



New lithostrotian specimens (Neosauropoda: Titanosauria) from the Mato Grosso State (western Brazil) and comments about tail injuries in sauropod dinosaurs

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ABSTRACT

Titanosaurs were a highly diverse group of sauropod dinosaurs, with hundreds of bones known from Brazil, mostly found isolated. The majority of them come from the Upper Cretaceous Bauru Basin, in southeastern Brazil. However, even though the Mato Grosso State (Midwest Brazil) provides the first historical findings of titanosaurs reported in the country, most of the recorded specimens remain undescribed. Here, we present newly titanosaur specimens collected in the 1950s in the Upper Cretaceous Cambambe Basin, near the Pedra Grande Creek, Chapada dos Guimarães municipality. The specimens are housed at the Museu de Ciências da Terra (Rio de Janeiro, Brazil) and comprise four incomplete caudal vertebrae and two portions of appendicular bones, including a probable fragmentary left ilium, which cannot be assigned to the same individual. Comparisons with more complete taxa allow us to identify this material as representative of two distinct morphotypes, both exhibiting a combination of primitive and derived morphological features. Additionally, the two caudal elements of Morphotype 1 present some pathological features, such as subchondral cysts, being the third case of this paleopathology reported in titanosaurs. Despite being fragmentary and lacking diagnostic features at a genus level, these new specimens demonstrate that Mato Grosso State holds great potential for the discovery of more material that can contribute to titanosaurian paleobiology.

1. Introduction

Titanosauria comprises the largest terrestrial animals that have ever lived on Earth (e.g., Carballido et al., 2017; Otero et al., 2021). With a worldwide distribution, the group represent approximately one-third of all sauropod diversity, demonstrating a substantial dominance during the Late Cretaceous period, particularly in South America (Cerdeira et al., 2012; Carballido et al., 2022). In Brazil, titanosaurs were the predominant herbivorous dinosaurs, with 14 nominal species described to date (Pereira et al., 2024). Titanosaur findings in Brazil have increased in recent years, especially in São Paulo and Minas Gerais states, all coming from deposits of the Bauru Basin (e.g., Santucci and Arruda-Campos, 2011; Bandeira et al., 2016; Navarro et al., 2022; Silva Junior et al.,

2022). This unit hosts most titanosaur occurrences in the country, as well as the most expressive taxonomic diversity (Bandeira et al., 2018). Additional titanosaur occurrences are also known from Lower Cretaceous strata, mainly in the northeast Brazil, but in smaller numbers (e.g., Zaher et al., 2011; Ghilardi et al., 2016; Carvalho et al., 2017).

Nonetheless, despite abundant and long dated known, titanosaur findings in Central-west Brazil remain elusive (e.g., Derby, 1890). The most expressive record originates from the Mato Grosso State, which is notable for being among the earliest regions to be explored in Brazilian vertebrate paleontology (e.g., Kellner and Campos, 1999; Gil et al., 2020). The first titanosaur specimen from this region was found in 1883 at the Pedra Grande site (Price, 1961), but the first mention about this specimen was made later by Huene (1931). The specimen, currently

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deposited in the Natural History Museum of London, was very incomplete and unfortunately not described in detail. Likewise, from a nearby locality, titanosaur materials were reported but remain undescribed, being found associated with the only named tetrapod taxon from this region, the abelisaurid theropod *Pycnonemosaurus nevesi* (Kellner and Campos, 2002).

Most of titanosaur findings in Mato Grosso State have been made at the Morro do Cambambe locality, a well-known site due to its prolific vertebrate record (see Sales et al., 2017; Bandeira et al., 2019 for a review). The first detailed anatomical description of a titanosaur specimen from this region with a tentative taxonomic identification was made

by Franco Rosas et al. (2004). The authors associated the specimen with the genus *Gondwanatitan*, previously known in the Bauru Group at São Paulo State, and erected the new Aeolosaurini, an endemic South American clade that would prove to be quite diverse, but with controversial relationships (Martinelli et al., 2011). In addition, some other titanosaur materials were recorded from this locality in the following years (e.g., Bandeira et al., 2019; Gil et al., 2020).

Here we report on new titanosaur specimens from the Pedra Grande locality, at Chapada dos Guimarães municipality that have been collected decades ago but remained undescribed until now. Moreover, we discuss the occurrence of pathological traits in caudal vertebrae of

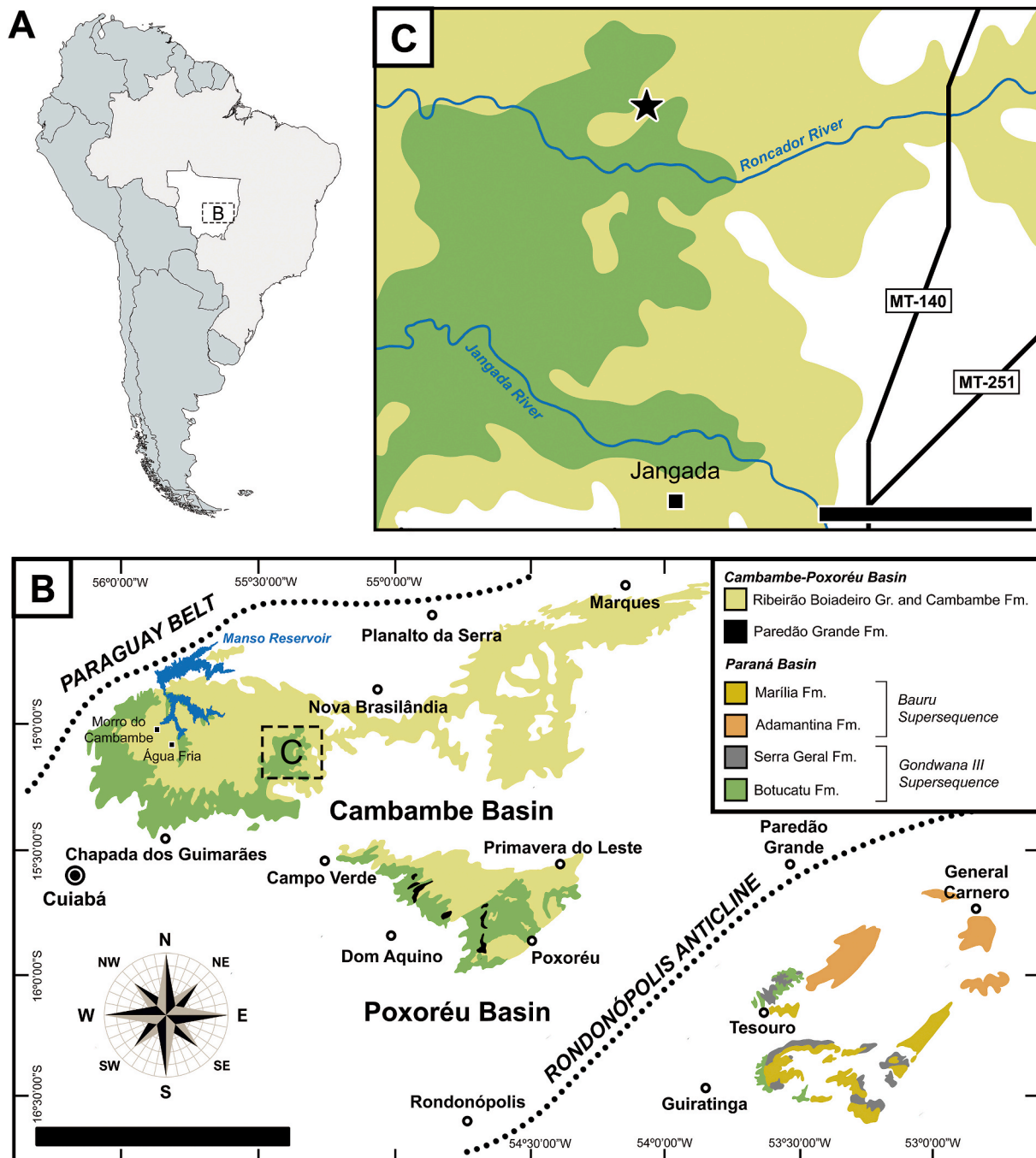


Fig. 1. The Cambambe–Poxoréu Basin in Mato Grosso State. (A) geographic localization of Mato Grosso State (white) in Brazil (light gray) and in South America (dark gray); (B) distribution of the fossiliferous Cretaceous strata in Mato Grosso State (based on Souza et al., 2004). Lithostratigraphy following Kuhn and da Paz (2020); (C) presumed localization of the Pedra Grande Creek and the homonymous farm (black star). Dotted lines indicate the main structural highs, while traced lines indicate enlarged areas. Scale bars equal 100 km (B) and 10 km (C).

sauropod dinosaurs and their paleobiological implications. The specimens described here not only represent new titanosaur occurrences in this region but also highlight the fossiliferous potential of Mato Grosso State.

