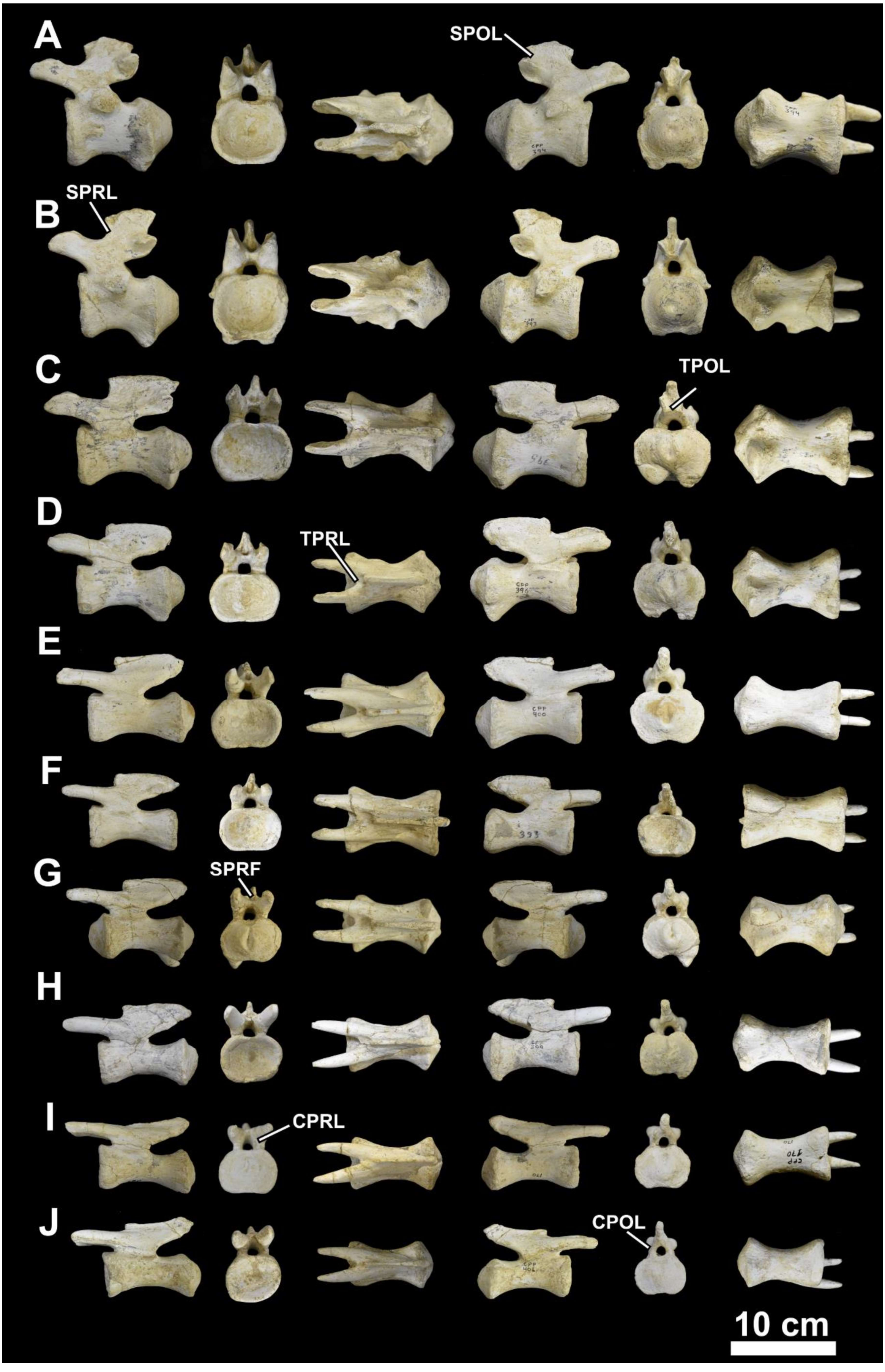
A
SPOL
B
SPRL
C
TPOL
D
TPRL
E
F
G
SPRF
H
I
CPRL
J
CPOL
10 cm

Figure 6. Scapular girdle. CPPLIP-444 (left scapula) in **A,** lateral and **B,** medial views. Abbreviations: **ac:** acromion; **acr:** acromial ridge; **lmc:** lateromedially projected crest; **lp:** lateral protuberance; **pdc:** proximodistally projected crest; **scb:** scapular blade.

