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Short communication

Description of a juvenile titanosaurian dinosaur from the Upper Cretaceous of Brazil

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ABSTRACT

We describe a juvenile specimen of a titanosaurian sauropod dinosaur consisting of two dorsal and three caudal vertebral centra, an ilium fragment, and an ischium unearthed in 1991 from Site Km 153.5 at BR-050 highway in the Serra da Galga region, municipality of Uberaba, state of Minas Gerais, Brazil. The outcrop at the site is assigned to the Serra da Galga Member of the Marília Formation (Bauru Basin: Bauru Group; Upper Cretaceous: Maastrichtian). Although the material is very incomplete, features such as strongly procoelous caudal centra suggest an affinity with the titanosaurian clade Lithostrotia. The extensive vertebral pneumaticity with deep pleurocoels and well-developed camerae supports the hypothesis that, in titanosaurs, the air sac system was already present and fully developed even at early ontogenetic stages.

1. Introduction

Titanosaurs represent the last great radiation of sauropod dinosaurs, with a globally distributed body-fossil record dating back to at least the late Early Cretaceous (D'Emic, 2012). They are easily differentiated from other sauropods by a characteristic suite of features such as anterior and middle caudal vertebrae with a ventral longitudinal hollow (convergent in diplodocids), a platelike ischium with no emargination distal to pubic peduncle, six or seven sacral vertebrae and reduction of the articular surfaces for the manual phalanges on the metacarpals (e.g., Salgado et al., 1997; Wilson and Sereno, 1998; Wilson, 2002; Wilson, 2006a). In the Cretaceous fossil record of Brazil titanosaurs represent the dinosaur clade with the highest taxonomic abundance (Kellner and Azevedo, 1999; Novas, 2009; Bittencourt and Langer, 2011), with ten species formally described to date. Of these, *Baurutitan britoi* Kellner, Campos, and Trotta 2005, *Trigonosaurus pricei* Campos, Kellner, Bertini and Santucci 2005, and *Uberabatitan ribeiroi* Salgado and Carvalho 2008 have been found in the region of Uberaba, in the state of Minas Gerais, in Upper Cretaceous rocks belonging to the Bauru Group of the Bauru Basin.

Fossils of juvenile sauropod individuals are rare, possibly because their small size made them more susceptible to taphonomic processes such as weathering, scavenging, and transport (Behrensmeyer et al., 1979; Carpenter and McIntosh, 1994). Although most juvenile sauropod specimens consist of fragmentary

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material (Peterson and Gilmore, 1902; Britt and Naylor, 1994; Martin, 1994; Foster, 2005; Candeiro et al., 2011), there are some notable exceptions, such as the enigmatic probable titanosauriform described by Schwarz et al. (2007) and Carballido et al. (2012), a juvenile of the titanosaur *Alamosaurus sanjuanensis* Gilmore, 1922 (Lehman and Coulson, 2002), some juvenile remains of *Europasaurus holgeri* Sander, Mateus and Knötschke, 2006 (Carballido and Sander, 2014), a juvenile *Rapetosaurus krausei* Curry Rogers and Forster, 2001 (Curry Rogers, 2009), the recent records of a juvenile specimen of *Barosaurus* March, 1890 (Melstrom et al., 2016), and a putative record from the Lower Cretaceous of Brazil (Ghilardi et al., 2016).

Here we describe a juvenile specimen of a titanosaurian sauropod dinosaur from the Marilia Formation, Bauru Basin, Brazil. This is the first juvenile specimen recovered from this formation and the most complete occurrence of a juvenile sauropod from Brazil.

2. Geological context

The material here was recovered from an exposure of the Serra da Galga Member of the Marília Formation (Upper Cretaceous: Maastrichtian) of the Bauru Group in the Bauru Basin (Fernandes and Coimbra, 1998, 2008; Dias-Brito et al., 2001; Paula e Silva, 2003). The Bauru Basin covers most of the western plateau of the state of São Paulo and also extends to the Triângulo Mineiro (i.e., the westernmost portion of Minas Gerais state), southern Goiás state, and southeastern Mato Grosso and northern Mato Grosso do Sul states (Ribeiro and Carvalho, 2007) (Fig. 1).

The subsurface of the Bauru Basin is composed of basalts of the Serra Geral Formation that are overlain by 300 m of sedimentary rocks that pertain to two chronologically correlated units, the Caiuá Group and the Bauru Group (Fernandes and Coimbra, 1998, 2008). The Caiuá Group includes the Rio Paraná, Goio Erê, and Santo Anastácio formations, which are composed of thin to very thin aeolian sandstones, that were deposited in a paleodesert that extended across the inner portion of the Bauru Basin during the Early Cretaceous (Fernandes and Coimbra, 2008). The Bauru Group is composed of the Vale do Rio do Peixe, Araçatuba, Presidente Prudente, São José do Rio Preto, Uberaba and Marília formations (*sensu* Fernandes, 2004). However, some authors disagree with this stratigraphic proposal. For example, Batezelli (2015) divided the Bauru Group into the Araçatuba, Uberaba, Adamantina, and Marília formations (Soares et al., 1980), with the latter including the Vale do Rio do Peixe, São José do Rio Preto and Presidente Prudente formations of Fernandes (2004).