2. Geological settings

The Upper Cretaceous strata in Mato Grosso State are distributed across four main deposits: Parecis, Paraná, Cambambe and Poxoréu basins (Fig. 1A and B). Regarding the latter units, both contain most of the fossil record known from this state (Sales et al., 2017). However, there is little consensus regarding the stratigraphic relations and hierarchy of their constituent units, given the lack of fossil taxa that allow a correlation with neighboring units. The Cambambe-Poxoréu deposits have already been referred to the Bauru Supersequence of the Paraná Basin (*sensu* Weska, 1996; Milani et al., 2007), as part of the Parecis Basin (e.g., Weska, 2006), or as composing individualized basins (Cambambe, Poxoréu and Itiquira; e.g., Coimbra, 1991; Kuhn et al., 2018). Nevertheless, most authors agree that the evolution of these small horst-grabens was associated with tectonic efforts related to the reactivation of the Trans Brazilian Lineament and the tectonic compartmentation of the Alto Garças Platform (Kuhn and da Paz, 2020).

Regarding the its stratigraphic succession, Coimbra (1991) divided these deposits into the Ribeirão Boiadeiro and Cambambe formations. On the other hand, Weska (1996) inserted those strata in the context of the Bauru Group, based on erosive unconformity with the Gondwana III Supersequence of the Paraná Basin, recognizing four units: Paredão Grande, Quilombinho, Cachoeira do Bom Jardim and Cambambe formations. In contrast, Kuhn et al. (2018) proposed the use of the term Ribeirão Boiadeiro Group to encompass the Cachoeira do Bom Jardim and Quilombinho formations, whose deposition correlates with the volcanic activity of the Paredão Grande Formation.

The Paredão Grande Formation is composed of coarse-to fine-grained pyroclastic rocks, associated with alkaline dykes and flows related with the Trindade Magmatic Plume event, aged at 83.9 ± 4 Ma ($^{40}\text{Ar}/^{39}\text{Ar}$ method; Gibson et al., 1997). The Quilombinho Formation predominantly consists of polymictic conglomerates with pebble-sized clasts of volcanic composition (probably coming from the Paredão Grande magmatism) in a sandy-clay matrix, interspersed with silexites, mudstones, siltstones, sandstones, and conglomeratic sandstones of a predominant tabular geometry (Kuhn and da Paz, 2020). The Cachoeira do Bom Jardim Formation which consists interdigitated with the Quilombinho Formation, consisting of stratified sandstones with carbonate cementation, laterally interspersed with continuous bodies of massive to laminated sandstones and intercalations of thick calcrete banks and fossiliferous silty levels. Laminated to massive reddish siltstones and levels of intraformational conglomerates also occur. The Cambambe Formation has its type-section in the homonymous hill (Fig. 1B), averaging 300 m in thickness. It lays in an erosive unconformity with the Ribeirão Boiadeiro Group and is composed predominantly of sandstones and rare polymictic orthoconglomerates. The Cretaceous succession is covered in a discordant way by the Cenozoic Cachoeirinha and Pantanal formations (Kuhn and da Paz, 2020).

According to the identification labels in the Museu de Ciências da Terra collection, all fossil elements described here were recovered in different years (1957–1958) from the same outcrop at Pedra Grande farm, near to a homonymous creek. The Pedra Grande Creek is an affluent of the Roncador River, emerging near the district of Jangada (Chapada dos Guimarães municipality). The titanosaur bones collected in 1883 mentioned by Derby (1890) and later by Huene (1931) were collected in a locality also named as “Pedra,” in the “municipality of Chapada”, which we assume that could corresponds to the same fossiliferous site. In the Pedra Grande fossil deposit, outcrops rocks from the Ribeirão Boiadeiro Group emerge, composed of the Quilombinho and Cachoeira do Bom Jardim formations (Fig. 1C). The specimens from Pedra Grande were attributed to the latter unit based on the reddish to

pinkish sandstones still adhered to the fossil material (Weska, 2006).

3. Materials and methods

3.1. Comparative osteology

Since the caudal vertebrae are the most complete and diagnostically informative elements, the description and comparisons were focused on these materials. To tentatively position of the examined caudal vertebrae within the caudal series, we conducted comparisons with the most complete taxa known (Table 1). Except for *Aeolosaurus*, the majority of taxa used for comparisons are monospecific. Therefore, we only mention the genera along the text. The anatomical and orientational nomenclature of the ‘Romerian’ descriptors was followed (Wilson, 2006). Vertebral laminae and fossae are identified and named using the landmark-based rationale applied to saurischian dinosaurs (Wilson, 1999, 2012; Wilson et al., 2011). The inference of epaxial and hypaxial musculature in the caudal series of sauropod dinosaurs was based on the osteological correlates provided by Díez Díaz et al. (2020).

3.2. CT-Scan imagery

We performed CT-Scan analyses using a General Eletrics CT 16 slice medical scanner, with more than 200 slices and a voxel size of 0.75 mm, belonging to the Centro Universitário de Controle do Câncer (CUCC) of the Universidade do Estado do Rio de Janeiro (UERJ). The acceleration voltage varied between 90 and 120 kV, with a electric current of 320 mA. The three-dimensional reconstruction was generated with the 3D Slicer software version 5.6.2 (available at <https://www.slicer.org/>).

Table 1
Selected specimens used in the comparisons.

Taxa	Specimen	Source
<i>Adamantisaurus mezzalirai</i>	MUGEO 1282,1289 and 1295	Firsthand examination; Santucci and Bertini (2006)
<i>Aeolosaurus rionegrinus</i>	MJG R-1	Firsthand examination; Powell (1987, 2003)
<i>Aeolosaurus colhuehuapensis</i>	UNPSJB-PV 959/1–27	Firsthand examination; Casal et al. (2007)
<i>Arrudaitan maximus</i>	MPMA 12-0001-97	Firsthand examination; Santucci and Arruda-Campos (2011)
<i>Baurutitan britoi</i>	MCT.R.1490	Firsthand examination; Kellner et al. (2005)
<i>Dreadnoughtus schrani</i>	MPM-PV 1156	Lacovara et al. (2014)
<i>Gondwanatitan faustoi</i>	MN 4111-V	Firsthand examination; Kellner and de Azevedo (1999)
<i>Mendozasaurus neguyelap</i>	IANIGLA-PV 065/1–22	Firsthand examination; González Riga et al. (2018)
<i>Menucocelsior arriagadai</i>	MPCN-PV-798	Aranciaga Rolando et al. (2022)
<i>Narambuenatitan palomoi</i>	MAU-Pv-N 425	Firsthand examination; Filippi et al. (2011)
<i>Neuquensaurus australis</i>	MCS-5	Firsthand examination; Salgado et al. (2005)
<i>Panamericansaurus schroederi</i>	MUCPv-417	Firsthand examination; Calvo and Porfiri (2010)
<i>Rinconosaurus caudamirus</i>	MAU-PV-CRS 25, 26 and 23/1–5	Firsthand examination; Pérez Moreno et al. (2021)
<i>Saltasaurus loricatus</i>	PVL 4017-22, 39, 91, 140, and 141	Firsthand examination; Powell (1992)
<i>Trigonosaurus pricei</i>	MCT.R.1719	Firsthand examination; Campos et al. (2005)
<i>Uberabatitan ribeiroi</i>	CPPLIP-1008–1012, 1014, 1019, 1020 and 1079	Firsthand examination; Silva Junior et al. (2019)

3.3. Institutional abbreviations

CPPLIP, Centro de Pesquisas Paleontológicas de Peirópolis Llewellyn Ivor Price from Universidade Federal do Triângulo Mineiro (UFTM), Peirópolis, Uberaba, Minas Gerais, Brazil; **MCT**, Museu de Ciências da Terra, Companhia de Pesquisas em Recursos Minerais – Serviço Geológico do Brasil, Rio de Janeiro, Brazil; **MUGEO**, Museu Geológico Valdemar Lefevre, São Paulo Brazil; **MJG**, Museo ‘Jorge Gerhold’, Río Negro, Argentina; **UNPSJB**, Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadavia, Argentina; **MPMA**, Museu de Paleontologia de Monte Alto, Monte Alto, São Paulo, Brazil; **MPM**, Museo Regional Padre Jesús Molina, Río Gallegos, Santa Cruz, Argentina; **MN**, Museu Nacional, Rio de Janeiro, Rio de Janeiro, Brazil; **IANIGLA**, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Mendoza, Argentina; **MPCN**, Colección Paleontología de Vertebrados, Museo Patagónico de Ciencias Naturales Juan Carlos Salgado, General Roca, Río Negro, Argentina; **MAU-Pv**, Paleontología de Vertebrados, Museo Municipal “Argentino Urquiza”, Rincón de los Sauces, Neuquén, Argentina; **MCS**, Museo de Cinco Saltos, Río Negro, Argentina; **MUCPv**, Museo de la Universidad Nacional del Comahue, Paleontología de Vertebrados, Neuquén, Argentina; **PVL**, Vertebrate Paleontology collection of the Instituto Miguel Lillo, Tucumán Province, Argentina.

4. Systematic paleontology

Dinosauria Owen, 1842.
Sauropoda Marsh, 1878.
Macronaria Wilson and Sereno, 1998.
Titanosauria Bonaparte and Coria, 1993.
Lithostrotia Upchurch et al., 2004.
Gen. et sp. indet.

4.1. Referred material

MCT.R.495, is represented by four but non-contiguous, caudal vertebrae collected in 1957; whereas MCT.R.412, which encompasses several fragmentary appendicular remains collected in 1958, including parts of long bones and a putative fragment of the posterior lobe of a left ilium. These materials are deposited in the paleontological collection (Reptiles) of MCT, Rio de Janeiro, Brazil.

