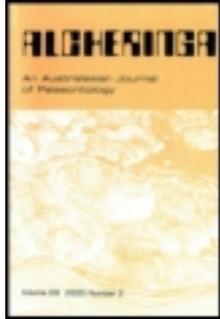


This article was downloaded by: [Jonathas Bittencourt]

On: 02 March 2012, At: 04:52

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



## Alcheringa: An Australasian Journal of Palaeontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/talc20>

### An additional basal sauropodomorph specimen from the Upper Triassic Caturrita Formation, southern Brazil, with comments on the biogeography of plateosaurids

Jonathas S. Bittencourt, Luciano A. Leal, Max C. Langer & Sérgio A. K. Azevedo

Available online: 02 Mar 2012

To cite this article: Jonathas S. Bittencourt, Luciano A. Leal, Max C. Langer & Sérgio A. K. Azevedo (2012): An additional basal sauropodomorph specimen from the Upper Triassic Caturrita Formation, southern Brazil, with comments on the biogeography of plateosaurids, *Alcheringa: An Australasian Journal of Palaeontology*, DOI:10.1080/03115518.2012.634111

To link to this article: <http://dx.doi.org/10.1080/03115518.2012.634111>



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.

# An additional basal sauropodomorph specimen from the Upper Triassic Caturrita Formation, southern Brazil, with comments on the biogeography of plateosaurids

JONATHAS S. BITTENCOURT, LUCIANO A. LEAL, MAX C. LANGER and SÉRGIO A. K. AZEVEDO

BITTENCOURT, J.S., LEAL, L.A., LANGER, M.C. & AZEVEDO, S.A.K., *iFirst* article. An additional basal sauropodomorph specimen from the Upper Triassic Caturrita Formation, southern Brazil, with comments on the biogeography of plateosaurids. *Alcheringa*, 1–10. ISSN 0311-5518.

We describe an additional saurischian specimen from the Caturrita Formation (Norian) of the Parana Basin, southern Brazil. This material was collected in the 1950s and remained unstudied due to its fragmentary condition. Detailed comparisons with other saurischians worldwide reveal that some characters of the ilium, including the low ventral projection of the medial wall of the acetabulum and its concave ventral margin, together with the short triangular shape of the pre-acetabular process and its mound-like dorsocaudal edge, resemble those of sauropodomorphs such as *Plateosaurus* and *Riojasaurus*. This set of traits suggests that MN 1326-V has affinities with basal Sauropodomorpha, probably closer to plateosaurians than to *Saturnalia*-like taxa. Previous records of this clade in the Caturrita Formation include *Unaysaurus*, which has been related to *Plateosaurus* within Plateosauridae. Alternative schemes suggest that plateosaurids include *Plateosaurus* plus the Argentinean ‘prosauropods’ *Coloradisaurus* and *Riojasaurus*. Both hypotheses raise biogeographic questions, as a close relationship between faunas from South America and Europe excluding Africa and North America is not supported by geological and biostratigraphical evidence. Additionally, the absence of plateosaurids in other continents suggests that the geographical distribution of this taxon is inconsistent with the geological history of western Pangaea, and this demands further investigations of the phylogeny of sauropodomorphs or improved sampling.

J.S. Bittencourt\* [[sigmaorionis@yahoo.com.br](mailto:sigmaorionis@yahoo.com.br)] Laboratório de Paleontologia, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Av. Bandeirantes 3900, 1404901, Ribeirão Preto, SP, Brazil. Fellow FAPESP; L.A. Leal, Departamento de Ciências Biológicas, Universidade Estadual do Sudoeste da Bahia, Rua José Moreira Sobrinho, s/n, 45206-190, Jequié, BA, Brazil; M.C. Langer, Laboratório de Paleontologia, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Av. Bandeirantes 3900, 1404901, Ribeirão Preto, SP, Brazil; S.A.K. Azevedo, Laboratório de Processamento de Imagem Digital, Departamento de Geologia e Paleontologia, Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista s/n, 20940-040, Rio de Janeiro, RJ, Brazil. Received 29.7.2011; revised 10.10.2011; accepted 18.10.2011.

Key words: Sauropodomorpha, Caturrita Formation, Late Triassic, Brazil, biogeography.

UNAMBIGUOUS dinosaur remains from the Late Triassic of southern Brazil have been known since the description of *Staurikosaurus* Colbert, 1970. Huene (1938) described *Spondylosoma* as a saurischian dinosaur, but its current status is unclear (Galton 2000, Langer 2004). Despite more recent discoveries (Bonaparte *et al.* 1999, 2007, Langer *et al.* 1999, Leal *et al.* 2004, Ferigolo & Langer 2007), several previously recovered dinosauriform specimens, including some collected early in the 20th century (Lyrio *et al.* 2003), await formal description (Kischlat 1999, Kischlat & Barberena 1999). Beltrão (1965) mentioned fossil bones collected during the 1950s in the Santa Maria area, central Rio Grande do Sul,

Brazil, widely known for its rich Triassic vertebrate fauna. The material has been housed at the Museu Nacional, Rio de Janeiro but, owing to its fragmentary condition (Couto in Beltrão 1965), has remained undescribed since then. Here, we describe and compare this specimen with several dinosauriforms in order to elucidate its taxonomic affinity.

