



## COMMENTS ON ADDITIONAL DINOSAUR SPECIMENS FROM THE JANNER SITE (UPPER TRIASSIC OF THE PARANÁ BASIN), SOUTHERN BRAZIL

RODRIGO TEMP MÜLLER

Centro de Apoio à Pesquisa Paleontológica, Universidade Federal de Santa Maria,  
Rua Maximiliano Vizzotto, 598, 97230-000, São João do Polêsine, RS, Brazil.  
*rodrigotmuller@hotmail.com*

MAURÍCIO SILVA GARCIA

Laboratório de Paleobiodiversidade Triássica, Departamento de Ecologia e Evolução, Universidade  
Federal de Santa Maria, Av. Roraima, 1000, 97105-900, Santa Maria, RS, Brazil.  
*maurissauro@mail.ufsm.br*

FLÁVIO AUGUSTO PRETTO

Centro de Apoio à Pesquisa Paleontológica, Universidade Federal de Santa Maria,  
Rua Maximiliano Vizzotto, 598, 97230-000, São João do Polêsine, RS, Brazil.  
*flavio.pretto@ufsm.br*

**ABSTRACT** – The Janner site (Upper Triassic of Southern Brazil) has been intensely explored, yielding constant new findings in recent years. Among these some fragmentary dinosaur specimens still not published were sampled. In this contribution, we describe these specimens, which represent five individuals, in order to increase our understanding on the anatomy of the dinosaurs that compose the paleofauna of the Janner site. The specimen CAPP/UFMS 0270 is comprised of a series of six articulated presacral vertebrae, plus two isolated vertebrae associated with a right femur. UFRGS-PV-1232-T comprises a sacrum and a left ilium. CAPP/UFMS 0271 comprises a right humerus that lacks the middle portion of the diaphysis. CAPP/UFMS 00272 and 2073 are both comprised of an isolated femur each. The fragmentary condition of the materials hampers any less inclusive assignment. However, the morphology of the elements resembles those of coeval dinosaurs. Furthermore, the new specimens increase our knowledge on the morphology of some structures poorly understood from the dinosaurs of Janner site, such as the hindlimb and axial skeleton.

**Keywords:** *Hyperodapedon* Assemblage Zone, Carnian, Saurischia, Sauropodomorpha, Archosauria, Dinosauria.

**RESUMO** – O sítio Janner (Triássico Superior do Sul do Brasil) tem sido explorado intensamente, produzindo constantes novos achados nos últimos anos. Dentre estes, restos de dinossauros ainda não publicados foram recuperados. Nesta contribuição nós descrevemos estes espécimes, que totalizam cinco indivíduos, com o objetivo de aumentar o entendimento sobre a anatomia e amostragem de dinossauros que compõem o conteúdo paleofaunístico do sítio Janner. O espécime CAPP/UFMS 0270 é composto por uma série de seis vértebras pré-sacrais articuladas, além de duas vértebras isoladas e um fêmur direito. UFRGS-PV-1232-T corresponde a um sacro e um ílio esquerdo. CAPP/UFMS 0271 compreende um úmero direito que carece de sua diáfise. CAPP/UFMS 0272 e 0273 compreendem um fêmur isolado cada. A condição fragmentária dos espécimes impede uma atribuição taxonômica menos inclusiva. Porém, a morfologia dos elementos lembra a de dinossauros coevos. Além disso, os novos espécimes aumentam nosso conhecimento sobre a morfologia de estruturas ainda pouco conhecidas de dinossauros do sítio Janner, como o membro anterior e o esqueleto axial.

**Palavras-chave:** Zona de Associação de *Hyperodapedon*, Carniano, Saurischia, Sauropodomorpha, Archosauria, Dinosauria.

### INTRODUCTION

The Triassic beds from Brazil yield some of the best-preserved skeletal remains of the oldest dinosaurs (*e.g.* Langer *et al.*, 1999; Cabreira *et al.*, 2011; 2016; Müller *et al.*, 2018a; Pacheco *et al.*, 2019; Pretto *et al.*, 2019). Indeed, regarding their age, dinosaurs from Brazil are comparable with those from the

Ischigualasto Formation, Argentina (*e.g.* Sereno *et al.*, 1993; Martínez *et al.*, 2011; Langer *et al.*, 2018). These findings are helping to build an evolutionary framework on the origin and early radiation of the dinosaurs. In addition, chronostratigraphic investigations dealing with Brazilian and Argentinean dinosaur-bearing outcrops are constraining the age that some evolutionary events took place (Martínez *et al.*, 2011; Langer *et al.*, 2018).

Despite the new findings, dinosaur specimens are still far less sampled than some other tetrapod groups. Actually, dinosaurs probably were rare components on the land ecosystems during the Carnian (Martínez *et al.*, 2013). Consequently, the fossil record of the group is relatively scarce, while other archosauromorphs and synapsids generally are better sampled in the same dinosaur-bearing outcrops. A classic example from Brazil is the fossiliferous content of the Janner site, in the municipality of Agudo, Rio Grande do Sul. The vertebrate paleofauna excavated from this site is considered Late Triassic in age (e.g. Langer *et al.*, 2007; Oliveira *et al.*, 2010; Cabreira *et al.*, 2011), and includes dinosaur records, including new taxa originally collected in this site. The first was the early sauropodomorph *Pampadromaeus barberenai* Cabreira *et al.*, 2011, which was described based on a partial skeleton of a single individual (ULBRA-PVT016). After that description, two additional specimens (CAPP/UFMSM 0027 and CAPP/UFMSM 0028), each represented by an isolated femur, were referred to *P. barberenai* (Müller *et al.*, 2016, 2019). The other dinosaur from the Janner site is a sauropodomorph as well and was named *Bagualosaurus agudoensis* Pretto, Langer & Schultz, 2019, also based in a partial skeleton of a single individual (UFRGS-PV-1099-T). So far, no additional specimens were ascribed to this taxon. In addition to these four aforementioned specimens, there is another described partial skeleton (UFRGS-PV-1240-T, Pretto *et al.*, 2015) that is slightly larger than the holotype of *B. agudoensis*. The general morphology of this specimen resembles that of *B. agudoensis*, but assignment of UFRGS-PV-1240-T to that taxon is not robust (Pretto *et al.*, 2019). The published fossil record of dinosaurs from the Janner site, therefore, comprises a total of five specimens. On the other hand, the cynodont genus *Exaeretodon* Cabreira, 1943, for example, is far more well-sampled, with dozens of specimens from the Janner site and deposited in the paleontological collections from Southern Brazil.

The Janner site has been intensely explored, yielding constant new findings in recent years. Among those findings are several fragmentary dinosaur specimens that are unpublished. In this contribution, we describe these specimens in order to increase our understanding on the anatomy of the dinosaurs that contribute to the paleofauna of the Janner site.

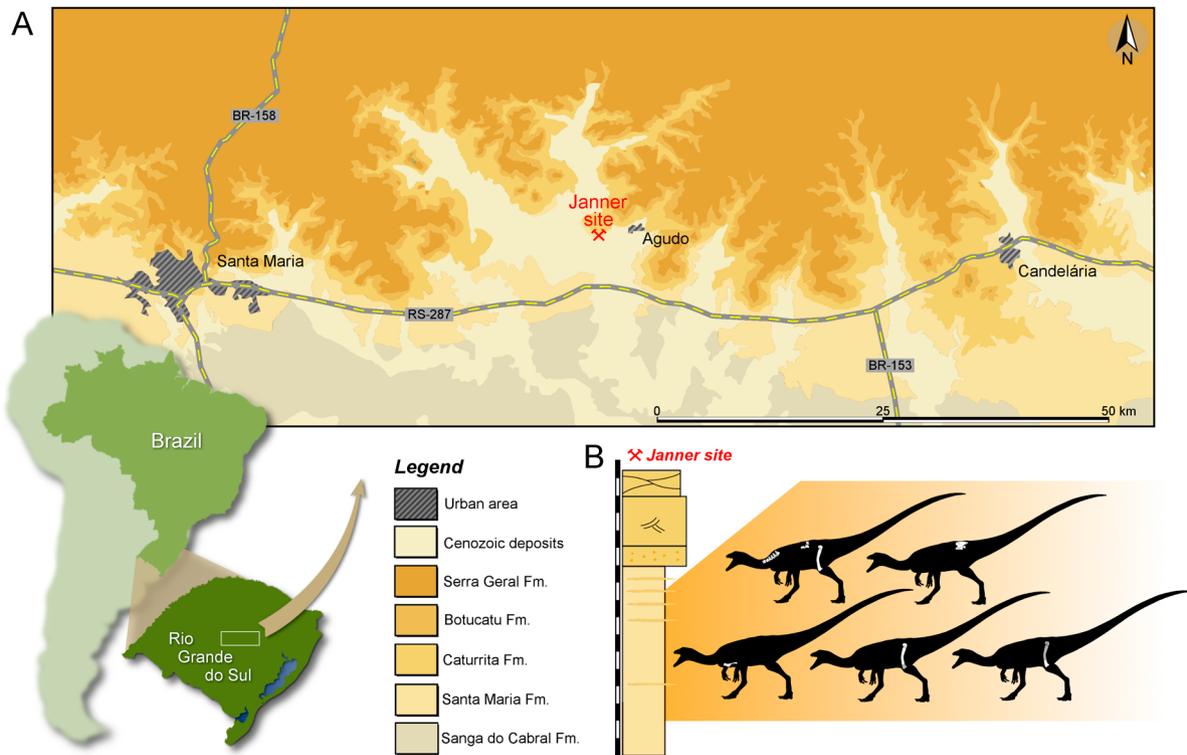
**Institutional abbreviations.** CAPP/UFMSM, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia, Universidade Federal de Santa Maria, São João do Polêsine, Rio Grande do Sul, Brazil; MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; NMT, National Museum of Tanzania, Dar es Salaam, Tanzania; PVL, Instituto Miguel Lillo, Tucumán, Argentina; PVSJ, División de Paleontología de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, San Juan, Argentina; ULBRA, Museu de Ciências Naturais, Universidade Luterana do Brasil, Canoas, Rio Grande do Sul, Brazil; UFRGS, Coleção de Paleontologia de Vertebrados, Universidade Federal do Rio Grande do Sul, Porto Alegre,

Rio Grande do Sul, Brazil; UFMSM, Coleção de Paleontologia, Laboratório de Estratigrafia e Paleobiologia, Universidade Federal de Santa Maria, Santa Maria, Rio Grande do Sul, Brazil; ZPAL, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

## GEOLOGICAL SETTING

The Janner (= “Várzea do Agudo”; Figure 1) site is located about 2 km west of the urban center of the municipality of Agudo (53°17'34.20"W, 29°39'10.89"S), Rio Grande do Sul State, southern Brazil. It is usually considered late Carnian (Late Triassic) in age (Langer *et al.*, 2007) and included in the *Hyperodapedon* Assemblage Zone (AZ) (Langer *et al.*, 2007), lower Candelária Sequence (Horn *et al.*, 2014) of the Santa Maria Supersequence of Zerfass *et al.* (2003) [equivalent to the uppermost portion of the Santa Maria Formation (Andreis *et al.*, 1980)]. As is typical of the Alemoa Member of the Santa Maria Formation (lower Candelária Sequence), its outcrops are composed of ravines of reddish massive to laminated mudstones, but also present yellowish cross-bedded sandstones and sandstones with mudstone interclasts, which are considered part of the Caturrita Formation (upper Candelária Sequence) (Da-Rosa, 2015). Furthermore, the mudstone portion comprises most of the site, being subdivided into proximal and distal floodplain deposits, while the sandstone is regarded as channel and crevasse deposits (Da-Rosa, 2015).

