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New dinosaur remains from the Late Triassic of southern Brazil (Candelária Sequence, *Hyperodapedon* Assemblage Zone)

FLÁVIO A. PRETTO, CESAR L. SCHULTZ and MAX C. LANGER

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The oldest unequivocal dinosaurian records come from Upper Triassic strata, mostly from Argentina and Brazil. Recent fieldwork in the Brazilian deposits of Ischigualastian age (late Carnian–earliest Norian) have resulted in the collection of a new specimen (UFRGS-PV-1240-T) identified as dinosaurian by the presence of a concave emargination on the ventral surface of the femoral head and a well-developed deltopectoral crest on the humerus, which extends for *ca* 40% of its estimated proximodistal length. Although fragmentary, the material increases the dinosaurian record from the Late Triassic of Brazil, which is still modest when compared with coeval Argentine strata. Additionally, UFRGS-PV-1240-T augments the dinosaurian diversity at the 'Sítio Janner' site, which was until now restricted to the sauropodomorph *Pampadromaeus barberenai*. The new specimen is larger than most early dinosaurians (except for herrerasaurids), implying that members of the group were already occupying niches otherwise explored by other larger-bodied taxa in the 'Sítio Janner' palaeofauna, and Late Triassic palaeoenvironments in general.

Flávio A. Pretto [flavio_pretto@yahoo.com.br] and Cesar L. Schultz [cesar.schultz@ufrgs.br] Universidade Federal do Rio Grande do Sul, Instituto de Geociências, Setor de Paleovertebrados, Av. Bento Gonçalves, 9500—Bloco J, Prédio 43127, Campus do Vale, Agronomia−Porto Alegre, Rio Grande do Sul, Brazil, CEP 91540-000; Max C. Langer [mclanger@ffclrp.usp.br] Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Departamento de Biologia, Av. Bandeirantes, 3900, CEP 14040-901, Ribeirão Preto, São Paulo, Brazil. *Received 9.4.2014; revised 24.11.2014; accepted 29.11.2014.*

Key words: Early dinosaurs, Triassic, Brazil, Candelária Sequence.

THE TRIASSIC witnessed one of the major evolutionary events in the history of life with the origin of Dinosauria, yet the timing of this event is not well constrained. Some putative Middle Triassic members of the group have been tentatively identified (Huene 1942, Nesbitt *et al*. 2013), but no unequivocal dinosaurian taxa are known from strata older than Late Triassic (Langer *et al*. 2010). Nonetheless, the presence of close dinosaurian outgroups in these older strata suggests that its ghost-lineage (and thus the origin of the group) extended at least into the Middle Triassic (Sereno & Arcucci 1993, 1994, Novas 1996, Nesbitt *et al*. 2010, 2013). Dinosaurians were probably uncommon elements in Middle Triassic terrestrial ecosystems (Irmis 2011), a scenario that may have lasted until the early stages of the Late Triassic (Carnian), when their diversity increased (Ezcurra 2010, Langer *et al*. 2010).

The oldest unambiguous dinosaurians come from the Ischigualasto Sequence of Argentina (Stipanicic & Marsicano 2002, Currie *et al*. 2009) and the Candelária Sequence (former Santa Maria 2 Sequence) of Brazil (Zerfass *et al*. 2003, Horn *et al*. 2014). Argentine dinosaurians of Ischigualastian age *sensu* Bonaparte (1982) and Langer (2005) include the herrerasaurids *Herrerasaurus ischigualastensis* Reig, 1963 (Novas 1993, Sereno & Novas 1993, Sereno 1993) and *Sanjuansaurus gordilloi* Alcober & Martínez, 2010; the sauropodomorphs *Eoraptor lunensis* Sereno *et al*., 1993, *Panphagia protos* Martínez & Alcober, 2009 and *Chromogisaurus novasi* Ezcurra, 2010; the theropod *Eodromaeus murphi* Martínez *et al*., 2011; and the ornithischian *Pisanosaurus mertii* Casamiquela, 1967 (Bonaparte 1976). In Brazil, this record is far less abundant, being represented only by the herrerasaurid *Staurikosaurus pricei* Colbert, 1970 (Bittencourt & Kellner 2009) and the sauropodomorphs *Saturnalia tupiniquim* Langer *et al*., 1999 (Langer 2003, Langer *et al*. 2007) and *Pampadromaeus barberenai* Cabreira *et al*., 2011. Much of this discrepancy may, however, be due to the smaller extent of the Brazilian outcrops and a reduced collection effort.

Intensive fieldwork conducted in the Candelária Sequence over the last few years by a research team from the Universidade Federal do Rio Grande do Sul (UFRGS) has resulted in the collection of several new specimens. Among these, dinosaurian remains (UFRGS-PV-1240-T) from the 'Sítio Janner' locality are presented here. This

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material suggests that dinosaurian dinosauromorphs were an important component of the local palaeofauna and implies that the Brazilian Upper Triassic strata are still relatively undersampled in terms of dinosaurian abundance and diversity.

Geological setting

The 'Sítio Janner' site is located on the outskirts of Agudo, Rio Grande do Sul, Brazil. Lithologically, it comprises massive red beds, including siltstones and very thin sandstones (Fig. 1). These locally incorporate mud inclusions and sporadic rhythmic intervals of various grainsizes. The red beds are divided into a non-fossiliferous portion at the base of the exposed section, and an upper fossiliferous unit. Based on sedimentology, and in the presence of coprolites and putative rhizoliths, the strata are interpreted to have accumulated in a distal floodplain palaeoenvironment. A light-coloured cross-bedded sandstone also occurs at the top of the exposure and represents a river channel. It is delimited by an erosive contact with the underlying red beds.

The 'Sítio Janner' site has produced an important suite of vertebrate fossils (Fig. 1), including the type-material of the sauropodomorph *Pampadromaeus* and the carnivorous cynodont *Trucidocynodon riograndensis* (Oliveira *et al*. 2010). The most abundant taxon is the herbivorous cynodont *Exaeretodon riograndensis* (Oliveira *et al*. 2007, Liparini *et al*. 2013); however, the presence of rhynchosaurs (Hyperodapedontidae) correlates the fossil suite with the *Hyperodapedon* Assemblage Zone (*sensu* Abdala *et al*. 2001) of presumed Ischigualastian age (Langer 2005).