Despite recent improvements, the Late Triassic dinosaur record is still sparse, and several aspects of the early evolution of the group are poorly understood (Brusatte *et al.* 2010, Langer *et al.* 2010). In the case of the Caturrita Formation, its dinosaur record (Leal *et al.* 2004) has implications for the biogeography of the Late Triassic ‘prosauropods’, which is discussed using previous phylogenetic hypotheses for basal sauropodomorphs (Upchurch *et al.* 2007, Yates 2007a, b, Rowe *et al.* 2010).

### *Institutional abbreviations*

GPIT: Institut für Geologie und Paläontologie, Tübingen, Germany; MCN: Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCP: Museu de Ciências e Tecnologia, Pontifícia Universidade Católica, Porto Alegre, Brazil; MN: Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; PVL: Instituto Miguel Lillo, San Miguel de Tucumán, Argentina; PVSJ: Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; SMNS: Staatliches Museum für Naturkunde, Stuttgart, Germany; UFRGS: Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; UFSM: Universidade Federal de Santa Maria, Santa Maria, Brazil.

### Geological setting

According to Beltrão (1965), the specimen described herein (MN 1326-V) was collected in Campinas, near São Martinho da Serra and Santa Maria, Rio Grande do Sul, southern Brazil (Fig. 1), although the precise locality is unknown. The material is embedded in reddish sandstone formerly assigned to the Botucatu Formation (Gordon 1947, Beltrão 1965), but now ascribed to the upper part of the Caturrita Formation, Rosario do Sul Group (Andreis *et al.* 1980, Scherer *et al.* 2000). Sequence-stratigraphic schemes

refer these strata to the upper part of ‘Sequence II’ of Faccini (1989), or the highstand systems tract of the Santa Maria 2 Sequence (Zerfass *et al.* 2003). No other fossils are known from Campinas, but the dinosaur fauna of the Caturrita Formation as a whole also includes the sauropodomorph *Unaysaurus* Leal *et al.*, 2004, collected from the ‘Água Negra’ site, located a few kilometres from Campinas (Fig. 1); the possible basal theropod *Guaibasaurus* Bonaparte *et al.*, 1999 (Bonaparte *et al.* 2007, Langer *et al.* 2011); and undescribed saurischian remains (Kischlat & Barberena 1999). Other fossil tetrapods from the Caturrita Formation include sphenodontians, procolophonids, rhynchosaurs, phytosaurs, silesaurids, cynodonts and dicynodonts (see Langer *et al.* 2007, for review), and this assemblage has been ascribed to the *Riograndia* Assemblage Zone (Rubert & Schultz 2004, Abdala & Ribeiro 2010, Soares *et al.* 2011). Although a possible Early Jurassic age has been proposed (Feringolo 2000), most authors agree with a Late Triassic age (possibly Norian) for the Caturrita Formation (Bonaparte *et al.* 1999, Langer *et al.* 2007, Abdala & Ribeiro 2010).