The Marília Formation consists of fining-upward cycles, including matrix-supported conglomerates with intra- and extraformational clasts, fine to very coarse sandstones, and rare mudstones (Menegazzo et al., 2016). The formation is divided into three members: the Serra da Galga, Ponte Alta, and Echaporã members, with the former cropping out exclusively in the Uberaba region. The Serra da Galga Member stands out as one of the most important paleontological units in the entire Bauru Group, having produced approximately 15 formally described fossil vertebrate taxa that collectively include fishes, frogs, lizards, turtles, crocodyliforms, and dinosaurs (sauropods and theropods, the latter including birds) (see Martinelli and Teixeira, 2015, and

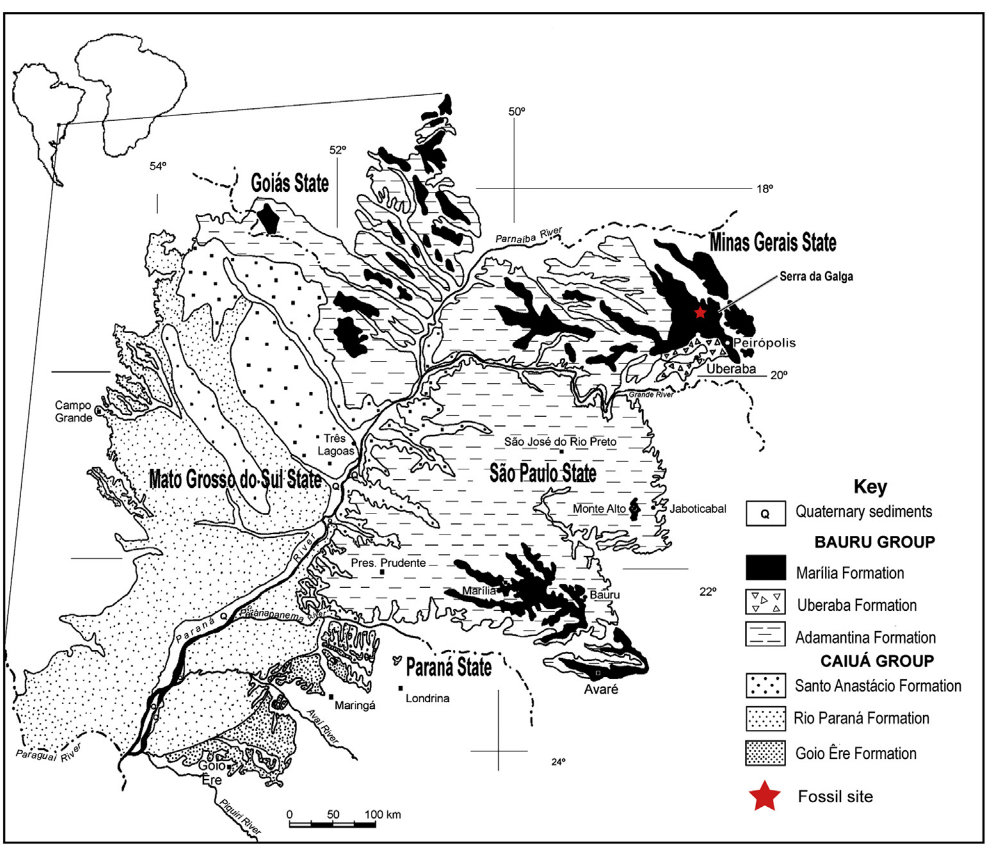

Fig. 1. Geological map of the Bauru Basin in Brazil. Modified from Fernandes and Coimbra (1996).

references therein). The Serra da Galga Member has also yielded remains of invertebrates (e.g., ostracods, gastropods, bivalves) and charophytes.

3. Materials and methods

The specimens were recovered in 1991 from a site about 500 m from the outcrops where the type materials of *Uberabatitan* were found. The remains are housed at the Centro de Pesquisas Paleontológicas “Llewelyn Ivor Price” (CPPLIP) of the Universidade Federal do Triângulo Mineiro (UFTM).

Throughout the description of the vertebrae we employ the terminology proposed by Wedel (2003a, 2003b) for the classification of pneumatic features, and the terminology proposed by Wilson (2006b) for the anatomical structures. Anterior and posterior are used in place of cranial and caudal, respectively.

Institutional abbreviations. CPPLIP: Centro de Pesquisas Paleontológicas Llwellyn Ivor Price.