Although hyperodapedontids are biostratigraphic markers, the composition of the 'Sítio Janner'

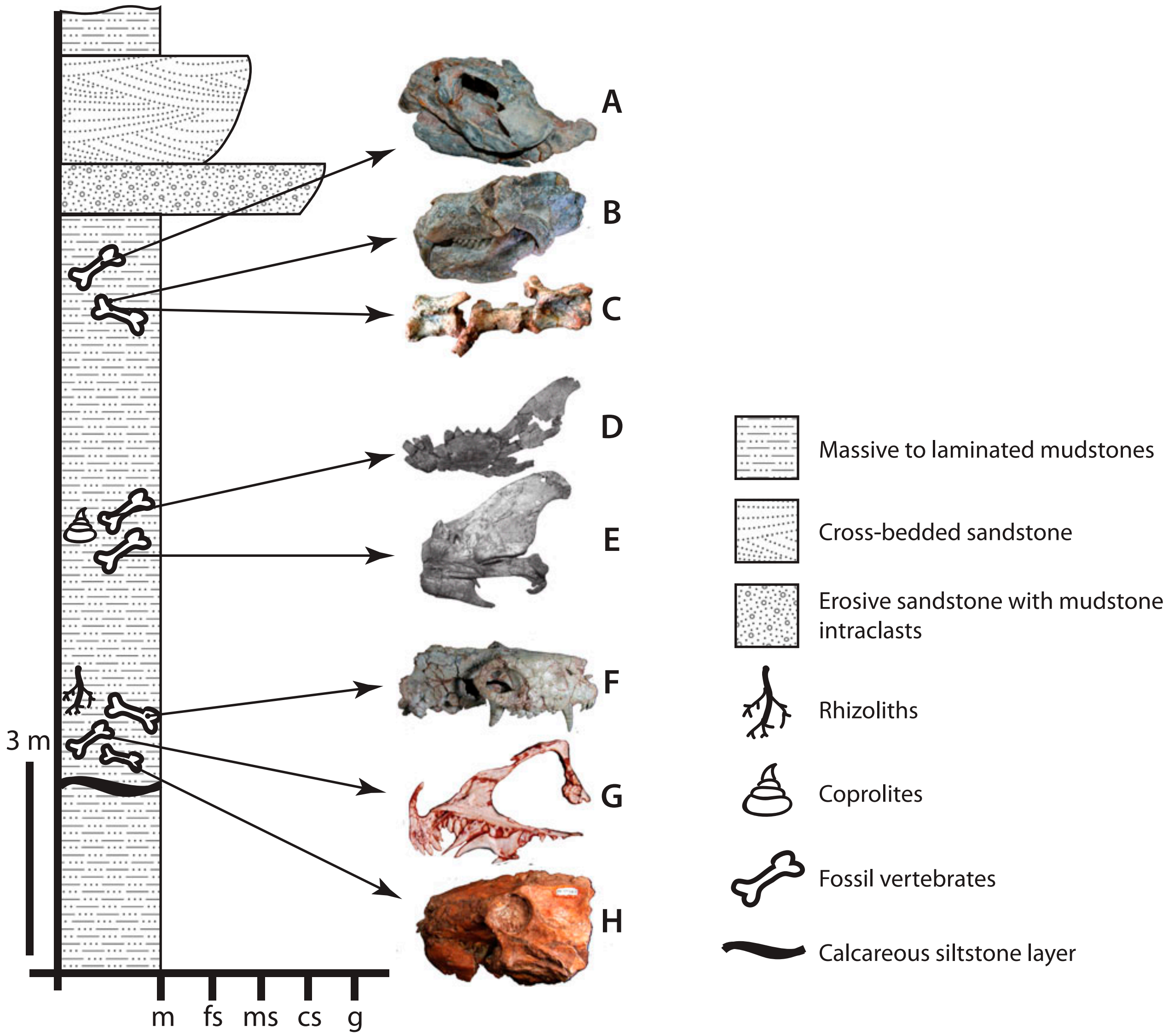

Fig. 1. Stratigraphic section of the 'Sítio Janner' outcrop (Candelária Sequence, Late Triassic, Brazil), with the position of some fossils found at the locality (specimen photographs not to scale). **A**, *Hyperodapedon* sp., MCN-PV-3509; **B**, **D**, **E**, *Exaeretodon riograndensis*, respectively UFRGS-PV-0715-T, 1096-T and 1177-T; **C**, Dinosauria indet., UFRGS-PV-1240-T; **F**, *Trucidocynodon riograndensis*, UFRGS-PV-1051-T; **G**, *Pampadromaeus barberenai*, ULBRA-PVT-016; **H**, juvenile traversodontid (possibly *E. riograndensis*), UFRGS-PV-1160-T.

palaeofauna differs from other coeval assemblages, which are typically dominated (*ca* 90%) by rhynchosaur remains (Schultz *et al*. 2000). In contrast, rhynchosaurs constitute only *ca* 10% of the sampled vertebrate fossils at 'Sítio Janner'; *Exaeretodon* comprises about 50% of the occurrences (Pretto *et al*. 2013). This is similar to the upper portion of the Ischigualasto Formation, where *Exaeretodon* is the most abundant taxon (Rogers *et al*. 1993, Martínez *et al*. 2011, 2013a), and prompts subdivision of the Brazilian *Hyperodapedon* Assemblage Zone into two distinct biostratigraphic units, as previously suggested by Oliveira & Schultz (2007).

Specimen overview

Although disarticulated, the dinosaurian bones (UFRGS-PV-1240-T) were in close spatial distribution (less than 1 m²), and their compatible size infers derivation from a single individual. All of the elements are diagenetically fractured and partly covered by carbonate concretionary material. The identified skeletal components include a left humerus, right femur, fragmentary right pubis and two semi-articulated series of caudal vertebrae. The latter were originally assigned to *Exaeretodon riograndensis* (UFRGS-PV-0715-T) by Oliveira *et al*. (2007), but are reinterpreted here as having dinosaurian affinities. Other co-occurring vertebrate fossils include: (1) a fairly complete individual of *Exaeretodon riograndensis* (UFRGS-PV-0715-T) with articulated skull and most of the postcranial elements (Oliveira *et al*. 2007); (2) the ilium of a smaller *Exaeretodon* specimen; and (3) a small cynodont dentary, possibly from an ontogenetically immature *Exaeretodon* individual.