Regarding vertebrate specimens sampled, the Janner site has a moderate diversity of cynodonts and archosauromorphs (Müller *et al.*, 2020). By far, cynodonts are the most abundant faunal element of the Janner paleofauna, mostly represented by the traversodontid *Exaeretodon* (Oliveira *et al.*, 2007; Liparini *et al.*, 2013; Müller *et al.*, 2015), although the ecteniniid *Trucidocynodon riograndensis* Oliveira, Soares & Schultz, 2010 is also present (Oliveira *et al.*, 2010; Stefanello *et al.*, 2018). In term of archosauromorphs, dinosauriforms are the most sampled group in this locality, as previously commented. However, the site has also rhynchosaur remains ascribed to *Hyperodapedon* Huxley, 1859 (see Langer *et al.*, 2007) and is the type locality of the ornithosuchid *Dynamosuchus collisensis* Müller *et al.*, 2020. The presence of *Hyperodapedon* and *Exaeretodon* places the Janner site in the *Hyperodapedon* AZ (Langer *et al.*, 2007). The age of this AZ has been constrained as approximately 233 Ma. (Langer *et al.*, 2018). Nevertheless, the overwhelming record of *Exaeretodon* in comparison to *Hyperodapedon* could indicate a younger age for the Janner site since the *Exaeretodon* biozone of the Ischigualasto Formation of Argentina overlaps the layers of the *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez *et al.*, 2011). Indeed, the sauropodomorph *Bagualosaurus agudoensis* is usually regarded as more derived in relation to other sauropodomorphs from the *Hyperodapedon* AZ (Müller *et al.*, 2018a; Langer *et al.*, 2019; Pretto *et al.*, 2019). However, additional dating is needed for a more reliable stratigraphic framework (for more details on this issue see Müller & Garcia, 2019).



**Figure 1.** Location and geological context of Janner site. **A**, location map of the Janner site and the surface distribution of the geologic units in the area (modified from Müller *et al.*, 2020). **B**, stratigraphic column of the Janner site (modified from Da-Rosa, 2015) depicting the specimens herein studied (silhouettes adapted from the artwork of Márcio L. Castro).

## SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA Cope, 1869  
 DINOSAUFORMES Benton, 1985  
 DINOSAURIFORMES Novas, 1992  
 DINOSAURIA Owen, 1842  
 (Figures 2–7)

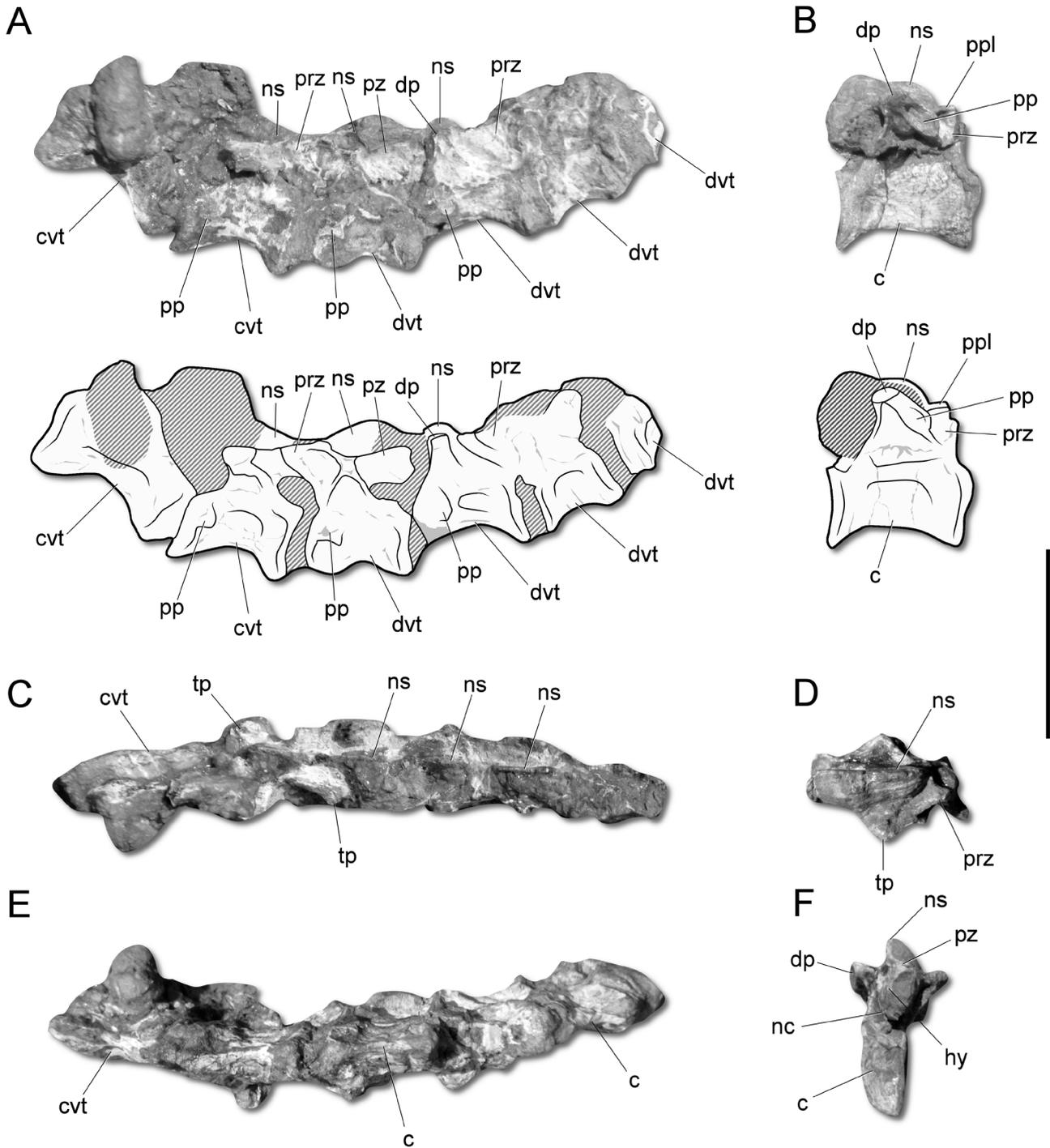
**Material.** CAPP/UFMS 0270. A series of six articulated presacral vertebrae plus two isolated vertebrae associated with a right femur (Figures 2–3).

**Diagnostic traits.** The specimen is assigned to Dinosauria due the presence of a concave emargination between the transition from the femoral shaft to the femoral head and the presence of a crest-like and asymmetrical fourth trochanter of the femur.

**Description and remarks.** The six articulated presacral vertebrae (Figure 2A) represent the last two cervical and the first four dorsal vertebrae. The first preserved cervical vertebra lacks the neural arch. The centrum is two times longer than its cranial height, which resembles the condition of *Buriolestes schultzi* Cabreira *et al.*, 2016 (CAPP/UFMS 0035). In *Macrocollum itaquii* Müller, Langer & Dias-da-Silva, 2018 (CAPP/UFMS 0001b), which bears a quite elongated neck, the anteroposterior length of the putative equivalent centrum is approximately three times longer than its dorsoventral height. There is a keel running longitudinally along the ventral surface of the centrum. The last cervical vertebra is craniocaudally shorter than the previous vertebra (approximately 0.7 times

shorter). Similar to the preceding, it bears a ventral keel, which is poorly developed ventrally. The cranial articular facet of the centrum is more developed ventrally than the caudal facet. The parapophysis lies on the lateral surface of the centrum, close to the cranial articular surface. Caudal to the parapophysis, the centrum bears a shallow fossa that runs craniocaudally reaching its caudal edge. The neural arch is approximately as tall as its respective centrum. The transverse process is lateroventrally directed and connected to the centrum by cranial and caudal centrodiapophyseal laminae. These laminae bound an infradiapophyseal fossa. Due to the preservation of the specimen, the presence of an epiphysis on the dorsal surface of the postzygapophysis is uncertain. The neural spine is low and subrectangular in lateral view. It lacks spine tables or any lateral process and is slightly cranially inclined, as in *Saturnalia tupiniquim* Langer *et al.*, 1999 (MCP-3845-PV) and distinct from the more cranially expanded spine of *Buriolestes schultzi* (CAPP/UFMS 0035).