4. Systematic paleontology

SAUROPODA Marsh 1878
MACRONARIA Wilson and Sereno 1998
TITANOSAURIFORMES Salgado, Coria and Calvo 1997
TITANOSAURIA Bonaparte and Coria 1993

Gen. et sp. Indet
Figs. 2–5

Referred material. The material consists of two dorsal centra (CPPLIP 0032 and CPPLIP 0115), three caudal centra (CPPLIP 0031, CPPLIP 0086, and CPPLIP 0114), a partial right ilium (CPPLIP 0029), and a partial right ischium (CPPLIP 0034).
Locality and horizon. Serra da Galga Member of the Marília Formation (Maastrichtian), in the Serra da Galga region at kilometer 153.5 of the highway BR-050, in the municipality of Uberaba, Minas Gerais state, Brazil.

4.1. Taphonomic observations

The outcrop where the specimen was found no longer exist, it was destroyed during a highway expansion, so only limited information regarding the stratigraphic environment could be recovered. However, it was found close to the outcrop where *Uberabatitan* was discovered within a braided fluvial system on a conglomeratic level, and the corresponding stratigraphy can be seen in Salgado and de Souza Carvalho, 2008.

Fossils discovered in the Serra da Galga Member of the Marília Formation mostly consist of disarticulated fragments, possibly related to strong seasonal fluctuations in sedimentary cycles (Garcia et al., 1999). The high degree of abrasion, including fractured and rounded surfaces, indicates that these taphonomic features were generated during transport in high-energy environments (Behrensmeyer, 1975; Behrensmeyer et al., 1979). This conclusion is supported by the transportability scheme introduced by Voorhies (1969), who demonstrated that elements of the axial column and pelvic girdle (his groups 1 and 2) display the highest potential for transport in fluvial systems – a situation that potentially accounts for the taphonomic signature of, e.g., the juvenile titanosaur taphocenosis.

Due to their close association in the field, corresponding size, and similar preservation, the elements are considered to belong to a single titanosaurian individual. The specimens are fragmentary, indicating possible prediagenetic transport, a hypothesis that is reinforced by the fact that the neural arches were not found associated. These are delicate structures that could have been easily destroyed or disarticulated in immature animals (Martin, 1994).

4.2. Descriptions and comparisons

Dorsal vertebrae: CPPLIP 0032 (Fig. 2A–E) is a well-preserved opisthocoelous dorsal centrum, lacking only a small portion of its right anterior face. The lateral faces are short with deep pleurocoels on both sides. The floor of the neural canal is deep and strongly concave, a feature commonly observed in juvenile sauropods, in which the neural canal is more conspicuously developed than in adults (Britt and Naylor, 1994). A small orifice, located roughly at the anterior portion of the neural canal, was made artificially during the preparation of the material. The contact surfaces with the neural arch show a pattern of ridges and grooves, indicating that the neurocentral suture was unfused, a typical feature of juveniles (Martin, 1994).

Dorsal centrum CPPLIP 0115 (Fig. 2F–J), the centrum is poorly preserved and heavily eroded on its left lateral face, but the right pleurocoel is preserved, measuring 28 mm anteroposteriorly and 15 mm dorsoventrally. The right contact surface for the neural arch is poorly preserved, as is the neural canal.

In both CPPLIP 0032 and CPPLIP 0115, the centrum is much less ventrally concave than in dorsal centra of the Patagonian saltasaurine titanosaur *Neuquensaurus australis* Lydekker, 1893 (Salgado et al., 2005). However, the new juvenile centra are similar to the middle dorsal centra of *Overosaurus paradasorum* Coria, Filippi, Chiappe, García, and Arcucci, 2013. In lateral view, the ventral limits of the anterior condyles are slightly more pronounced than those of the posterior cotyles, but without the ventral crest present in *Overosaurus* (Coria et al., 2013).

The pleurocoels are located on the anterior-most portion of the centrum as in *Bonatitan reigi* Martinelli and Forasiepi, 2004. CPPLIP 0032 is also similar to dorsal centra of *Trigonosaurus* in that both pleurocoels occupy the dorsal-most portion of the centrum.

CPPLIP 0032 and CPPLIP 0115 differ from the dorsal centra of a juvenile specimen of the diplodocid *Brontosaurus parvus* (Tschopp et al., 2015) with respect to the ventral extension of the condyles and cotyles, which do not surpass the ventral margins of the main body of the centra in the latter. Furthermore, the pleurocoels of *Brontosaurus* are located on the posterior portion of the centrum, connected to the cotyle.