### Systematic palaeontology

DINOSAURIA Owen, 1842 *sensu* Padian & May, 1993

SAURISCHIA Seeley, 1888 *sensu* Gauthier, 1986

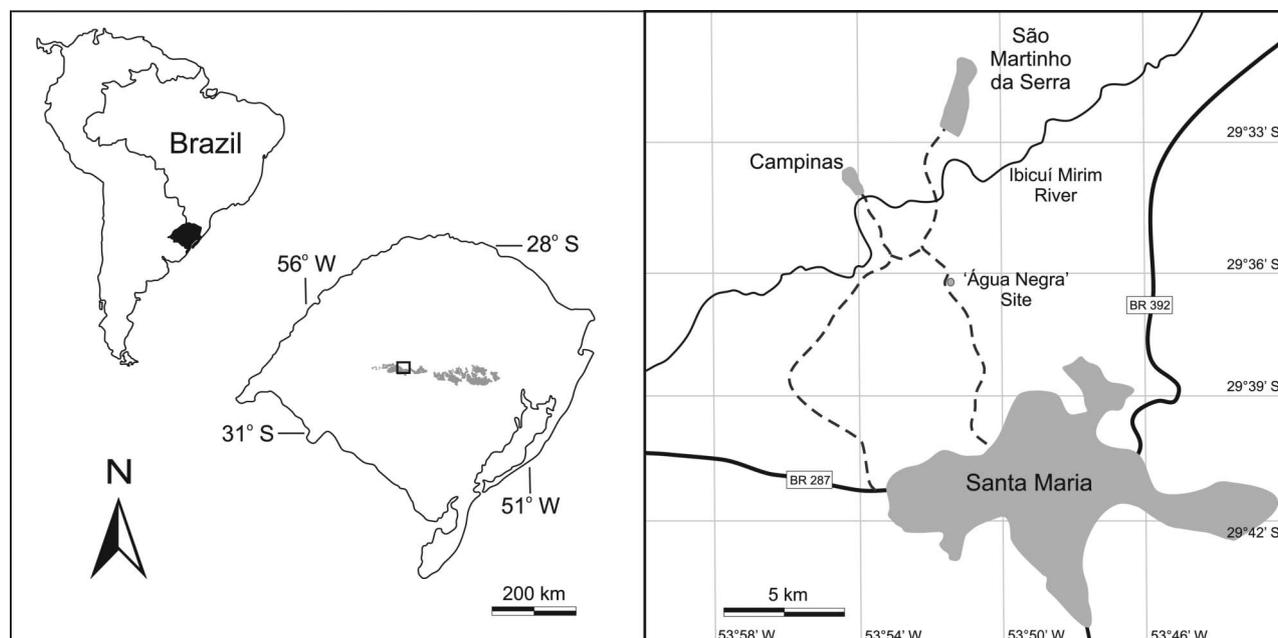


Fig. 1. Composite map showing the region of Campinas and its closest municipalities (Santa Maria and São Martinho da Serra), in central Rio Grande do Sul, southern Brazil. Continuous thick lines represent main highway and dashed lines denote secondary or unimproved roads. Continental map modified from Langer (2005).

SAUROPODOMORPHA Huene, 1932 *sensu* Upchurch, 1997

Sauropodomorpha indet.

*Material.* The specimen MN 1326-V (Figs 2, 3), previously numbered MN 2247-V (Beltrão 1965, p. 40), is preserved in a reddish sandstone block and consists of an incomplete right ilium, uninformative vertebral remains and other indeterminate fragments, plus four isolated and incomplete bones including a possible pubis, an ischium, a possible tibia and a metatarsal IV. These elements were found in close association and are considered parts of the same specimen.

*Description and comparison.* The preserved vertebra is located behind the ilium due to post-mortem displacement, and it shows the centrum plus a portion of the right transverse process (Fig. 2A–B). This latter is ventrally ornamented by an elongated crest, which borders a conspicuous infradiapophyseal fossa. The available information does not allow identification to a particular series of the vertebral column.

The preserved parts of the right ilium include the pre-acetabular process, partial pubic peduncle, the ischiadic peduncle, the medial wall of the acetabulum and part of the supra-acetabular crest (Fig. 2A–B). The pre-acetabular process is subtriangular in lateral view, being much shorter than the space between the