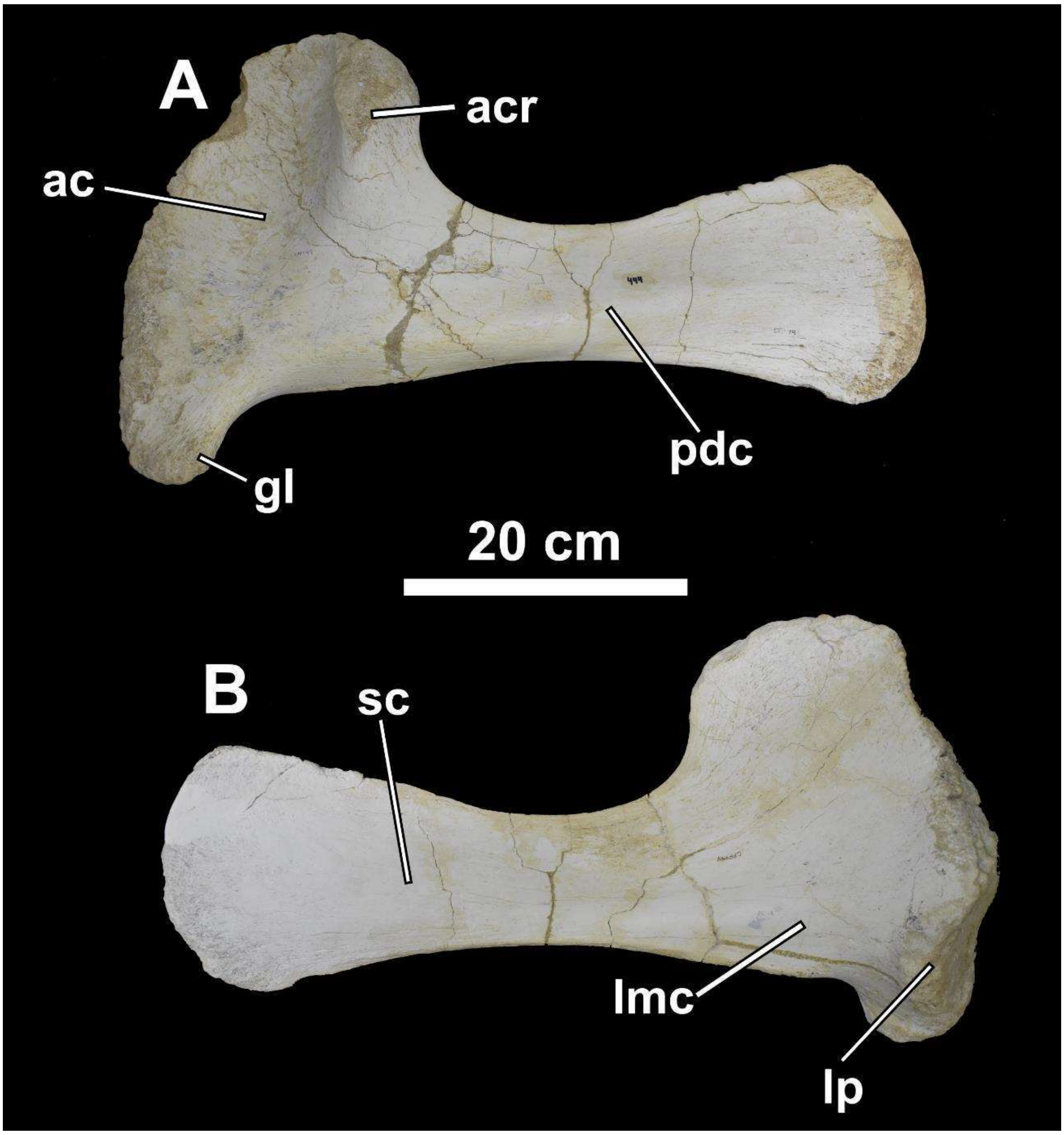

Figure 7. Humeri. **A,** CPPLIP-119 (left humerus) in 1, anterior; 2, posterior; 3, proximal and 4, distal views. **B,** CPPLIP-897 (right humerus) in 1, anterior; 2, posterior and 3, distal views. **C,** CPPLIP-408 (right humerus) in 1, anterior; 2, posterior; 3, proximal and 4, distal views. **D,** CPPLIP-1174 in 1, anterior; 2, posterior; 3, proximal and 4, distal views. Abbreviations: **dc:** deltapectoral crest; **lpc:** laterally projected crest; **rac:** radial condyle; **ulc:** ulnar condyle.