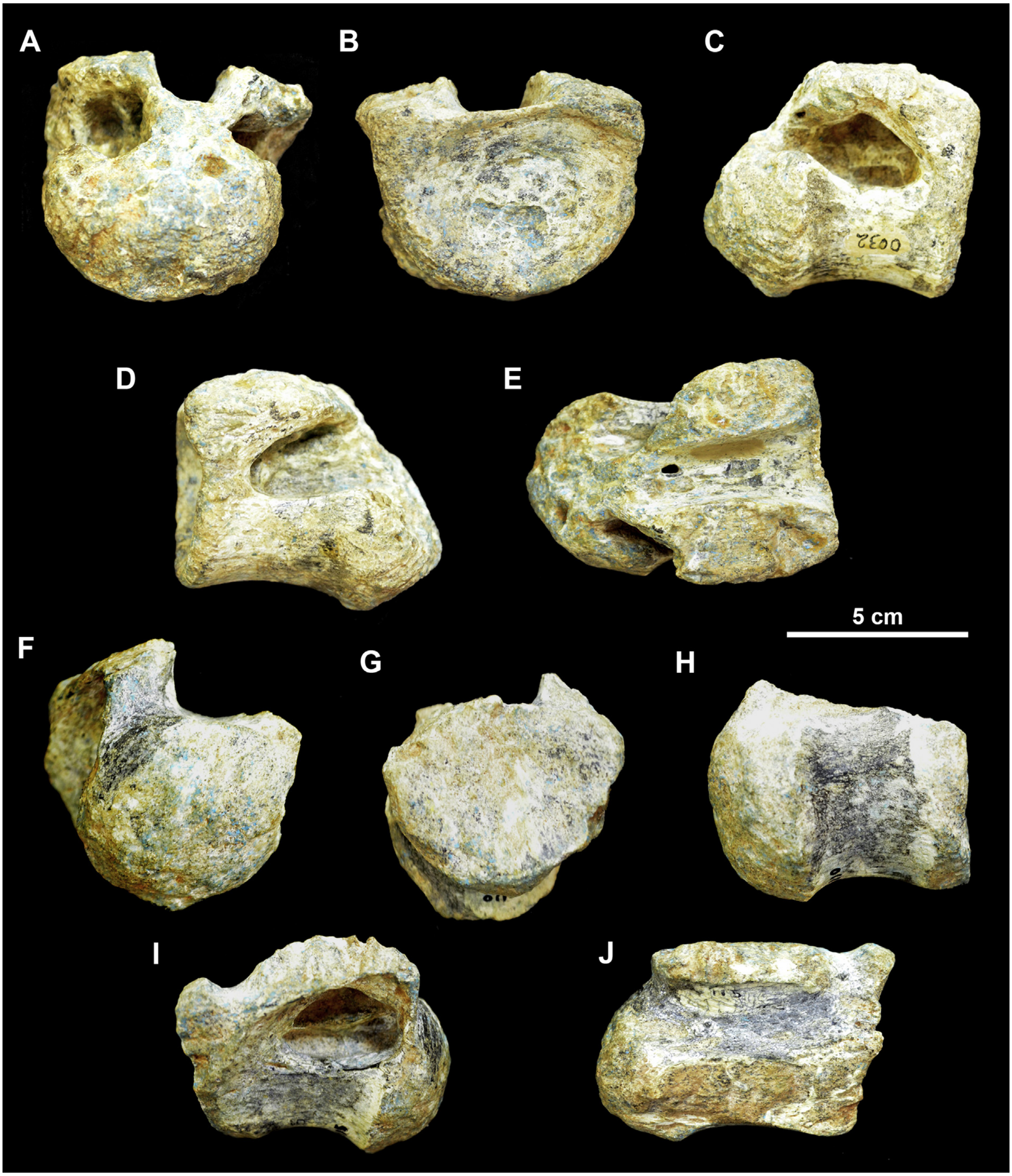

Fig. 2. Juvenile Titanosauria indet. from the Serra da Galga Member of the Marília Formation. Dorsal centrum CPPLIP 0032 in anterior (A), posterior (B), left lateral (C), right lateral (D), and dorsal (E) views. Dorsal centrum CPPLIP 0115 in anterior (F), posterior (G), left lateral (H), right lateral (I), and dorsal (J) views.

Caudal vertebrae: CPPLIP 0031 (Fig. 3A–D) is a well-preserved procoelous caudal vertebral centrum. Based on these measurements, and comparisons with the other two preserved caudal centra, this centrum clearly pertained to an anterior caudal vertebra. The lateral faces are short, with the posterior condyle occupying one-third of the anteroposterior length of the centrum. The contact surfaces for the neural arch are well defined and short, reinforcing the identification of the vertebra as an anterior caudal.

CPPLIP 0114 (Fig. 3E–F) is a very poorly preserved caudal centrum. The posterior condyle is broken and the lateral faces are short. The contact surface of the neural arch is not preserved and its right portion is fragmented. The neural canal is very large, which may indicate that the centrum belonged to another anterior caudal vertebra, but one that was positioned more posteriorly than CPPLIP 0031.

CPPLIP 0086 (Fig. 3G–H) is another fragmentary caudal centrum that is similar in size to CPPLIP 0114. The contact surfaces for the neural arch are poorly preserved, as are both lateral sides of the centrum. The neural canal is large and well preserved. Its diameter and proportions indicate that the centrum was also positioned near CPPLIP 0031, and therefore probably represents part of another anterior caudal.