4.2. Locality and horizons

The elements were recovered at the Pedra Grande farm locality (Chapada dos Guimarães Municipality, Mato Grosso State) by Llewellyn Ivor Price and his team, during the expeditions with the National Commission of Nuclear Energy from Brazil. In this locality, rocks from the Ribeirão Boiadeiro Group emerge, composed of the Quilombinho and Cachoeira do Bom Jardim formations, Cambambe Basin (*sensu Kuhn and da Paz, 2020*). The Ribeirão Boiadeiro Group is dated from the Upper Santonian to Lower Campanian interval, based on the absolute ages of the underlying Paredão Grande Formation, which has been constrained at 83.9 ± 0.4 Ma (latest Santonian) using the $^{40}\text{Ar}/^{39}\text{Ar}$ method (*Gibson et al., 1997*).

4.3. Description

4.3.1. Caudal vertebrae

General remarks — The caudal vertebrae described here were tentatively identified as the possible 11th–12th? and 18th–19th? elements, followed by another 18th–19th? and 20th–23rd? elements. We assume the positionings based on the conspicuous reduction of the transverse process, the development of the centra and some vertebral laminae when compared with more complete caudal series (see *Table 1*). Given the putative overlapping between the 18th–19th? elements, we consider these materials as pertain to two different individuals

(hereafter MCT.R.495a and MCT.R.495b). Moreover, both individuals exhibit notable differences in the preservation of the bone remains. Although the remains of MCT.R.495a individual lack minor parts of the zygapophyses, the periosteum is well-preserved in both elements. In contrast, the materials pertaining to MCT.R.495b exhibit several oxide impregnations and are severely weathered, with caudal elements missing the left lateral part of centrum and the entire neural arch. Thus, anatomical comparisons will be quite restricted.

In all vertebrae analyzed, a well-marked and strongly concave cotyle is present, as well as a developed procoely, where the condyle apex is orientated above the transversal axis. As in several titanosaurs, the neural arch is placed over the anterior half of the centrum (*Salgado et al., 1997*; but also see *Lerzo et al., 2024*), but not surpassing the anterodorsally margin of the cotyle as observed in Aeolosaurini taxa (*Casal et al., 2007*; *Martinelli et al., 2011*). The morphology and position of these elements in the caudal series further allows us to infer that the specimens correspond to advanced lithostrotians (e.g., *Powell, 2003*; *Upchurch et al., 2004*). Additionally, despite some morphological differences between the caudal elements could be reflect variations throughout the caudal series, such as length-to-width ratios and average elongation indexes (*Table 2*). Several characters allow us to allocate MCT.R.495a and MCT.R.495b not only as distinct individuals but also as two distinct morphotypes. These differences are discussed and detailed below.

Morphotype 1 (MCT.R.495a) — Morphotype 1 is distinguished by having caudal centra that are proportionally more elongated than those in Morphotype 2 (see *Table 2*), with the apex of the condyle more deflected dorsally than in the latter. Comparing both morphotypes, the centra of Morphotype 1 are wider compared to Morphotype 2, with the cotyle being as wide as high, presenting subcircular to subquadrangular outlines. Laterally, both vertebral centra of Morphotype 1 are poorly compressed dorsoventrally, exhibiting pronounced marks reminiscent of transverse processes in the transition to the neural arch. In turn, the neural arches are anteriorly placed in the centra and extend anteroposteriorly following the length of the centrum.

The 11th–12th? vertebra is quite incomplete, missing only the dorsal edge of the neural spine and the right prezygapophysis (*Fig. 2*). In the anterior view, the cotyle presents a thick border, with maximum

Table 2

Selected measurements (in mm) of the caudal elements from Pedra Grande specimens (MCT.R.495a and MCT.R.495b).

Measurements	Morphotype 1 (MCT.R.495a)		Morphotype 2 (MCT.R.495b)	
	11th–12th	18th–19th	18th–19th	20th–23rd
Centrum, maximum anteroposterior length (with condyle)	172	137	105	111
Centrum, minimum anteroposterior length (without condyle)	135	110	74	80
Cotyle, maximum dorsoventral height	112	73	63	61
Cotyle, maximum width	118	75	64	41
Condyle, maximum dorsoventral height	110	84	64	62
Condyle, maximum width	131	80	71	25
Total dorsoventral height (with neural arch)	191	141	85	79
Length-to-Height Ratio (LHR) ^a	1.56	1.63	1.64	1.79
Average Elongation Index (aEI) ^b	1.17	1.49	1.17	1.57

^a LHR corresponds to maximum anteroposterior length of the centrum (with articular condyles) divided by the dorsoventral height of the posterior surface.

^b aEI corresponds to minimum anteroposterior length of the centrum (excluding articular condyles) divided by the mean average value of the maximum width and dorsoventral height of the cotyle.

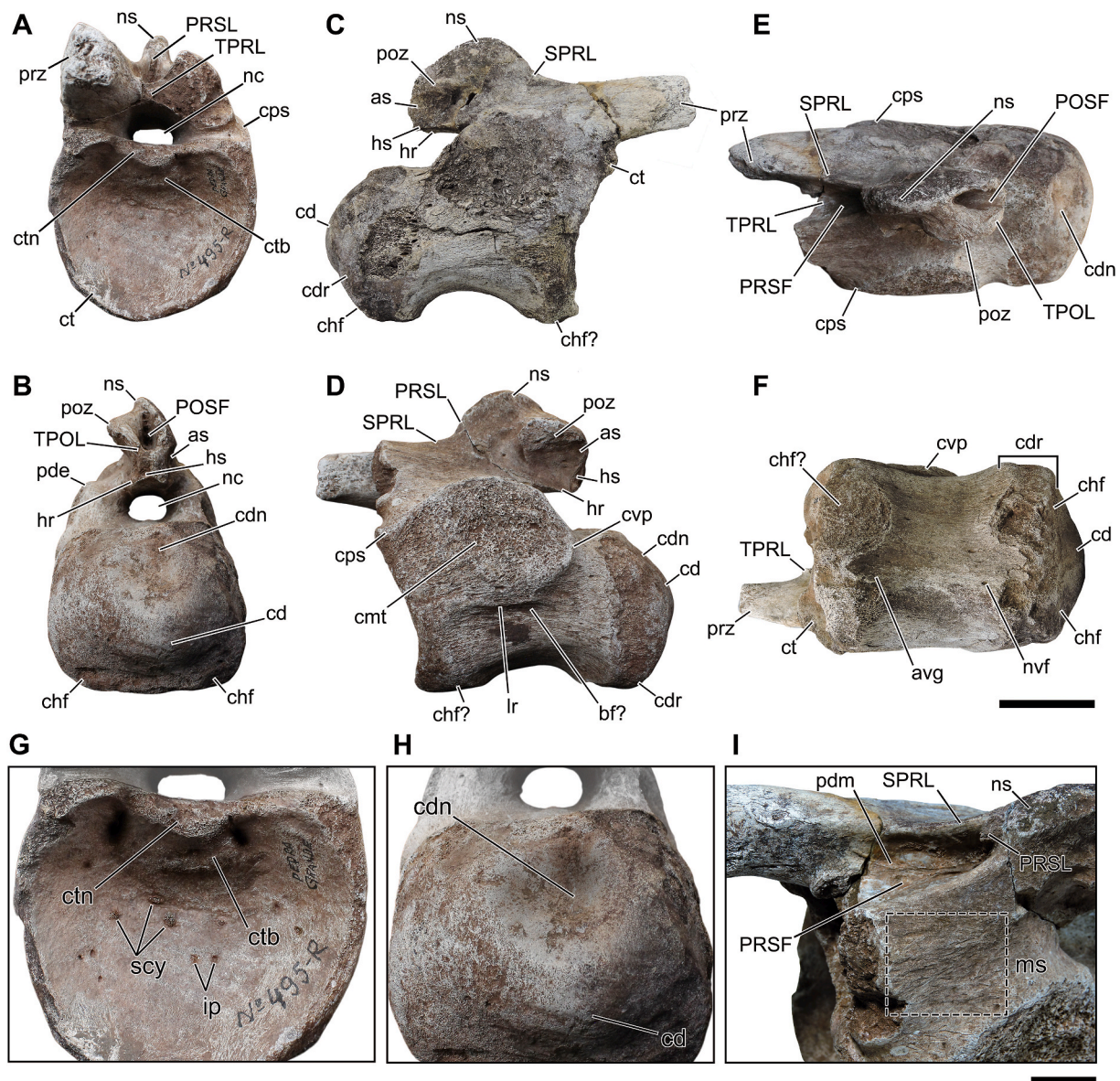


Fig. 2. Pedra Grande titanosaur (Morphotype 1). Probable 11th–12th caudal vertebra in (A) anterior, (B) posterior, (C) right lateral, (D) left lateral, (E) dorsal and (F) ventral views. (G–I) detail from the neural arch and centrum. Anatomical abbreviations: as, articular surface; avg, anteroventral groove; bf, blind fossa; cd, condyle; cnd, condylar notch; cdr, condylar ridge; chf, chevron facet; cmt, camellate tissue; cps, costovertebral process scar; ct, cotyle; ctb, cotylar bulge; ctn, cotylar notch; cvp, costovertebral process; hr, hyposphenal ridge; hs, hyposphene; ip, invagination pit; lr, lateral ridge; ms, muscular striae; nc, neural canal; ns, neural spine; pde, posterodorsal eminence; pdm, pneumatic diverticula mark; POSF, postspinal fossa; poz, postzygapophysis; PRSF, prespinal fossa; PRSL, prespinal lamina; prz, prezygapophysis; scy, subcondral cyst; SPRL, spinoprezygapophyseal lamina; TPRL, intraprezygapophyseal lamina. Scale bars equal 50 mm (A–F) and 20 mm (G–I).

thickening in the dorsolateral portion where a cotylar notch is observed medially (Fig. 2A–G). Additionally, below this notch and entering the cotyle, a trapezoidal and well-developed bulge is present, fading inward towards the cotyle center. In the posterior view, the condyle apex is slightly deflected ventrally and exhibits a concave depression forming a broad condylar notch (Fig. 2B–H). We interpret these characters as codependent and distributed serially, as they are also present in the most posterior element (see below). These structures have never been observed in other titanosaurs until now, particularly the cotylar bulge, leading us to interpret them as a putative autapomorphy of this morphotype.

