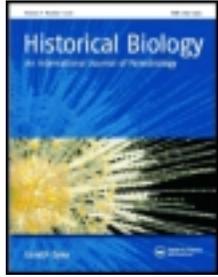


This article was downloaded by: [Jonathas Souza Bittencourt]

On: 17 August 2012, At: 06:23

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Historical Biology: An International Journal of Paleobiology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ghbi20>

Dinosaur remains from the 'Botucaraí Hill' (Caturrita Formation), Late Triassic of south Brazil, and their stratigraphic context

Jonathas Souza Bittencourt^{a b}, Átila Augusto Stock da Rosa^c, Cesar Leandro Schultz^d & Max Cardoso Langer^a

^a Departamento de Biologia, Universidade de São Paulo, Av. Bandeirantes 3900, 1404-901, Ribeirão Preto (SP), Brazil

^b Departamento de Geologia, Universidade Federal de Minas Gerais, Av. Antônio Carlos 6670, 31270-901, Belo Horizonte (MG), Brazil

^c Departamento de Geociências, Universidade Federal de Santa Maria, Av. Roraima 1000, 97105-900, Santa Maria (RS), Brazil

^d Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves 9500, 91501-970, Porto Alegre (RS), Brazil

Version of record first published: 17 Aug 2012

To cite this article: Jonathas Souza Bittencourt, Átila Augusto Stock da Rosa, Cesar Leandro Schultz & Max Cardoso Langer (2012): Dinosaur remains from the 'Botucaraí Hill' (Caturrita Formation), Late Triassic of south Brazil, and their stratigraphic context, *Historical Biology: An International Journal of Paleobiology*, DOI:10.1080/08912963.2012.694881

To link to this article: <http://dx.doi.org/10.1080/08912963.2012.694881>



PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Dinosaur remains from the ‘Botucaraí Hill’ (Caturrita Formation), Late Triassic of south Brazil, and their stratigraphic context

Jonathas Souza Bittencourt^{a,b,*}, Átila Augusto Stock da Rosa^c, Cesar Leandro Schultz^d and Max Cardoso Langer^a

^aDepartamento de Biologia, Universidade de São Paulo, Av. Bandeirantes 3900, 1404-901 Ribeirão Preto (SP), Brazil; ^bDepartamento de Geologia, Universidade Federal de Minas Gerais, Av. Antônio Carlos 6670, 31270-901 Belo Horizonte (MG), Brazil; ^cDepartamento de Geociências, Universidade Federal de Santa Maria, Av. Roraima 1000, 97105-900 Santa Maria (RS), Brazil; ^dInstituto de Geociências, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves 9500, 91501-970 Porto Alegre (RS), Brazil

(Received 16 March 2012; final version received 15 May 2012)

Vertebrate fossils recovered from sites nearby the Botucaraí Hill and Candelária (Caturrita Formation) depict a diverse Late Triassic tetrapod fauna from south Brazil. These records are of key importance to the biostratigraphy of the upper sections of the Rosario do Sul Group. A lithological and biostratigraphic survey on the main fossil localities of the Botucaraí Hill area confirms the occurrence of the lower *Hyperodapedon* and the upper *Riograndia* Assemblage Zones in the region, the latter yielding early saurischians. In this paper, three incomplete dinosaur specimens, an isolated sacral vertebra, an articulated left pubis–ischium and an isolated right ischium, from the ‘Botucaraí Hill’ site are described. A comparative survey suggests that these specimens have sauropodomorph affinities, but probably more primitive than typical ‘prosauropods’ from the Norian–Early Jurassic. Regardless of the phylogenetic position of *Guaibasaurus* as theropod or sauropodomorph, their occurrence in the Caturrita Formation, which also yielded ‘core prosauropods’ from the Santa Maria region, suggests either the survival of early members of the clade with more derived ‘prosauropods’ or that heterochronous faunas are sampled from that stratigraphic unit.

Keywords: Dinosauria; Sauropodomorpha; Caturrita Formation; Botucaraí Hill

Institutional abbreviations: BMNH, The Natural History Museum, London, UK; GPIT, Institut für Geologie und Paläontologie, Tübingen, Germany; HMN, Humboldt Museum für Naturkunde, Berlin, Germany; MCN, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCP, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica, Porto Alegre, Brazil; MMACR, Museu Municipal Aristides Carlos Rodrigues, Candelária, Brazil; MCZ, Harvard Museum of Comparative Zoology, Cambridge, USA; PVL, Instituto Miguel Lillo, San Miguel de Tucumán, Argentina; PVSJ, Instituto y Museo de Ciencias Naturales de la Universidad Nacional de San Juan, San Juan, Argentina; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UFPel, Universidade Federal de Pelotas, Pelotas, Brazil; UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; ZPAL, Institute of Paleobiology of the Polish Academy of Science, Warsaw, Poland

Introduction

The Upper Triassic strata of the Rosario do Sul Group, south Brazil, yields a rich saurischian fauna (Langer et al. 2007), including some of the earliest dinosaurs. Herrerasaurids (Colbert 1970) and basal sauropodomorphs (Langer et al. 1999; Cabreira et al. 2011) are known from the Santa Maria Formation; the abundance and richness of which is only outreached by the coeval Ischigualasto Formation of Argentina (Serenó and Novas 1992; Sereno et al. 1993; Martínez and Alcober 2009; Alcober and Martínez 2010; Ezcurra 2010; Martínez et al. 2011). In contrast, the dinosauriform fauna of the younger Caturrita Formation, composed of a silesaurid (Frigolo and Langer 2007), a putative theropod (Bonaparte et al. 1999; Langer et al. 2011) and ‘prosauropods’ (Leal et al. 2004; Bittencourt et al. 2012), is relatively less abundant than

some coeval faunas worldwide (Bonaparte 1971; Yates 2003a; Galton and Upchurch 2004; Langer et al. 2010).

Several authors have emphasised the importance of describing and identifying fragmentary early dinosauriform specimens (Nesbitt and Chatterjee 2008; Nesbitt and Stoker 2008), which can help to (1) fulfil biostratigraphic or biogeographic gaps, (2) erect new characters for systematic studies and (3) increase the knowledge of morphological diversity within the group. In this paper, we provide a detailed description of three saurischian specimens recovered from the Botucaraí Hill area (Caturrita Formation), coupled with a new biostratigraphic framework for nearby fossil localities.

Material and methods

The material described herein includes three specimens: an isolated second sacral vertebra (UFPel 014), articulated

*Corresponding author. Email: sigmaorionis@yahoo.com.br

left pubis and ischium (UFRGS-PV-0761-T) and an isolated right ischium (MMACR PV 037-T), all collected in the ‘Botucaraí Hill’ site (Figures 1, 2; see ‘Discussion’ section). Some of these specimens were briefly mentioned in previous studies (Kischlat and Lucas 2003), and Kischlat (2003) carried out a preliminary study on both UFPel 014 and UFRGS-PV-0761-T in his PhD thesis, but formal descriptions are lacking. Their affinities have been assessed based on comparisons with a large sample of archosaur taxa, not only on an apomorphy-based approach (Nesbitt and Stoker 2008), but also analysing typical features of the more common Middle and Late Triassic archosaur clades (i.e. phytosaurs, aetosaurs, ‘rauisuchians’ and dinosauromorphs). This is necessary when dealing with faunas composed of multiple-lineage taxa that share

morphological traits to one another, as typically represented by the Late Triassic archosaur radiation.

Comparative description

UFPel 014, sacral vertebra

The vertebra is almost complete, lacking only the distal part of the neural spine (Figure 3). Similarly to *Guaibasaurus*, the robust centrum is as long as broad in ventral view, but broader at the level of the parapophyses (Figure 3(A),(B)). There is no evidence of sacral fusion as observed in some pseudosuchians (Weinbaum and Hungerbühler 2007) and non-tetanuran theropods (Tykoski 2005). The ventral surface bears a shallow sagittal sulcus, laterally bordered by shallow depressions.