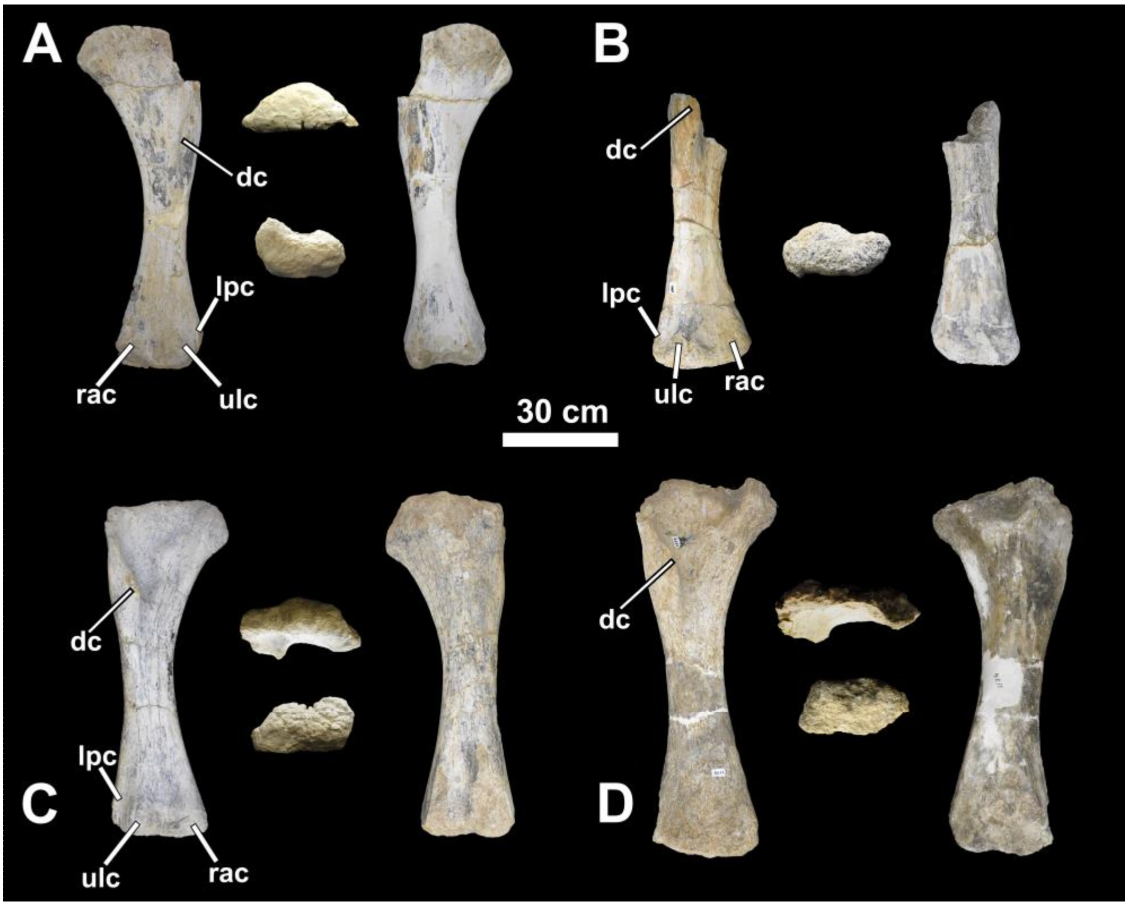

Figure 8. Femora. **A,** CPPLIP-653 (left femur) in 1, anterior/oblique and 2, posterior/ oblique views. **B,** CPPLIP-881 (left femur) in 1, anterior/oblique and 2, posterior/ oblique views. Abbreviations: **fic:** fibular condyle; **ft:** fourth trochanter; **dec:** proximodistally expanded crest; **gtr:** great trochanter; **lmd:** lateromedial depression; **tic:** tibial condyle; **trf:** trochanteric shelf.

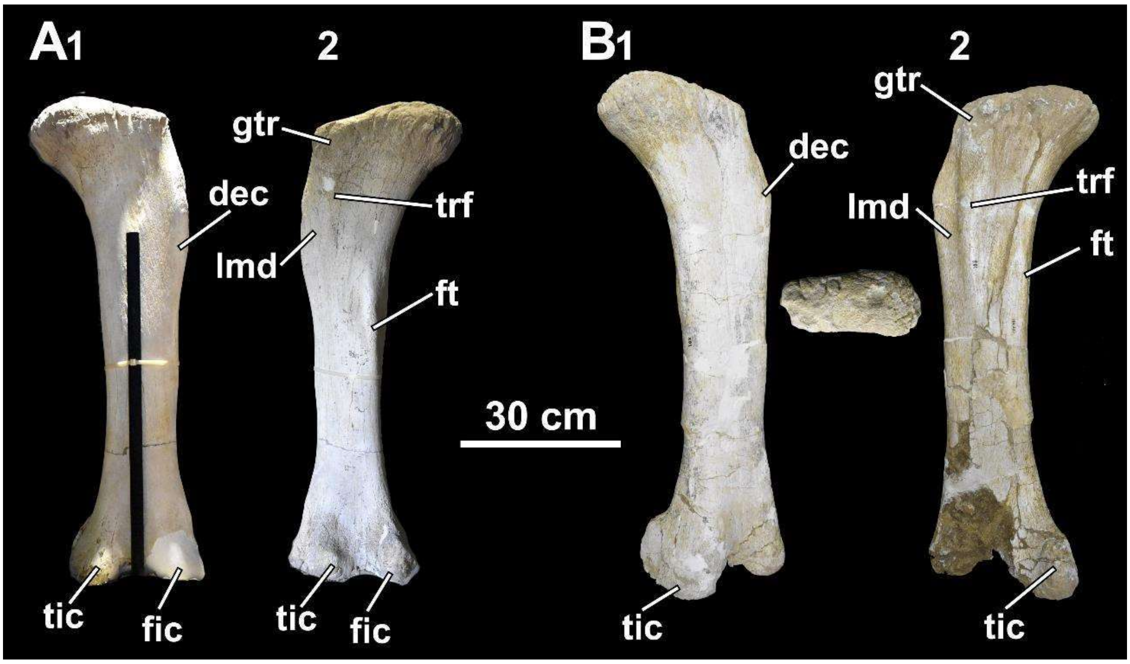

Figure 9. Crural elements. **A,** CPPLIP-493 (right tibia) in 1, lateral; 2, medial; 3, proximal and 4, distal views. **B,** CPPLIP-262 (left fibula) in 1, lateral; 2, medial; 3, proximal and 4, distal views. **C,** CPPLIP-403 (right fibula) in 1, lateral; 2, medial; 3, proximal and 4, distal views. Abbreviations: **cc:** cnemial crest; **fk:** fibular knob; **fvl:** fovea ligamentosa; **jc:** joint capsule; **lt:** lateral protuberance; **tp:** tibial protuberance.