In the lateral view, the dorsal margin of the centrum is flattened and almost rectilinear, while the ventral surface is slightly concave (Fig. 2C and D). Costovertebral processes are broad, occupying almost the entire anteroposterior extension of the neural arch. The left side of the centrum

is better preserved, showing that the costovertebral process develops both dorsally and ventrally. However, although weathered, the processes are poorly developed laterally, giving a rectangular aspect to the centrum in the dorsal and ventral views (Fig. 2E and F). Ventrally to it, a ridge delimits an incipient fossa with no connection to the internal part of the vertebrae (i.e., blind fossa), which is possibly a remnant insertion point of the medial *M. ilioischio-caudalis*.

A slight median constriction is present, being more pronounced ventrally due to a robust ridge that bounds the posterior condyle. This condylar ridge becomes thicker most in the lateral and ventral edges, being undifferentiated from the posterior condyle in posterior view. The ventral surface of the centrum presents a marked anteroventral groove, but ventrolateral ridges are absent. The anteroventral groove appears to be longitudinally shallow and delimited by anterior chevron facets (Fig. 2F). Posterior facets for chevrons appear to be broader and more

developed in the condyle rather than on the ventral surface.

The infrazygapophyseal region of neural arches ('pedicel') is mediolaterally wider and dorsoventrally shorter in anterior view, with an ellipsoid neural canal that is wider than tall (Fig. 2A). In contrast, the neural arch pedicel extends anteriorly in the posterior view bearing a posterodorsal eminence (Fig. 2B–D). The neural arch is positioned anteriorly on the centrum, with its anteroventral margin blending seamlessly with the dorsal edge of the cotyle. A remarkable scar is present anteriorly to the costovertebral of processes, being more developed in the right side (Fig. 2D and E).

The neural arch is low dorsoventrally and has approximately the same height as the centrum. The preserved prezygapophysis is robust and anteroposteriorly short, projecting slightly anterodorsally. Several striations are present on the lateral surface of the left prezygapophysis,

which probably correspond to scars of the epaxial musculature, such as the *M. articulospinalis* and *M. tendinoarticularis*. The intra-prezygapophyseal lamina (TPRL) is well-developed and extends close to the cotyle, creating a deep prespinal fossa (Fig. 2I). In addition, the prespinal fossa has paired striations that extend into the neural spine, likely representing impressions of the *M. multifidus* or pneumatic diverticula. Marked spinoprezygapophyseal laminae run from the anteromedial margin of the prezygapophyses into the neural spine, and are separated by a rough and incipient prespinal lamina (PRSL).

The neural spine is low, transversely compressed, and slightly inclined anteriorly (Fig. 2C–E). In dorsal view, the neural spine exhibits a pendant-like shape, with a deep postspinal fossa between the postzygapophyses. However, a postspinal lamina is absent. The postzygapophyses are positioned posteriorly with respect to the

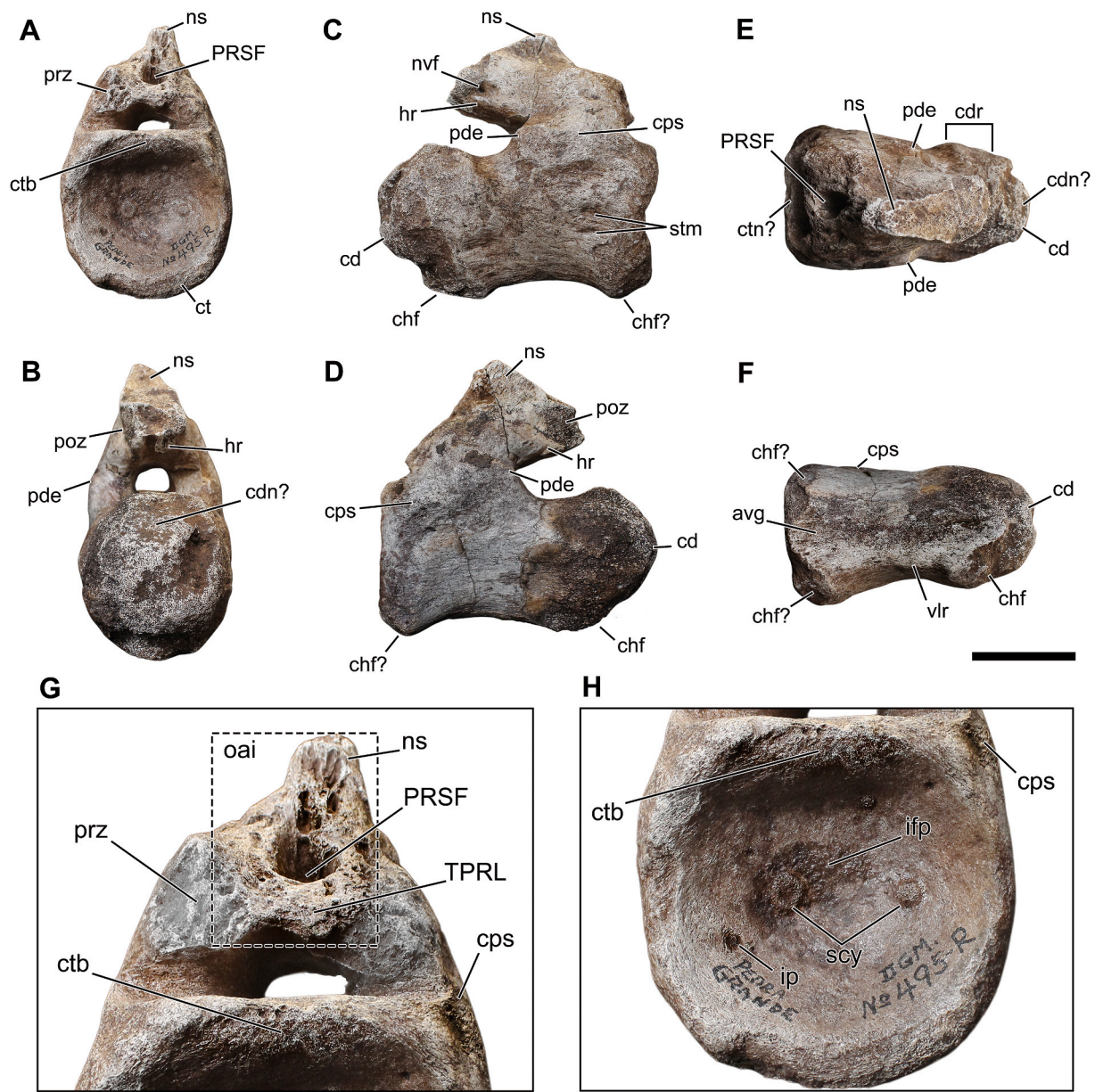


Fig. 3. Pedra Grande titanosaur (Morphotype 1). Probable 18th–19th caudal vertebra in (A) anterior, (B) posterior, (C) right lateral, (D) left lateral, (E) dorsal and (F) ventral views. (G–H) detail from the neural arch and centrum. Anatomical abbreviations: **avg**, anteroventral groove; **cd**, condyle; **cdn**, condylar notch; **cdr**, condylar ridge; **chf**, chevron facet; **cps**, costovertebral process scar; **ct**, cotyle; **ctb**, cotylar bulge; **ctn**, cotylar notch; **hr**, hyposphenal ridge; **ifp**, inflammatory process; **ip**, invagination pit; **ns**, neural spine; **oai**, osteoarthritis inflammatory; **pde**, posterodorsal eminence; **poz**, postzygapophysis; **PRSF**, prespinal fossa; **prz**, prezygapophysis; **scy**, subchondral cyst; **stm**, scratches marks; **TPRL**, intra-prezygapophyseal lamina. Scale bars equal 50 mm (A–F) and 20 mm (G–H).

costovertebral processes in the lateral view and exhibit large, flat articular surfaces oriented obliquely, with bony processes developing dorsolaterally. Ventrally to postzygapophyses, a thick hyposphene is present bounding the intrapostzygapophyseal lamina (TPOL). This structure exhibits laterally marked ridges, but which do not form hyposphenal laminae.