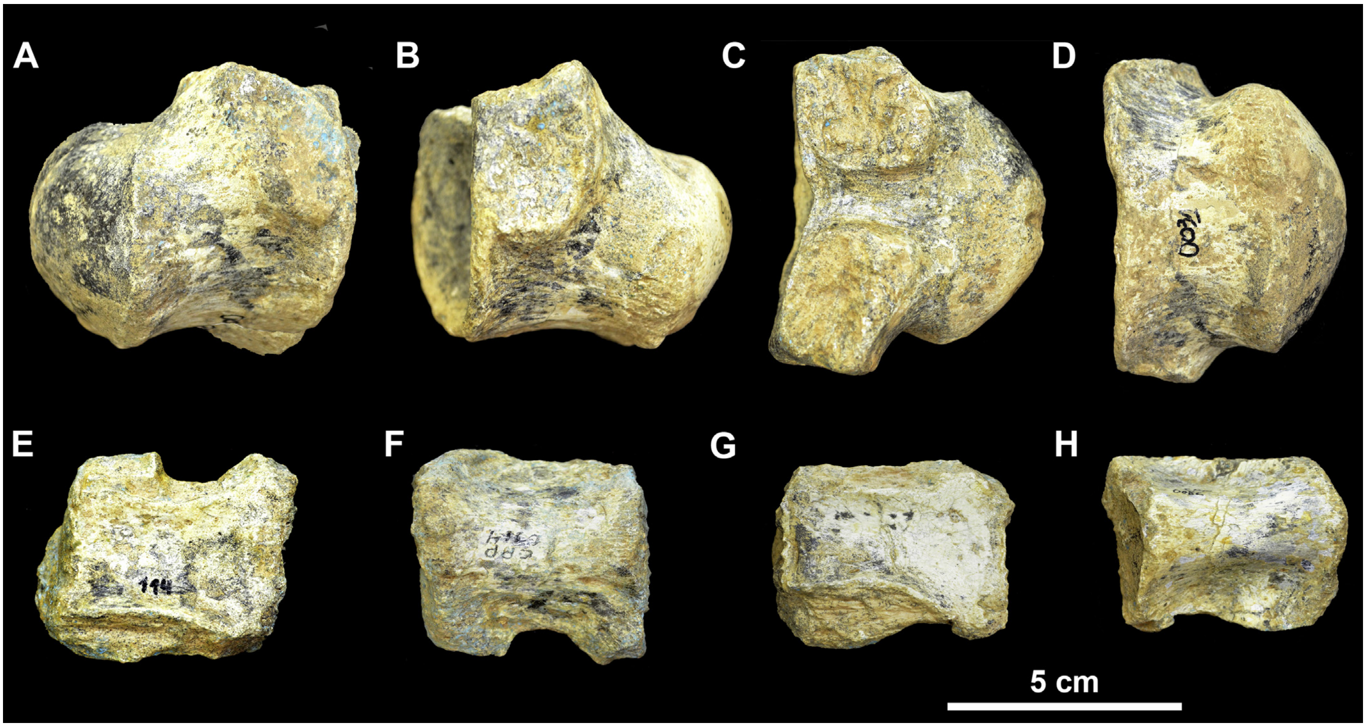

Fig. 3. Juvenile Titanosauria indet. from the Serra da Galga Member of the Marília Formation. Caudal centrum CPPLIP 0031 in right lateral (A), left lateral (B), dorsal (C), and ventral (D) views. Caudal centrum CPPLIP 0114 in ventral (E) and dorsal (F) views. Caudal centrum CPPLIP 0086 in ventral (G) and dorsal (H) views.

The absence of the neural arches precludes the identification of the position of both CPPLIP 0086 and CPPLIP 0114. However, assuming that they belong to the same individual as CPPLIP 0031, it is probable that they derive from the middle section of the caudal series insofar as they are not much smaller than the latter centrum. Relative to the anterior centrum, which shows a strongly procoelous condition and a robust condyle, the condyles and the cotyles of both mid caudal are only slightly developed.(See Table 1).

Table 1
Vertebral measurements (mm). The values followed by a * represents complete structures.

Identification	Element	Maximum length	Maximum width	Maximum height	Condyle height	Condyle width	Cotyle height	Cotyle width
CPPLIP 0032	Dorsal	62	60	48	37	52	46*	55*
CPPLIP 0115	Dorsal	62	60	66	43	51	32	63
CPPLIP 0031	Caudal	70*	59*	50*	46*	75*	49*	90*
CPPLIP 0086	Caudal	47	43	30	34	54	35	55
CPPLIP 0114	Caudal	47	40	24	32	55	32	59

The caudal centra clearly differ from those of *Baurutitan* due primarily to the absence of a pronounced rim framing the posterior condyle, the lack of a deep depression in its central portion, and the absence of a 'heart-shaped' anterior cotyle. This latter feature also differentiates the centra from those of *Bonitasaura salgadoi* Apesteguía, 2004. The new caudals also differ from those of *Trigonosaurus* in having lateral and ventral margins that are less concave and bounded by the condyle. Despite the fact that the transverse processes are not fully preserved in CPPLIP 0031, they are similar to those of *Neuquensaurus* in being positioned anteriorly on the centrum.

Ilium: CPPLIP 0034 (Fig. 4A–B) is a fragment of a right ilium. It measures 134 mm in maximum length and 84 mm in preserved height. The proximal portion of the pubic peduncle is preserved; it is robust and anteroposteriorly flattened. A small portion of the preacetabular process is also present as a thin lamina.