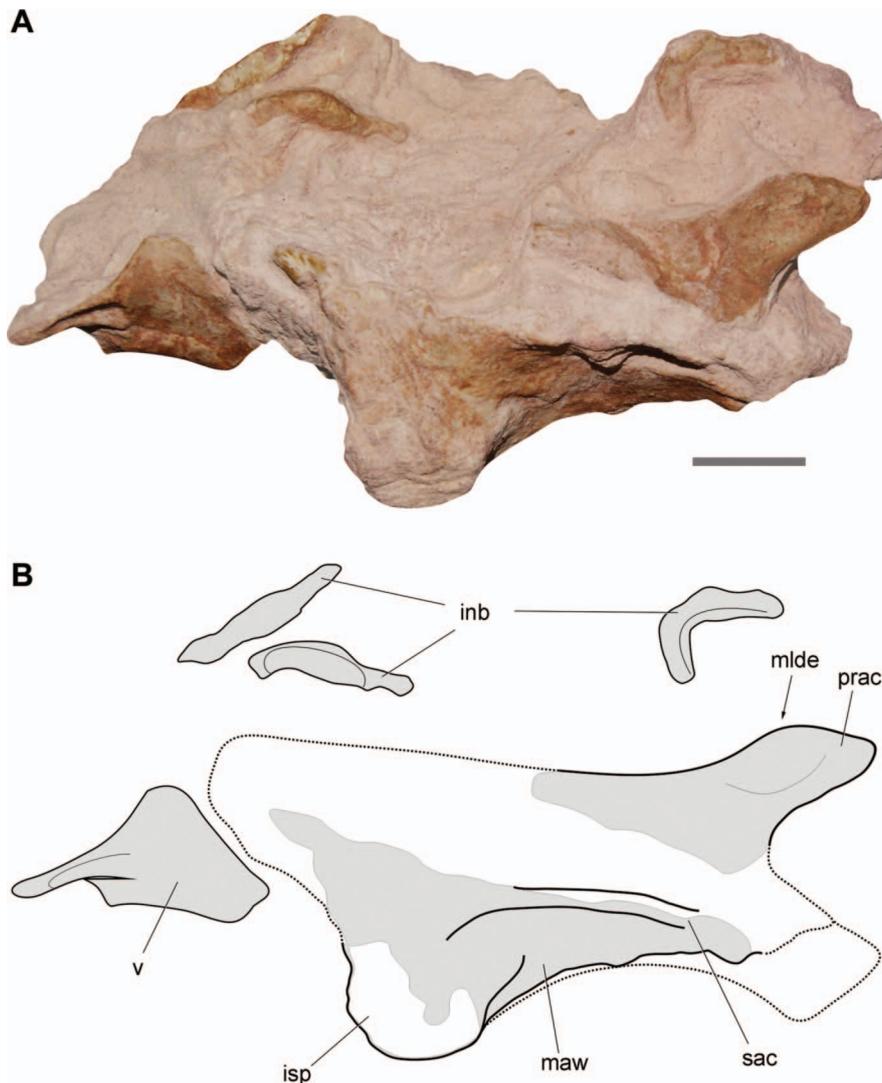


Fig. 2. Specimen MN 1326-V. **A**, Photograph and, **B**, drawing of the block containing the right ilium, in lateral view, and other bone fragments. Abbreviations: maw = medial acetabular wall; mlde = mound-like dorsal edge; isp = ischiadic peduncle; prac = pre-acetabular process; sac = supra-acetabular crest; inb = indeterminate bones; v = vertebra remnant. Grey areas represent preserved bone surface. Scale bar = 20 mm.

pre- and post-acetabular embayments of the bone. Dorsally, this process bears a distinct mound-like margin on its caudal edge, followed by a concavity of the dorsal margin of the iliac lamina. There is no evidence of a robust lateral margin of the pre-acetabular fossa, as observed in herrerasaurids (Bittencourt & Kellner 2009), *Guaibasaurus* (Langer *et al.* 2011) and at least one specimen of *Efraasia* (SMNS 17928). The distance between the proximal portion of both the pubic and ischiadic peduncles is more than twice the length of the pre-acetabular process. The medial wall of the acetabulum is dorsoventrally shallow and ventrally concave, as seen in most dinosaurs (Langer & Benton 2006, Nesbitt *et al.* 2009). There is no evidence of an excavation on the antitrochanteric portion of the acetabulum, a feature regarded as a possible autapomorphy of *Guaibasaurus* (Langer *et al.* 2011). The pubic peduncle is incomplete, so its relative extension can not be evaluated, and the ischiadic peduncle is short relative to the total height of the iliac blade.

A thick-walled, rod-like bone shaft with an expanded flange is also preserved (Fig. 3A–B). Its shape matches a pubis shaft, but further information is unavailable due to its incomplete preservation.

Another elongated and flattened partial bone is preserved (Fig. 3C–E). Its maximal width fits that of a fibula, based on the size of the putative tibia (see below; Fig. 3F–G). However, both the deep sulcus on its ‘dorsomedial’ surface and the flat, oblique ‘cranial’ margin (Fig. 3C, E) hamper its assignment to the pelvic epipodium. The transversely compressed shaft with rounded outer margin and a hint of an inner flange on its cranial surface fits the morphology of an archosaur right ischium (Bonaparte 1984, Sereno 1991). Its proximal portion is dorsoventrally broader than lateromedially wide. A proximodistally oriented groove, extending along the dorsomedial portion of the shaft (Fig. 3C), appears as an L-shaped notch in cross-section (Fig. 3E). A similar structure is evident on the dorsolateral margin of the ischium of many dinosaurs (e.g., *Plateosaurus*, SMNS 13200; see also