The 18th–19th? vertebra is less complete than the anterior one (Fig. 3). This element exhibits some scars and scratches in the lateral side, together with signal of bone remodeling and some abnormal tissue in the neural arch. These unusual features are explained in more detail in the “Paleopathological features” section.

In anterior view, the cotyle has a thick border as in the other Morphotype 1 vertebra, but no cotylar notch is observable. The dorsal surface of the centrum, above the posterior end, has a shallow concavity which is limited posteriorly by the dorsal rim of the posterior articulation. A shallow dorsal concavity is present on the posterior portion of the centrum, where a bony edge limits the very pronounced and slightly dorsally inclined posterior end. The neural arch is asymmetrically developed (Fig. 3A and B), with a strong inclination to the right side. The element lacks both prezygapophyses, where only the most basal portion of the pedicel is preserved. In this region, a deep but not extended prespinal fossa (PRSF) is observed. In the posterior view, the centrum exhibits a more circular outline. The postzygapophyses are well developed, featuring a proportionally wider, flattened and inclined articulation surface (Fig. 3B). A pair of hyposphenal ridges is present, though they are less developed compared to the other caudal vertebra.

Laterally, the centrum bears two lateral projections oriented ventrally for the chevron (Fig. 3C and D), with stretch marks (possibly from muscle scar) predominantly visible on the left side. A pair of small circular openings, likely neurovascular foramina, are developed laterally on each side of the neural arch, positioned more anteriorly than the facet articulation of the postzygapophyses (Fig. 3C). The centrum is more compressed laterally than the putative 11th–12th? caudal vertebra of Morphotype 1.

The neural spine, although incomplete, presents the vertical projection of its anterior corner placed behind the middle part of the

centrum. The posterior corner of the neural spine also rests over the distal articulation. Pre- and postspinal laminae are not observable.

The transverse processes are missing, as expected due to its more distal position in comparison with the 11th–12th? vertebra, as this structure is lost within the titanosaurian caudal sequence (Kellner et al., 2005). However, a costovertebral process scar is observed instead of the transverse processes, especially in the left side. This costovertebral process scar presents a thickening in a posterior direction. Dorsally, a posterodorsal eminence is visible on both sides of the caudal vertebra, placed before the middle part of the centrum.

Morphotype 2 (MCT.R.495b) — The caudal elements belonging to the Morphotype 2 are quite incomplete, and thus very detailed comparisons are difficult. Nonetheless, the Morphotype 2 caudal vertebrae are proportionally shorter when compared with the caudal elements from the Morphotype 1. Overall, the caudal elements of this morphotype tend to be more compressed laterally, presenting a squarer outline.

In anterior view, the caudal 18th–19th? has a relatively short centrum, entirely lacking the neural arch. The centrum has a subcircular outline, being higher than wider, presenting the dorsal and ventral margins somewhat flattened (Fig. 4A). A transverse process eminence is also observable, but solely in the right side.

The posterior part of the centrum has a condyle dorsoventrally oriented, with a lateral margin of the anterior articulation surface slightly rounded. A shallow dorsal concavity is present on the posterior portion of the centrum at the dorsal surface, as in the caudal elements of the Morphotype 1. However, the concavity is more pronounced, and the posterior end of the centrum is more inclined dorsally. The ventral face presents a prominent ventrolateral ridge, which is preserved in the left side (Fig. 4D). Ventrally, an eroded articulation surface could represent the chevron facets.

The neural arch suture is restricted and placed on the anterior portion of the centrum, presenting a strong neural arch pedicel. The neural canal is quite broad, being developed strongly laterally. A prominent bulge, indicative of the fusion of the transverse process and the centrum or neural arch can be observed.

Lastly, the 20th–23rd caudal vertebra (Fig. 5) is the most incomplete

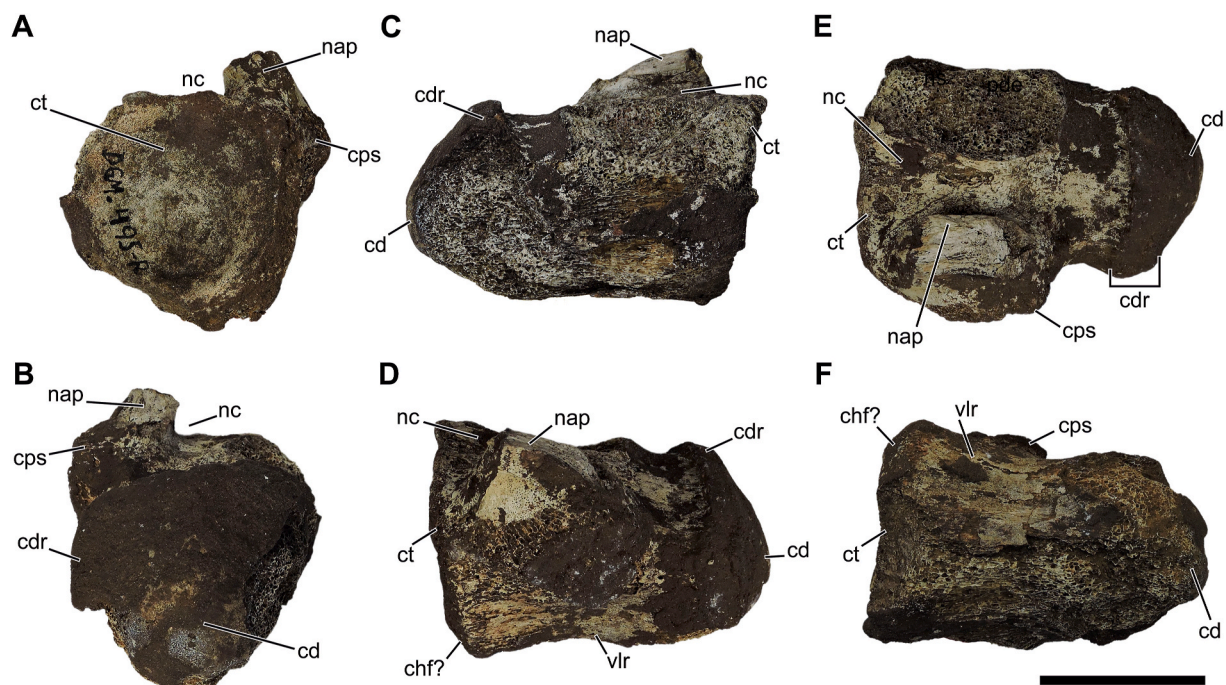


Fig. 4. Pedra Grande titanosaur (Morphotype 2). Probable 18th–19th caudal vertebra in (A) anterior, (B) posterior, (C) right lateral, (D) left lateral, (E) dorsal and (F) ventral views. Anatomical abbreviations: **cd**, condyle; **cdr**, condylar ridge; **chf?**, chevron facet; **ct**, cotyle; **nap**, neural arch pedicel; **nc**, neural canal; **tp**, transverse process; **vlr**, ventrolateral ridge. Scale bar equals 50 mm.