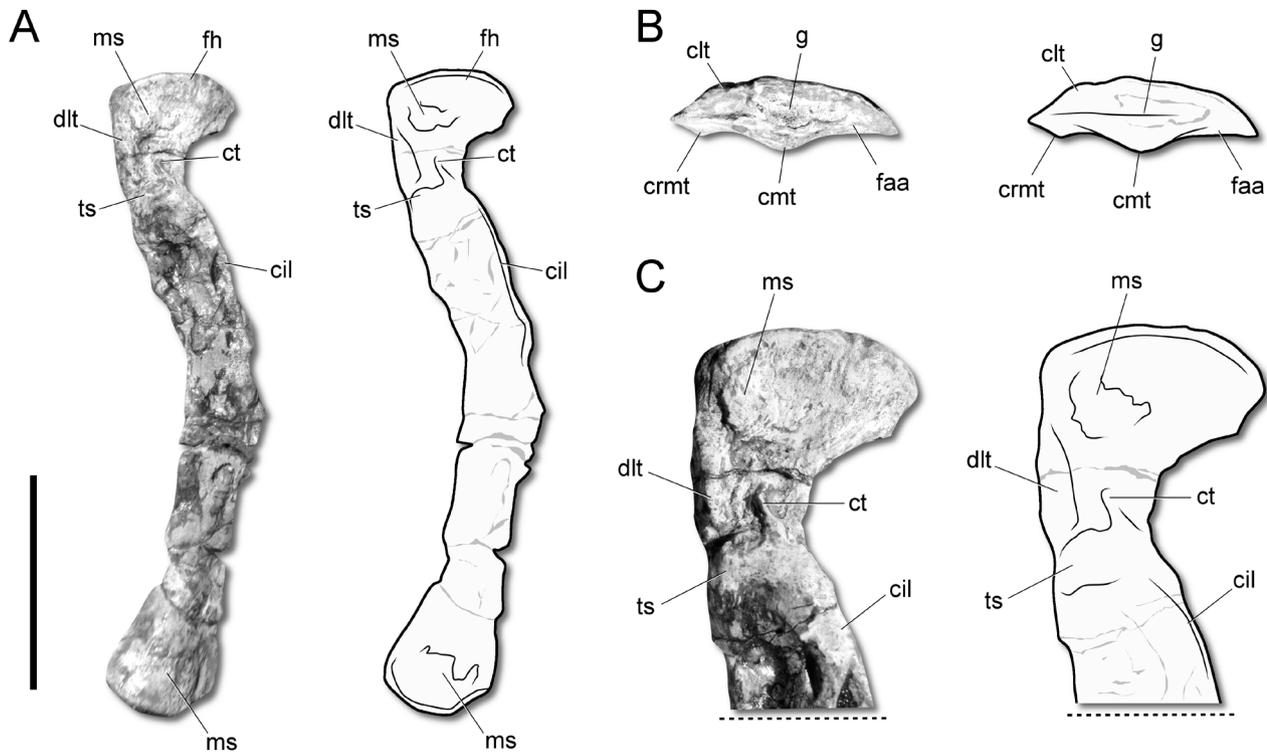
The centrum of the first dorsal vertebra is approximately as long as the centrum of the last cervical vertebra. A longitudinal keel runs along the ventral surface of the centrum, as in the previous vertebrae. The parapophysis is located on the lateral surface of the centrum, close to the cranial margin. There are three infradiapophyseal fossae at the lateral surface of the neural arch. The neural spine is low and craniocaudally short. The ventral surface is poorly preserved and severely worn and, as a result, it is not possible to assess the presence of a ventral keel. In the subsequent dorsal vertebrae, the



**Figure 2.** Axial skeleton of CAPPA/UFSM 0270. **A**, a series of six articulated vertebrae in left lateral view. **B**, caudal dorsal vertebra in right lateral view. **C**, a series of six articulated vertebrae in dorsal view. **D**, caudal dorsal vertebra in dorsal view. **E**, a series of six articulated vertebrae in ventral view. **F**, caudal dorsal vertebra in caudal view. Abbreviations: **c**, centrum; **cvt**, cervical vertebra; **dp**, diapophysis; **dvt**, dorsal vertebra; **hy**, hyosphene; **nc**, neural canal; **ns**, neural spine; **pp**, parapophysis; **ppl**, prezygapophyseal lamina; **prz**, prezygapophysis; **pz**, postzygapophysis; **tp**, transverse process. Scale bar = 20 mm.

parapophysis is located progressively more dorsally. By the third dorsal vertebra, the parapophysis is almost entirely located on the neural arch. The neural spine of the third dorsal vertebra is craniocaudally longer than the spine of the previous vertebrae. There is no ventral keel in the centrum of the third dorsal vertebra.

One of the two isolated vertebrae preserves the centrum and the neural arch (Figure 2B). This vertebra belongs to the caudal portion of the dorsal series. This identification relies on the position of the parapophysis, which is close to the diapophysis. The craniocaudal length of the centrum is approximately 1.85 times longer than is dorsoventral

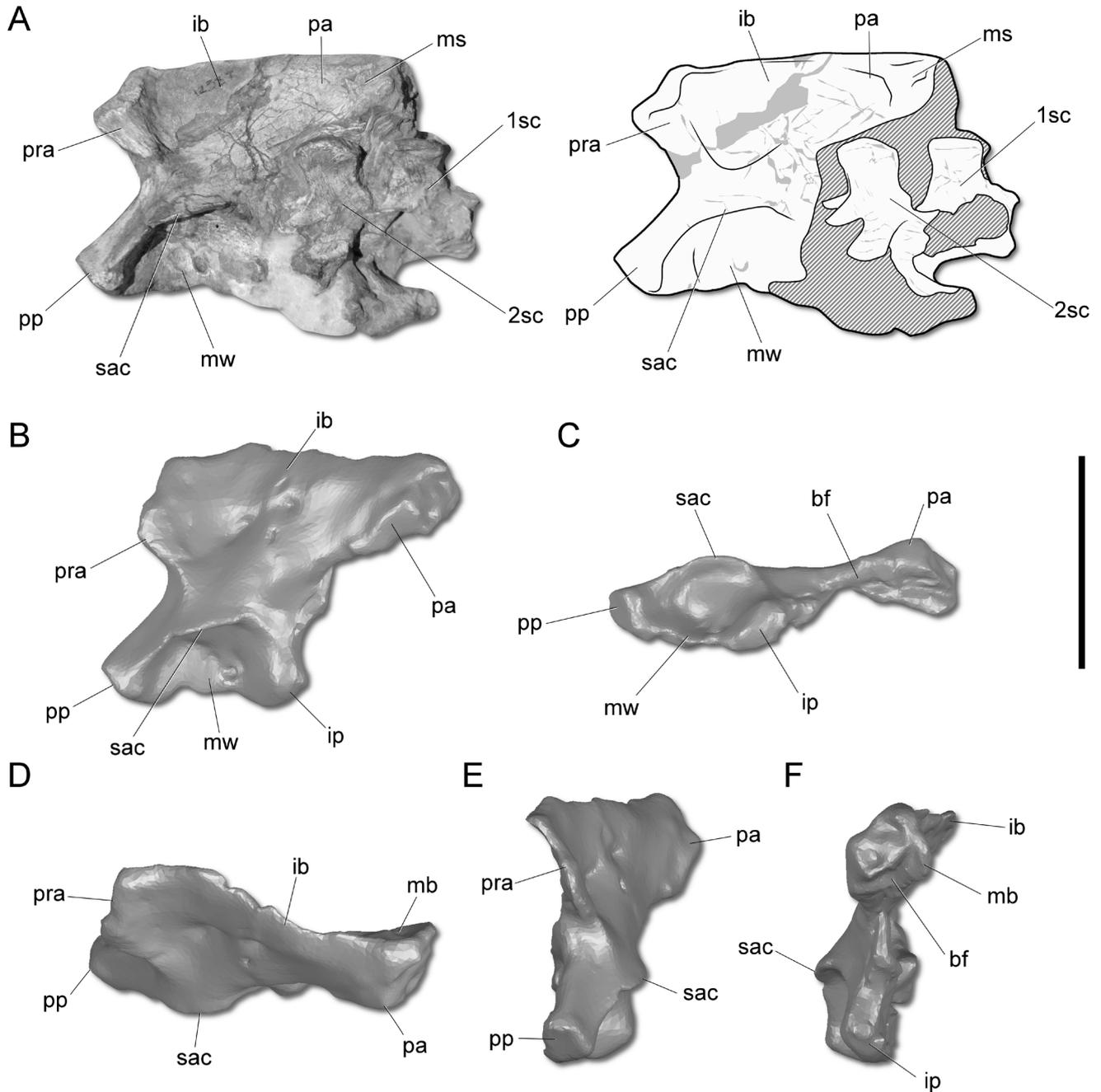


**Figure 3.** Right femur of CAPPA/UFSM 0270. **A**, craniolateral view. **B**, proximal view. **C**, detail of the proximal portion in craniolateral view. **Abbreviations:** cil, cranial intermuscular line; clt, craniolateral tuber; cmt, caudomedial tuber; crmt, craniomedial tuber; ct, cranial trochanter; dlt, dorsolateral trochanter; faa, facies articularis antitrochanterica; fh, femoral head; g, groove; ms, muscle scar; ts, trochanteric shelf. Scale bars: A = 50 mm; B–C = 20 mm.

height. This condition differs from herrerasaurids, which bear craniocaudally short dorsal centra (*e.g.* *Herrerasaurus ischigualastensis* Reig, 1963 – PVL 2566; *Staurikosaurus pricei* Colbert, 1970 – MCZ 1669; *Sanjuansaurus gordilloi* Alcober & Martínez, 2010 – PVSJ 605; Novas, 1993; Bittencourt & Kellner, 2009; Alcober & Martínez, 2010). There are two infradiapophyseal fossa below the transverse process. However, there is an additional fossa cranial to the parapophysis, which is roofed by a prezygoparapophyseal lamina. This lamina represents the prezygodiapophyseal lamina of the previous vertebrae. However, the dorsal displacement of the parapophysis interrupts the connection between the prezygapophysis and the diapophysis. The medial portion of the ventral surface of the postzygapophysis projects ventrally to form a dorsoventrally short and sheet-like hyposphene accessory articulation, which is usually present in saurischian dinosaurs (Nesbitt, 2011). The base of the neural spine is approximately as long as the craniocaudal length of the neural arch (excluding the pre- and postzygapophyses). The distal portion of the spine is missing. The other isolated vertebra is composed of an isolated centrum that lacks parapophyses. Therefore, it probably belongs to a mid/caudal dorsal vertebra or a caudal vertebra. The size and proportions of the element resemble those of the isolated dorsal vertebra previously mentioned. The centrum is constricted at the mid length, lacks any keel, and bears a lateral fossa.