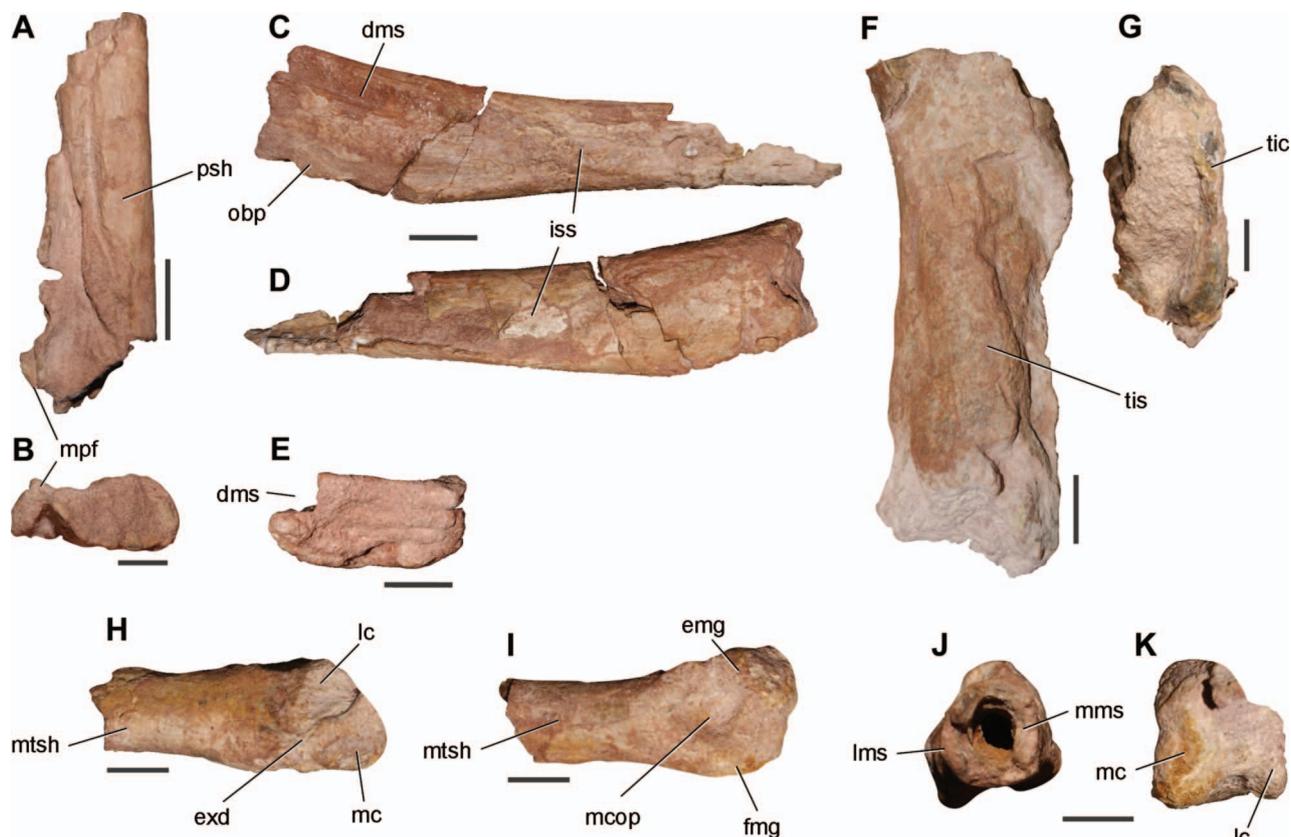


Fig. 3. Specimen MN 1326-V. A–B, Possible pubis. C–E, Ischium, in medial (C), lateral (D), and proximal (E) view. F–G, Tibia in lateral or medial (F), and cross-sectional (G) views. H–K, Left metatarsal IV in cranial (H), medial (I), proximal (J), and distal (K) views. Abbreviations: dms = dorsomedial sulcus; emg = extensor margin of the ginglymoid condyle; exd = extensor depression; fmg = flexor margin of the ginglymoid condyle; iss = ischial shaft; lms = lateral metatarsal shaft; mc = medial condyle; mcp = medial collateral pit; mms = medial metatarsal shaft; mpf = medial pubic flange; mtsh = metatarsal shaft; obp = obturator plate remnant; psh = pubic shaft; tic = tibial cortex; tis = tibial shaft. Scale bars (A, C, D, F) = 20 mm; (B, E, G–K) = 10 mm.

Langer 2003, Yates 2003a, b, Langer *et al.* 2011). The cranioventral margin of the bone is damaged, but the flange appears to be a remnant of the obturator plate (Fig. 3C). On the caudal two-thirds of the preserved bone, the ventral margin flattens dorsoventrally and projects caudally, giving a rod-like appearance to the shaft. The distal portion of the bone is incomplete and the presence of a dorsoventral expansion, as seen in several early dinosaurs (Bonaparte *et al.* 1999, Langer 2003, Galton & Upchurch 2004) can not be evaluated. Most of the medial surface of the proximal half of the shaft is slightly concave and bears longitudinal striations for muscle attachment (Fig. 3C). The symphyseal area is evidenced both by the rugose distal half of the medial surface of the shaft and by a crescentic rim cranially bordering this area.

Another elongated, flattened bone is preserved, but most of its surface is missing or damaged (Fig. 3F). The general transverse compression is typical of both tibiae and fibulae of Late Triassic saurischians (Novas 1994, Langer 2003, Bittencourt & Kellner 2009). Accordingly, owing to its large dimensions in comparison with the ilium, we tentatively regard it as a tibia. Its orientation can not be determined, but one side is concave, suggesting an expansion toward the tips. Its thin cortex (Fig. 3G) differs from the condition in most non-theropod dinosaurs (Sereno 1999, Holtz *et al.* 2004). However, thin-walled bones have been reported among other taxa from the Caturrita Formation, including *Guaibasaurus* (Langer *et al.* 2011) and *Unaysaurus* (UFSM 11069). On the other hand, the putative tibia of MN 1326-V is not uniformly wide around the medullar portion of the bone. In one of the broken surfaces, the wall in the flattened portion is thinner than in the corners (Fig. 3G).