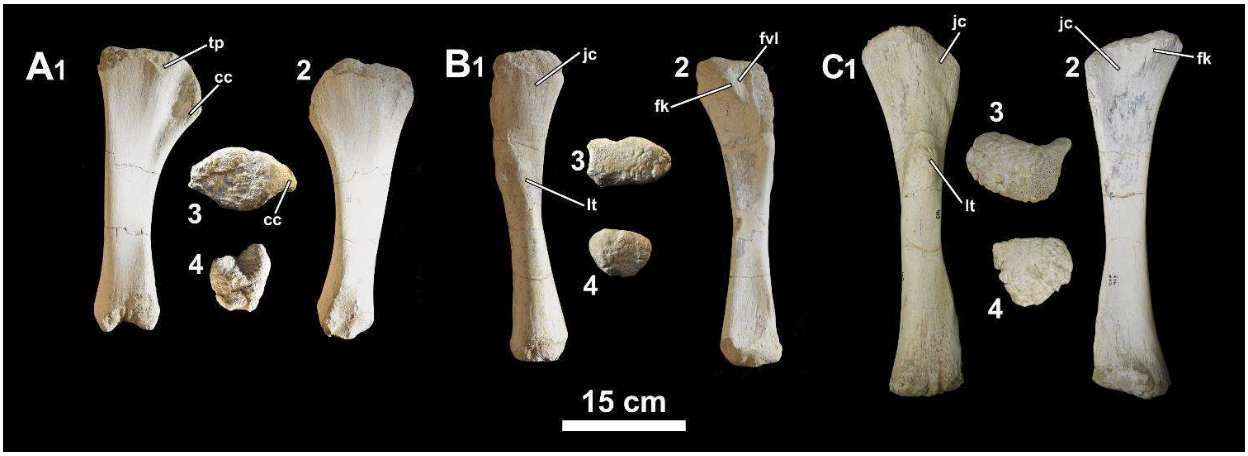

Table 1. Measurements (cm) of axial elements. * = incomplete values; ---- = structure not preserved. **CE:** cervical, **CA:** caudal; **P1:** Ponto 1, **P2:** Ponto 2; **aEI:** average elongation index; **AMCH:** anterior maximum centrum height; **AMCW:** anterior maximum centrum width; **ML1:** maximum length (with condyle); **ML2:** maximum length (without condyle); **NSH:** neural spine height; **PMCH:** posterior maximum centrum height; **PMCW:** posterior maximum centrum width.