The femur (Figure 3) is approximately 144 mm in length and diagenetically altered in its transverse dimension by sedimentary compression (minimum circumference of the

shaft approximately 42 mm). The bone is sigmoid (Figure 3A), with a slender shaft and expanded extremities. The maximum lateromedially width of the femoral head is approximately 29.5 mm. There is a shallow transverse groove running on the proximal surface (Figure 3B). The craniolateral margin of the proximal end is convex, while the opposite side bears two concavities formed by the presence of the craniomedial and caudomedial tubera. These are subequal in size. The facies articularis antitrochanterica is ventrally directed, distinct from the condition of silesaurids (Nesbitt, 2011) where this surface is elevated in comparison. The greater trochanter is angled and the transition between the femoral head and the shaft is marked by a ventral concavity, a diagnostic trait of dinosaurs (Nesbitt *et al.*, 2010). The dorsolateral trochanter forms a raised process with smooth margins. In addition, there is a raised muscle scar (Figure 3C) slightly dorsal to this trochanter, which also occurs in some dinosauriforms, such as *Silesaurus opolensis* Dzik, 2003 (ZPAL AbIII/361/21 – Piechowski *et al.*, 2014), *Asilisaurus kongwe* Nesbitt *et al.*, 2010 (NMT RB159 – Griffin & Nesbitt, 2016), *Buriolestes schultzi* (CAPPA/UFSM 0035 – Müller *et al.*, 2018a), and *Gnathovorax cabreirai* Pacheco *et al.*, 2019 (CAPPA/UFSM 0009 – Pacheco *et al.*, 2019). Lateral to the dorsolateral trochanter runs a sharp longitudinal ridge that represents the cranial trochanter. This trochanter differs from several theropods and ornithischians by the shape of the proximal end, which connects smoothly to the femoral shaft. The distal end of this trochanter is connected to a pronounced, transversely oriented ridge. This structure represents the trochanteric shelf and is absent in post-Carnian

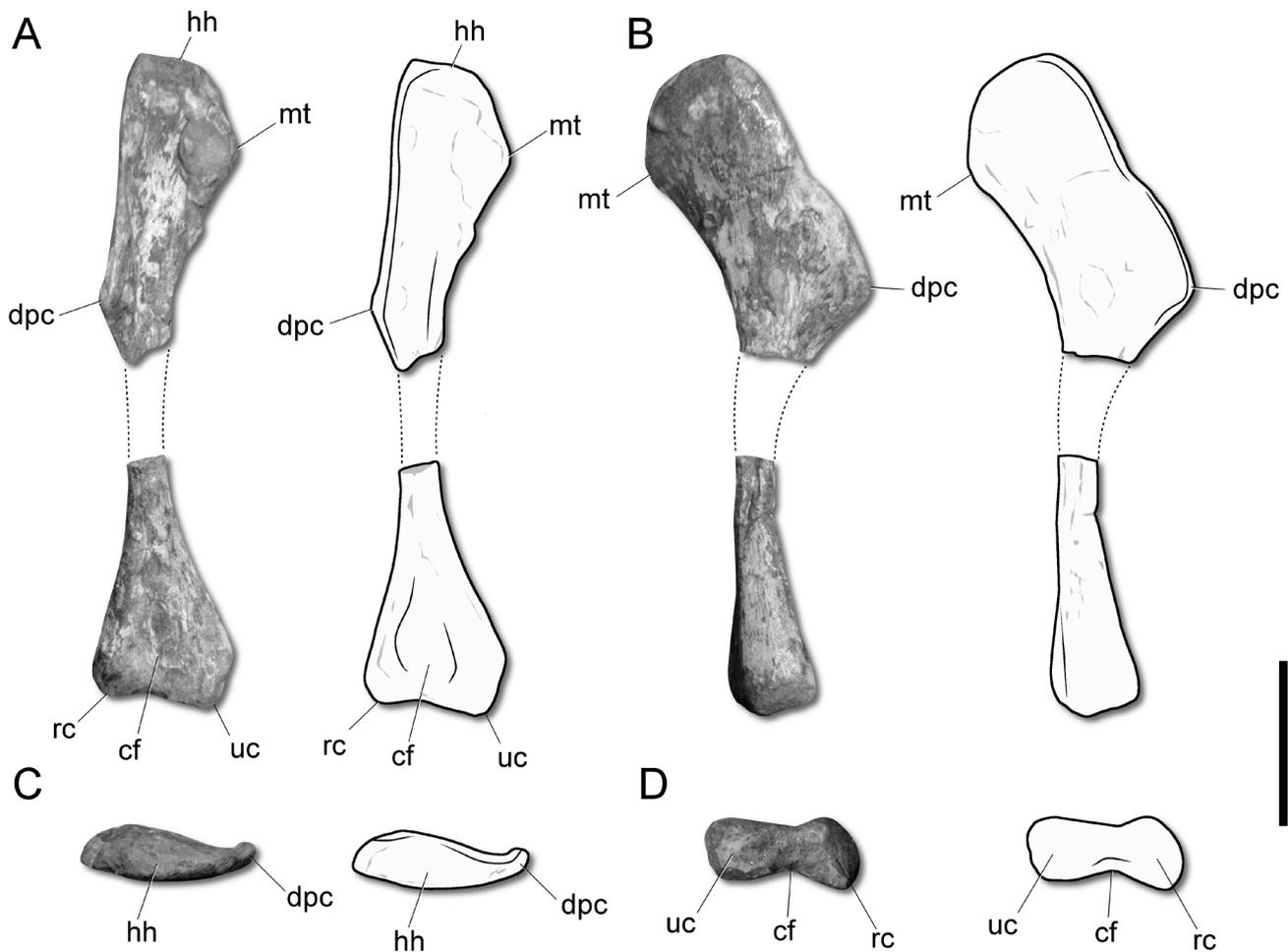


**Figure 4.** Sacrum of UFRGS-PV-1232-T. **A**, left ilium in lateral view and sacral vertebrae in right lateral view. **B**, three-dimensional rendering of the left ilium in lateral view. **C**, three-dimensional rendering of the left ilium in ventral view. **D**, three-dimensional rendering of the left ilium in dorsal view. **E**, three-dimensional rendering of the left ilium in cranial view. **F**, three-dimensional rendering of the left ilium in caudal view. Abbreviations: **1sc**, first primordial sacral vertebra; **2sc**, second primordial sacral vertebra; **bf**, brevis fossa; **ib**, iliac blade; **ip**, ischiodic peduncle; **mb**, medial blade; **ms**, muscle scar; **mw**, medial wall; **pa**, postacetabular ala; **pp**, pubic peduncle; **pra**, preacetabular ala; **sac**, supracetabular crest. Note that the sacral vertebrae are not articulated with the ilium and rotated 180°. Scale bar = 50 mm.

sauropodomorphs, like *Macrocollum itaquii* (CAPPA/UFSM 0001b) and *Coloradisaurus brevis* (Bonaparte, 1978) (PVL 5904). However, the trochanteric shelf is a typical trait of Carnian dinosaurs, recognized in herrerasaurids (Novas, 1993; Pacheco *et al.*, 2019), sauropodomorphs (Ezcurra, 2010; Cabreira *et al.*, 2016; Pretto *et al.*, 2019), and putative theropods (Martínez *et al.*, 2011). A sharp longitudinal ridge that corresponds to the cranial intermuscular line runs

ventral to the craniolateral corner of the trochanteric shelf. The fourth trochanter is crest-like and asymmetrical, with the distal margin forming a steeper angle to the shaft. The medial surface of that trochanter bears a fossa that probably represents the insertion point of the musculus caudofemoralis longus (see Langer, 2003).

On the craniolateral surface of the distal portion there is a point densely marked by muscle scars (Figure 3A). A



**Figure 5.** Right humerus of CAPPA/UFSM 0271. **A**, cranial view. **B**, lateral view. **C**, proximal view. **D**, distal view. Abbreviations: **cf**, cuboid fossa; **dpc**, deltopectoral crest; **hh**, humeral head; **mt**, medial tuberosity; **rc**, radial condyle; **uc**, ulnar condyle. Scale bar = 20 mm.

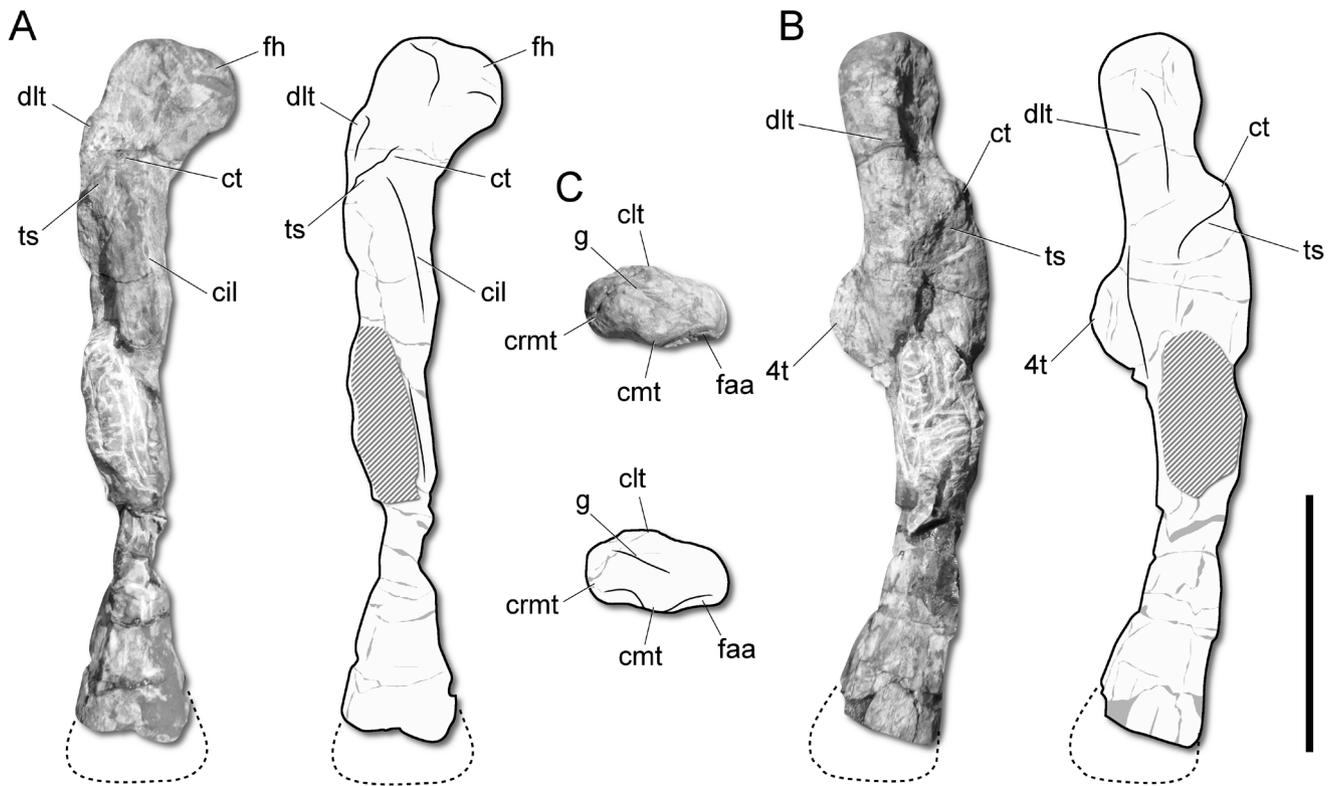
similar condition was also reported for other coeval dinosaurs, like *Saturnalia tupiniquim* (MCP 3944-PV – Langer, 2003) *Buriolestes schultzi* (CAPPA/UFSM 0035 – Müller *et al.*, 2018a), and *Pampadromaeus barberenai* Cabreira *et al.*, 2011 (CAPPA/UFSM 0027 – Müller *et al.*, 2016). The popliteal surface occupies approximately 20% of the total length of the bone, distinct from several silesaurids (*e.g.* *Silesaurus opolensis*, *Sacisaurus agudoensis* Ferigolo & Langer, 2006), which bear proximodistally longer fossae (Nesbitt *et al.*, 2010). In distal view, the fossa is wide and U-shaped. The distal articular surface is strongly affected by sedimentary compression. Therefore, it is hard to discern the crista tibiofibularis from the lateral condyle. Nevertheless, both are clearly smaller than the medial condyle. There is a groove between the craniomedial and the caudolateral portions of the distal articular surface.