A metapodial element (Fig. 3H–K) can be regarded as a metatarsal (Mt) owing to the persistent transverse width of the preserved shaft along its extension (Sereno & Arcucci 1994a, b, Langer 2003). The metacarpal shaft of most early dinosaurs (e.g., *Heterodontosaurus*, Santa Luca 1980; *Efraasia*, SMNS 12667; *Plateosaurus*, SMNS 13200k; *Guaibasaurus*, UFRGS PV0725T; *Coelophysis*: Colbert 1989) is usually thinner towards its mid-length, and the distal condyles are more expanded lateromedially (Galton 1973, 2001, Santa Luca 1980, Colbert 1989, Bonaparte *et al.* 2007, Langer *et al.* 2011). The assignment of the associated bones of MN 1326-V to the pelvic girdle reinforces this interpretation.

The thin-walled shaft of the metatarsal is elliptical in cross-section (Fig. 3J) and flattened on its right

side, suggesting that it articulated with another metatarsal along most of its extension. This is a common feature of dinosaur metatarsals, whereas metacarpals articulate to one another only at their proximal ends (Galton 1973, Santa Luca 1980, Sereno 1994). In dorsal view, the right distal condyle is longer and deeper than the left condyle, and extends further distally (Fig. 3H, K). This contrasts with the nearly symmetrical configuration of the metatarsal condyles of basal dinosauriforms, such as *Marasuchus* (Sereno & Arcucci 1994b) and *Silesaurus* (Dzik 2003), but resembles those of Mt I and IV of several basal dinosaurs, including *Herrerasaurus* (PVL 2566), *Guaibasaurus* (MCN PV2356; Langer *et al.* 2011), *Dilophosaurus* (Welles 1984), *Plateosaurus* (SMNS 13200k), *Riojasaurus* (PVL 3808) and *Heterodontosaurus* (Santa Luca 1980), in which the distal margin of the largest condyle (the lateral and medial condyles of Mt I and IV, respectively) slopes continuously towards the distal margin of the smaller adjacent condyle (Fig. 3H). A notch or concavity separating the distal condyles of metatarsal III in the taxa mentioned above (also in metatarsal II of *Plateosaurus*) is not seen in cranial aspect of the metatarsal of MN 1326-V. Metatarsal I of *Herrerasaurus* and *Dilophosaurus* possesses a distinct lateral kink on the dorsal margin of the lateral condyle, a feature not observed in MN 1326-V. Metatarsal I of some ‘prosauropods’ (*Plateosaurus*, *Riojasaurus*) bears the enlarged lateral condyle evident in MN 1326-V, but, unlike the material described here, it is a more robust bone, with a broader and shorter shaft. The opposite is apparent in metatarsal I of *Saturnalia* and *Herrerasaurus*, in which the shaft is quite elongated and thinner than in MN 1326-V. Metatarsal II of *Saturnalia* (MCP 3844-PV), *Herrerasaurus*, *Dilophosaurus* and *Plateosaurus* (GPIT mounted skeletons) are asymmetrical, but the distal projection of the lateral condyle with regard to the medial one is smaller than that of the metatarsal IV. Because of the set of characters discussed above, we regard the preserved metatarsal of MN 1326-V as the left metatarsal IV (Fig. 3H–K). The medial collateral pit is deeper than the left one, but this was probably increased by overpreparation. The flexor margin surrounding the collateral pit is deeper than the extensor portion in both condyles (Fig. 3I). The axis through the condyles is rotated about 40° in relation to the lateromedial plane of the shaft (Fig. 3J). Because of this rotation, the left condyle is projected ventrally with respect to the right one. The extensor depression is shallow (Fig. 3H), bordered proximally by a faint C-shaped rim, and confluent with the dorsal wall of both right and left condyles. The flexor

depression is as broad as long and splits the ginglymoid articulation ventrally.

## Discussion

Most of the preserved bones of MN 1326-V are not informative. Yet, relevant data may be gathered from the ilium, the anatomy of which allows the taxonomic assessment of the specimen.

A short subtriangular pre-acetabular process is a common feature among archosaurs, including crurotarsians (e.g., aetosaurs, rauisuchians and basal crocodylomorphs; Huene 1929, Colbert & Mook 1951, Krebs 1977, Gebauer 2004, Gower & Schoch 2009), basal dinosauriforms (e.g., *Marasuchus*, PVL 3870) and sauropodomorphs (Fig. 4A–C; Bonaparte 1971, Galton 1984, Yates 2003a, Galton & Upchurch 2004). In contrast, the pre-acetabular process in MN 1326-V differs greatly from the elongated rod-like

structure found in ornithischians (Sereno 1999, Norman *et al.* 2004). In theropods (Madsen 1976, Holtz *et al.* 2004, Tykoski & Rowe 2004), this process is at least as high as the iliac blade above the acetabulum, being commonly rounded or with a ventrocaudal fold in the cranial margin (Rauhut 2003: characters 168, 171). In herrerasaurids (Novas 1994, Bittencourt & Kellner 2009), it is proportionally shorter than in theropods but is also cranially rounded owing to a peculiar dorsoventral bulging (Fig. 4D) and is not pointed as in sauropodomorphs.