Description

Caudal vertebrae. Remnants of five caudal vertebrae were found in two discrete sequences. Their morphological similarity (e.g., craniocaudally elongated centra, neural spines caudally displaced, caudolaterally directed transverse processes, ventral surface of the centrum with a longitudinal ventral groove in some vertebrae) to other basal dinosaurian taxa (e.g., Yates 2003, Bittencourt & Kellner 2009, Ezcurra 2010, Sereno *et al*. 2013) advocates referral to UFRGS-PV-1240-T. The cranial-most preserved vertebra (Fig. 2) bears an incomplete transverse processes and neural spine. It articulates with the cranial third of the subsequent vertebra, with the base of a chevron interposed between them. The length/height ratio of the most proximal centrum is 1.19 (31 x 26 mm), which, in conjunction with the well-developed transverse processes, indicates derivation from the proximal part of the tail (Grillo & Azevedo 2011b). The neurocentral sutures are also closed, inferring osteological maturity.

The exposed cranial articular surface is excavated and roughly circular; the caudal articular surface is obscured. The ventral surface is strongly concave and lacks a ventral groove. The lateral margin is slightly depressed just ventral to the transverse process and forms a faint lateral fossa. The neural spine occupies the entire dorsal margin, with its more robust portion interposed between the postzygapophyses, which are in turn separated by a deep median notch similar to that seen in *Saturnalia* and *Guaibasaurus* (Ezcurra 2010) and *Chromogisaurus* (Martínez *et al*. 2013b, *contra* Ezcurra 2010). The articular surfaces of the prezygapophyses face mediodorsally and articulate with the ventrolaterally oriented postzygapophyses.

The second series of three probable mid-caudal vertebrae (Fig. 3) are preserved in articulation, also preserving the proximal end of a chevron. The neurocentral sutures are closed, and the centrum bodies are more elongate (length/height ratio of 1.94, or 35 x 18 mm). The transverse processes are small and laterally projecting. The centra are amphicoelous but with shallower articular facets relative to the more proximal caudals. The ventral surfaces bear faint longitudinal grooves extending along the entire centrum length. The prezygapophyses are robust with dorsomedially oriented articular facets. The neural spines are situated in the caudal half of the centrum and interposed between the postzygapophyses, likewise separated by a median notch. The articular facets of the postzygapophyses are ventrolaterally oriented.

The better-preserved chevron is distoventrally directed and encloses the haemal canal, and none of the chevrons is fused to the centra.

Humerus. Part of a left humerus is preserved, lacking the ectepicondylar area and most of the proximal end (Fig. 4). The bone is 130 mm in maximum preserved length. The humeral shaft is slightly bowed cranially and sub-circular in cross-section with a smooth outer surface. The caudal surface on the distal third of the shaft bears a faint depression dividing the entepicondylar and ectepicondylar (not preserved) portions of the distal humerus. Although the distal extremity is incomplete, the ulnar articulation is still visible. The radial condyle is broken off. The deltopectoral crest is likewise incomplete, but its remnants indicate development consistent with other early dinosaurians (Bakker & Galton 1974, Langer & Benton 2006, Langer *et al.* 2010, Nesbitt 2011). The deltopectoral crest would have extended for about 40% of the estimated total humeral length and has a rugose lateral surface for attachment of the mm. supracoracoideus and deltoideus scapularis inferior (Langer *et al.* 2007).

Pubis. The partial right pubis lacks the proximal articular surfaces, and the medial portion of the apron and its distal half (Fig. 5). The shaft is lacriform in cross-section being very robust laterally, but becoming thinner medially where it would have converged with its counterpart. The proximal portion of the bone bears

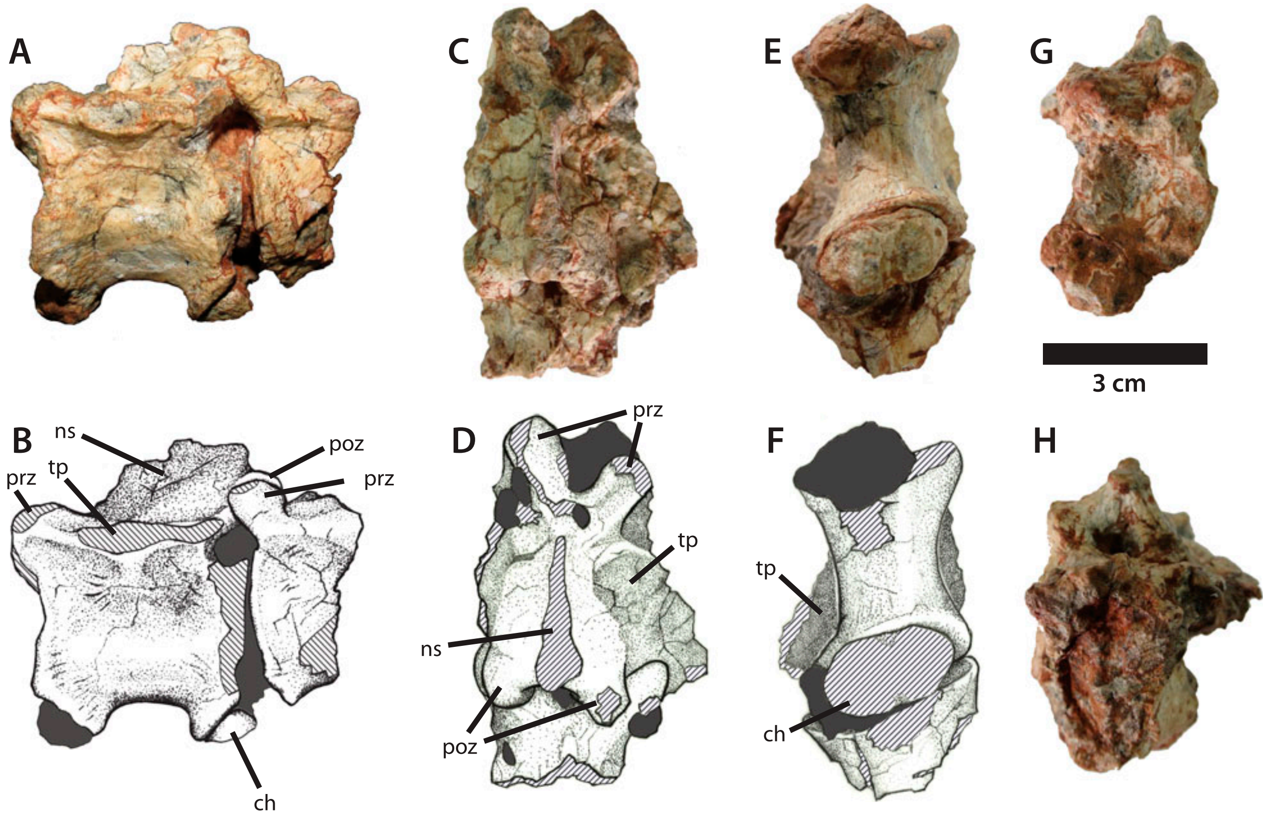

Fig. 2. UFRGS-PV-1240-T, Dinosauria indet. (Candelária Sequence, Late Triassic, Brazil). Proximal caudal vertebrae in lateral (**A, B**), dorsal (**C, D**) ventral (**E, F**), cranial (**G**) and caudal (**H**) views. Grey areas are covered by sediment and dashed areas indicate fractured bone. ch, chevron; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process.