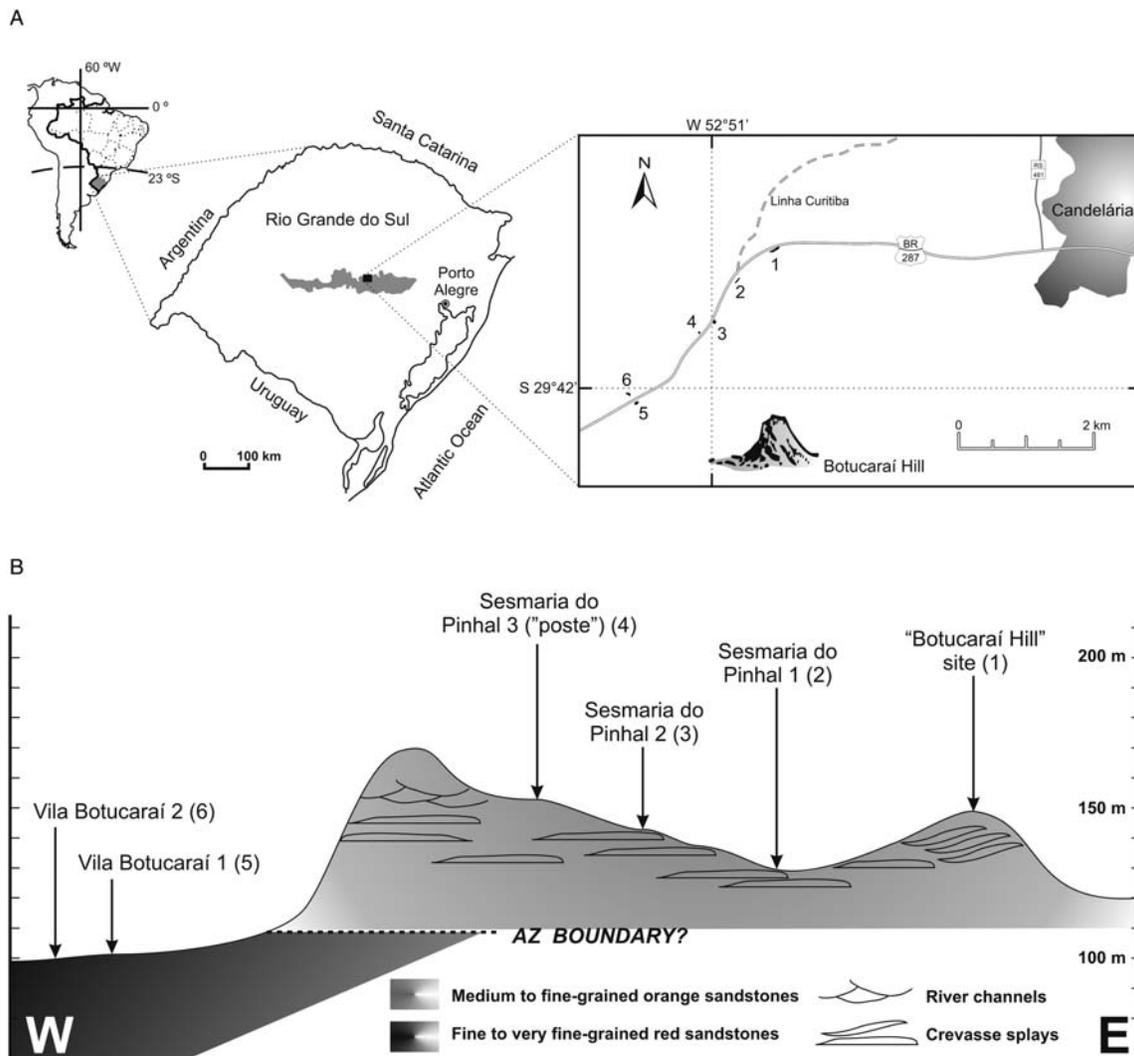


Figure 1. Fossil sites of the Botucaraí Hill area. (A) Composite map showing the location of the fossil sites nearby the Botucaraí Hill and Candelária, Rio Grande do Sul; (B) east-western section of the outcrops numbered on the map, depicting their lithofacies and scaled with the altitude. The ‘Vila Botucaraí’ sites correspond to the *Hyperodapedon* AZ, whereas the ‘Botucaraí Hill’ and Sesmaria do Pinhal sites may be assigned to the *Riograndia* AZ. AZ, assemblage zone.



Figure 2. Overview of the 'Botucaraí Hill' site, southern margin of BR 287 road, with provenance of main fossils. (1) Dinosaurs described herein, (2) *J. candelariensis* and (3) *R. guaibensis* (isolated tooth). Arrow indicates the level that yielded a stereospondyl interclavicle on the northern part of the outcrop. Photograph by C.L. Schultz (see also Dias-da-Silva et al. 2009).

Two obliquely oriented furrows bound the parasagittal depressions caudally (Figure 3(A),(B)). The flat ventral surface of the centrum is not as strongly constricted as in pseudosuchians, such as *Batrachotomus* (Gower and Schoch 2009) and *Arizonasuchus* (Nesbitt 2005) and basal dinosauriforms (e.g. *Silesaurus*, ZPAL AbIII 361; Dzik 2003).

The ventral surface of UFPel 014 also resembles that of the putative second sacral of *Guaibasaurus* (MCN-PV 2355; Langer et al. 2011), which possesses the sagittal sulcus and the oblique furrows. Among sauropodomorphs, the latter trait is seen in the second primordial sacral centrum of *Adeopapposaurus* (PVSJ 610) and *Sellosaurus* (SMNS 12685; Galton 2000). The first primordial sacral of *Panphagia* (PVSJ 874; Martínez and Alcober 2009) also has a flattened ventral surface, but the centrum is much longer than wide. This is also the case of the two primordial sacral vertebrae of *Saturnalia* (MCP 3845-PV), the second of which does not bear a median ventral sulcus. Basal neotheropods (e.g. *Coelophysis*, NMMNHS P-42200; Rinehart et al. 2009) and ornithischians (e.g. *Scelidosaurus*, BMNH R1111) bear typical spool-shaped elongated sacrals, which are unlike UFPel 014. On the contrary, the herrerasaurids *Herrerasaurus* (PVL 2566; Novas 1994) and *Staurikosaurus* (MCZ 1669) have axially shortened sacral centra, and the second sacral of both taxa has a flat ventral surface that lacks the sagittal sulcus.

The ventrolateral margins of the cranial and caudal ends of the centrum in UFPel 014 bear striation for muscle attachment, and both articular facets are slightly concave. The cranial facet is broader than high (Figure 3(C)), as in the second primordial sacral vertebra of herrerasaurids (*Staurikosaurus*, MCZ 1669; *Herrerasaurus*, PVL 2566; Novas 1994) and most sauropodomorphs (*Efraasia*, SMNS 17928; *Riojasaurus*, PVL 3808; *Plateosaurus gracilis*, SMNS 5715). Otherwise, in some theropods [e.g. Shake-N-Bake coelophysoid (Tykoski 2005), 'Syntarsus' *kayentakatae* (Tykoski 2005), *Dilophosaurus* (UCMP 7720; Welles 1984)], rauisuchians [e.g. *Postosuchus* and

Batrachotomus (Long and Murry 1995; Gower and Schoch 2009)], *Silesaurus* (Dzik 2003) and *Spondylosoma* (Galton 2000), the centrum is at least as high as wide. As a consequence, the rib attachment area in the centrum is placed more dorsally relative to the ventral margin of the cranial articular facet than in basal sauropodomorphs, herrerasaurids and the material described here.

The width of the cranial facet in UFPel 014 is increased by two lateral knobs right below the mid-height of the centrum, which are cranial extensions of the rib articulation areas (Figure 3(C)). The cranial facet also bears two dorsolateral excavations, dorsal to the knobs. The caudal facet is rounded and expands slightly below the ventral margin of the cranial facet (Figure 3(E),(F)). The border of the caudal articular facet is craniocaudally thicker than that of the cranial facet (Figure 3(A),(B)), suggesting the presence of a robust subsequent vertebra.

The parapophyses of UFPel 014 correspond to low lateral expansions on the craniodorsal portion of the centrum (Figure 3(A)–(C)). Five small foramina surround the right parapophysis caudoventrally (Figure 3(G)). This area is not as well preserved on the left side, but three foramina are seen below the parapophysis. A single foramen on the caudal surface of the centrum is present in the second sacral vertebra of *Saturnalia* (MCP 3844-PV) and *Guaibasaurus* (MCN-PV 2355). The second sacral centrum of another specimen of *Saturnalia* (MCP 3845-PV) lacks lateral foramina, suggesting intraspecific variation.

Sacral foramina have not been reported in basal pseudosuchians, non-dinosaurian dinosauriforms and other basal dinosaurs, but pleurocoels were described for tetanuran theropods (Rauhut 2003; O'Connor 2006). Yet, these are much larger and less numerous (Frey and Martill 1995; Harris 1998), and the multiple foramina of UFPel 014 seem unique among early saurischians.

Each sacral rib is formed by an lamina projecting from the lateral margin of the neural arch, at the base of the transverse process, and a robust process attached to the

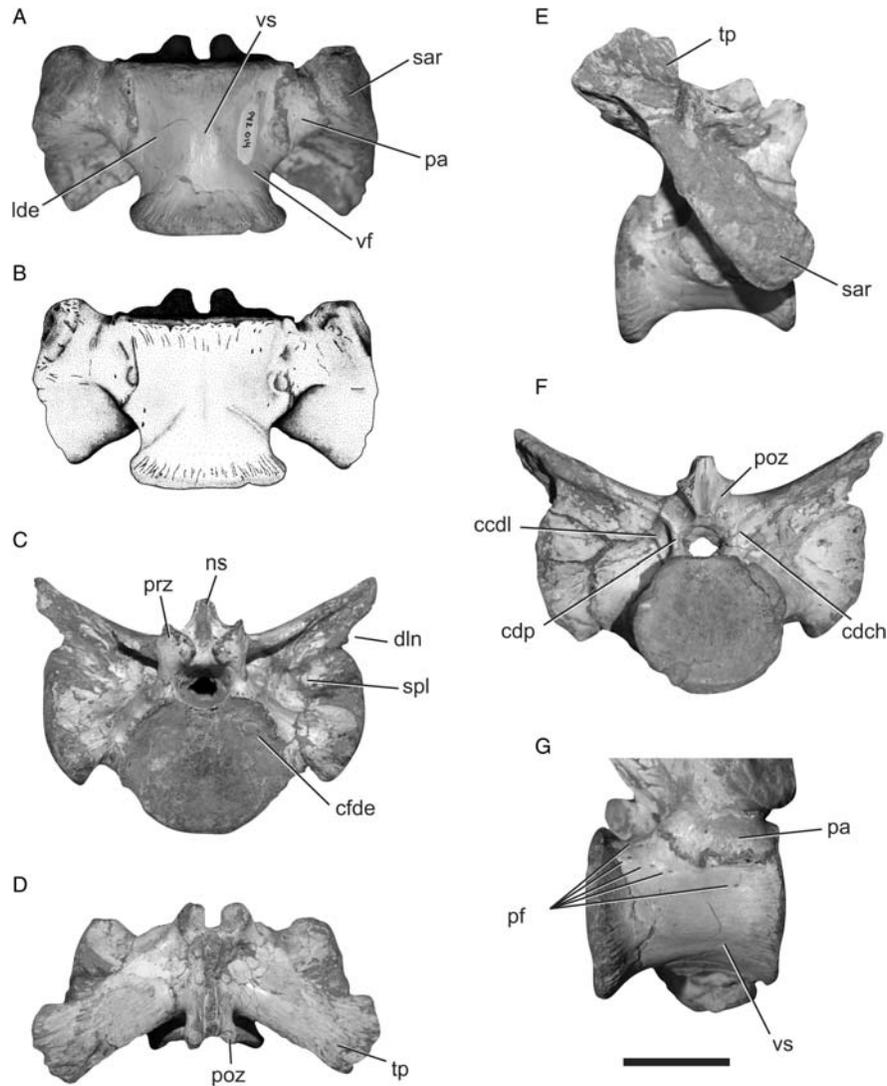


Figure 3. Second sacral vertebra of UFPel 014. (A) Photograph in ventral view, (B) interpretative drawing of the ventral view, (C) photograph in cranial view, (D) photograph in dorsal view, (E) photograph in right lateral view, (F) photograph in caudal view and (G) photograph in right ventrolateral view. cccl, caudal centrodiapophyseal lamina; cdch, caudal chonos; cdp, caudal pedicel; cfde, cranial articular facet dorsal excavation; lde, lateral depression; dln, dorsolateral notch; spl, sacral plate; ns, neural spine; pa, parapophysis; pf, pneumatic foramen; poz, postzygapophysis; prz, prezygapophysis; sar, sacral rib; tp, transverse process; vf, ventral furrow; vs, sagittal ventral sulcus. Scale bar equals 30 mm (all images at scale).