Ischium: CPPLIP 0029 (Fig. 4C–D) is an almost complete right ischium that measures 208 mm in greatest length and 120 mm in preserved height. It has a semilunar shape in medial and lateral views. The iliac peduncle is short and its anterior face is concave where it forms part of the acetabulum. The pubic peduncle is not preserved (See Table 2).

Table 2
Pelvic girdle measurements (mm).

Identification	Element	Preserved length	Preserved height
CPPLIP 0034	Ilium	134	84
CPPLIP 0029	Ischium	208	120

The ilium is too fragmented for comparisons, However the ischium, although heavily abraded, is a narrow, lamina-like structure, similar in appearance to those of *Neuquensaurus* and *Saltasaurus loricatus* Bonaparte and Powell, 1980. The iliac peduncle appears to have been relatively gracile and less robust than in *Rapetsaurus* or *Nequensaurus*.

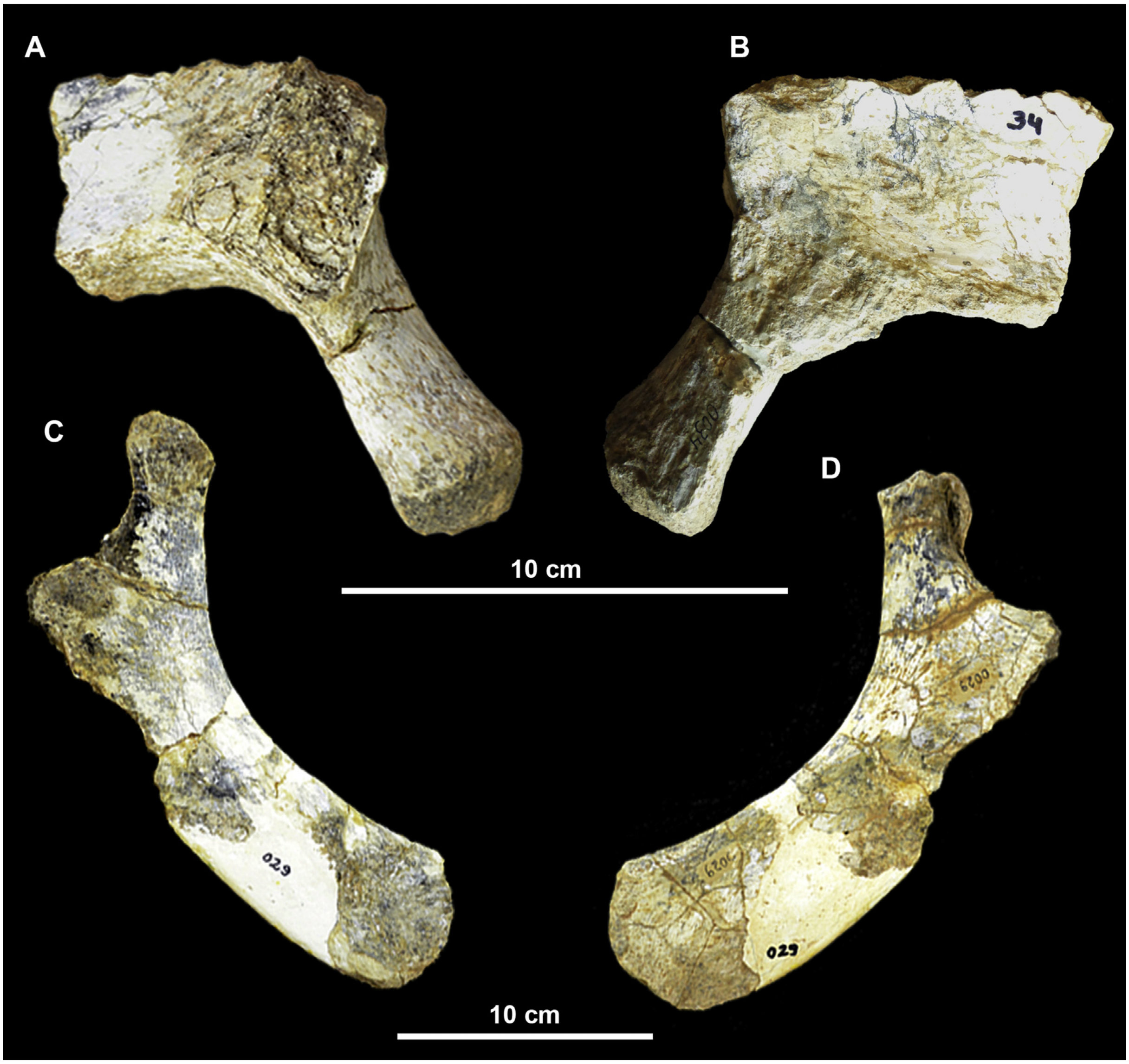

Fig. 4. Juvenile Titanosauria indet. from the Serra da Galga Member of the Marília Formation. Right lium CPPLIP 0034 in lateral (A) and medial (B) views. Right ischium CPPLIP 0029 in medial (C) and lateral (D) views.