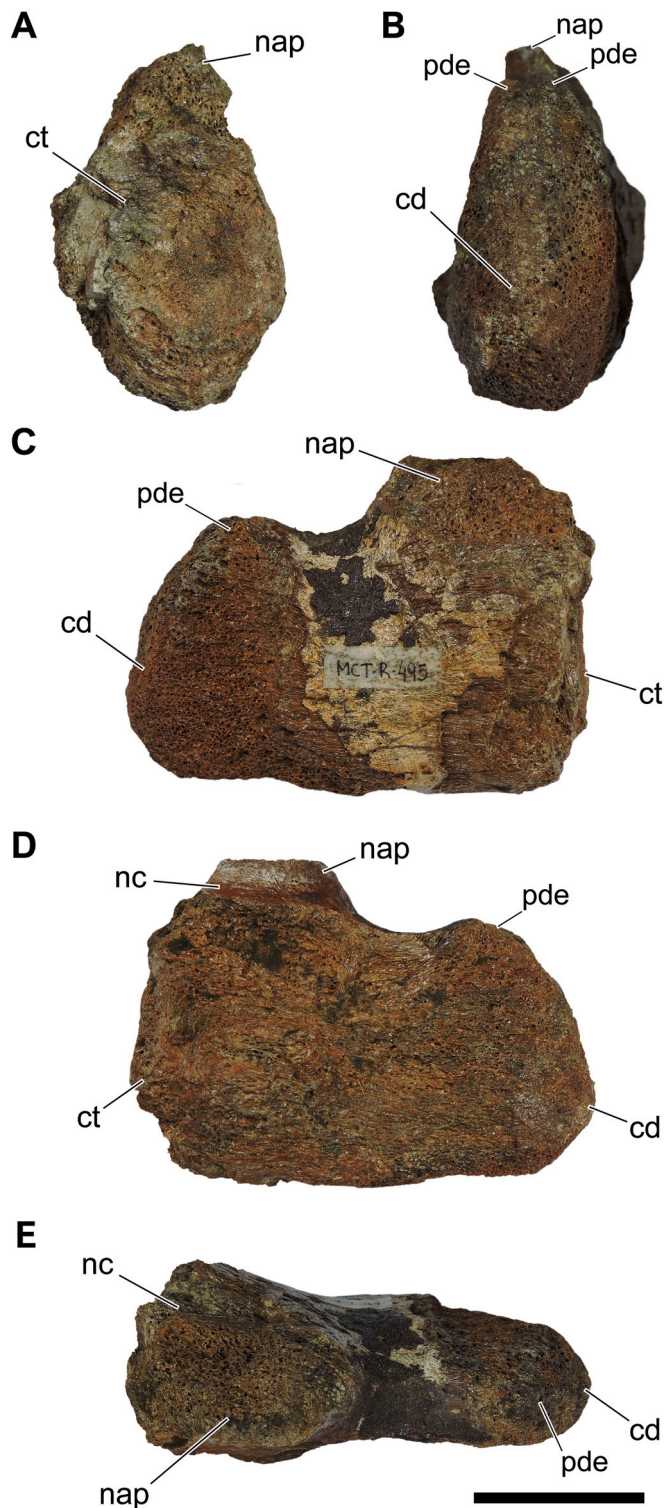


Fig. 5. Pedra Grande titanosaur (Morphotype 2). Probable 20th–23rd caudal vertebra in (A) anterior, (B) posterior, (C) right lateral, (D) left lateral, and (E) dorsal views. Anatomical abbreviations: **cd**, condyle; **chf**, chevron facet; **ct**, cotyle; **nap**, neural arch pedicel; **nc**, neural canal; **pde**, posterodorsal eminence. Scale bar equals 50 mm.

element, with the left side missing and with some internal spongy tissue exposed. Even so, it is possible to notice that the vertebral centrum is apparently short. As in the former caudal vertebra, this element presents the posterior end of the centrum well-inclined dorsally, being preceded by a dorsal concavity. The neural arch pedicel appears to be robust

laterally, occupying almost half of the total length of the vertebra.

4.3.2. Appendicular remains (MCT.R.412)

Unfortunately, the appendicular elements cannot be attributed to any of the caudal vertebral morphotypes previously described. This is due to the lack of detailed information regarding the materials association, collection and stratigraphic control. Without this critical contextual data, it is not possible to accurately correlate these elements with specific vertebral morphotypes, so we prefer to treat them as separate specimens.

The long bones cannot be properly identified due to their poor preservation, characterized by nonterminal portions and only slight curvature, which do not correspond to any specific bone (Figs. 6 and 7). These bones exhibit an outer layer of tissue that aligns with the typical growth pattern of bone, and an inner spongy pattern, like that observed in other titanosaurs (Kellner et al., 2006).

The element possibly represents a portion of the postacetabular

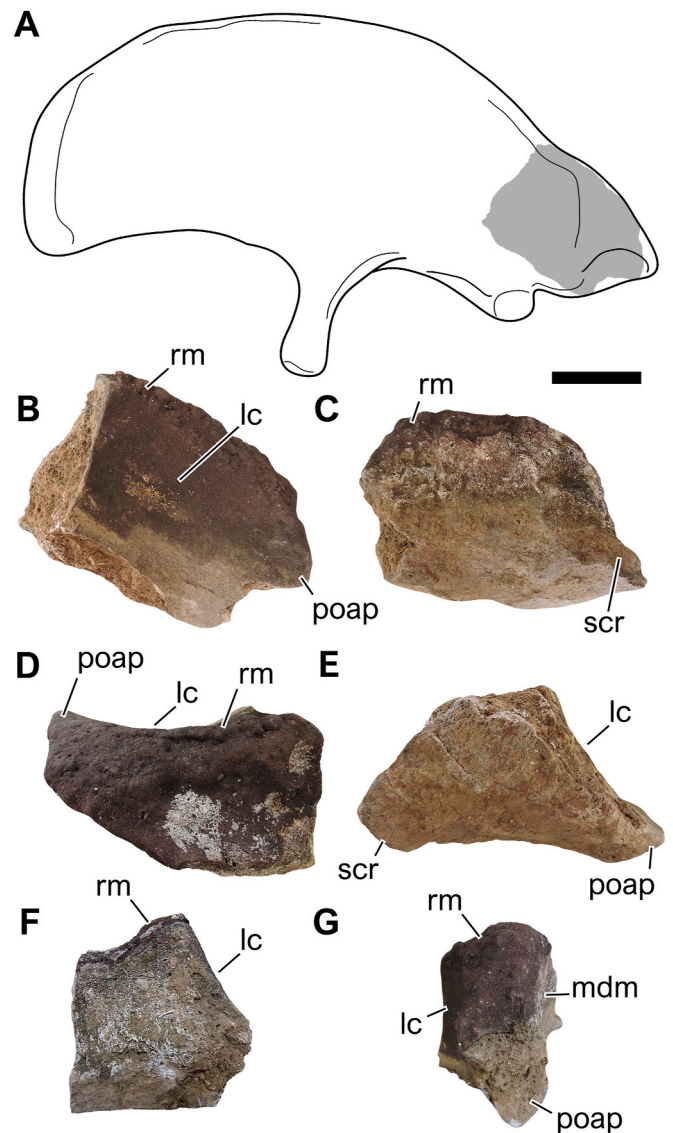


Fig. 6. Fragment of a putative left ilium from Pedra Grande farm. (A) schematic outline of a titanosaur ilium, depicting preserved part within Pedra Grande specimen (redrawn from Curry Rogers, 2009, Fig. 39). Ilium from Pedra Grande farm in (A) lateral, (B) medial, (C) dorsal, (D) ventrolateral, (E) anterior and (F) posterior views. Anatomical abbreviations: **lc**, lateral concavity; **mdm**, medial margin; **poap**, post acetabular process; **rm**, rough margin; **scr**, sacral rib. Scale bar equals 50 mm.

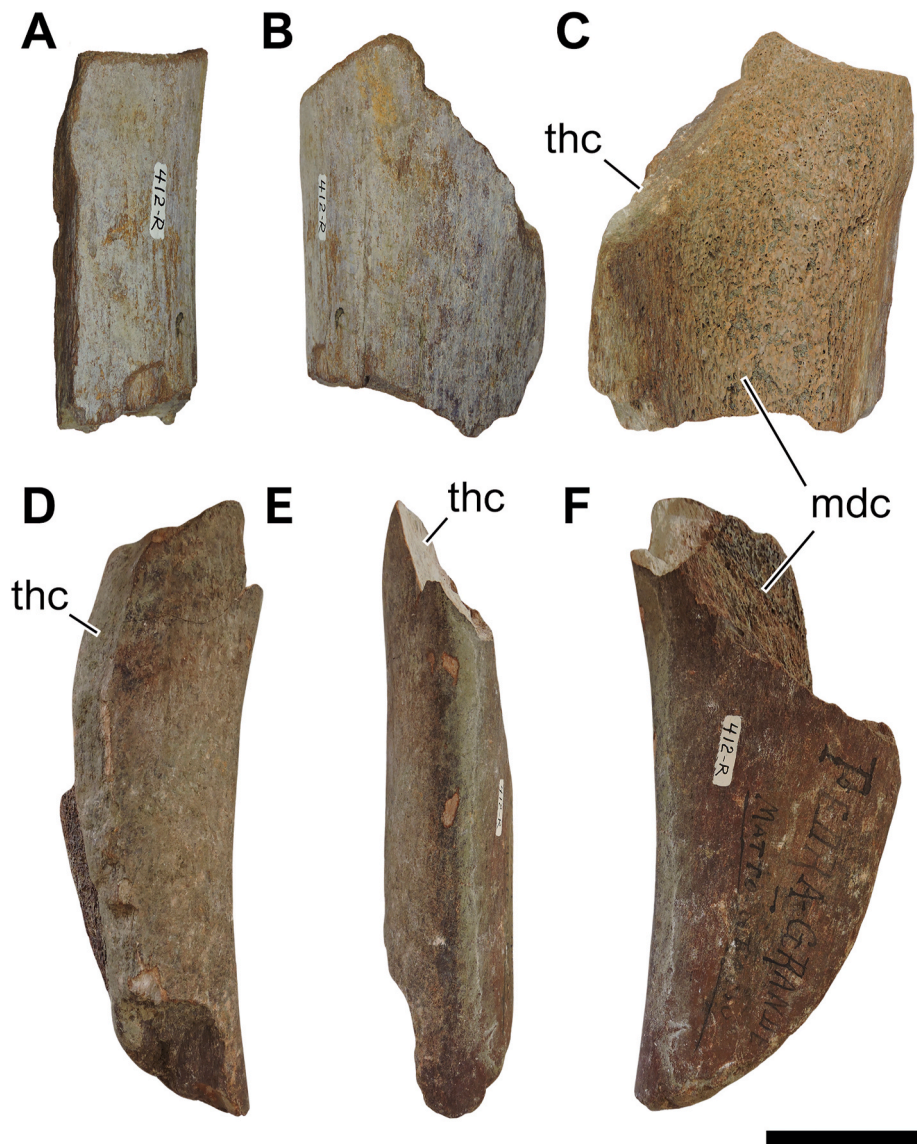


Fig. 7. Appendicular remains from the Pedra Grande farm. Long bone in (A) anterior, (B) lateral, and (C) medial views; Putative femur in (D) anterior, (E) lateral, and (F) posterior views. Anatomical abbreviations: **mdc**, medullary cavity; **thc**, thick cortex. Scale bar equals 50 mm.

process of an ilium (MCT.R.412; Fig. 6). This element presents an iron impregnation, contributing to a heterogeneous appearance. Although its incomplete nature, MCT.R.412 bears a long postacetabular lobe, and a pronounced curvature can provide some information into its morphology (Fig. 6B). In lateral view, the ilium fragment exhibits a slight lateral concavity (Fig. 6C). The surface shows significant preserved periostium, and a rough margin is evident along the dorsolateral edge. The postacetabular process is somewhat distinctly visible, and its general development can be approximated.