**Material.** UFRGS-PV-1232-T. A sacrum and a left ilium (Figure 4).

**Diagnostic traits.** The specimen is assigned to Dinosauria due the presence of a brevis shelf, a ventrally oriented brevis

fossa, and the straight to slightly convex ventral margin of the acetabular wall of the ilium.

**Description and remarks.** The sacrum preserves the two primordial sacral vertebrae and their respective ribs (Figure 4A). The centrum of the first sacral vertebra is elongated. The cranial articular surface is concave and crescent shaped in cranial view. The caudal articular surface is articulated against the cranial articular surface of the second sacral vertebra. However, both elements are not co-ossified. The size of the centrum of the second sacral vertebra is uncertain as it is obscured by a dense layer of sediment. The prezygapophysis of the first sacral vertebra is cranially short and does not extend past the level of the cranial margin of its centrum. The transverse process roofs partially the first sacral rib. The ventral portion of the first sacral rib is not preserved. However, the morphology of the preserved parts that it was “C”-shaped in lateral view, matching the morphology of coeval saurischians, like *Pampadromaeus barberenai* (ULBRA-PVT016), *Saturnalia tupiniquim* (MCP 3944-PV), and *Bagualosaurus agudoensis* (UFRGS-PV-1099-T). The transverse process of the second sacral vertebra



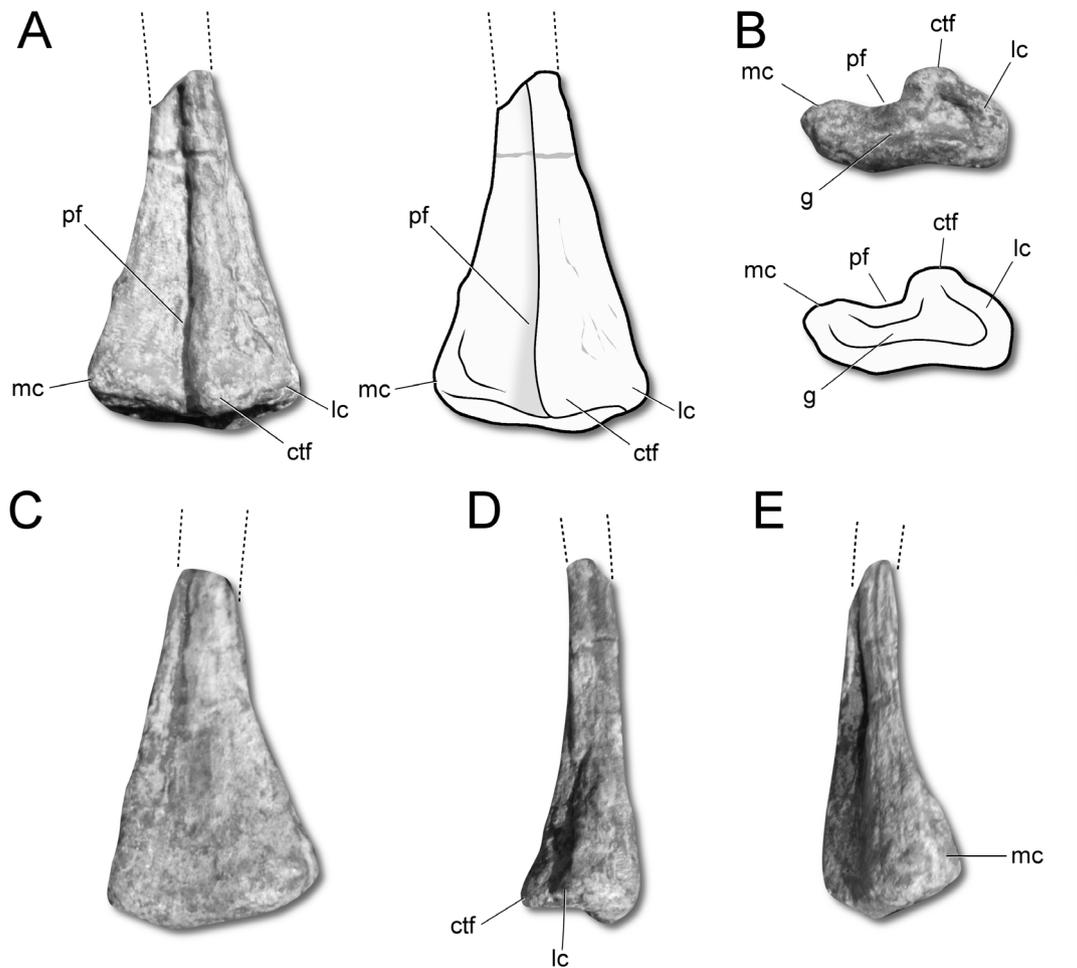
**Figure 6.** Right femur of CAPP/UFMS 0272. **A**, cranial view. **B**, lateral view. **C**, proximal view. Abbreviations: **4t**, fourth trochanter; **cil**, cranial intermuscular line; **clt**, craniolateral tuber; **cmt** caudomedial tuber; **crmt**, craniomedial tuber; **ct**, cranial trochanter; **dlt**, dorsolateral trochanter; **faa**, facies articularis antitrochanterica; **fh**, femoral head; **g**, groove; **ts**, trochanteric shelf. Scale bar = 50 mm.

is caudolaterally directed, while its rib runs cranioventrally, resulting in an “S” shape in lateral view. The putative ventral contact with the first sacral rib is not visible as the caudal end of the first sacral rib is not preserved. On the other hand, a dorsal contact between the elements is clearly absent in the specimen. This condition resembles the morphology of coeval sauropodomorphs (e.g. *Pampadromaeus barberenai* – ULBRA-PVT016; *Buriolestes schultzi* – CAPP/UFMS 0035), whereas in *Herrerasaurus ischigualastensis* (PVL 2566) a caudal expansion of the transverse process of the first sacral vertebra attaches against a cranial expansion of the transverse process of the second element (Novas, 1993). The neural spines of both sacral vertebrae are subequal in size. In contrast, in *Bagualosaurus agudoensis* (UFRGS-PV-1099-T) the neural spine of the first sacral vertebra is craniocaudally shorter than the spine of the second element. This specimen is distinct from *Herrerasaurus ischigualastensis* (PVL 2566), because UFRGS-PV-1232-T lacks spine tables. On the other hand, the specimen bears gently striated expansions on the distal tip of the neural spines, which resemble the holotype (ULBRA-PVT016) of *Pampadromaeus barberenai* (Langer *et al.*, 2019).

The ilium is 83 mm in length (Figure 4). The cranial margin of the preacetabular ala does not exceed the cranial margin of the pubic peduncle. Resembling the holotype (ULBRA-PVT280) of *Buriolestes schultzi*, the tip of the

preacetabular process is sub-rectangular and tall. On the other hand, the same structure is pointed to sub-triangular in the post-Carnian sauropodomorphs, *Macrocollum itaquii* (CAPP/UFMS 0001b) and *Saturnalia tupiniquim* (MCP 3946-PV). Moreover, there is a raised scar (Figure 4A) that resembles those present in the holotype (ULBRA-PVT280) of *Buriolestes schultzi*, *Saturnalia tupiniquim* (MCP 3945-PV), and a putative saturnaliin from Brazil (CAPP/UFMS 0200 – Garcia *et al.*, 2019). However, in the indeterminate saturnaliin, the raised scar is mostly horizontally oriented and more rugous, while in UFRGS-PV-1232-T the scar is more vertical and less rough. In addition, a specimen referred to *Buriolestes schultzi* (CAPP/UFMS 0035) also has a scar, but it does not form a raised process, similar to a condition observed in the holotype of *Pampadromaeus barberenai* (ULBRA-PVT016; Langer *et al.*, 2019). The scar of UFRGS-PV-1232-T extends longitudinally along the dorsal surface of the iliac blade, but it does not form a raised process. Nevertheless, at the caudal portion of the postacetabular ala, the scars becomes a raised process again, resembling the condition of *Buriolestes schultzi* (ULBRA-PVT280, CAPP/UFMS 0035), *Chromogisaurus novasi* Ezcurra, 2010 (PVSJ 845), *Saturnalia tupiniquim* (MCP 3944-PV, 3945-PV), and CAPP/UFMS 0200 (Langer, 2003; Ezcurra, 2010; Müller *et al.*, 2018a; Garcia *et al.*, 2019).

The postacetabular ala is more developed than the preacetabular ala (Figure 4B), exceeding the ischiadic



**Figure 7.** Right femur of CAPPA/UFSM 0273. **A**, caudal view. **B**, distal view. **C**, cranial view. **D**, lateral view. **E**, medial view. Abbreviations: **ctf**, crista tibiofibularis; **g**, groove; **lc**, lateral condyle; **mc**, medial condyle; **pf**, popliteal fossa. Scale bar = 20 mm.

peduncle. In herrerasaurids such as *Herrerasaurus ischigualastensis* (PVL 2566), *Gnathovorax cabreirai* (CAPPA/UFSM 0009), and especially *Staurikosaurus pricei* (MCZ 1669) the postacetabular process is considerable shorter. As typical of dinosaurs, there is a brevis fossa on the ventral surface of the postacetabular ala (Figure 4C). The iliac blade is dorsoventrally larger than the dorsoventral height of the iliac acetabulum. The dorsal margin of the iliac blade is almost straight along its entire length. The supracetabular crest runs along the pubic peduncle and forms the roof of the acetabulum. However, the cranial tip of the crest does not reach the cranial end of the pubic peduncle and also merges caudally with the ilium distant from the cranial portion of the brevis shelf. Moreover, the crest is well-developed laterally and slightly ventrally oriented. The medial wall of the acetabulum reaches the ventral margin of the bone, almost completely closing the acetabulum, a usual condition in Carnian dinosaurs, except for herrerasaurids (e.g. *Herrerasaurus ischigualastensis* – PVL 2566; *Staurikosaurus pricei* – MCZ 1669; *Gnathovorax cabreirai* – CAPPA/USFM 0009).

**Material.** CAPPA/UFSM 0271. A right humerus that lacks the middle portion of the diaphysis (Figure 5).

**Diagnostic traits.** The specimen is assigned to Dinosauria due the presence of a dorsoventrally well developed and subrectangular deltopectoral crest of the humerus.