centrum (Figure 3(A)–(C),(E)–(G)). Both the sacral rib and the transverse process are closely articulated, forming the ‘sacral plate’ of Upchurch et al. (2004). The suture between the rib and the transverse process extends from the dorsolateral to the ventromedial portions of the ‘sacral plate’. In lateral view, the flat distal margin of the rib forms an angle of 45° to the craniocaudal axis of the vertebra (Figure 3(E)). Its cranioventral portion is broader than the caudodorsal area and folds medially at the tip. This results in a notch between the rib and the lateral margin of the cranial articular facet of the centrum (Figure 3(C),(F)). In contrast to herrerasaurids (Novas 1994; Bittencourt and

Kellner 2009), a dorsolateral recess between the rib and the transverse process, similar to that of *Riojasaurus* (PVL 3808), is present in UFPel 014 (Figure 3(C),(F)).

The rib of the third sacral vertebra of *Silesaurus*, presumably equivalent to the second primordial sacral vertebra of other archosaurs (Nesbitt 2011), also projects caudodorsally and articulates with the ventral margin of the transverse process (Dzik and Sulej 2007). However, it differs from UFPel 014 by its conspicuous C-shaped distal outline. The ‘sacral plate’ in the second sacral vertebra of *Staurikosaurus*, including the cranial excavation of the dorsoventral lamina (Bittencourt and Kellner

2009), is similar to that of UFPel 014. Its transverse process is laterally, caudally and dorsally directed, as also described in *Saturnalia* (MCP 3845-PV), *Efraasia* (SMNS 17289), *Plateosaurus* (SMNS 5715) and *Riojasaurus* (PVL 3808). Herrerasaurids, on the other hand, have horizontal transverse processes (Bittencourt and Kellner 2009).

Among theropods, the caudosacral vertebra 1 (sensu Welles 1984) of *Dilophosaurus* (UCMP 37302) bears a fan-shaped rib which is superficially similar to that of UFPel 014. Yet, its parapophysis is more dorsally and caudally positioned, the rib is directed dorsally, and the constricted area between the proximal rib attachment and the distal fan-shaped expansion are craniocaudally shorter than in UFPel 014. The remaining sacral vertebrae of *Dilophosaurus* are poorly preserved, preventing further comparisons (Tykoski 2005). The sacral vertebrae of *Liliensternus* (HMN MB.R. 2175) possess strongly dorsally directed 'sacral plates', with a concave lateral margin for articulation with the expanded medial surface of the ilium. Yet, no recess between the transverse process and the sacral rib is seen. Basal tetanurans (e.g. *Allosaurus*, Madsen 1976) also have strongly dorsally directed sacral transverse processes, but the ribs are significantly less robust than in more basal saurischians (Langer and Benton 2006).

The cranial margin of the transverse process in UFPel 014 bulges cranially at its distal tip (Figure 3(D)). Proximally, it merges with the prezygapophysis, forming the diapoprezygapophyseal lamina, which roofs a deep infraprezygapophyseal fossa. A caudal centrodiapophyseal lamina spans ventrally, bounding the caudal chonos cranially. The caudal margin of the transverse process merges with the caudoventral surface of the neural arch (Figure 3(F)), roofing the caudal chonos. Both pre- and postzygapophyses are similar to those described for early dinosaurs (Novas 1994; Langer 2003; Bittencourt and Kellner 2009), with postzygapophyses separated by a deep crevice. The latter is bounded ventrally by a faint 'hyosphenal ridge' (Yates 2007b) and the broad recess ventral to the postzygapophysis that receives the prezygapophysis.

UFRGS-PV-0761-T, left pubis and ischium

The pubis and ischium were discovered in close association and may correspond to the same individual. Only the proximal portion of the pubis is preserved (Figure 4), including the articular surfaces for the other pelvic bones, and the proximal portions of the shaft and blade. The ischium includes the partial proximal area and most of the shaft (Figure 5).

The pubic body is craniocaudally elongated and encompasses three distinct portions in its proximal margin

(Figure 4(A)): (1) the articulation area for the pubic peduncle of the ilium, (2) the cranial acetabular area and (3) the acetabular fossa. Only the proximal portion of the shaft is preserved, and its orthogonal orientation in relation to the proximal surface of the bone suggests a propubic pelvis.

The articulation area for the ilium is as long as broad. It is cranially rounded in proximal view and medially displaced in relation to the cranial portion of the pubic acetabular area. The latter is concave, with two distinct prominences on its lateral margin. The cranial prominence (Figure 4(A)) is laterally projected and can be observed in other dinosauriforms, such as *Marasuchus* (PVL3870) and *Silesaurus* (ZPAL AbIII 361). The caudal prominence is distally pointed, forming a triangle-like process in lateral view (Figure 4(A),(E),(F)), very similar to that of *Silesaurus* (ZPAL AbIII 361) and saurischians, such as *Eoraptor* (PVL 512), *Saturnalia* (MCP 3844-PV) and *Liliensternus* (HMN MB.R. 2175; Huene 1934). Similar processes are seen in *Batrachotomus* (SMNS 80269) and poposaurids (Long and Murry 1995; Weinbaum and Hungerbühler 2007), but these are more ventrally projected than that of UFRGS-PV-0761-T.

The ischiadic process of the pubis bears a deep and transversely broad acetabular fossa on its dorsal portion (Figure 4(A),(E),(F)). This fossa does not pierce the medial wall of the pubis, and its lateral opening appears like a wedged sulcus. A similar structure is seen in *Saturnalia* (Langer 2003), *Silesaurus* (Dzik 2003) and *Guaibasaurus* (Langer et al. 2011), and corresponds to an enlarged version of the ischio-acetabular groove of some dinosauriforms (Sullivan and Lucas 1999; Langer 2003; Ezcurra 2006; Langer et al. 2011). In *Eoraptor* (PVL 512), the pubis is not well preserved, but an ischio-acetabular groove is also present, which seems equivalent to the fossa connecting the articulation area for the ilium and the ischiadic process in herrerasaurids (e.g. *Herrerasaurus*, PVL 2566), early sauropodomorphs (e.g. *Plateosaurus*, GPIT-mounted skeletons; *Riojasaurus*, PVL 3808) and theropods (e.g. *Coelophysis*, NMMNHS P-42200; *Megapnosaurus*, Raath 1977; *Liliensternus*, HMN MB.R. 2175). Basal archosauriforms (Romer 1956), phytosaurs (Chatterjee 1978), pseudosuchians (e.g. *Postosuchus*; Long and Murry 1995) and basal dinosauriforms (e.g. *Marasuchus*, PVL 3870; Novas 1996) also bear an acetabular fossa. Yet, its medial wall projects dorsally and reaches the ventral margin of the iliac acetabular wall, closing the acetabulum. In fact, most archosauriforms with a dorsally projected medial margin of the acetabular portion of the pubis have a convex to straight ventral margin of the iliac acetabulum (Bonaparte 1984; Hutchinson 2001; Dzik 2003). *Guaibasaurus* (UFRGS PV-0725-T; Langer et al. 2011) bears two sulci on the proximal acetabular surface of the pubis, but there is no evidence of a convex ventral margin of the medial