a rugose pubic tubercle, which probably associated with the ambiens musculature (Hutchinson 2001a, Langer 2003, Grillo & Azevedo 2011a). The preserved portion of the shaft is straight in lateral view. Distally, a proximodistally oriented sulcus extends over less than three-quarters of the preserved pubis fragment. In cranial view, the proximomedial surface is laterally curved where it formed the margin of the pelvic canal. The remaining caudal surface is otherwise obscured by encrusting carbonate matrix.

Femur. The right femur has suffered significant damage to its articular ends and the fourth trochanter is missing (Fig. 6). The preserved component is 265 mm in maximum length and has an elliptical midshaft cross-section, with a maximum craniocaudal length of 32 mm and lateromedial width of 24 mm measured across the shaft distal to the presumed position of the fourth trochanter. The compact bone wall thickness does not exceed 25% of the maximum femoral diameter, as seen close to the midlength of the shaft. The femoral shaft is slightly sigmoid in lateral view, and although incomplete, the preserved portion of the femoral head forms a 45° angle to the lateromedial axis of the distal condyles. As in most dinosaurians (Novas 1996, Nesbitt 2011), a concave emargination is evident ventral to the femoral head. A pronounced rugosity on the caudolateral surface of the proximal extremity marks the distal insertion point of m. obturatorius, at the same position observed in *Saturnalia* (Langer 2003). The lesser trochanter is well developed, though considerably lower than in ornithischians and neotheropods (Langer & Benton 2006, Nesbitt 2011). It is fully connected to the shaft and contiguous with a caudally projected trochanteric shelf that extends along the lateral surface of the femur, to terminate in a faint caudolateral swelling. A rugose cranial intermuscular line extends distally from the lesser trochanter to occupy approximately one-third of the femoral length.

Interpretation of the condylar extremity is hindered by damage. The condyles (especially the lateral condyle) are also distorted by crushing. Caudally, the popliteal surface is low, not reaching 25% of the total proximodistal length of the bone.

Phyogenetic analysis

In order to assess the affinities of UFRGS-1240-T within Dinosauromorpha, the specimen was scored (Appendix A) into the data matrix of Nesbitt *et al.* (2010), as modified by Kammerer *et al.* (2012). Our analysis was conducted under equally weighted parsimony in TNT v1.1 (Goloboff *et al.* 2008) with a heuristic search of 10 000 replications of Wagner trees (with random addition sequence), and the tree bisection reconnection (TBR) algorithm enforced (10 trees saved per replication).