In turn, the medial view (Fig. 6D), in turn, reveals the inner aspect of this iliac fragment, where the bone's structure is heavily compromised, with much of the cortical bone eroded away. The medial margin (mdm) is discernible, but poorly defined. Indorsal view, the fragment appears curved and poorly flattened, and the slight lateral curvature is more pronounced. The iron layer covers much of the exposed surface, creating a rugose, crust-like appearance. In ventrolateral view (Fig. 6E), the curvature of the ilium is apparent, along with a pronounced lateral concavity. This view highlights the asymmetry in preservation, where certain areas are more heavily eroded than others. The attachment site for the sacral rib (scr) can be inferred but is not well-preserved.

The fragment exhibits a slight curvature and the iron layer's is less

impregnated. The medial margin can be seen but is not well-defined. In the posterior view, the curvature is less discernible from this angle. The rough margin and the medial margin are visible along the posterior edge, further illustrating the poorly preservation status.

The remaining elements are severely eroded, with only portions possibly corresponding to the preserved diaphysis (Fig. 7). These elements exhibit some trabecular tissue, though without any evidence of pneumaticity (e.g., Wedel, 2003). Based on these morphological traits, it is concluded that these bones most likely belong to appendicular elements rather than vertebrae fragments, such as diapophyses or neural spines.

Both elements are relatively straight, lacking any significant curvature. However, one of the them (Fig. 7A–C). appears to be less flattened anteroposteriorly than the other (Fig. 7D–F). The former element appears to be somewhat medially curved, in the shape of a wedge. This general shape resembles, to some degree, the fossa preceding the deltopectoral crest on the humeral head, or the proximal fossa in ulnae of titanosaurs. Also, at its “proximal” end, the element is broader, while the “distal” or the putative diaphysis is comparatively straight, as in those forelimb elements.

The second indeterminate appendicular element is somewhat

flattened anteroposteriorly. In general, no significant differences are observed in terms of thickness, torsion or bone development.

5. Pathological features on morphotype 1

The caudal vertebrae of Morphotype 1 exhibit some paleopathological features (Fig. 8), as subrounded lesions with smooth edges but with well-defined borders. The infrazygapophyseal part of neural arches also shows an incipient pneumatization, especially on right side, which is observed close to the level of the postzygapophyses. This means there are early signs of air-filled spaces developing within these bony structures, a feature that is often seen in bones that have experienced infection or other pathological processes. These lesions are conspicuous on the anterior articular surfaces (Fig. 8E), appearing as subrounded suppurative eruptions with smooth edges, particularly more widespread in the 11th–12th? caudal vertebrae.

On the condyle, the lesion measures around 20–30 mm dorsoventrally and ~30 mm mediolaterally. Some scars and scratches are

presented in the vertebral centra in both elements, especially in the left lateral side, together with signal of bone remodeling with smooth edges. On the condyle of the more posterior caudal vertebra, an elongated region just above one of the cysts shows some superficial bone erosion, probably due to a recurrent inflammatory process. Both vertebrae also present an irregular pneumatic bone overgrowth in the ventral portion of the neural arch, near to the prezygapophysis pedicels, which extends on both lateral sides of the vertebra but developed an aggressive pneumatization in the left side. Just below this lesion, some stretch marks with superficial indentations are observed on the left side of both vertebrae. The neural arch shows some irregular distension and more asymmetrical bone remodeling in lateral view. These features combined, could point to a complex history of disease or trauma affecting the vertebrae.

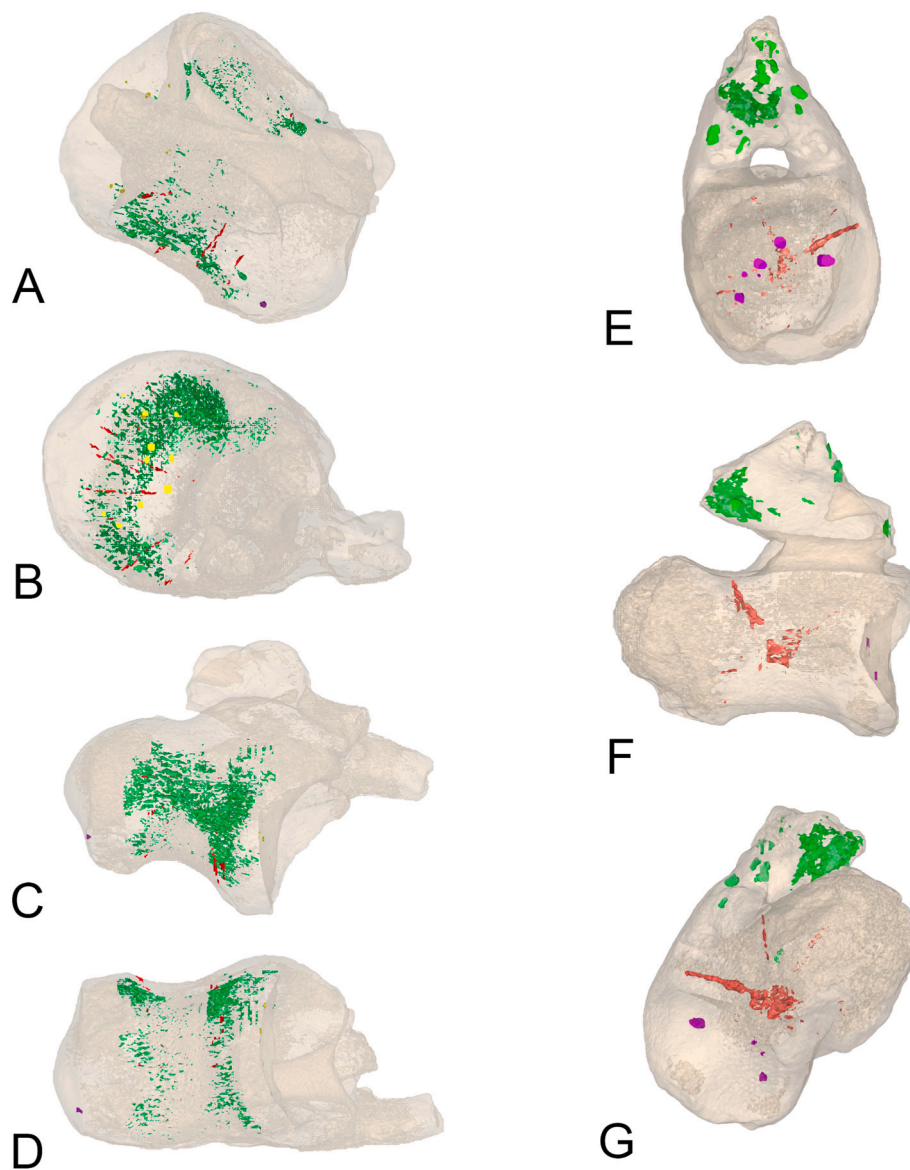


Fig. 8. Paleopathological features on Morphotype 1 caudal vertebrae. Probable 11–12th caudal vertebra in (A) dorsolateral, (B) anterior, (C) right lateroventral, and (D) ventral views; Probable 18th–19th caudal vertebra in (E) anterior, (F) right lateral, (G) dorsolateral views. Structures colored in green indicates the aggressive pneumatization compatible with osteoarthritis. Colored in red are possibly related to the vascular system, which can be related or not with the paleopathology discussed. Yellow dots in (A–B), and purple dots (E–G), are the subchondral cysts, interpreted here as products of some inflammatory process.

6. Discussion

6.1. Systematic affinities of the Pedra Grande specimens

Despite the difficulty of establishing a precise taxonomic affinity of the Pedra Grande specimens due to its incompleteness, these clearly represent advanced lithostrotian titanosaurs given the strongly procoelous condition along the middle to posterior caudal elements. There are several morphological differences between the specimens studied here and the known titanosaurs species to date, which prevents us from tentatively attributing these specimens to some already known genus. However, regarding their putative phylogenetic position, we can conclude that they are not a primitive species, because of the presence of strongly procoelous caudal vertebra in all preserved elements.

Due to the abovementioned, our specimens differ from the basal titanosaur *Andesaurus* (Mannion and Calvo, 2011), the lognkosaurian lithostrotians such as *Mendozasaurus* (González Riga et al., 2018) and the basal lithostrotian *Malawisaurus*, for example (Gomani, 2005). Additionally, our specimens also lack the hyposphene-hypantrum articulation observed in anterior and middle caudal vertebrae of the basal eutitanosaurian *Epachthosaurus* (Martínez et al., 2004). However, the 11th–12th? vertebra shares with some caudal elements of *Epachthosaurus* the very large with slightly displaced dorsally condyle.