The ilium attributed to *Caseosaurus* (Nesbitt *et al.* 2007) bears a distally pointed pre-acetabular process, however, in contrast to MN 1326-V, the ventral margin of the pre-acetabular process is strongly projected dorsally. Problematic basal saurischians such as *Eoraptor* (PVSJ 512) and *Guaibasaurus* (UFRGS PV0725T) have a short pre-acetabular process but, in the former genus, the dorsal margin

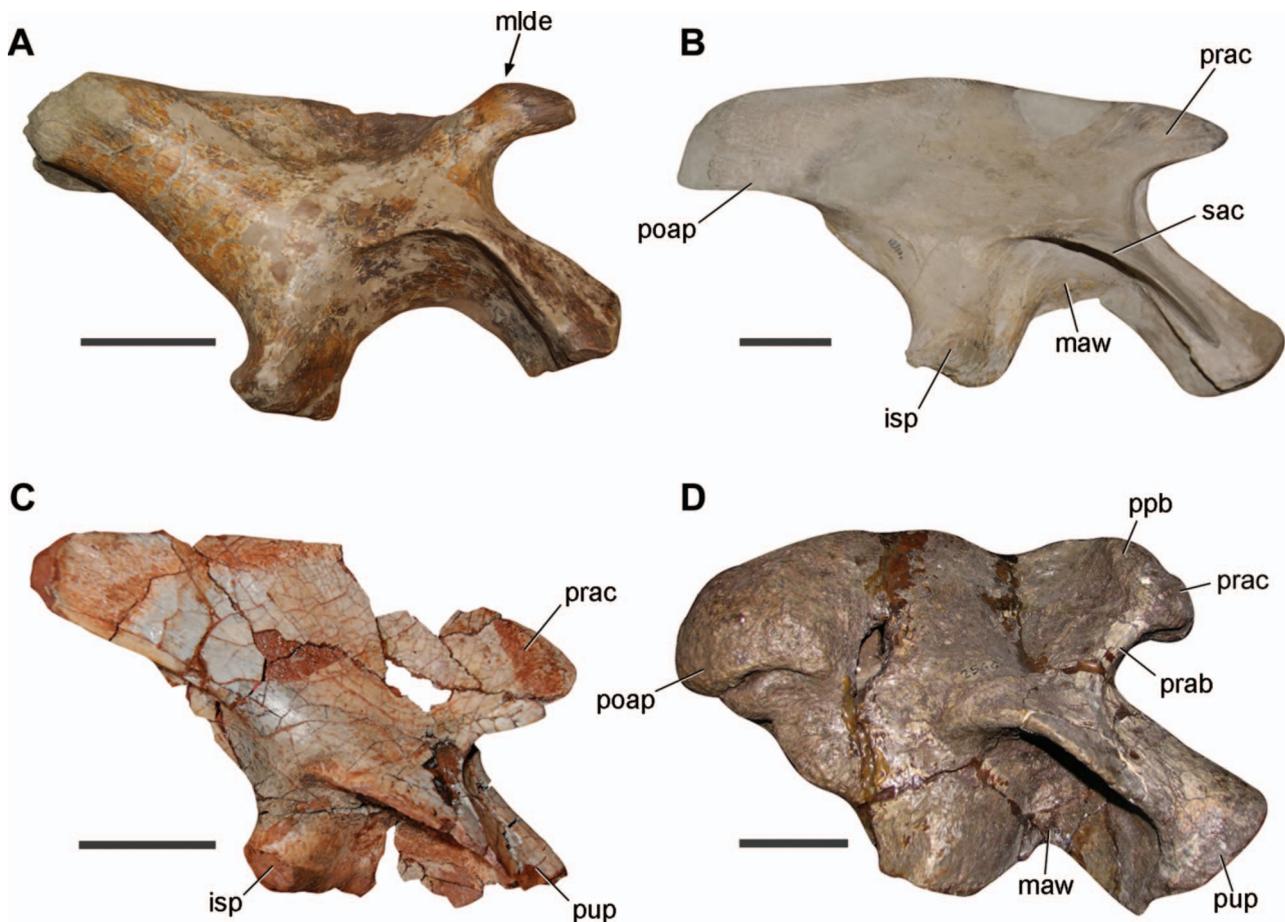


Fig. 4. Right ilia of assorted early saurischian taxa, in lateral view. **A**, cf. *Plateosaurus*, SMNS 12250; **B**, *Efraasia minor*, SMNS 12354; **C**, *Saturnalia tupiniquim*, MCP 3846-PV; **D**, *Herrerasaurus ischigualastensis*, PVL 2566. Abbreviations: maw = medial acetabular wall; mlde = mound-like dorsal edge; isp = isquiadic peduncle; poap = post-acetabular process; ppb = pre-acetabular process bulging; prab = pre-acetabular buttress; prac = pre-acetabular process; pup = pubic peduncle; sac = supra-acetabular crest. Scale bars (A) = 10 cm; (B, D) = 50 mm; (C) = 20 mm.

of the process is strongly convex and, in the latter, it is rounded distally. In the basal sauropodomorph *Saturnalia* (MCP 3845-PV), the pre-acetabular process is convex in both ventral and dorsal margins and its cranial tip reaches the cranial edge of the pubic peduncle (Fig. 4C). The ilium of MN 1326-V also differs from those of *Saturnalia* (Langer 2003), *Chromogisaurus* (Ezcurra 2010), *Guaibasaurus* (Langer *et al.* 2011) and herrerasaurids (Novas 1994, Bittencourt & Kellner 2009) by its shallower ventral projection of the medial acetabular wall, approaching the condition of more derived saurischians, such as 'prosauropods' (Galton & Upchurch 2004, Yates 2007a, b) and coelophysoids (Tykoski & Rowe 2004).