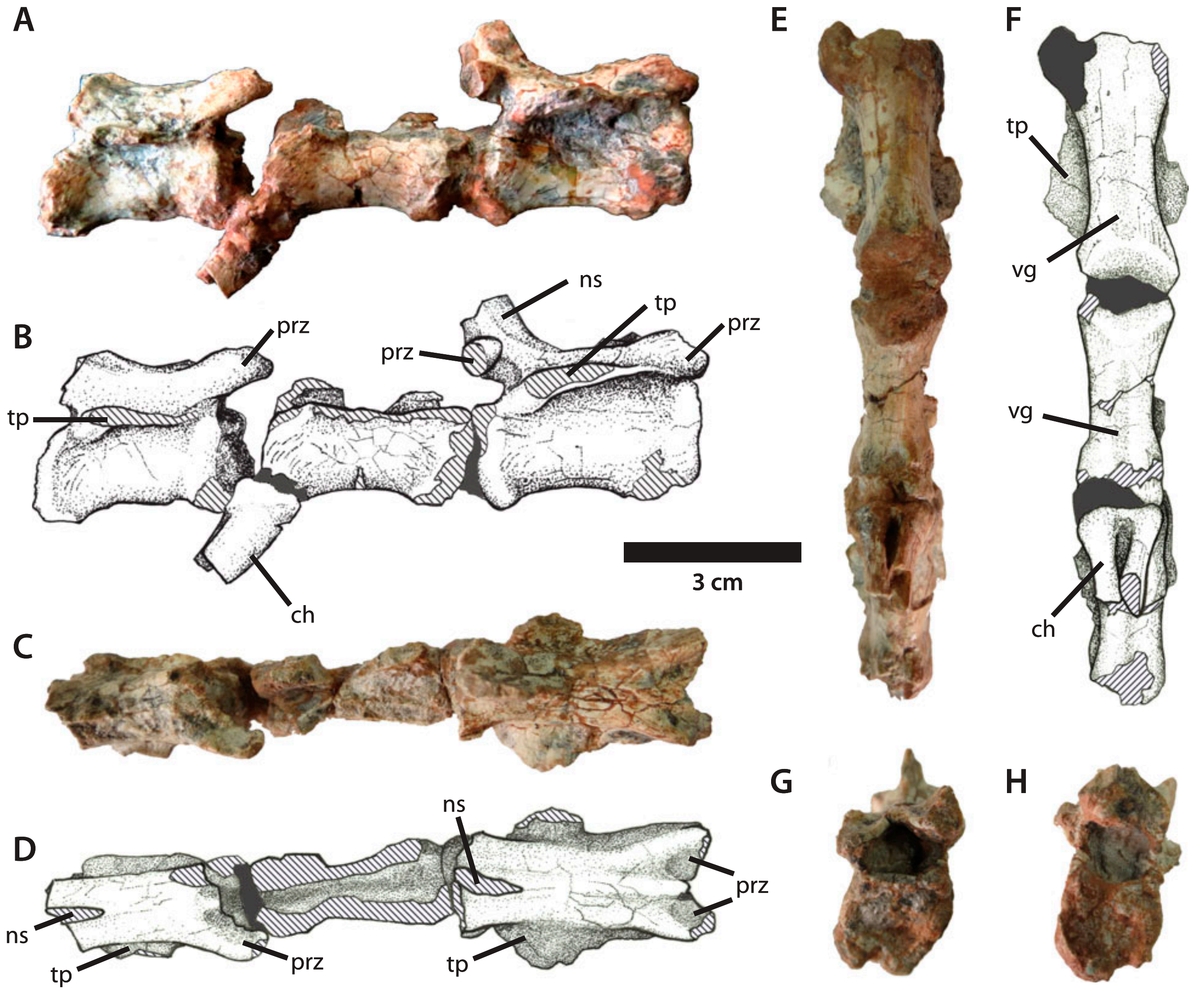

Fig. 3. UFRGS-PV-1240-T, Dinosauria indet. (Candelária Sequence, Late Triassic, Brazil). Mid-caudal vertebrae in lateral (**A, B**), dorsal (**C, D**) ventral (**E, F**), cranial (**G**) and caudal (**H**) views. Grey areas are covered by sediment and dashed areas indicate fractured bone. ch, chevron; ns, neural spine; prz, prezygapophysis; tp, transverse process; vg, ventral longitudinal groove.

The search resulted in 32 most parsimonious trees of 748 steps (CI = 0.465; RI = 0.704). The strict consensus tree (Fig. 7A) nested UFRGS-PV-1240-T within a polytomy of dinosaurians, and this uncertain resolution is likely a product of missing data in the new specimen. Although UFRGS-PV-1240-T can not be confidently positioned in any of the less inclusive clades within Dinosauria (Fig. 7B), its referral to the group is supported by at least two dinosaurian synapomorphies: (1) the deltopectoral crest of UFRGS-PV-1240-T is situated more than 30% down the length of the humerus, a trait exclusive to dinosaurian dinosauromorphs (Langer & Benton 2006, Langer *et al*. 2010, Nesbitt 2011); and (2) the presence of a concave emargination on the ventral surface of the femoral head, which might also be indicative of Dinosauria (Nesbitt 2011).

Discussion

UFRGS-PV-1240-T shows morphological traits typical of early dinosaurians, such as the well-developed deltopectoral crest on the humerus and the concave emargination of the ventral surface of the femoral head (Novas 1996, Langer & Benton 2006, Nesbitt 2011). The sigmoid shape of the femur, although present in many early dinosaurians, such as *Eoraptor*, *Herrerasaurus*, *Saturnalia* and *Eodromaeus* (Novas 1993, Langer 2003, Martínez *et al*. 2011, Sereno *et al*. 2013), is also common to some non-dinosaurian archosaurs (Hutchinson 2001b, Ezcurra 2006, Langer *et al*. 2013) and non-dinosaurian dinosauromorphs, such as *Lagerpeton*, *Marasuchus* and *Silesaurus* (Romer 1971, 1972, Sereno & Arcucci 1993, 1994, Dzik 2003, Langer *et al*. 2013). The somewhat inwardly turned femoral head, angled at 45° relative to the distal intercondylar axis, is also a feature of early dinosaurians and dinosauromorphs (Carrano 2000, Hutchinson 2001b), but appears elsewhere among early archosaurs (Nesbitt 2011). Pointedly, UFRGS-PV-1240-T differs from more advanced sauropodomorphs, theropods and ornithischians, in which the femoral head is medially oriented (Carrano 2000, Hutchinson 2001b).

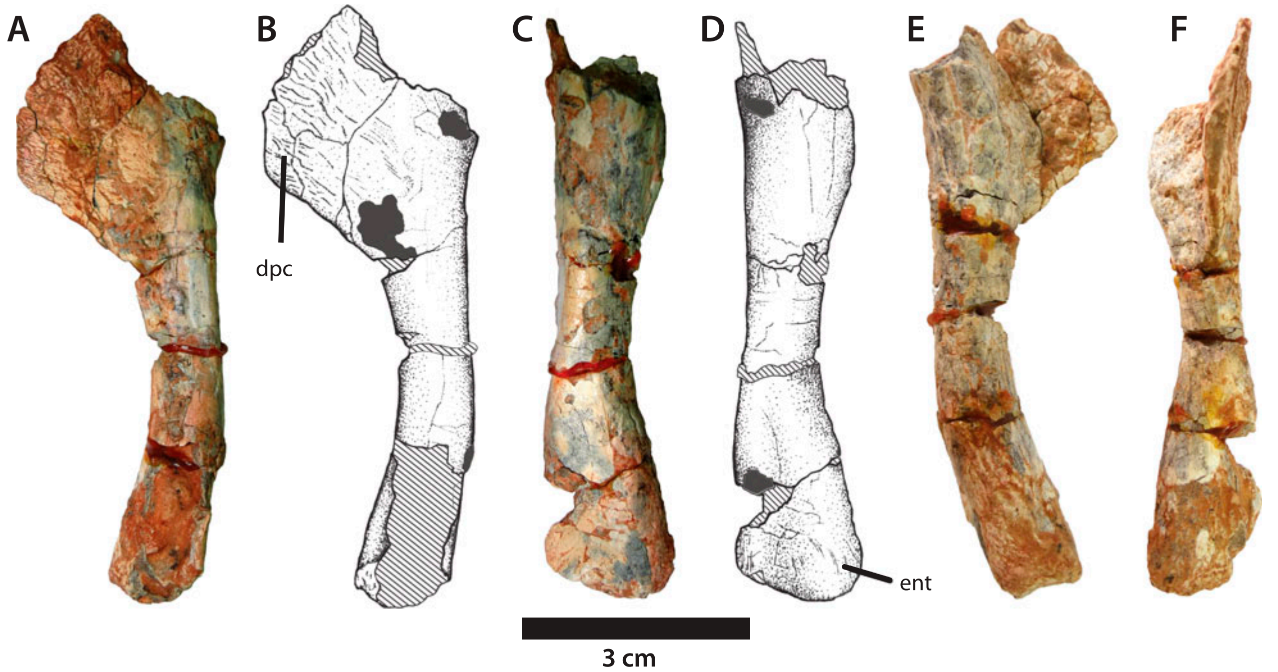

Fig. 4. UFRGS-PV-1240-T, Dinosauria indet. (Candelária Sequence, Late Triassic, Brazil). Left humerus in lateral (**A, B**), caudal (**C, D**), medial (**E**) and cranial (**F**) views. Grey areas are covered by sediment and dashed areas indicate fractured bone. dpc, deltopectoral crest; ent, entepicondyle.