The Pedra Grande specimens also can be excluded from the clade *Aeolosaurini*, since they lack the extremely anteriorly displaced neural arch, the anterodorsally projected neural spine, the postzygapophyses significantly exceed the middle of the vertebral centrum, and the constricted ventral part of the centrum, as observed in both *Aeolosaurus* species and in *Gondwanatitan* (Kellner and Azevedo, 1999; Powell, 2003; Casal et al., 2007). Also, the condyle in the two *Aeolosaurus* species previously described tend to be displaced dorsally, differing from the Pedra Grande specimens.

We can exclude the Pedra Grande specimens from the Saltasaurinae clade, since the vertebrae described here lack synapomorphic features, like the strongly dorsoventrally flattened centrum of the anterior caudal with centrum significantly wider than high (as represented here by the 18th–19th? vertebra), and the position of the neural spine, whose is only observable in the 11th–12th? vertebra. In turn, this element lacks the anterodorsally edge positioned posteriorly relative to the anterior border of the postzygapophyses, as commonly observed in Saltasaurinae species (Powell, 1992).

Comparing with other Brazilian titanosaur species with caudal vertebrae presented, we can exclude the Pedra Grande specimens from *Trigonosaurus*, since it has a well-developed prespinal lamina, which is absent in the specimens described here (Campos et al., 2005). Also, the Pedra Grande specimens are different from *Baurutitan*, since they lack thick postspinal laminae (Kellner et al., 2005).

The Pedra Grande specimens also differ from *Maxakalisaurus* since the latter presents well-developed articulation surfaces for the chevrons, unknown for the Mato Grosso specimens (Kellner et al., 2006). Also, the anterior caudal vertebra of *Maxakalisaurus* presents a very large and wide neural channel, having convex lateral walls in the vertebral centra, differing from the specimens described here.

Since the Pedra Grande specimens presents both comparatively primitive and advanced morphological features, is very difficult to precise to which titanosaurian clade they are more related to. In addition, the caudal elements of Morphotype 1 exhibit a distinctive notch that enters the cotyle, which is associated with the trapezoidal and well-developed bulge, fading inward towards the cotyle in both specimens.

Since the presence of the bulge and the notch potentially could be serially distributed, this lead us to propose them as a potential autapomorphy for this morphotype. The bulge likely served as a reinforcement structure, contributing to the stability and articulation of the vertebrae.

These fragments yield valuable insights into the array of titanosaurs that inhabited the region, contributing to the reconstruction of the paleobiological diversity of this specific group of dinosaurs in the given

geographic area. Beyond species identification, the analysis of these fragments may unveil distinct anatomical features, such as the medial laminae presented in the neural channel of the 11th–12th? vertebra. This could represent a new potential in the search for new species in future expeditions to the Pedra Grande farm or even in the municipality Chapada dos Guimarães.

Concerning the appendicular elements, little can be said since the state of preservation is poor. However, the overall morphology resembles titanosaurs whose ilia are proportionally shorter and more robust, as in *Rinconsaurus* and *Muyelensaurus*. The curvature and the rounded end are morphological features compatible with the preacetabular lobe observed in other neosauropod ilia, but less elongated and laterally projected than in some derived titanosaurs, such as *Epachthosaurus*.

6.2. Nature of the lesions in the morphotype 1 and its implications

Paleopathological lesions in sauropods remain relatively under-reported in the scientific literature. The paleopathological pattern of Morphotype 1 resembles that is exhibited by other titanosaur caudal vertebra with known bone lesions. However, in the specimens reported here, the paleopathological features is observed in more posterior caudal elements, and not in most anterior ones, being in the 11th–12th? and in the 18th–19th? vertebrae examined in our study. This sheds light on the prevalence of such conditions and being more widespread in this clade.

By identifying these lesions as subchondral cysts, we can interpret that those inflammatory nodules are protrusions of disc material into the surface of the vertebral body, which may contact the marrow of the vertebra and lead to inflammation. This process typically occurs when abnormal stress is applied over joint surfaces, resulting in the progressive loss of cartilage and exposure of the subchondral spongy bone. Subsequently, this exposure permits the intrusion of synovial fluid into the bone, leading to the resorption of bone trabeculae. A less common scenario involves the onset of bone necrosis due to synovial fluid intrusion, representing a secondary inflammatory event in response to another pathological cause (Rhaney and Lamb, 1955).

In the literature, there are only two other reported cases of subchondral cysts in caudal vertebrae of dinosaurs, making this paleopathology one of the rarest. The first case corresponds to an indeterminate sauropod specimen from the Jurassic of Niger (Witzmann et al., 2016); whereas the second case is probably represented by a middle caudal of the indeterminate titanosaur from the Açú Formation, Potiguar Basin (Barbosa et al., 2018). Thus, the present report reinforces that the subchondral cysts described are still rare in the fossil record, while reinforcing the presence of this type of injury in the middle caudal vertebrae, at least in sauropods. However, another unusual feature for caudal vertebrae in general, particularly in the middle region, is the “pneumatic” zone observed in the neural arches of the Morphotype 1 caudal vertebrae. Since some saltasaurine titanosaurs from Argentina are reported with some pneumatization in the neural arch in caudal vertebrae (Cerdeira et al., 2012), could the pneumatization observed in the Morphotype 1 of Pedra Grande as the same pneumatization? We believe that not is.

Comparing with the saltasaurines described by Cerdeira et al. (2012) pneumatization observed presents trabecular-organized tissue (known as camellate bone tissue) and have an communication with pneumatic foramina. Those communication with the foramina are generally located in the base of the neural arch or in the spinoprezygapophyseal fossa (Cerdeira et al., 2012). But in the Morphotype 1 described here, the pneumatization is quite different.

The aggressive pneumatization in the left side, together with the stretch marks with superficial indentations observed in Morphotype 1 is compatible with osteoarthritis, a type of degenerative disease that results from breakdown of joint cartilage and underlying bone. This condition is normally caused by biomechanical stress on the joint and low-grade inflammatory processes, where a gradual loss of cartilage

develops and the underlying bone is affected. In this scenario, the cartilage wears away, spurs emerge from the edge of the bone, and synovial fluid increases (Berenbaum, 2013).

Osteoarthritis, as a degenerative joint disease, typically causes significant cartilage loss and morphological damage to other joint tissues. More subtle biochemical changes occur and development of the asymmetrical muscle growth during the earliest stages of osteoarthritis progression.

Bone distension, associated with the asymmetric remodeling in the neural arch of MCT.R.495 suggests that the pneumatization in could be attributed to paleopathological bone remodeling, probably linked to metabolic diseases, rather than the presence of air sacs. The *M. caudofemoralis* positioned more laterally on the caudal vertebrae, is a crucial element in the locomotion of dinosaurs, especially in titanosaurs. The inflammatory process of this muscle could be related to the development of the costovertebral process scar observed in the Morphotype 1 caudal vertebrae. We assume this, since both elements present an asymmetric development on one side but not on the other. This asymmetry is particularly notable when considering that the vertebrae have internal pneumatization developed on the side opposite to the costovertebral process scar.

These characteristics suggest the presence of a chronic inflammation of the *M. caudofemoralis*, which could have caused or exacerbated the observed bone morphological changes. Prolonged inflammation may have led to increase bone tissue formation as an adaptive or reinforcing response, resulting in the asymmetry observed in the costovertebral process scars. Finally, asymmetric internal pneumatization may indicate a pressure relief or load redistribution mechanism, compensating for the additional tension caused by inflammation and altered muscle movement.

7. Conclusions

Mato Grosso State is characterized by the predominance of Cretaceous strata and marks the debut of titanosaur discoveries in the country. The specimens described here were unearthed in the 1950s near the Pedra Grande Creek and, despite their fragmentary nature and the absence of generic-level diagnostic features, the newly described specimens play a pivotal role in elucidating faunal gaps in the Brazilian Cretaceous. The caudal elements with paleopathologies document the third known case of subchondral cysts in caudal vertebrae of dinosaurs, highlighting the rarity of such cysts in the fossil record, particularly among sauropod dinosaurs. Lastly, the Pedra Grande specimens underscore the vast potential of Mato Grosso State in uncovering more complete specimens, further enriching our understanding of dinosaur diversity and paleobiology in this region.

CRedit authorship contribution statement

Leticia Lacerda: Writing – original draft, Investigation, Formal analysis. **Kamila L.N. Bandeira:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Investigation, Data curation, Conceptualization. **Bruno A. Navarro:** Writing – review & editing, Writing – original draft, Validation, Investigation, Formal analysis, Data curation, Conceptualization. **Maria L.P. Bertolossi:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Valéria Gallo:** Writing – review & editing, Methodology, Investigation. **Rafael C. da Silva:** Writing – review & editing, Writing – original draft, Validation, Investigation, Data curation. **Diogenes de A. Campos:** Writing – review & editing, Writing – original draft, Visualization, Validation, Data curation. **Alexander W.A. Kellner:** Writing – review & editing, Writing – original draft, Visualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data was used for the research described in the article.

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