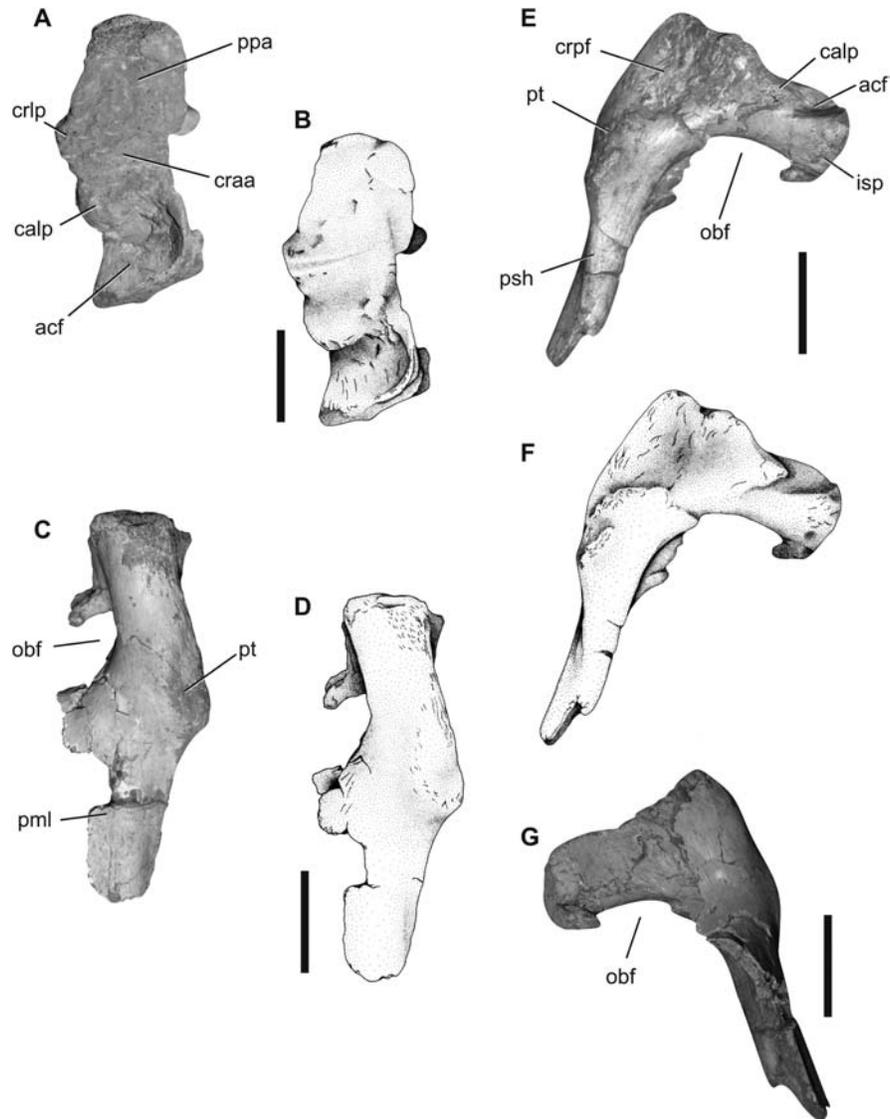


Figure 4. Left pubis of UFRGS-PV-0761-T. (A) Photograph in proximal view, (B) interpretative drawing of the proximal view, (C) photograph in cranial view, (D) interpretative drawing of the cranial view, (E) photograph in lateral view, (F) interpretative drawing of the lateral view and (G) photograph in medial view. acf, acetabular fossa; calp, caudolateral prominence; craa, cranial acetabular area; crlp, cranio-lateral prominence; crpf, cranial pubic fossa; isp, ischiadic process of the pubis; obf, obturator fenestra; pml, pubic medial lamina; ppa, peduncle pubic attachment area; psh, pubic shaft; pt, pubic tubercle. Scale bars equal 20 mm (A, B) and 30 mm (C–G).

acetabular wall, nor of a dorsal projection of the medial portion of the proximal pubis.

The ischiadic process of UFRGS-PV-0761-T is elongated and hatchet-shaped in lateral view (Figure 4(E)–(G)). Its ventral margin projects craniomedially, forming the obturator plate (incompletely preserved). The concave ventral margin of the process roofs the elliptical, craniocaudally elongated obturator fenestra, which is visible in both cranial and caudal aspects. The ischiadic process of UFRGS-PV-0761-T is very similar to that of *Silesaurus* (ZPAL AbIII 361) and *Saturnalia* (MCP 3844-PV). This specimen shares with early theropods the

craniocaudal elongation of the proximal pubis, but seems to lack the co-ossified pubis and ischium of adult coelophysoid individuals (Raath 1969; Tykoski and Rowe 2004). In addition, the obturator fenestra in basal theropods is craniocaudally shorter than in UFRGS-PV-0761-T and *Saturnalia* (right pubis of the holotype, MCP 3844-PV).

The cranial margin of the pubic body of UFRGS-PV-0761-T (Figure 4(C),(D)) is proximally straight and not dorsally projected as in *Batrachotomus* (Gower and Schoch 2009). Its cranio-lateral surface bears the conspicuously striated cranial pubic fossa (‘triangular

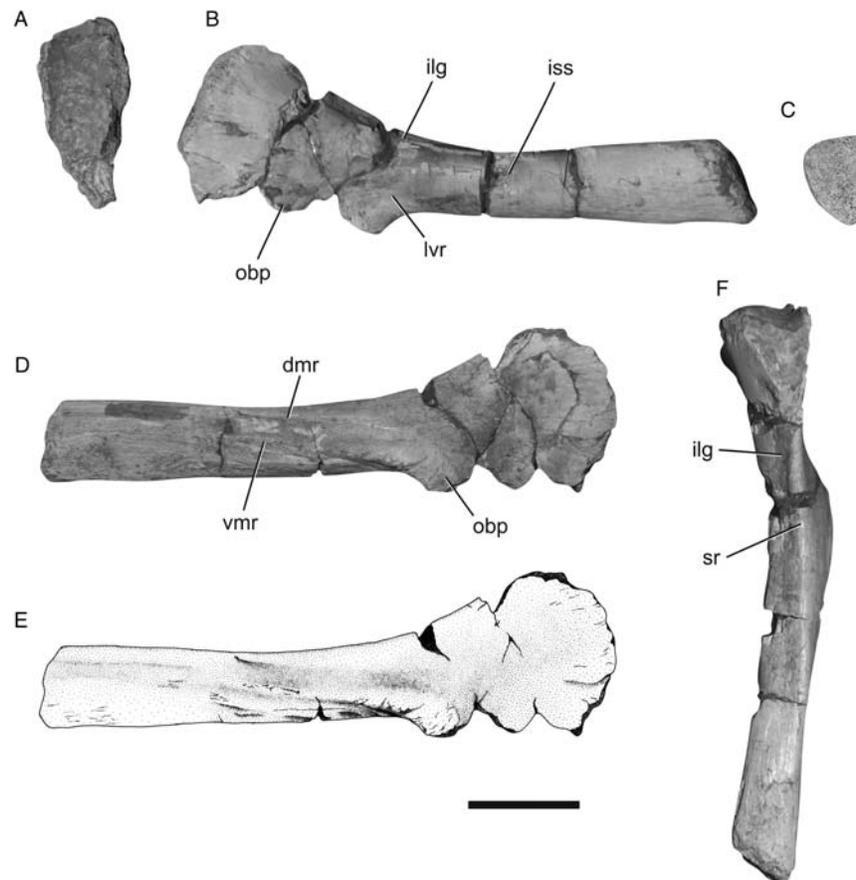


Figure 5. Left ischium of UFRGS-PV-0761-T. (A) Photograph in proximal view, (B) photograph in lateral view, (C) photograph in distal view, (D) photograph in medial view, (E) interpretative drawing of the medial view and (F) photograph in dorsal view. dmr, dorsomedial ridge; ilg, ischial longitudinal groove; iss, ischial shaft; lvr, lateroventral recess; obp, obturator plate; sr, symphyseal ridge; vmr, ventromedial ridge. Scale bar equals 30 mm (all images at scale).

fossa', Sereno and Arcucci 1994). The pubic tubercle (= 'ambiens' tuberosity; Hutchinson 2001) is stout and rugose, spanning onto most of the cranio-lateral portion of the boundary between the pubic body and the shaft. In cranial view, it forms a pendant, proximodistally elongated process, with a laterodistal apex, obliquely oriented relative to the pubic shaft. At the proximal edge of the pubic body, the caudal margin of the pubic tubercle is bounded by a raised margin, which also borders the cranio-lateral concavity of the proximal pubis caudally.

The pubic tubercle of *Marasuchus* (PVL 3870) and *Silesaurus* (ZPAL AbIII 361) is closer to the caudal edge of the pubic body than that of UFRGS-PV-0761-T, which is more similar to that of *Guaibasaurus* (MCN-PV 2355), both in position and in morphology. It slightly differs from the narrower and more proximodistally elongated tubercle of early neotheropods (e.g. *Coelophysis*, NMMNHS P-42200). The pubic tubercle of herrerasaurids is smaller than those of other basal saurischians (Novas 1994; Bittencourt and Kellner 2009; Alcober and Martínez 2010), whereas the basal sauropodomorphs *Saturnalia*

(MCP 3844-PV) and *Efraasia* (SMNS 12354; Yates 2003c) possess a moderately to strongly expanded pubic tubercle, pyramid-shaped in cranial view.

The medial surface of the pubic body is mostly flat in its cranial portion (Figure 4(G)), but slightly concave in the acetabular portion and obturator process. Striations for muscle attachment are widespread across that surface. The proximal portion of the shaft comprises a bulged lateral axis, and a thinner medial lamina, continuous to the obturator plate.

The ischial body of UFRGS-PV-0761-T is deep and the obturator process, although incompletely preserved, is restricted to the proximal third of the bone (Figure 5(A),(B),(D),(E)). This is typical of dinosaurs (Novas 1996; Langer and Benton 2006), the obturator process of which is followed by a slender shaft (Santa Luca 1980; Sereno and Novas 1994; Langer 2003; Bittencourt and Kellner 2009; Martínez et al. 2011), as also seen in *Silesaurus* (Dzik 2003).

Most of the proximal margin of the ischium is missing in UFRGS-PV-0761-T (Figure 5(A),(B)), and it is

ambiguous if it had the dinosauriform waisted margin (Irmis et al. 2007). As common to archosaurs, the dorsal portion of the proximal ischium is lateromedially wider than the ventral part. The medial surface of the obturator process is slightly concave (Figure 5(D),(E)), and the lateral surface is convex on its cranioproximal portion. As in other saurischians (e.g. *Saturnalia*, MCP 3845-PV; *Liliensternus*, HMN MB.R. 2175), a recess is located on the ventrolateral part of the obturator plate, above the area where it merges with the ischial shaft (Figure 5(B)). The dorsal margin of the proximal ischial body is continuous to a broad crest ('symphyseal ridge' of Bonaparte et al. 1999; Langer 2003; Langer et al. 2011) on the dorsal margin of the shaft (Figure 5(F)), which extends from a more lateral position in the ischial body to the dorsomedial corner of the shaft. In addition, the shaft bears a longitudinal groove, which has been reported in various basal dinosaurs (Yates 2003b; Martínez 2009; Langer et al. 2011). This groove begins as a narrow excavation at the dorsolateral region of the ischial body and expands caudally onto the dorsal surface of the shaft, merging caudally with the flattened dorsolateral portion of the ischium, as also observed in *Saturnalia* (MCP 3844-PV).