**Description and remarks.** The bone is separated in two portions. The proximal portion is approximately 42.5 mm in length and encompasses the entire deltopectoral crest. The proximal articular surface is straight to gently convex. There is no caudal tuberosity in the head, contrasting with many dinosaurs like *Buriolestes schultzi* (ULBRA-PVT280), *Herrerasaurus ischigualastensis* (PVSJ 373), and *Macrocollum itaquii* (CAPPA/UFSM 0001b). The medial tuberosity is ventrally directed, while in *Herrerasaurus ischigualastensis* (PVSJ 373) it forms a dorsally projected, finger-shaped process (Serenó *et al.*, 1993). Moreover, the transition between the proximal articular surface and the medial tuberosity is smooth, while in *Buriolestes schultzi* (ULBRA-PVT280) and *Herrerasaurus ischigualastensis* (PVSJ 373) there is a marked gap. The condition of the specimen resembles post-Carnian sauropodomorphs, like

*Unaysaurus tolentinoi* Leal *et al.*, 2004 (UFSM 11069) and *Adeopapposaurus mognai* Martinez, 2009 (PVSJ 610). The deltopectoral crest is well developed, as typical for dinosaurs. The structure is subrectangular and bears a faint concavity in the proximal portion, at the contact with the main body of the bone. In cranial view the crest is straight, rather than strongly sinuous as in some sauropodomorphs like *Coloradisaurus brevis* (PVL 5904 – Apaldetti *et al.*, 2013). The lateral surface of the crest lacks a longitudinally oriented ridge, which is present in *Buriolestes schultzi* (ULBRA-PVT280), *Saturnalia tupiniquim* (MCP 3844-PV) and *Unaysaurus tolentinoi* (UFSM 11069).

The distal preserved portion of the humerus is approximately 37 mm in length. As preserved, the shaft is remarkably slender (5 to 6 mm wide and minimum circumference of the shaft approximately 17 mm), while the distal end is transversely expanded (maximum width is approximately 19.2 mm). The cranial surface of the distal portion is gently concave. The radial condyle is more developed cranially than the ulnar condyle. In contrast, the latter is more developed distally, which resembles *Buriolestes schultzi* (ULBRA-PVT280) and *Saturnalia tupiniquim* (MCP 3844-PV). Both condyles are separated by a shallow cuboid fossa. Distinct from *Buriolestes schultzi* (ULBRA-PVT280) and *Herrerasaurus ischigualastensis* (PVSJ 373), the specimen lacks a rugose swelled crest on the entepicondylar surface.

**Material.** CAPP/UFMS 0272. A partial right femur that lacks the distal articular surface (Figure 6).

**Diagnostic traits.** The specimen is assigned to Dinosauria due the presence of a concave emargination between the transition from the femoral shaft to the femoral head.

**Description and remarks.** The preserved length is approximately 130 mm and the minimum circumference of the shaft is approximately 39 mm. The bone is sigmoid as typical for dinosaurs, and the femoral head is medially projected, but this is accentuated by taphonomic distortion. The maximum length of the proximal end is approximately 27 mm. A transverse groove lies on the proximal articular surface, and a tuber marks its craniolateral margin. There are two additional tubers on the caudal margin, one craniomedial and the other caudomedial. Both tubers are subequal in size and are separated by a sulcus for the ligament of the femoral head. In contrast to the morphology observed here, the caudomedial tuber is generally expanded in non-dinosaur dinosauriforms (Novas, 1996). The facies articularis antitrochanterica is ventrally oriented. The dorsolateral trochanter forms a sharp raised process and does not lie on the cranial surface of the femoral head. The cranial trochanter is proximodistally oriented and is connected to a trochanteric shelf that reaches the caudomedial margin of the bone. An intermuscular line runs longitudinally from the distal portion of the cranial trochanter. The fourth trochanter is symmetrical and crest-like, with both proximal and distal margins forming low angles with the shaft. This condition differs from several coeval dinosaurs (*e.g.* *Buriolestes schultzi*, CAPP/UFMS 0035; *Pampadromaeus barberenai*, CAPP/UFMS 0027; *Saturnalia tupiniquim*, MCP3944-PV)

where the distal margin of the trochanter forms a steeper angle to the shaft, resulting in an asymmetrical trochanter. However, a symmetrical fourth trochanter is recognized in non-dinosaur dinosauromorphs (*e.g.* *Ixalerpeton polesinensis* Cabreira *et al.*, 2016, *Dromomeron gregorii* Nesbitt *et al.*, 2009, *Sacisaurus agudoensis*), *Staurikosaurus pricei* (MCZ 1669), and theropods [*e.g.* *Coelophysis bauri* (Cope, 1887), *Liliensternus liliensterni* (Huene, 1934), *Dilophosaurus wetherilli* (Welles, 1954) – Nesbitt, 2011] as well as in one of the femora of *Bagualosaurus agudoensis*, though Pretto *et al.* (2019) argued that its morphology represents overpreparation. In addition, this trochanter is proportionally proximodistally shorter than that of CAPP/UFMS 0027, another dinosaur femur from the same fossiliferous site (Müller *et al.*, 2016). The distal end of the femur is expanded, but the fragmentary condition of the distal portion hinders any further observations on its structure.

**Material.** CAPP/UFMS 0273. Distal articular surface of a right femur (Figure 7).

**Diagnostic traits.** The taxonomic assignment proposed here is tentative, given the fragmentary condition of the specimen, lacking clear synapomorphies of Dinosauria. The assignment relies, as such, on the similar morphology shared with CAPP/UFMS 0028 (see below).

**Description and remarks.** This specimen is the most fragmentary of the sample. The preserved portion is 32.8 mm in length and the minimum circumference of the shaft is approximately 18 mm. The maximum length of the distal articular surface is approximately 19.5 mm. Regardless of the fragmentary condition, the size of the specimen is also smaller compared to the other dinosaur specimens from the same site, except CAPP/UFMS 0028, a putative skeletally immature specimen of *Pampadromaeus barberenai* (Müller *et al.*, 2019). Therefore, this specimen could belong to an immature individual. Indeed, there is an unusual deep groove on the distal articular surface, which resembles CAPP/UFMS 0028. The cranial surface of the bone collapsed as a result of postmortem processes, creating a longitudinal sulcus, which is taphonomic in origin, the same possibly being the case for the concave cranial margin of the distal end. The popliteal fossa is well-developed proximodistally. However, the depression of this region also seems affected by postmortem processes. All three condyles are subequal in length, whereas *Pampadromaeus barberenai* (ULBRA-PVT016; CAPP/UFMS 0027) has a reduced crista tibiofibularis (Müller *et al.*, 2016). This condition also differs from the condition in lagerpetids, where the crista tibiofibularis is remarkable expanded (Irmis *et al.*, 2007; Nesbitt *et al.*, 2009; Cabreira *et al.*, 2016; Garcia *et al.*, 2019).

## DISCUSSION AND CONCLUSION

The morphology of the new specimens described here match those of coeval dinosaurs, especially non-herrerasaurid saurischians. Although the sizes of the recovered elements resemble those of *Pampadromaeus barberenai*, rather than *Bagualosaurus agudoensis*, a less-inclusive designation based

on an apomorphic approach is difficult due to of the recent phylogenetic controversies concerning the earliest dinosaurs. For instance, the theropod/sauropodomorph split still is obscure in anatomical terms (Langer, 2014). In some analyses, putative basal members of Theropoda (*e.g.* *Eodromaeus*, *Guaibasaurus*, *Daemonosaurus*) are recovered as saurischians basal to this dichotomy (*e.g.* Cabreira *et al.*, 2016; Pacheco *et al.*, 2019). Therefore, the synapomorphies of each dinosaur clade are, for now, poorly understood.

The new specimens, which represent five individuals, increase the number of dinosaurs collected from the Janner site, actually doubling the number of dinosaurs sampled from the locality. Yet, this content of dinosaurs is still low when compared to the record of cynodonts from the same locality. Taking solely the collection housed at CAPP/UFMS until the end of 2019, the number of cynodonts from the Janner site is approximately five times higher than the total of dinosaurs (Table 1). Indeed, the paleofauna present at the Janner site (upper *Hyperodapedon* AZ/*Exaeretodon* sub-AZ - Müller & Garcia, 2019) is consistent with the latest Carnian-earliest Norian records of the Ischigualasto Formation of Argentina (*Exaeretodon* biozone), where traversodontid cynodonts are the most abundant faunal element. Another quantification of the ecosystem parcel occupied by dinosaurs during the late Carnian indicates that dinosaurs correspond to ~1.5% of the tetrapod record from the Ischigualasto Formation, Argentina (Martínez *et al.*, 2013). Both quantifications agree that dinosaurs were rare components on the land ecosystems during the Carnian.

Therefore, it is not a surprise that some portions of the skeleton are yet unknown for the dinosaurs from the Janner site. For instance, the humerus (which is described here) is poorly preserved in *Pampadromaeus barberenai* and unknown in *Bagualosaurus agudoensis*. Moreover, the cervical series is completely unknown for both. Thus, the new specimens bring anatomical information that was, so far, unknown for the dinosaurs of the Janner site. Unfortunately, as previously mentioned, a less inclusive identification of the isolated elements is not possible at this time. Nevertheless, some comments are pertinent. For instance, the shape of the preserved cervical vertebrae does not match with that of Norian sauropodomorphs, like *Macrocollum itaquii*, which bears elongated vertebrae (Müller *et al.*, 2018b). So, if the specimen CAPP/UFMS 0270 belongs to one of the previously known dinosaurs from the Janner site, this dinosaur probably does not have an elongated neck, typical for a Carnian sauropodomorph. In addition, the preserved presacral vertebrae of this specimen are not craniocaudally short, as seen only in the cranialmost and caudalmost dorsal vertebrae of herrerasaurids among basal dinosauriforms. Thus, the condition of CAPP/UFMS 0270 is more similar to that of basal sauropodomorphs such as *Buriolestes schultzi* and *Saturnalia tupiniquim*. The presence of a trochanteric shelf in the described femora is also more related to the typical condition of Carnian dinosaurs, with the exception of *Staurikosaurus pricei* (Bittencourt & Kellner, 2009; Garcia *et*

*al.*, 2019) or immature specimens (*e.g.* Marsola *et al.*, 2018; Müller *et al.*, 2019).