4.3. Pneumaticity

Postcranial pneumaticity in sauropod dinosaurs has been the subject of much investigation in recent years (Cerda et al., 2012; Wedel and Taylor, 2013). Pneumatization of the axial skeleton would have dramatically reduced its total mass and undoubtedly helped sauropods reach their massive body sizes (Wedel, 2009). Vertebral laminae (the series of thin, bony struts connecting the major vertebral landmarks) are thus best conceived of as a correlate of axial pneumaticity in saurischians, bounding negative space filled by pneumatic diverticula (Wilson, 1999).

Wedel (2003a) introduced a classificatory scheme in order to standardize the defining characteristics of pneumaticity in sauropod vertebrae. Among these, two types of pneumaticity were described in titanosaurs: (1) camellate pneumaticity, which is characterized by the presence of camellae with generally small, angular cavities bearing irregular margins; and (2) camerate pneumaticity, which is characterized by the presence of camerae with generally larger, rounded cavities having regular margins (*sensu* Wedel, 2003a).

In the right pleurocoel of CPPLIP 0115 there are three rounded camerae with well-defined margins (Fig. 5). In contrast, the pleurocoels of CPPLIP 0032, there are two deeper and larger camerae. The preserved elements thus demonstrate that, in this juvenile titanosaur, axial skeletal pneumaticity extended to the thoracic region and did not have a homogeneous distribution. CPPLIP 0115 is an anterior dorsal centrum with camerae that are smaller and shallower than those of the more posterior centrum CPPLIP 0032. In this respect, CPPLIP 0032 and CPPLIP 0115 differ conspicuously from dorsal vertebrae of adult specimens of *Uberabatitan* (e.g., CPPLIP 1077), which have only a single deep camera with well-defined margins. The juvenile vertebrae also differ from dorsal vertebrae of *Trigonosaurus* (CPPLIP 0361), which have a deep camera that lacks defined margins.

The new material also differs from dorsal vertebrae of *Gondwanatitan faustoi* Kellner and Azevedo, 1999 with respect to the morphology of its pleurocoels, which in the latter are located on the Uppermost portions of the centra, immediately ventral to the neural arch, and are deep and elongated with poorly defined camerae. Similarly, the Early Cretaceous titanosaur *Tapuiasaurus* *macedoi* Zaher, Pol, Carvalho, Nascimento, Riccomini, Larson, Juárez Valieri, Silva, and Campos, 2011 has proportionally larger pleurocoels with poorly defined camerae (Zaher et al., 2011).

The caudal centrum of the juvenile specimen does not show any pneumaticity, differing from some Saltasaurinae taxa (Cerda et al., 2012) and other sauropods (Wedel and Taylor, 2013).

caudals followed by a series of amphicoelous, opisthocoelous and biconvex centra, and *Baurutitan* has the first caudal biconvex – a condition that may also be present on *Neuquensaurus* (D'emic and Wilson, 2010).

Most, if not all, Brazilian Late Cretaceous titanosaur taxa such as *Baurutitan* (Santucci and Arruda-Campos, 2011), *Trigonosaurus*

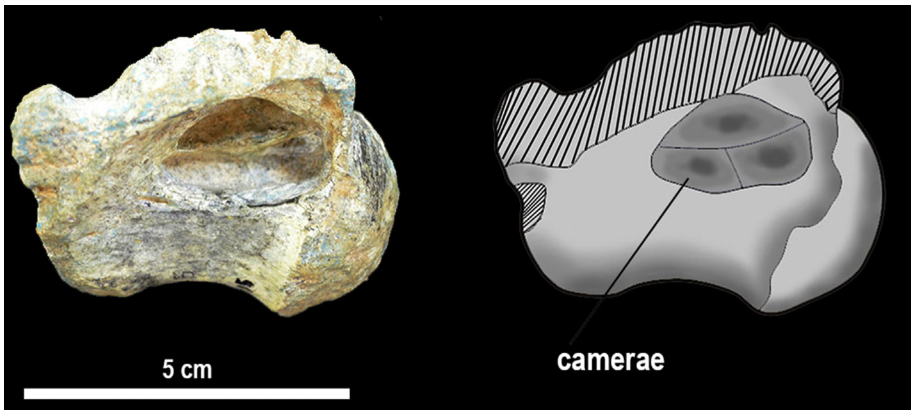

Fig. 5. Photograph (left) and interpretive drawing (right) of dorsal centrum CPPLIP 0115 in right lateral view, showing three camerae within the pleurocoel. This stage of development corresponds to morphological ontogenetic stage 3 proposed by Carballido and Sander (2014).