The ischial shaft of UFRGS-PV-0761-T is subtriangular in cross-section and rod-like along most of its extension (Figure 5(B)–(F)). It is subtly distinct from the ischial shafts of *Saturnalia*, *Guaibasaurus* and most 'core prosauropods', which are dorsoventrally narrower proximally and quite expanded distally. UFRGS-PV-0761-T also differs from the ischium of early theropods, which have a relatively longer and narrower shaft (Rauhut 2003; Tykoski 2005). The shaft lacks a medial keel along its proximoverventral margin as seen in pseudosuchians (Serenó 1991) and early dinosauromorphs (Novas 1996). The ischial shafts of herrerasaurids (Novas 1994; Bittencourt and Kellner 2009) and silesaurids (Dzik 2003) differ from that of UFRGS-PV-0761-T by the absence of a distal expansion.

The flat medial surface of the ischium is rugose and bears craniocaudally directed striations for the articulation with its counterpart (Figure 5(D),(E)). A groove extending from the proximal portion of the shaft until its preserved distal end is limited dorsally by a longitudinal ridge and ventrally by an other elongated ridge (the 'medial ridge' of Hutchinson 2001). The latter is a caudal continuation of the ventral margin of the obturator process, which enters the medial surface of the shaft, becoming thinner towards the distal end of the bone. Both the dorsal and the medial ridges are also seen in *Panphagia* (PVSJ 874) and *Adeopapposaurus* (PVSJ 610). The lateral surface of the shaft bears a lateral crest along its entire extension, resulting in a subtriangular cross-section (Figure 5(C)). In some sauropodomorphs (e.g. *Plateosaurus*, SMNS 13200), the apex of the lateral expansion is ventrally projected and not

dorsally as in UFRGS-PV-0761-T. The distal end of the ischium is missing.

MMACR PV 037-T, right ischium

This additional isolated ischium is more complete than that described above, but their anatomy and size are very similar. It bears a proximal smooth dorsocaudal surface, which corresponds to the articulation with the ischiadic peduncle of the ilium (Figure 6(A),(B),(F)). This area also encompasses the antitrochanter, which projects laterally from the edge of the articular surface. Similar to that of basal dinosaurs (Irmis et al. 2007), the area between the iliac articulation and the obturator process shows a lateral acetabular fossa, medially bound by a sheet of bone. In the ventral margin of the ischium, the boundary between the obturator process and the ischial shaft is marked by notch (Figure 6(A),(B)). This is more common in theropods (Rauhut 2003), but a fainter version of it is also seen in *Plateosaurus* (GPIT-mounted skeletons; Yates 2003c). The apparent absence of this structure in UFRGS-PV-0761-T is more likely due to its incompleteness.

The flattened medial surface of the shaft preserves the ventral longitudinal ridge as described for UFRGS-PV-0761-T, but the dorsal ridge is not as conspicuous as in that specimen (Figure 6(A)). Likewise, MMACR PV 037-T also bears a dorsal symphyseal crest and a dorsolateral longitudinal groove (Figure 6(D)). The distal portion of the bone is clearly expanded caudodorsally, but not to the extent seen in most saurischians (Bonaparte et al. 1999; Langer 2003; Rauhut 2003). The distal outline is medially flat and laterally rounded (Figure 6(C)), and the subtriangular outline typical of sauropodomorphs (Galton and Upchurch 2004) is lacking.

Discussion

Affinity of the dinosaur specimens

The affinities of UFPel 014 with sauropodomorphs are supported by the presence of a dorsolateral recess in the 'sacral plate' (Upchurch et al. 2007). This structure is associated with the craniocaudal crest on the dorsomedial surface of the postacetabular process of the ilium, which is especially conspicuous in basal members of the group (Bonaparte 1971; Galton 2001). UFPel 014 shares sacral foramina with *Saturnalia* and *Guaibasaurus*, but the paucity of the material prevents its assignment to either of these genera. Indeed, no apomorphic features of *Saturnalia* and *Guaibasaurus*, or even Guaibasauridae, are based on the sacral vertebra anatomy (Langer et al. 1999, 2007, 2011; Ezcurra 2010).

UFRGS-PV-0761-T shares various characters with *Saturnalia*, including a wedged lateral opening of the ischio-acetabular groove and a hatchet-shaped ischiadic

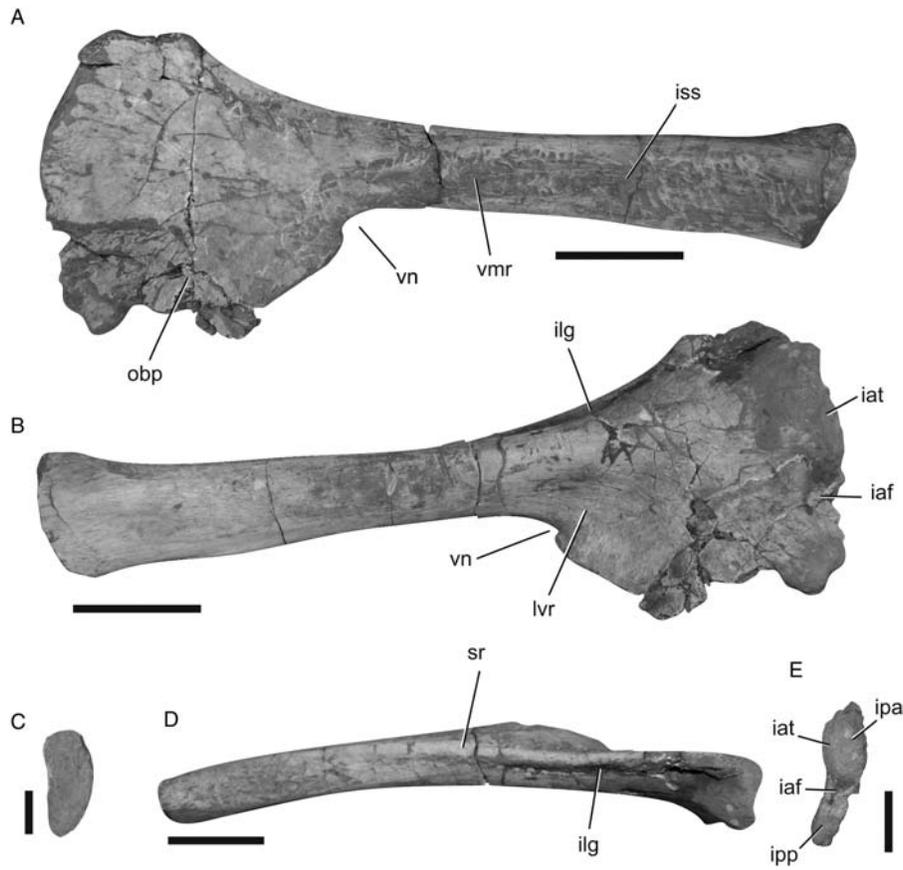


Figure 6. Right ischium of MMACR PV 037-T. (A) Photograph in medial view, (B) photograph in lateral view, (C) photograph in distal view, (D) photograph in dorsal view and (E) photograph in proximal view. iaf, ischial acetabular fossa; ipa, ischiadic peduncle articular area; iat, ischial antitrochanter; ilg, ischial longitudinal groove; iss, ischial shaft; lvr, lateroventral process; obp, obturator plate; sr, symphyseal ridge; vmr, ventromedial ridge; vn, ventral notch. Scale bars equal 30 mm (A, B, D–E) and 10 mm (C).

process of the pubis. Both characters are also seen in *Silesaurus*, and *Guaibasaurus* has a similar ischio-acetabular groove lateral opening. Yet, UFRGS-PV-0761-T differs from *Saturnalia* in its larger size and the more robust and subtriangular ischial shaft, suggesting that it is a distinct taxon. In addition, the absence of typical ‘core prosauropods’ (i.e. plateosaurids, riojasaurids and massospondylids; Yates 2007a) features, including an enlarged pubic fenestra and a lateromedially expanded and craniocaudally short pubic blade (Galton and Upchurch 2004), precludes the assignment of UFRGS-PV-0761-T to that group, and suggests a basal position within Sauropodomorpha. There is no positive evidence supporting the assignment of MMACR PV 037-T and UFRGS-PV-0761-T to the same individual, but their matching anatomy suggests that they belong to the same taxon.

The similarity of the specimens described here to both *Guaibasaurus* and sauropodomorphs is not surprising, as affinities between that genus and *Saturnalia* have been noticed by previous authors. In fact, Bonaparte et al. (2007) and Ezcurra (2010) argued for a close relationship between

Guaibasaurus and *Saturnalia*, mainly based on the anatomy of the ilium. Yet, Langer et al. (2011) suggested that the sauropodomorph affinity of *Guaibasaurus* may result from symplesiomorphies shared by basal saurischians in general. Their study indicates that various phylogenetic analyses of basal dinosaurs lack characters that account for a greater variability among early saurischians. Indeed, Langer et al. (2011) showed that the phylogenetic position of various basal taxa is sensitive to small variations in character sampling. In this sense, some features discussed here, as the sacral foramina, the composition of the ‘sacral plate’, the shape of the proximal portion of the pubis and the variation on the pubic tubercle, may be considered in future phylogenetic studies. This may add evidence that *Guaibasaurus* is a sauropodomorph, rather than a theropod. On the other hand, the lack of more complete material of that genus, including cranial parts, hampers a definitive assessment of its phylogenetic position.

Correlations of the Botucaraí Hill paleofauna

The surroundings of the Botucaraí Hill, about 8 km southwest of Candelária, represent one of the best sampled areas for Triassic tetrapods in Rio Grande do Sul, Brazil. It was defined as a 'Local Fauna' by Barberena et al. (1985) and has yielded an abundant record of fossil tetrapods including temnospondyls, rhynchosaurs, archosaurs, dicynodonts and cynodonts (Langer et al. 2007; Dias-da-Silva et al. 2009; Soares et al. 2011). Yet, the specimens have not been recovered from a single site, but from a series of outcrops along the BR 287 road, on the NW slope of the hill (Figure 1(A)). Accordingly, the name Botucaraí Hill cannot be strictly applied to any of the sites, although it has been usually (and will be here) employed with reference to the first of those localities to be dug up for fossils, yielding the dicynodont *Jachaleria candelariensis* (Araújo and Gonzaga 1980). More importantly, it has been long suspected (Schultz et al. 2000) that not all sites of the Botucaraí Hill area belong to a single stratigraphic unit. The 'Botucaraí Hill' site itself corresponds to a 15-m thick road cut, with specimens coming from different levels of the outcrop (Figure 2).