Regarding UFRGS-PV-1232-T, the overall morphology of the ilium and sacrum matches that of basal saurischians, such as *Eodromaeus murphi* Martínez *et al.*, 2011, and early sauropodomorphs such as *Buriolestes schultzi* and *Eoraptor lunensis* Sereno *et al.*, 1993. A peculiar feature of the ilium is the presence of rugosities related to muscle attachment scars. These rugosities have been used as a trait of saturnaliin sauropodomorphs (mainly *Saturnalia tupiniquim* and *Chromogisaurus novasi*), but a comparative study of basal dinosaurs ilia showed that this feature is more widespread among the group (Garcia *et al.*, 2019). Indeed, other basal dinosaurs such as the holotype of *Buriolestes schultzi* and *Herrerasaurus ischigualastensis*, as well as non-dinosaurian dinosauriforms (*e.g.* *Silesaurus opolensis*, *Ignotosaurus fragilis* Martínez *et al.*, 2013) also bear these rugosities. On the other hand, although widespread among basal dinosaurs, in sauropodomorphs these rugosities seem to be restricted to the basalmost forms, since they are absent in *Pampadromaeus barberenai*, *Panphagia protos* Martínez & Alcober 2009, *Bagualosaurus agudoensis*, and Norian sauropodomorphs such as *Macrocollum itaquii*. Therefore, UFRGS-PV-1232-T has a condition similar to that of Carnian sauropodomorphs. Moreover, this specimen has a relatively craniocaudally short ilium, like *Buriolestes schultzi* (CAPP/UFMS 00035) and *Eoraptor lunensis* (PVSJ 512), but slightly differing from the more elongated ilium of *Saturnalia tupiniquim* (MCP 3945-PV; MCP 3946-PV), *Chromogisaurus novasi* (PVSJ 845), and *Panphagia protos* (PVSJ 874), and also differing from the much more craniocaudally short ilium typical of herrerasaurids (*e.g.* *Herrerasaurus ischigualastensis* - PVSJ 373 and *Staurikosaurus pricei* - MCZ 1669). Nevertheless, several factors that may have influence in this feature (*e.g.* ontogeny) are still poorly understood in basal dinosaurs (Garcia *et al.*, 2019).

Furthermore, the Janner site might represent a key window in deep time to a faunal turnover regarding major herbivores/omnivores in the Carnian land ecosystems. While deposits of the latest Ladinian-early Carnian include stenaulorhynchine rhynchosaurs (*e.g.* *Brasinorhynchus* Schultz, Langer & Montefeltro, 2016) and traversodontid cynodonts (*e.g.* *Massetognathus* Romer, 1967) as major herbivores/omnivores (Ezcurra *et al.*, 2017; Schmitt *et al.*, 2019), the mid to late Carnian ecosystems witnessed the rise and fall of the hyperodapedontine rhynchosaurs (*e.g.* *Hyperodapedon*), possibly to the benefit of traversodontid cynodonts (Langer *et al.*, 2007), which become dominant on the latest Carnian-earliest Norian (Martínez *et al.*, 2013). Nonetheless, the latter are also virtually substituted by herbivorous/omnivorous dinosauriforms (*i.e.* sauropodomorphs and silesaurids/ornithischians - see Cabreira *et al.*, 2016; Ezcurra *et al.*, 2017; Garcia *et al.*, 2019). Therefore, the specimens herein presented are an addition to the paleofauna of an important fossiliferous locality of the Late Triassic of southern Brazil, and expand the knowledge of some anatomical traits of the dinosaurs of this age.

Table 1. Dinosaurs and cynodonts deposited at the CAPPA/UFSM collection.

Specimen	Anatomical element	Taxonomic ascription	Dinosauria (D) or Cynodontia (C)
CAPPA/UFSM 0027	Femur	cf. <i>Pampadromaeus barberenai</i>	D
CAPPA/UFSM 0028	Femur	cf. <i>Pampadromaeus barberenai</i>	D
CAPPA/UFSM 0029	Skull and lower jaw	<i>Trucidocynodon riograndensis</i>	C
CAPPA/UFSM 0030	Skull and lower jaw	<i>Exaeretodon</i>	C
CAPPA/UFSM 0030	Skull and lower jaw	<i>Exaeretodon</i>	C
CAPPA/UFSM 0030	Skull and lower jaw	<i>Exaeretodon</i>	C
CAPPA/UFSM 0030	Lower jaw	<i>Exaeretodon</i>	C
CAPPA/UFSM 0033	Skull and lower jaw	<i>Exaeretodon</i>	C
CAPPA/UFSM 0036	Skull	Cynodontia	C
CAPPA/UFSM 0199	Femur	Cynodontia	C
CAPPA/UFSM 0201	Lower jaw	Traversodontidae	C
CAPPA/UFSM 0202	Lower jaw	Traversodontidae	C
CAPPA/UFSM 0203	Skull	<i>Exaeretodon</i>	C
CAPPA/UFSM 0204	Lower jaw	<i>Exaeretodon</i>	C
CAPPA/UFSM 0205	Lower jaw	cf. <i>Exaeretodon</i>	C
CAPPA/UFSM 0208	Lower jaw	Probainognathia	C
CAPPA/UFSM 0215	Canine tooth	cf. <i>Exaeretodon</i>	C
CAPPA/UFSM 0216	Maxilla	<i>Exaeretodon</i>	C
CAPPA/UFSM 0217	Post-canine tooth	<i>Exaeretodon</i>	C
CAPPA/UFSM 0220	Lower jaw	<i>Exaeretodon</i>	C
CAPPA/UFSM 0222	Skull	<i>Exaeretodon</i>	C
CAPPA/UFSM 0223	Humerus	cf. Traversodontidae	C
CAPPA/UFSM 0231	Lower jaw	Traversodontidae	C
CAPPA/UFSM 0232	Lower jaw	Traversodontidae	C
CAPPA/UFSM 0235	Lower jaw	Traversodontidae	C
CAPPA/UFSM 0239	Lower jaw	Traversodontidae	C
CAPPA/UFSM 0243	Partial skeleton	Traversodontidae	C
CAPPA/UFSM 0250	Autopodium	Cynodontia	C
CAPPA/UFSM 0251	Lower jaw	<i>Exaeretodon</i>	C
CAPPA/UFSM 0263	Lower jaw	<i>Exaeretodon</i>	C
CAPPA/UFSM 0264	Lower jaw	<i>Exaeretodon</i>	C
CAPPA/UFSM 0265	Lower jaw	<i>Exaeretodon</i>	C
CAPPA/UFSM 0266	Lower jaw	<i>Exaeretodon</i>	C
CAPPA/UFSM 0267	Lower jaw	<i>Exaeretodon</i>	C
CAPPA/UFSM 0270	Partial postcranium	cf. Saurischia	D
CAPPA/UFSM 0271	Humerus	Dinosauria	D
CAPPA/UFSM 0272	Femur	Dinosauria	D
CAPPA/UFSM 0273	Femur	cf. Dinosauria	D

## ACKNOWLEDGEMENTS

We thank C.L. Schultz (curator of UFRGS), who made the specimen UFRGS-PV-1232-T available for study. We also extend our gratitude to J. Choiniere and A.B. Heckert for comments and suggestions that improved the quality of this manuscript.