6. Discussion

The dorsal centra reported herein (CPPLIP 0032 and CPPLIP 0115) differ from those of other juvenile titanosaurs, such as the juvenile skeleton of *Rapetosaurus* (Curry Rogers, 2009), in which the dorsoventral diameter of the centrum is greater than its width and the posterior articular cotyle is deeper. The new centra are nearly as wide as tall, and their cotyles are not as deep as in *Rapetosaurus*. The same applies to dorsal centra of juvenile individuals of the Jurassic macronarian *Europasaurus* (Carballido and Sander, 2014), which have more strongly concave ventral faces and posterior cotyles that are larger than their respective anterior condyles. Similarly, in a juvenile dorsal centrum of *Phuwiangosaurus sirindhornae* Martin, Buffetaut, and Suteethorn, 1994, the ventral face is also more concave, and the pleurocoel is located more posteriorly than in the new Serra da Galga specimen (Martin, 1994).

Despite their generally poor preservation, it is notable that the caudal centra of the new specimen have less concave ventral surfaces than in those of caudals of the three titanosaurian genera previously described from the same region: *Baurutitan*, *Trigonosaurus*, and *Uberabatitan*. Nevertheless, with its slightly concave ventral face and a posterior condyle that is slightly larger than the anterior cotyle, CPPLIP 0031 is more similar to the most anterior preserved caudal of *Rapetosaurus*.

Even though the juvenile elements described herein collectively preserve few diagnostic features, the strongly procoelous condition of the anterior caudal centrum is a character of Titanosauria (Filippi et al., 2011; D'Emic, 2012), and allow us to include CPPLIP 0031 (and all of the elements presuming they belong to the same individual) in this clade.

Wilson (2002) proposed the character “anterior and middle caudal vertebrae procoelous” as a synapomorphy of the clade Lithostrotia (Upchurch, Barrett, and Dodson, 2004). However, this character appears several times outside Lithostrotia, such as *Dreadnought schrani* Lacovara et al., 2014, *Mendozasaurus neguyelap* González Riga, 2003 and *Malawisaurus dixeyi* Jacobs et al., 1993. Even in some lithostrotian titanosaurian species the procoelous condition of the anterior caudal centra are variable: *Rincosaurus caudimirus* Calvo and González Riga, 2003 has procoelous anterior (Mannion and Otero, 2012; Juárez Valieri and Ríos Díaz, 2013), and *Uberabatitan* are also considered to be members of Lithostrotia. Based on the geological and geographical context, we also suggest that the Peirópolis specimen has affinities with Lithostrotia. CPPLIP 0086 and 0114 possesses a dorsoventrally compressed centrum, a characteristic of Saltasaurinae (Powell, 2003) and may be related with this clade.

The presence of pneumatic camerae in the dorsal centra indicates that the specimen was not extremely immature at death; rather, it corresponds to the morphological ontogenetic stage (MOS) 3 of Carballido and Sander (2014) (which was proposed by these authors based on their study of the ontogeny of *Europasaurus*). In a recent study, Melstrom et al. (2016) supported the hypothesis that, in neosauropods, vertebral pneumaticity developed early in ontogeny, first in the cervical series and later extending to other vertebrae.

The Serra da Galga specimen pertains to MOS 3; furthermore, based on the presence of pneumatic camerae in its dorsal centra, it probably already possessed air sac diverticula in the thoracic region. Therefore, the titanosaurian respiratory system was probably completely developed at an early ontogenetic stage and a correspondingly small body size. This supports the hypothesis of “ontogenetic canalization” in titanosaurs proposed by Curry Rogers et al. (2016), who demonstrated via studies of the juvenile *Rapetosaurus* that osteologically immature titanosaurs were nearly identical in morphology to adults except for their size.

The dorsal centra CPPLIP 0032 and CPPLIP 0115 bear pneumatic fossae that differ in morphology from those of other titanosaurian taxa found in the same region, such as *Trigonosaurus* and *Uberabatitan*. This suggests that the new juvenile specimen may belong to a different lithostrotian species, and that the pleurocoels may become progressively smaller but not change in overall shape. During growth the vertebral pneumaticity of sauropod individual becomes better developed due to the expansion of either the cervical or abdominal air sac diverticulae (Wedel, 2003b; Salgado et al., 2006); a change hypothesized to reduce the weight of the skeleton and/or increase oxygen consumption in response to the elevated metabolic demands brought about by large body size.

Finally, some workers have argued that sauropods show signs of gregarious behavior (Salgado et al., 2012). With respect to titanosaurs, it has been suggested that if this behavior was not present, females at least would have aggregated periodically during the ovipositional season (Chiappe et al., 2005; García et al., 2015). Price (1951) reported sauropods eggs within the Marília Formation, and although no juveniles have been found associated with these eggs, the synformational presence of both eggs and juveniles with adult titanosaurs suggests that animals of different ontogenetic stages shared a common environment.

7. Conclusions

In conclusion, although fragmentary, the juvenile titanosaurian specimen described herein lends further support to hypotheses of isometric growth in titanosaurs, and may also represent a species distinct from those that have already been found in the Uberaba region. Furthermore, the presence of titanosaur eggs and individuals of different ontogenetic stages in the area bolsters the idea that the local paleoenvironment was conducive to both titanosaurian nesting as well as supporting a taxonomically diverse sauropod fauna.

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