A detailed investigation of all sites, with historical inventory of their fossil record and *in situ* geologic studies, allowed a more precise characterisation of the Botucaraí Hill area. Such studies are vital to the understanding of fossiliferous deposits such as those of Triassic age in Rio Grande do Sul, which are composed of isolated anthropogenic outcrops with poor stratigraphic control. In these conditions, attempts to a fine correlation among nearby sites are necessary before biostratigraphic studies are conducted on a larger scale, perhaps using structural blocks as units to be cross-correlated (Da-Rosa and Faccini 2005). In this context, the Botucaraí Hill area belongs to the 'Candelária Block' of Da-Rosa and Faccini (2005), which is particularly important, because it preserves the most complete record of biostratigraphic units in the Santa Maria Supersequence (Zerfass et al. 2003; Langer et al. 2007). Yet, this study focuses on the uppermost portions of the sequence, which are those that crop out in the Botucaraí Hill area.

Six different fossiliferous sites are known on the NW slope of the Botucaraí Hill, along BR 287 road (Figure 1). The easternmost of them is that frequently referred to as the 'Botucaraí Hill' site (Figure 2). The single fossil record from its lower third corresponds to a stereospondyl interclavicle possibly referable to Mastodonsauroidea (Dias-da-Silva et al. 2009). This came from the northern margin of the road, whereas all other remains were collected from the main outcrop, which lies on the southern side of the road. The specimens dealt with here came from its middle third (Figure 2), along with all specimens referred to *J. candelariensis* (Araújo and Gonzaga 1980; Vega-Dias et al. 2004) and a still

undescribed ictidosaur (MMACR PV-0003-T), whereas an isolated first lower incisor of *Riograndia guaibensis* (Soares et al. 2011, p. 83) was recovered from the upper third of the outcrop (Figure 2). Other fossils collected in the site, i.e. isolated archosaur teeth (Dornelles 1990) and a partial phytosaur rostrum (Kischlat and Lucas 2003), were found scattered on the ground, with no clear indication of its stratigraphic provenance.

The three next outcrops westward of the 'Botucaraí Hill' site have been referred to as Sesmaria do Pinhal 1–3 (Soares et al. 2011). The first of these bears an accumulation of small tetrapod remains on its psamitic basal portion (Martinelli et al. 2005), which yielded the type specimens of *R. guaibensis* (Bonaparte et al. 2001) and *Irajatherium hernandezi* (Martinelli et al. 2005). Other recovered small tetrapods (Feringolo 2000, p. 243; Soares et al. 2011) include *Brasilodon quadrangularis*, *Brasilitherium riograndensis* and sphenodontians, possibly referred to *Clevosaurus brasiliensis*. The type specimens of *Guaibasaurus candelariensis* (Bonaparte et al. 1999) represent the only material recovered from Sesmaria do Pinhal 2, whereas Sesmaria do Pinhal 3, also referred to as 'poste', has yielded teeth of *B. riograndensis*, teeth and the partial maxilla of a traversodontid with affinities to *Exaeretodon* and remains of indeterminate sphenodontians and archosaurs (Ribeiro et al. 2011; Soares et al. 2011).

The next westward outcrops are the most problematic of the Botucaraí area in terms of fossil content, because most specimens were collected during the 1970s, lacking field notes regarding their provenance. Yet, personal communications from independent sources allow the definition of an area about 3 km southwest of the 'Botucaraí Hill' site, along BR 287 road (Figure 1(A)), as the most likely type locality of *Proterochampsia nodosa* (Barberena 1982), *Charruodon tetracuspidatus* (Abdala and Ribeiro 2000) and *Exaeretodon riograndensis* (Abdala et al. 2002). More recently, a rhynchosaur with affinities to *Hyperodapedon* (MCN-PV 3598) was also collected in this area, as well as from another site 0.5 km northward (MMACR PV 017-T). These will be referred to here as, respectively, 'Vila Botucaraí' 1 and 2.

The 'Botucaraí Hill' site, as well as Sesmaria do Pinhal 1 and 2, preserves massive fine sandstones, orange to brown, with tabular or lensoid geometry, indicating depositional lobes of crevasse splays (Figure 1(B)), typical of the Caturrita Formation, whereas the Sesmaria do Pinhal 3 site includes medium sandstones with through cross bedding, characterising the alluvial channels of that unit. On the contrary, the 'Vila Botucaraí' sites preserve massive/laminated mudstones with rhizocretions, desiccation marks and carbonate concretions, intercalated with very fine tabular sandstones (Figure 1(B)). Within the Santa Maria 2 Sequence (Zerfass et al. 2003), these deposits are typical of the Alemoa Member of the Santa Maria Formation.

The lithofaciological context suggests that ‘Botucaraí Hill’ and Sesmária do Pinhal 1–3 are coeval sites, and the occurrence of *R. guaibensis* in two of the localities allows their correlation to the *Riograndia* Assemblage Zone (AZ) of Soares et al. (2011). Instead, the ‘Vila Botucaraí’ sites are lower in the local stratigraphy, and the record of *Hyperodapedon* suggests an assignment to the eponymous biostratigraphic unit (Abdala et al. 2001; Langer et al. 2007). Accordingly, around Botucaraí Hill, the contact between the *Hyperodapedon* AZ (below) and *Riograndia* AZ (above) matches a lithofaciological shift from distal floodplain to alluvial channels and crevasse splays. Although erosional, the contact is formed by very fine tabular sandstones, with no evidence of erosional surfaces. In other areas of the east-western ‘Triassic belt’ of Rio Grande do Sul, the deposits yielding the *Hyperodapedon* AZ are linked to highly sinuous rivers, whereas the overlying rocks represent braided river systems. This shift in fluvial style marks the transition from the Santa Maria to the Caturrita formations, or the end of the Transgressive systems tract of the Santa Maria Sequence 2. It is noteworthy that the *Hyperodapedon* AZ is less than 50 m thick in the ‘Candelária’ structural block, whereas the *Riograndia* AZ has a thickness of more than 150 m. This may be explained by the lower depositional rate of floodplain deposits, which have more paedogenesis when compared to the channel deposits.

Some authors have attempted to refine the biostratigraphy of the Santa Maria 2 sequence beyond the *Hyperodapedon*–*Riograndia* AZs dichotomy. Langer et al. (2007) and Oliveira and Schultz (2007) identified a *Hyperodapedon* Acme Zone and a younger *Exaeretodon*-rich zone within the *Hyperodapedon* AZ. This was based both on correlations to the Ischigualasto Formation, in NW Argentina, where *Exaeretodon* abounds upper in the section (Martínez et al. 2011), as well as on apparent peculiarities of the deposits yielding *Exaeretodon* in the Santa Maria sequence, including the Vila Botucaraí 1 site. This was even suggested to belong to the Caturrita Formation by Barberena et al. (1985), representing the start of the coarsening up succession that replaces the Alemoa Member. On the contrary, the present study found no lithological basis to segregate the Vila Botucaraí sites from localities in Rio Grande do Sul where the Alemoa Member yields typical fossils of the *Hyperodapedon* Acme Zone fossils. Indeed, except for the ambiguous *Exaeretodon major*, from the Middle Triassic deposits of the Chiniquá area (Abdala et al. 2002; Liu 2007) and the specimens mentioned by Ribeiro et al. (2011), all currently known remains of *Exaeretodon* appears to come from the Transgressive systems tract of the Santa Maria Sequence 2. This is also the case of a new outcrop in the area of Vera Cruz (Horn et al. 2011), where an erosional surface occurs within the massive mudstones of the Alemoa member, splitting records of *Hyperodapedon* (below) and *Exaer-*

etodon (above). Indeed, an *Exaeretodon*-rich zone appears to occur in the Triassic of south Brazil, but there is no lithologic evidence to identify corresponding strata in isolated outcrops. Besides, it was recently proposed (Ribeiro et al. 2011) that the fauna of Sesmária do Pinhal 3 may be somewhat intermediate between the *Hyperodapedon* and *Riograndia* AZs. Yet, this is unlikely given that Sesmária do Pinhal 3 occurs at the same stratigraphic level as sites (‘Botucaraí Hill’ and Sesmária do Pinhal 1) that yield typical *Riograndia* AZ fossils. Besides, the occurrence of *B. riograndensis* also suggests that the fauna of Sesmária do Pinhal 3 belongs to the *Riograndia* AZ.

The Caturrita Formation yielded typical ‘prosauro-pods’, including *Unaysaurus tolentinoi* (Leal et al. 2004), with probable affinities to Jurassic forms, and other fragmentary remains (Bittencourt et al. 2012), as well as probable non ‘core prosauropod’ basal sauropodomorphs, i.e. the specimens described here and the ilium/femora (Ferigolo and Langer 2007) recovered from the type locality of *Sacisaurus agudoensis*. *Guaibasaurus* may be also included, but its phylogenetic position is still debated. This suggests either the occurrence of basal sauropodomorphs together with more ‘derived’ members of the clade, as already known in Late Triassic stratigraphic units of other parts of the world (Yates 2003a, 2003c; Galton and Upchurch 2004; Galton 2007; Novas et al. 2011), or that the dinosauriforms of the Caturrita Formation have been sampled from stratigraphic levels at different ages (Scherer et al. 2000; Bittencourt and Langer 2011).