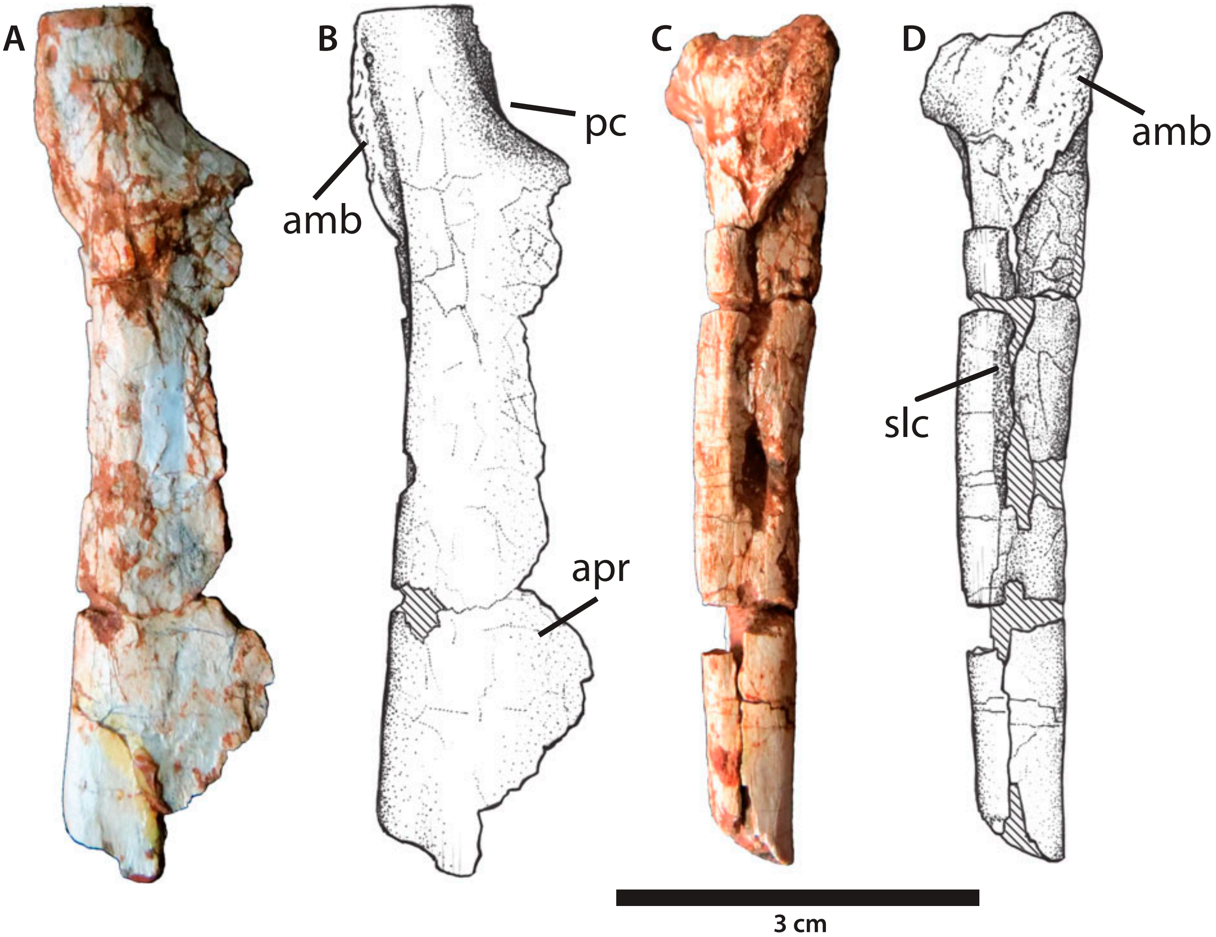

Fig. 5. UFRGS-PV-1240-T, Dinosauria indet. (Candelária Sequence, Late Triassic, Brazil). Right pubis in cranial **A, B** and lateral **C, D**, views. Dashed areas indicate fractured bone. amb, tuberosity for the insertion of m. *ambiens*; apr, pubic apron; pc, pubic canal; slc, lateral sulcus.