Specimen	Element	Locality	aEI	ML1	ML2	AMCH	AMCW	PMCH	PMCW	NSH
CPPLIP-234	CE	RO	3,58	38,40	32,73	8,98	13,74	10,10	11,32	17,18
CPPLIP-258	CE	P2	1,19	28,32	20,66	14,55	23,44	14,55	32,73	19,86*
CPPLIP-1457	CE	P2	1,53	33,53	25,06	15,35	23,43	19,39	24,24	----
CPPLIP-1130	CA	P1	1,74	13,39	10,54	6,53	8,82	9,17	9,06	3,88*
CPPLIP-248	CA	P2	1,53	15,07	10,90	8,35	11,36	8,81	13,23	3,48*
CPPLIP-899	CA	P2	1,5	14,14	9,27	8,35	10,44	8,11	12,29	----
CPPLIP-1175	CA	P2	----	14,15*	10,66*	6,72	12,05	9,05	12,76	----
CPPLIP-393	CA	P1	1,57	9,06	6,77	5,33	6,22	4,5	6,23	4,62*
CPPLIP-394	CA	P1	1,56	9,6	6,94	6,04	6,22	4,44	5,86	3,73*
CPPLIP-395	CA	P1	1,66	10,49	8,53	4,98	7,64	4,99	7,64	3,56*
CPPLIP-396	CA	P1	1,92	9,95	8,71	3,91	6,41	4,09	6,75	----
CPPLIP-400	CA	P1	1,77	9,73	8,8	4,68	6,26	5,2	6,8	----
CPPLIP-397	CA	P1	1,69	8,13	8,13	4	5,61	3,33	5,34	----
CPPLIP-398	CA	P1	2,14	10	6,53	3,73	5,6	3,3	5,2	----
CPPLIP-390	CA	P1	1,81	9,06	7,73	4,26	5,73	4,54	5,2	----
CPPLIP-170	CA	P1	1,81	8,93	7,73	3,86	6,01	3,61	4,81	----
CPPLIP-401	CA	P1	1,91	8,54	7,47	4,15	4,8	3,46	4,93	----

Table 2. Measurements (cm) of scapular girdle. * = incomplete measures. **P1:** Ponto 1. **MPL:** maximum proximodistal length; **MMB:** maximum mediolateral breadth.

Specimen	Element	Locality	MPL	MMB
CPPLIP-444	Scapula	**P1**	5,47	30,83

Table 3. Measurements (cm) of humeri. ---- = structure not preserved; * = incomplete measures. **P1:** Ponto 1, **RO:** Rodovia. **DAW**: distal anteroposterior width; **DWI:** distal width index; **ECC:** eccentricity index; **ML:** maximum proximodistal Length; **MPTB:** maximum proximal transverse breadth; **MMB:** midshaft mediolateral breadth; **MSC:** midshaft circumference; **MDTB:** maximum distal transverse breadth; **PAW:** proximal anteroposterior width; **PWI:** proximal width index.

Specimen	Element	Locality	DAW	DWI	ECC	ML	MPTB	MMB	MSC	MDTB	PAW	PWI
CPPLIP-119	Humerus	RO	11,33	0,24	1,10	87,93	28,51	11,69	37,3	21,64	11,72	0,13
CPPLIP-877	Humerus	RO	13,07	----	1,08	68,73 *	----	10,31	42,8	27,47	----	----
CPPLIP-408	Humerus	P1	10,91	0,12	1,26	87,25	31,48	12,71	43,3	26,74	10,73	0,12
CPPLIP-1174	Humerus	P1	13,05	----	1,45	95,83 *	35,41	14,76	45,8	28,26	10,34	----

Table 4. Measurements (cm) of forelimb elements. ---- = structure not preserved; * = incomplete measures. **P1:** Ponto 1, **P2:** Ponto 2. **DAW**: distal anteroposterior width; **DWI:** distal width index; **ML:** maximum proximodistal Length; **MPTB:** maximum proximal transverse breadth; **MMB:** midshaft mediolateral breadth; **MSC:** midshaft circumference; **MDTB:** maximum distal transverse breadth; **PAW:** proximal anteroposterior width; **PWI:** proximal width index.

Specimen	Element	Locality	DAW	DWI	ML	MPTB	MMB	MSC	MDTB	PAW	PWI
CPPLIP-653	Femur	P1	17,8	0,19	90,73	26,22	9,8	54,3	24,64	8,95	0,98
CPPLIP-881	Femur	P2	----	----	98,59	27,89	10,7	58,9	27,17*	10,31	0,10
CPPLIP-493	Tibia	P1	8,05	----	33,45*	12,71	5,83	22,3	6,22	6,87	----
CPPLIP-262	Fibula	P2	5,44	0,14	37,98	9,86	4,28	25,2	7,64	7,13	0,18
CPPLIP-403	Fibula	P2	7,78	0,17	45,12	11,44	5,33	26,5	9,22	7,14	0,2