Acknowledgements

We are indebted to Alexander Hohloch (GPIT), Ana Maria Ribeiro and Jorge Ferigolo (MCN), Angela Milner and Sandra Chapman (BMNH), Claudia Malabarba (MCP), David Unwin (HMN), Jaime Powell (PVL), Jerzy Dzik and Tomasz Sulej (ZPAL), Ricardo Martínez and Oscar Alcober (PVSJ) and Rainer Schoch (SMNS) who allowed examination of specimens under their care. We also thank the crew of Laboratório de Paleontologia (FFCLRP-USP), and especially Carlos Nunes Rodrigues (MMACR), for help during the fieldwork on the Botucaraí area. Maíra Massarani is thanked for the drawings. Part of this research was funded by FAPESP (Proc. 2010/08891-3).

References

- Abdala F, Barberena MC, Dornelles J. 2002. New species of the traversodontid cynodont *Exaeretodon* from the Santa Maria Formation (Middle/Late Triassic) of southern Brazil. *J Vert Paleontol.* 22(2):313–325.
- Abdala F, Ribeiro AM. 2000. A new therioherpetid cynodont from the Santa Maria Formation (middle Late Triassic), southern Brazil. *Geodiversitas.* 22(4):589–596.
- Abdala F, Ribeiro AM, Schultz CL. 2001. A rich cynodont fauna of Santa Cruz do Sul, Santa Maria Formation (Middle-Late Triassic), southern Brazil. *N Jahrb Geol Paläont M.* 11:669–687.
- Alcober O, Martínez RN. 2010. A new herrerasaurid (Dinosauria, Saurischia) from the Upper Triassic Ischigualasto Formation of northwestern Argentina. *Zookeys.* 63:55–81.

- Araújo DC, Gonzaga TD. 1980. Uma nova espécie de *Jachaleria*, Therapsida, Diconodontia to Triássico do Brasil. In: Actas. II Congreso Argentino de Paleontología y Biostratigrafía y I Congreso Latinoamericano de Paleontología. Buenos Aires: Asociación Paleontológica Argentina.
- Barberena MC. 1982. Uma nova espécie de *Proterochampsia* (*P. nodosa*, sp. nov.) do Triássico do Brasil. An Acad Brasil Cienc. 54(1):127–141.
- Barberena MC, Araújo DF, Lavina EL, Azevedo SAK. 1985. O estado atual do conhecimento sobre os tetrápodes permianos e triássicos do Brasil meridional. In: Campos DA, Ferreira CS, Brito IM, Viana CF, editors. Paleontologia e Estratigrafia, Coletânea de Trabalhos Paleontológicos. Brasília: DNPM. p. 21–28.
- Bittencourt JS, Kellner AWA. 2009. The anatomy and phylogenetic position of the Triassic dinosaur *Staurikosaurus pricei* Colbert, 1970. Zootaxa. 2079:1–56.
- Bittencourt JS, Langer MC. 2011. Mesozoic dinosaurs from Brazil and their biogeographic implications. An Acad Brasil Cienc. 83(1):23–60.
- Bittencourt JS, Leal LA, Langer MC, Azevedo SAK. 2012. An additional basal sauropodomorph specimen from the Upper Triassic Caturrita Formation, southern Brazil, with comments on the biogeography of plateosaurids. Alcheringa, doi: 10.1080/03115518.2012.634111.
- Bonaparte JF. 1971. Los tetrápodos del sector superior de la Formación Los Colorados, La Rioja, Argentina (Triásico Superior). I Parte. Opera Lilloana. 22:1–183.
- Bonaparte JF. 1984. Locomotion in rauisuchid thecodonts. J Vert Paleontol. 3(4):210–218.
- Bonaparte JF, Brea G, Schultz CL, Martinelli AG. 2007. A new specimen of *Guaibasaurus candelariensis* (basal Saurischia) from the Late Triassic Caturrita Formation of southern Brazil. Hist Biol. 19(1):73–82.
- Bonaparte JF, Ferigolo J, Ribeiro AM. 1999. A new early Late Triassic saurischian dinosaur from Rio Grande do Sul State, Brazil. Natl Sci Mus Monogr. 15:89–109.
- Bonaparte JF, Ferigolo J, Ribeiro AM. 2001. A primitive Late Triassic 'ictidosaur' from Rio Grande do Sul, Brazil. Palaeontology. 44(4):623–635.
- Cabreira SF, Schultz CL, Bittencourt JS, Soares MB, Fortier DC, Silva LR, Langer MC. 2011. New stem-sauropodomorph (Dinosauria, Saurischia) from the Triassic of Brazil. Naturwissenschaften. 98(12):1035–1040.
- Chatterjee S. 1978. A primitive parasuchid phytosaur reptile from the Upper Triassic Maleri Formation of India. Palaeontology. 21(1):83–128.
- Colbert EH. 1970. A saurischian dinosaur from the Triassic of Brazil. Am Mus Novit. 2405:1–39.
- Da-Rosa AAS, Faccini UF. 2005. Delimitação de blocos estruturais de diferentes escalas em seqüências mezozóicas do Estado do Rio Grande do Sul: implicações bioestratigráficas. GAEA. 1(1):16–23.
- Dias-da-Silva S, Dias EV, Schultz CL. 2009. First record of stereospondyls (Tetrapoda, Temnospondyli) in the Upper Triassic of Southern Brazil. Gondwana Res. 15(1):131–136.
- Dornelles JEF. 1990. Registro sobre a ocorrência de dentes de um arcossáurio para a Formação Caturrita, Triássico superior do Rio Grande do Sul. Cienc Nat. 12:99–101.
- Dzik J. 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. J Vert Paleontol. 23(3):556–574.
- Dzik J, Sulej T. 2007. A review of the early Late Triassic Krasiejow biota from Silesia, Poland. Palaeontol Pol. 64:3–27.
- Ezcurra MD. 2006. A review of the systematic position of the dinosauriform archosaur *Eucoelophysis baldwini* Sullivan & Lucas, 1999 from the Upper Triassic of New Mexico, USA. Geodiversitas. 28(4):649–684.
- Ezcurra MD. 2010. A new early dinosaur (Saurischia: Sauropodomorpha) from the Late Triassic of Argentina: a reassessment of dinosaur origin and phylogeny. J Syst Palaeontol. 8(3):371–425.
- Ferigolo J. 2000. Esfenodontídeos do Neo-triássico/Jurássico do Estado do Rio Grande do Sul. In: Holz M, De Ros LF, editors. Paleontologia do Rio Grande do Sul. Porto Alegre: CIGU/UFGRS. p. 236–245.
- Ferigolo J, Langer MC. 2007. A Late Triassic dinosauriform from south Brazil and the origin of the ornithischian predeceps bone. Hist Biol. 19(1):23–33.
- Frey E, Martill DM. 1995. A possible oviraptorosaurid theropod from the Santa Formation (Lower Cretaceous, ?Albian) of Brazil. N Jahrb Geol Paläont M. 7:397–412.
- Galton PM. 2000. Are *Spondylosoma* and *Staurikosaurus* (Santa Maria Formation, Middle-Upper Triassic, Brazil) the oldest saurischian dinosaurs? Paläontol Z. 74(3):393–423.
- Galton PM. 2001. The prosauropod dinosaur *Plateosaurus* MEYER, 1837 (Saurischia: Sauropodomorpha; Upper Triassic). II. Notes on the referred species. Rev Paleobiol. 20(2):435–502.
- Galton PM. 2007. Notes on the remains of archosaurian reptiles, mostly basal sauropodomorph dinosaurs, from the 1834 fissure fill (Rhaetian, Upper Triassic) at Clifton in Bristol, southwest England. Rev Paleobiol. 26(2):505–591.
- Galton PM, Upchurch P. 2004. Prosauropoda. In: Weishampel DB, Dodson P, Osmólska H, editors. The Dinosauria. Berkeley, CA: University of California Press. p. 232–258.
- Gower DJ, Schoch RR. 2009. Postcranial anatomy of the rauisuchian archosaur *Batrachotomus kupferzellensis*. J Vert Paleontol. 29(1):103–122.
- Harris JD. 1998. A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and palaeobiogeographic implications, based on a new specimen from Texas. Bull NM Mus Nat Hist Sci. 13:1–75.
- Horn BLD, Pretto FA, Neto VDP, Raugust T, Schultz CL. 2011. New fossil-bearing outcrops of the Triassic (Carnian) of southern Brazil, and its biostratigraphic significance. In: IV Congreso Latinoamericano de Paleontología de Vertebrados. San Juan: Universidad Nacional de San Juan.
- Huene F. 1934. Ein neuer Coelurosaurier in der thüringschen Trias. Paläontol Z. 16:145–168.
- Hutchinson JR. 2001. The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). Zool J Linn Soc. 131(2):123–168.
- Irmis RB, Nesbitt SJ, Padian K, Smith ND, Turner AH, Woody D, Downs A. 2007. A Late Triassic dinosauriform assemblage from New Mexico and the rise of dinosaurs. Science. 317(5836):358–361.
- Kischlat EE. 2003. Padrão muscular da coxa de arcossauromorfos fósseis. Aplicação do cladismo reverso e teste de hipóteses [PhD thesis]. Porto Alegre: Universidade Federal do Rio Grande do Sul.
- Kischlat EE, Lucas SG. 2003. Phytosaur from the Upper Triassic of Brazil. J Vert Paleontol. 23(2):464–467.
- Langer MC. 2003. The pelvic and hind limb anatomy of the stem-sauropodomorph *Saturnalia tupiniquim* (Later Triassic, Brazil). Paleobios. 23(2):1–40.
- Langer MC, Abdala F, Richter M, Benton MJ. 1999. A sauropodomorph dinosaur from the Upper Triassic (Carnian) of southern Brazil. C R Acad Sci Paris Sci Terre et Planét. 329(7):511–517.
- Langer MC, Benton MJ. 2006. Early dinosaurs: a phylogenetic study. J Syst Palaeontol. 4(4):309–358.
- Langer MC, Bittencourt JS, Schultz CL. 2011. A reassessment of the basal dinosaur *Guaibasaurus candelariensis*, from the Late Triassic Caturrita Formation of south Brazil. Earth Environ Sci Trans R Soc Edinburgh. 101(3-4):301–332.
- Langer MC, Ezcurra MD, Bittencourt JS, Novas FE. 2010. The origin and early evolution of dinosaurs. Biol Rev. 85(1):55–110.
- Langer MC, Ribeiro AM, Schultz CL, Ferigolo J. 2007. The continental tetrapod-bearing Triassic of South Brazil. Bull NM Mus Nat Hist Sci. 41:201–218.
- Leal LA, Azevedo SAK, Kellner AWA, Da Rosa AAS. 2004. A new early dinosaur (Sauropodomorpha) from the Caturrita Formation (Late Triassic), Parana Basin, Brazil. Zootaxa. 690:1–24.
- Liu J. 2007. The taxonomy of the traversodontid cynodonts *Exaeretodon* and *Ischnognathus*. Rev Bras Paleontol. 10(2):133–136.
- Long RA, Murry PA. 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. Bull NM Mus Nat Hist Sci. 4:1–254.
- Madsen JH. 1976. *Allosaurus fragilis*: a revised osteology. Utah Geol Miner Surv Bull. 109:1–163.
- Martinelli AG, Bonaparte JF, Schultz CL, Rubert R. 2005. A new tritheledontid (Therapsida, Eucynodontia) from the Late Triassic of Rio Grande do Sul (Brazil), and its phylogenetic relationships among