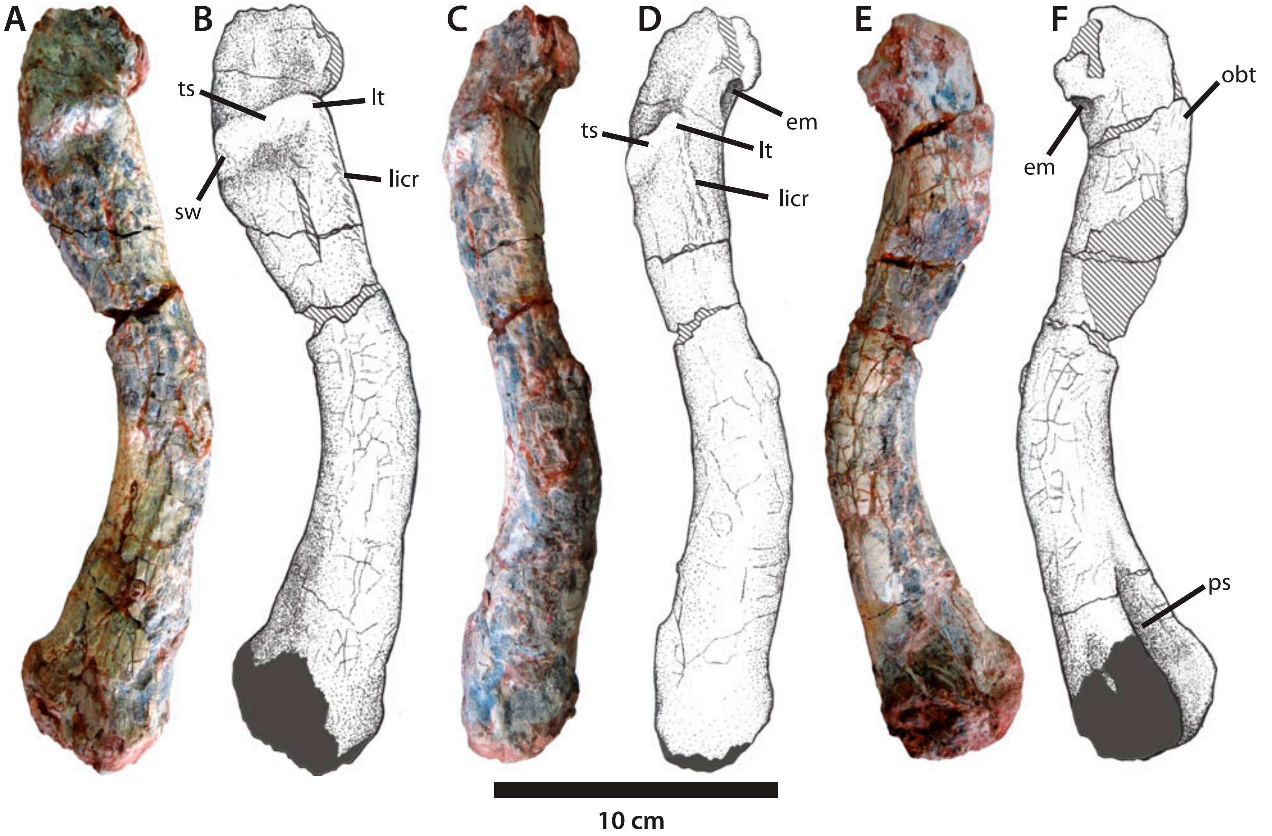

Fig. 6. UFRGS-PV-1240-T, Dinosauria indet. (Candelária Sequence, Late Triassic, Brazil). Right femur. **A, B**, Lateral view, **C, D**, cranial view and **E, F**, medial view. Grey areas are covered by sediment and dashed areas indicate fractured bone. em, ventral emargination of the femoral head; licr, cranial intermuscular line, lt, lesser trochanter; obt, insertion area of m. *obturatorius*; ps, popliteal surface; sw, caudolateral swelling of the trochanteric shelf; ts, trochanteric shelf.

The cranial trochanter and the trochanteric shelf of UFRGS-PV-1240-T are well developed, as in most non-dinosaurian dinosauromorphs and early dinosaurians (Langer & Benton 2006, Nesbitt 2011). However, separation of the cranial trochanter from the shaft by a cleft, which characterizes many advanced theropods and ornithischians (Langer & Benton 2006, Nesbitt 2011), is not evident. Furthermore, the condition of the trochanteric shelf is controversial. Although common among dinosauromorphs (Novas 1992, 1996, Ezcurra 2006, Langer & Benton 2006, Nesbitt *et al*. 2009a, Nesbitt 2011), the expression of this feature is highly variable, with reversals occurring in Silesauridae (Langer *et al*. 2013) and Dinosauria (Langer & Benton 2006, Nesbitt 2011). Some authors also suggest that this feature might be related to ontogeny (Nesbitt *et al*. 2009a). The trochanteric shelf of UFRGS-1240-T differs somewhat from the condition evident in early dinosaurians, such as *Herrerasaurus*, *Saturnalia* and *Pampadromaeus* (Novas 1993, Langer 2003, Cabreira *et al*. 2011), in being less developed and not forming a well-marked rugose crest. Unlike those taxa, UFRGS-PV-1240-T also apparently lacks a dorsolateral trochanter.

The distal portion of the enlarged deltopectoral crest on the humerus of UFRGS-PV-1240-T creates an obtuse angle against the longitudinal axis of the shaft, resembling *Eoraptor* (Sereno *et al*. 2013) and *Tawa* (Nesbitt *et al*. 2009b). In contrast, it is almost perpendicular in *Saturnalia* (Langer *et al*. 2007). In addition, the entepicondyle of UFRGS-PV-1240-T is not as medially pronounced as in *Saturnalia* (Langer *et al*. 2007), being otherwise reminiscent of *Eoraptor* (Sereno *et al*. 2013).

Pampadromaeus is the only dinosaurian taxon thus far recorded from ‘Sítio Janner’ (Cabreira *et al*. 2011), but a dinosauriform has also been recently reported (Müller *et al*. 2014). UFRGS-PV-1240-T is significantly larger than these coeval specimens, with the femur being 265 mm long compared with 155 mm in *Pampadromaeus* and around 105 mm for the indeterminate ‘Sítio Janner’ dinosauriform. Indeed, UFRGS-PV-1240-T is larger than most dinosaurians of the same age, except for a putative sauropodomorph from southern Brazil (Da-Rosa *et al*. 2006, Ezcurra 2012), and the herrerasaurids *Staurikosaurus* (which was of similar size) and *Herrerasaurus*, known from larger specimens (Sereno & Novas 1992, Bittencourt & Kellner 2009). Notably, no traits unambiguously support the affinity of UFRGS-PV-1240-T with herrerasaurids. The neural spines of the proximal caudal vertebrae (Fig. 2) could be interpreted as vertical like those apomorphically occurring in Herrerasauridae (Novas 1992, Langer &