## REFERENCES

- Alcober, O.A. & Martinez, R.N. 2010. A new herrerasaurid (Dinosauria, Saurischia) from the Upper Triassic Ischigualasto formation of northwestern Argentina. *ZooKeys*, **63**:55–81. doi:10.3897/zookeys.63.550
- Andreis, R.R.; Bossi, G.E. & Montardo, D.K. 1980. O Grupo Rosário do Sul (Triássico) no Rio Grande do Sul, Brasil. In: CONGRESSO BRASILEIRO DE GEOLOGIA, 31, 1980. *Anais, Camboriú*, p. 659–673.
- Apaldetti, C.; Pol, D. & Yates, A. 2013. The postcranial anatomy of *Coloradisaurus brevis* (Dinosauria: Sauropodomorpha) from the Late Triassic of Argentina and its phylogenetic implications. *Palaeontology*, **56**:277–301. doi:10.1111/j.1475-4983.2012.01198.x
- Bittencourt, J.S. & Kellner, A.W.A. 2009. The anatomy and phylogenetic position of the Triassic dinosaur *Staurikosaurus pricei* Colbert, 1970. *Zootaxa*, **2079**:1–56. doi:10.11646/zootaxa.2079.1.1
- Cabreira, S.F.; Kellner, A.W.A.; Dias-da-Silva, S.; Roberto-da-Silva, L.; Bronzati, M.; Marsola, J.C.A.; Müller, R.T.; Bittencourt, J.S.; Batista, B.J.; Raugust, T.; Carrilho, R.; Brodt, A. & Langer, M.C. 2016. A unique Late Triassic dinosauromorph assemblage reveals dinosaur ancestral anatomy and diet. *Current Biology*, **26**:3090–3095. doi:10.1016/j.cub.2016.09.040
- Cabreira, S.F.; Schultz, C.L.; Bittencourt, J.S.; Soares, M.B.; Fortier, D.C.; Silva, L.R. & Langer, M.C. 2011. New stem-sauropodomorph (Dinosauria, Saurischia) from the Triassic of Brazil. *Naturwissenschaften*, **98**:1035–1040. doi:10.1007/s00114-011-0858-0
- Da-Rosa, A.A.S. 2015. Geological context of the dinosauriform bearing outcrops from the Triassic of Southern Brazil. *Journal of South American Earth Sciences*, **61**:108–119. doi:10.1016/j.jsames.2014.10.008
- Ezcurra, M.D. 2010. A new early dinosaur (Saurischia: Sauropodomorpha) from the Late Triassic of Argentina: a reassessment of dinosaur origin and phylogeny. *Journal of Systematic Palaeontology*, **8**:371–425. doi:10.1080/14772019.2010.484650
- Ezcurra, M.D.; Fiorelli, L.E.; Martinelli, A.G.; Rocher, S.; Baczkó, M.B. von; Ezpeleta, M.; Taborda, J.R.A.; Hechenleitner, E.M.; Trotteyn, M.J. & Desojo, J.B. 2017. Deep faunistic changes preceded the rise of dinosaurs in southwestern Pangaea. *Nature Ecology & Evolution*, **1**:1477–1483. doi:10.1038/s41559-017-0305-5
- García, M.S.; Müller, R.T.; Da-Rosa, Á.A. & Dias-da-Silva, S. 2019. The oldest known co-occurrence of dinosaurs and their closest relatives: a new lagerpetid from a Carnian (Upper Triassic) bed of Brazil with implications for dinosauromorph biostratigraphy, early diversification and biogeography. *Journal of South American Earth Sciences*, **91**:302–319. doi:10.1016/j.jsames.2019.02.005
- Griffin, C.T. & Nesbitt, S.J. 2016. The femoral ontogeny and long bone histology of the Middle Triassic (?late Anisian) dinosauriform *Asilisaurus kongwe* and implications for the growth of early dinosaurs. *Journal of Vertebrate Paleontology*, **36**:e1111224. doi:10.1080/02724634.2016.1111224
- Horn, B.L.D.; Melo, T.P.; Schultz, C.L.; Philipp, R.P.; Kloss, H.P. & Goldberg, K. 2014. A new third-order sequence stratigraphic framework applied to the Triassic of the Paraná Basin, Rio Grande do Sul, Brazil, based on structural, stratigraphic and paleontological data. *Journal of South American Earth Sciences*, **55**:123–132. doi:10.1016/j.jsames.2014.07.007
- Irmis, R.B.; Nesbitt, S.J.; Padian, K.; Smith, N.D.; Turner, A.H.; Woody, D. & Downs, A. 2007. A Late Triassic dinosauromorph assemblage from New Mexico and the rise of dinosaurs. *Science*, **317**:358–361. doi:10.1126/science.1143325
- Langer, M.C. 2003. The pelvic and hind limb anatomy of the stem sauropodomorph *Saturnalia tupiniquim* (Late Triassic, Brazil). *PaleoBios*, **23**:1–40.
- Langer, M.C. 2014. The origins of Dinosauria: much ado about nothing. *Palaeontology*, **57**:469–478. doi:10.1111/pala.12108
- Langer, M.C.; Abdala, F.; Richter, M. & Benton, M.J. 1999. A sauropodomorph dinosaur from the Upper Triassic (Carnian) of southern Brazil. *Comptes Rendus de l'Academie des Sciences Paris*, **329**:511–517. doi:10.1016/S1251-8050(00)80025-7
- Langer, M.C.; McPhee, B.W.; Marsola, J.C.; Roberto-da-Silva, L. & Cabreira, S.F. 2019. Anatomy of the dinosaur *Pampadromaeus barberenai* (Saurischia—Sauropodomorpha) from the Late Triassic Santa Maria Formation of southern Brazil. *PloS ONE*, **14**:e0212543. doi:10.1371/journal.pone.0212543
- Langer, M.C.; Ramezani, J. & Da Rosa, Á.A. 2018. U-Pb age constraints on dinosaur rise from south Brazil. *Gondwana Research*, **57**:133–140. doi:10.1016/j.gr.2018.01.005
- Langer, M.C.; Ribeiro, A.M.; Schultz, C.L. & Ferigolo, J. 2007. The continental tetrapod-bearing Triassic of South Brazil. *Bulletin of the New Mexico Museum of Natural History and Science*, **41**:201–218.
- Liparini, A.; Oliveira, T.V.; Pretto, F.A.; Soares, M.B. & Schultz, C.L. 2013. The lower jaw and dentition of the traversodontid *Exaeretodon riograndensis* Abdala, Barberena & Dornelles, from the Brazilian Triassic (Santa Maria 2 Sequence, *Hyperodapedon* Assemblage Zone). *Alcheringa*, **37**:331–337. doi:10.1080/03115518.2013.752607
- Marsola, J.C.; Bittencourt, J.S.; Butler, R.J.; Da Rosa, Á.A.; Sayão, J.M. & Langer, M.C. 2018. A new dinosaur with theropod affinities from the Late Triassic Santa Maria Formation, South Brazil. *Journal of Vertebrate Paleontology*, **38**:e1531878. doi:10.1080/02724634.2018.1531878
- Martínez, R.N.; Apaldetti, C.; Alcober, O.A.; Colombi, C.E.; Sereno, P.C.; Fernandez, E.; Malnis, P.S.; Correa, G.A. & Abelin, D. 2013. Vertebrate succession in the Ischigualasto Formation. *Journal of Vertebrate Paleontology*, **32**:10–30. doi:10.1080/02724634.2013.818546
- Martínez, R.N.; Sereno, P.C.; Alcober, O.A.; Colombi, C.E.; Renne, P.R.; Montañez, I.P. & Currie, B.S. 2011. A basal dinosaur from the dawn of the dinosaur era in southwestern Pangaea. *Science*, **331**:206–210. doi:10.1126/science.1198467
- Müller, R.T.; Araújo-Júnior, H.I.; Aires, A.S.S.; Silva Roberto-da-Silva, L. & Dias-da-Silva, S. 2015. Biogenic control on the origin of a vertebrate monotypic accumulation from the Late Triassic of southern Brazil. *Geobios*, **48**:331–340. doi:10.1016/j.geobios.2015.05.001

- Müller, R.T.; Baczko, M.B.; Desojo, J.B. & Nesbitt, S.J. 2020. The first ornithosuchid from Brazil and its macroevolutionary and phylogenetic implications for Late Triassic faunas in Gondwana. *Acta Palaeontologica Polonica*, **65**:1–10. doi:10.4202/app.00652.2019
- Müller, R.T. & Garcia, M.S. 2019. Rise of an empire: analysing the high diversity of the earliest sauropodomorph dinosaurs through distinct hypotheses. *Historical Biology*, in press. doi:10.1080/08912963.2019.1587754
- Müller, R.T.; Langer, M.C.; Bronzati, M.; Pacheco, C.P.; Cabreira, S.F. & Dias-da-Silva, S. 2018a. Early evolution of sauropodomorphs: anatomy and phylogenetic relationships of a remarkably well preserved dinosaur from the Upper Triassic of southern Brazil. *Zoological Journal of the Linnean Society*, **184**:1187–1248. doi:10.1093/zoolinlean/zly009
- Müller, R.T.; Langer, M.C.; Cabreira, S.F. & Dias-da-Silva, S. 2016. The femoral anatomy of *Pampadromaeus barberenai* based on a new specimen from the Upper Triassic of Brazil. *Historical Biology*, **28**:656–665. doi:10.1080/08912963.2015.1004329
- Müller, R.T.; Langer, M.C. & Dias-da-Silva, S. 2018b. An exceptionally preserved association of complete dinosaur skeletons reveals the oldest long-necked sauropodomorphs. *Biology Letters*, **14**:20180633. doi:10.1098/rsbl.2018.0633
- Müller, R.T.; Langer, M.C.; Pacheco, C.P. & Dias-da-Silva, S. 2019. The role of ontogeny on character polarization in early dinosaurs: a new specimen from the Late Triassic of southern Brazil and its implications. *Historical Biology*, **31**:794–805. doi:10.1080/08912963.2017.1395421
- Nesbitt, S.J. 2011. The early evolution of archosaurs: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History*, **352**:1–292. doi:10.1206/352.1
- Nesbitt, S.J.; Irmis, R.B.; Parker, W.G.; Smith, N.D.; Turner, A.H. & Rowe, T. 2009. Hindlimb osteology and distribution of basal dinosauiromorphs from the Late Triassic of North America. *Journal of Vertebrate Paleontology*, **29**:498–516. doi:10.1671/039.029.0218
- Nesbitt, S.J.; Sidor, C.A.; Irmis, R.B.; Angielczyk, K.D.; Smith, R.M.H. & Tsuji, L.A. 2010. Ecologically distinct dinosaurian sister group shows early diversification of Ornithodira. *Nature*, **464**:95–98. doi:10.1038/nature08718
- Novas, F.E. 1993. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. *Journal of Vertebrate Paleontology*, **13**:400–423. doi:10.1080/02724634.1994.10011523
- Novas, F.E. 1996. Dinosaur monophyly. *Journal of Vertebrate Paleontology*, **16**:72–741. doi:10.1080/02724634.1996.10011361
- Oliveira, T.V.; Schultz, C.L. & Soares, M.B. 2007. O esqueleto pós craniano de *Exaeretodon riograndensis* Abdala et. al. (Cynodontia, Traversodontidae), Triássico do Brasil. *Revista Brasileira de Paleontologia*, **10**:79–94. doi:10.4072/rbp.2007.2.02
- Oliveira, T.V.; Soares, M.B. & Schultz, C.L. 2010. *Trucidocynodon riograndensis* gen. nov. et sp. nov. (Eucynodontia), a new cynodont from the Brazilian Upper Triassic (Santa Maria Formation). *Zootaxa*, **2382**:1–71. doi:10.11646/zootaxa.2382.1.1
- Pacheco, C.; Müller, R.T.; Langer, M.; Pretto, F.A.; Kerber, L. & da Silva, S.D. 2019. *Gnathovorax cabreirai*: a new early dinosaur and the origin and initial radiation of predatory dinosaurs. *PeerJ*, **7**:e7963. doi:10.7717/peerj.7963
- Piechowski, R.; Tałanda, M. & Dzik, J. 2014. Skeletal variation and ontogeny of the Late Triassic Dinosauriform *Silesaurus opolensis*. *Journal of Vertebrate Paleontology*, **34**:1383–1393. doi:10.1080/02724634.2014.873045
- Pretto, F.A.; Langer, M.C. & Schultz, C.L. 2019. A new dinosaur (Saurischia: Sauropodomorpha) from the Late Triassic of Brazil provides insights on the evolution of sauropodomorph body plan. *Zoological Journal of the Linnean Society*, **185**:388–416. doi:10.1093/zoolinlean/zly028
- Pretto, F.A.; Schultz, C.L. & Langer, M.C. 2015. New dinosaur remains from the Late Triassic of southern Brazil (Candelária Sequence, *Hyperodapedon* Assemblage Zone). *Alcheringa*, **39**:264–273. doi:10.1080/03115518.2015.994114
- Schmitt, M.R.; Martinelli, A.G.; Melo, T.P. & Soares, M.B. 2019. On the occurrence of the traversodontid *Massetognathus ochagaviae* (Synapsida, Cynodontia) in the early late Triassic *Santacruzodon* Assemblage Zone (Santa Maria Supersequence, southern Brazil): taxonomic and biostratigraphic implications. *Journal of South American Earth Sciences*, **93**:36–50. doi:10.1016/j.jsames.2019.04.011
- Sereno, P.C.; Forster, C.A.; Rogers, R.R. & Monetta, A.M. 1993. Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. *Nature*, **361**:64–66. doi:10.1038/361064a0
- Stefanello, M.; Müller, R.T.; Kerber, L.; Martínez, R.N. & Dias-da-Silva, S. 2018. Skull anatomy and phylogenetic assessment of a large specimen of Ecteniniidae (Eucynodontia: Probainognathia) from the Upper Triassic of southern Brazil. *Zootaxa*, **4457**:351–378. doi:10.11646/zootaxa.4457.3.1
- Zerfass, H.; Lavina, E.L.; Schultz, C.L.; Garcia, A.J.V.; Faccini, U.F. & Chemale, F. 2003. Sequence stratigraphy of continental Triassic strata of Southernmost Brazil: a contribution to Southwestern Gondwana palaeogeography and palaeoclimate. *Sedimentary Geology*, **161**:85–105. doi:10.1016/S0037-0738(02)00397-4

Received in 16 March, 2020; accepted in 09 June, 2020.