- carnivorous non-mammalian eucynodonts. *Ameghiniana*. 42(1):191–208.
- Martínez RN. 2009. *Adeopapposaurus mognai*, gen. et sp. nov. (Dinosauria: Sauropodomorpha), with comments on adaptations of basal Sauropodomorpha. *J Vert Paleontol*. 29(1):142–164.
- Martínez RN, Alcober OA. 2009. A basal sauropodomorph (Dinosauria: Saurischia) from the Ischigualasto Formation (Triassic, Carnian) and the early evolution of Sauropodomorpha. *PLoS ONE*. 4(2):1–12.
- Martínez RN, Sereno PC, Alcober O, Colombi CE, Renne PR, Montañez IP, Currie BS. 2011. A basal dinosaur from the dawn of the dinosaur era in southwestern Pangaea. *Science*. 331(6014):206–210.
- Nesbitt SJ. 2005. Osteology of the Middle Triassic pseudosuchian archosaur *Arizonasaurus babbitti*. *Hist Biol*. 17(1–4):19–47.
- Nesbitt SJ. 2011. The early evolution of archosaurs: relationships and the origin of major clades. *Bull Am Mus Nat Hist*. 352:1–292.
- Nesbitt SJ, Chatterjee S. 2008. Late Triassic dinosauriforms from the Post Quarry and surrounding areas, west Texas, USA. *N Jah Geol Paläont A*. 249(2):143–156.
- Nesbitt SJ, Stoker MR. 2008. The vertebrate assemblage of the Late Triassic Canjilon Quarry (Northern New Mexico, USA), and the importance of apomorphy-based assemblage comparisons. *J Vert Paleontol*. 28(4):1063–1072.
- Novas FE. 1994. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. *J Vert Paleontol*. 13(4):400–423.
- Novas FE. 1996. Dinosaur monophyly. *J Vert Paleontol*. 16(4):723–741.
- Novas FE, Ezcurra MD, Chatterjee S, Kutty TS. 2011. New dinosaur species from the Upper Triassic Upper Maleri and Lower Dharmaram formations of Central India. *Earth Environ Sci Trans R Soc Edinburgh*. 101(3–4):333–349.
- O'Connor PM. 2006. Postcranial pneumaticity: an evaluation of soft-tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. *J Morphol*. 267(10):1199–1226.
- Oliveira TV, Schultz CL. 2007. La predominancia de *Exaeretodon* Cabrera 1943 en una sección Triásica de Brasil y su probable correlación con el mismo evento en la porción mediana superior de la Formación Ischigualasto (Triásico de Argentina). In: XXIII Jornadas Argentinas de Paleontología de Vertebrados. Trelew: Museo Paleontológico Egidio Feruglio.
- Raath MA. 1969. A new coelurosaurian dinosaur from the forest sandstone of Rhodesia. *Arnoldia*. 4(28):11–25.
- Raath MA. 1977. The anatomy of the Triassic theropod *Syntarsus rhodesiensis* (Saurischia: Podokesauridae) and a consideration of its biology [PhD thesis]. Salisbury: Rhodes University.
- Rauhut OWM. 2003. The interrelationships and evolution of basal theropod dinosaurs. *Spec Pap Palaeontol*. 69:1–213.
- Ribeiro AM, Abdala F, Bertoni RS. 2011. Traversodontid cynodonts (Therapsida–Eucynodontia) from the Upper Triassic localities of the Paraná Basin, southern Brasil. In: IV Congreso Latinoamericano de Paleontología de Vertebrados. San Juan: Universidad Nacional del Comahue.
- Rinehart LF, Lucas SG, Heckert AB, Spielmann JA, Celsky MD. 2009. The paleobiology of *Coelophysis bauri* (Cope) from the Upper Triassic (Apchean Whitaker quarry, New Mexico), with detailed analysis of a single quarry block. *Bull NM Mus Nat Hist Sci*. 45:1–260.
- Romer AS. 1956. *Osteology of Reptiles*. Chicago, IL: The University of Chicago Press.
- Santa Luca AP. 1980. The postcranial skeleton of *Heterodontosaurus tucki* (Reptilia, Ornithischia) from the Stormberg of South Africa. *Ann South Afr Mus*. 79(7):159–211.
- Scherer CMS, Faccini UF, Lavina EL. 2000. Estratigráfico do Mesozóico da Bacia do Paraná. In: Ros LF, Holz M, editors. *Geologia do Rio Grande do Sul*. Porto Alegre: Universidade Federal do Rio Grande do Sul. p. 335–354.
- Schultz CL, Scherer CMS, Barberena MC. 2000. Biostratigraphy of southern Brazilian Middle-Upper Triassic. *Rev Bras Geocien*. 30(3):495–498.
- Sereno PC. 1991. Basal archosaurs: phylogenetic relationships and functional implications. *Soc Vertebr Paleontol Mem*. 2:1–53.
- Sereno PC, Arcucci AB. 1994. Dinosaurian precursors from the Middle Triassic of Argentina: *Lagerpeton chanarensis*. *J Vert Paleontol*. 13(4):385–399.
- Sereno PC, Forster CA, Rogers RR, Monetta AM. 1993. Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. *Nature*. 361(6407):64–66.
- Sereno PC, Novas FE. 1992. The complete skull and skeleton of an early dinosaur. *Science*. 258(5085):1137–1140.
- Sereno PC, Novas FE. 1994. The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*. *J Vert Paleontol*. 13(4):451–476.
- Soares MB, Schultz CL, Horn BLD. 2011. New information on *Riograndia guaibensis* Bonaparte, Ferigolo & Ribeiro, 2001 (Eucynodontia, Tritheledontidae) from the Late Triassic of southern Brazil: anatomical and biostratigraphic implications. *An Acad Brasil Cienc*. 83(1):329–354.
- Sullivan RM, Lucas SG. 1999. *Eucoelophysis baldwini*, a new theropod dinosaur from the Upper Triassic of New Mexico, and the status of the original types of *Coelophysis*. *J Vert Paleontol*. 19(1):81–90.
- Tykoski RS. 2005. Anatomy, ontogeny, and phylogeny of coelophysoid theropods [Ph.D. thesis]. Austin, TX: University of Texas.
- Tykoski RS, Rowe T. 2004. Ceratosauria. In: Weishampel DB, Dodson P, Osmólska H, editors. *The Dinosauria*. Berkeley, CA: University of California Press. p. 47–70.
- Upchurch P, Barrett PM, Dodson P. 2004. Sauropoda. In: Weishampel DB, Dodson P, Osmólska H, editors. *The Dinosauria*. Berkeley, CA: University of California Press. p. 259–322.
- Upchurch P, Barrett PM, Galton PM. 2007. A phylogenetic analysis of basal sauropodomorph relationships: implications for the origin of sauropod dinosaurs. *Spec Pap Palaeontol*. 77:57–90.
- Vega-Dias C, Maisch MW, Schultz CL. 2004. A new phylogenetic analysis of Triassic dicynodonts (Therapsida) and the systematic position of *Jachaleria candelariensis* from the Upper Triassic of Brazil. *N Jah Geol Paläont A*. 231:145–166.
- Weinbaum JC, Hungerbühler A. 2007. A revision of *Poposaurus gracilis* (Archosauria: Suchia) based on two new specimens from the Late Triassic of the southwestern USA. *Paläontol Z*. 81(2):131–145.
- Welles SP. 1984. *Dilophosaurus wetherilli* (Dinosauria, Theropoda). Osteology and comparisons. *Palaeontographica*. 185(4–6):85–180.
- Yates AM. 2003a. A definite prosauropod dinosaur from the Lower Elliot Formation (Norian: Upper Triassic) of South Africa. *Palaeontol Afr*. 39:63–68.
- Yates AM. 2003b. A new species of the primitive dinosaur *Thecodontosaurus* (Saurischia: Sauropodomorpha) and its implications for the systematics of early dinosaurs. *J Syst Palaeontol*. 1(1):1–42.
- Yates AM. 2003c. The species taxonomy of the sauropodomorph dinosaurs from the Lowenstein Formation (Norian, Late Triassic) of Germany. *Palaeontology*. 46(2):317–337.
- Yates AM. 2007a. The first complete skull of the triassic dinosaur *Melanorosaurus* Haughton (Sauropodomorpha: Anchisauria). *Spec Pap Palaeontol*. 77:9–55.
- Yates AM. 2007b. Solving a dinosaurian puzzle: the identity of *Aliwalia rex* Galton. *Hist Biol*. 19(1):93–123.
- Zerfass H, Lavina EL, Schultz CL, Garcia AGV, Faccini UF, Chemale F, Jr. 2003. Sequence stratigraphy of continental Triassic strata of southernmost Brazil, a contribution to Southwestern Gondwana palaeogeography and palaeoclimate. *Sediment Geol*. 161(1–2): 85–105.