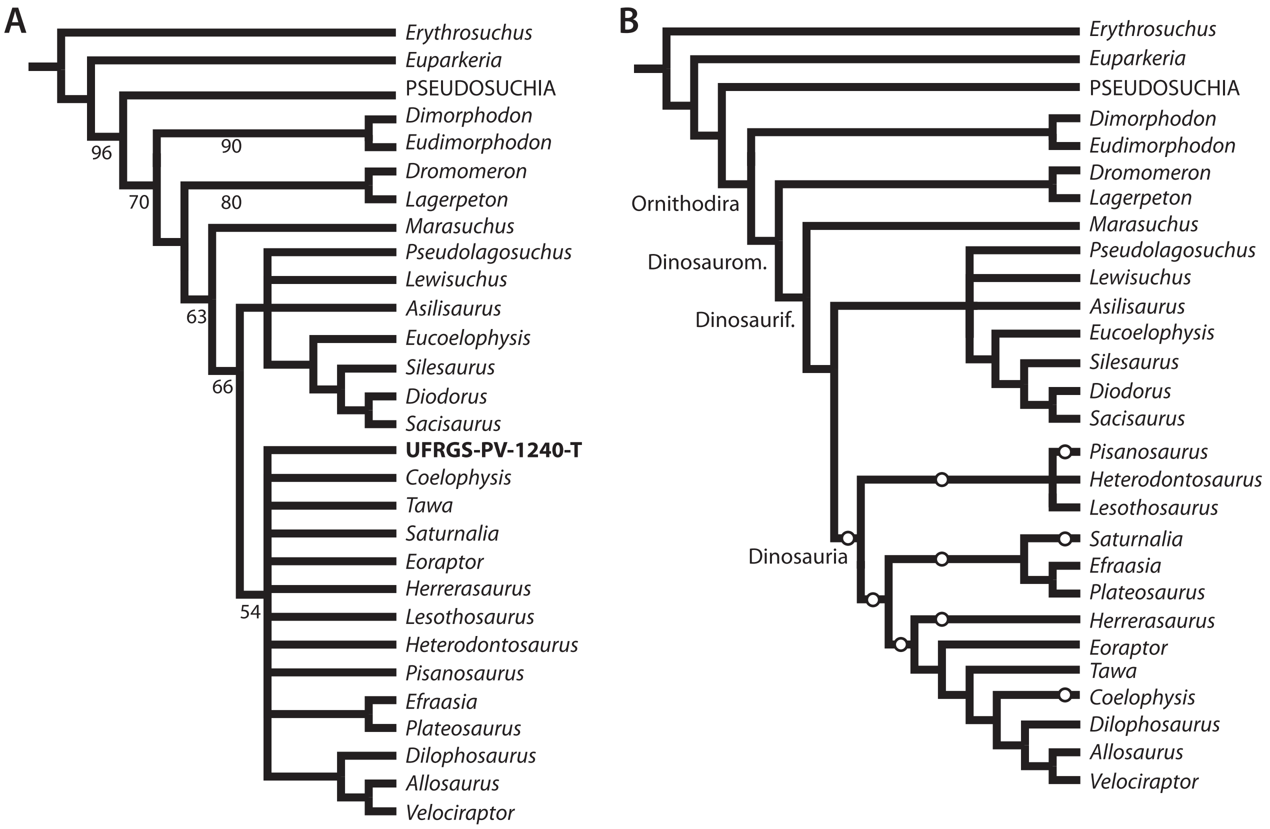

Fig. 7. Strict consensus (**A**) of the 32 most parsimonious trees (tree length = 748 steps; CI = 0.465; RI = 0.704). Numbers indicate bootstrap index for some nodes. **B**, Reduced strict consensus (after the exclusion of UFRGS-PV-1240-T). White circles indicate the different positions UFRGS-PV-1240-T can adopt when included in the analysis. Some nodes (Pseudosuchia, *Dromomeron*) were collapsed in both trees to reduce the image size. Dinosaurif., Dinosauriformes; Dinosaurom., Dinosauromorpha.

Benton 2006, Bittencourt & Kellner 2009). However, they are too fragmentary for determination to be precise. In addition, UFRGS-PV-1240-T lacks the typically herrerasaurid shortened caudal vertebral centra (Novas 1993).

Although the abundance of dinosaurian remains is low compared with those of other vertebrate groups found at 'Sítio Janner' (e.g., *Exaeretodon*), UFRGS-PV-1240-T shows that larger dinosaurian body sizes were already represented in the *Hyperodapedon* Assemblage Zone. Direct comparison of the femur length of UFRGS-PV-1240-T with those of more complete basal dinosaurians (Sereno & Novas 1992, Langer *et al.* 1999, Sereno *et al.* 2013) indicates that UFRGS-PV-1240-T could have reached a maximum estimated body length of at least 2.5 m. This is substantially larger than *Pampadromaeus* or the coeval carnivorous cynodont *Trucidocynodon*, and rivals the dominant herbivores *Exaeretodon* and *Hyperodapedon* (Fig. 8). Body size is regarded as a key factor in organismal fitness and the capacity to obtain food or territory (Brown & Maurer 1986, Hone & Benton 2005, Sookias *et al.* 2012). Thus,

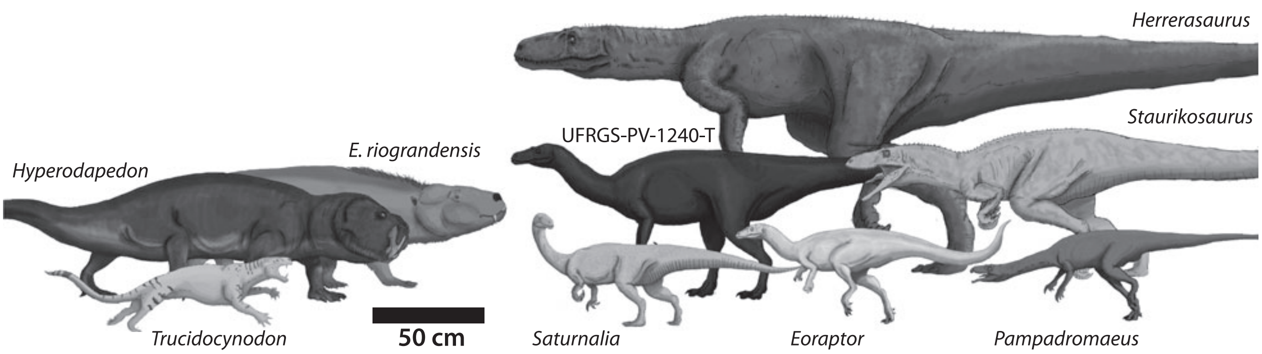

Fig. 8. Schematic diagram comparing the estimated and observed body sizes of selected Ischigualastian taxa. *Herrerasaurus* body size interpreted from Sereno & Novas (1992); *Eoraptor* interpreted from Sereno *et al.* (2013); *Staurikosaurus* interpreted from Grillo & Azevedo (2011b); *Saturnalia* interpreted from Langer *et al.* (1999); *Pampadromaeus* interpreted from Cabreira *et al.* (2011); *Hyperodapedon* based on MCN-PV-3509; *Exaeretodon riograndensis* based on UFRGS-PV-0715-T; *Trucidocynodon* interpreted from Oliveira *et al.* (2010). Reconstructions by Voltaire Dutra Paes Neto (UFRGS).

the large size of UFRGS-PV-1240-T might imply that dinosaurian dinosauromorphs were already important competitors for resources in some Late Triassic ecosystems, a trend that would increase toward the end of the period and throughout the remainder of the Mesozoic (Langer *et al*. 2010).

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Appendix A

Scoring of UFRGS-PV-1240-T in the data matrix of Kammerer *et al.* (2012)

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