A mound-like dorsal margin of the pre-acetabular process of MN 1326-V is similar to that of some specimens assigned to cf. *Plateosaurus* (SMNS 12250, SMNS 6014, Galton 2001, Moser 2003; Fig. 4A) and *Riojasaurus* (PVL 3808). However, it should be noted that not all specimens assigned to these taxa possess this feature (Bonaparte 1971, Galton 2001, Moser 2003). Both *Plateosaurus* and *Riojasaurus* have been grouped into the Plateosauridae in some phylogenetic schemes (Upchurch *et al.* 2007, Martínez 2009), but most hypotheses (Leal *et al.* 2004, Yates 2007a, b, 2010, Rowe *et al.* 2010) favour *Riojasaurus* to be closely related to the South African *Eucnemesaurus*, and *Plateosaurus* to be allied with *Unaysaurus*, forming a more restricted Plateosauridae. One ilium attributed to *Adeopapposaurus*, which has been related to *Massospondylus* (Martínez 2009), also bears the mound-like structure, but its pre-acetabular process is longer and dorsoventrally thinner than that of MN 1326-V, with a straight and horizontal ventral margin. Due to the incompleteness of the specimen described herein, its close affinity to any of the aforementioned genera can not be confirmed. Indeed, because no unambiguous synapomorphy shared by MN 1326-V and plateosaurians was found, the material described herein is considered simply as an indeterminate Sauropodomorpha until further material is available. The configuration of its pre-acetabular process coupled with conspicuous differences between its acetabular region and that of basal saurischians suggest that MN 1326-V is closer to Plateosauria (*sensu* Yates 2007a) than to *Saturnalia*-like basal-most sauropodomorphs (Langer *et al.* 1999, Martínez & Alcober 2009, Ezcurra 2010). Unfortunately, no pelvic bone of the coeval *Unaysaurus* was recovered, preventing detailed comparisons with MN 1326-V. The lack of more diagnostic material also prevents its assignment to that species or to a new taxon. Nevertheless, the occurrence of MN 1326-V

corroborates the presence of 'prosauropods' in the upper sections of the Caturrita Formation.

Despite recent advances, the phylogeny of the sauropodomorphs remains controversial (Yates 2003a, 2007a, b, Smith & Pol 2007, Upchurch *et al.* 2007, Ezcurra 2010, Langer *et al.* 2010, Rowe *et al.* 2010, Pol *et al.* 2011). The framework in which the Brazilian 'prosauropods' are more closely related to plateosaurids from central Europe than to the sauropodomorphs from coeval strata in Argentina (Leal *et al.* 2004, Yates 2007a, b) is unexpected, since an isolation between the Brazilian and Argentinean sauropodomorph faunas during the Late Triassic is not supported by geological and biostratigraphical evidence (Bonaparte 1982, Schultz *et al.* 2000, Zeffass *et al.* 2003, 2004). Indeed, the geographic position of Europe and South America during the Late Triassic, as part of a broadly emergent western Pangean landmass (Scalera 2001, Scotese 2002), is incongruent with a faunal distribution restricted to these areas. Accordingly, the range of this clade ought to minimally include northern Africa or North America (Nesbitt *et al.* 2009), which are devoid of unambiguous plateosaurids (Galton & Upchurch 2004, Nesbitt *et al.* 2007). The recently described *Seitaad*, from the Early Jurassic of North America may represent a plateosaurid (Sertich & Loewen 2010), but this was not supported in a more recent study (Rowe *et al.* 2010).

The absence of plateosaurids in areas other than Europe and South America could be explained by poor sampling or a spurious phylogenetic signal. In the case of North America, the former explanation is less likely, because its Norian dinosaur fauna is well studied, and the absence of sauropodomorphs may represent a true biogeographic pattern (Nesbitt *et al.* 2007). Indeed, recent studies suggest that the expansion of the geographic distribution of sauropodomorphs to North America was constrained until the Early Jurassic by physical barriers, such as the Appalachian–Ouachita orogeny and the Central Atlantic Magmatic Province (Coney 1982, Rowe *et al.* 2010).

Terrestrial faunal interchange between Africa and southern South America should not have been hampered until the Early Jurassic, at which time the first Gondwanide hotspots responsible for the break-up of southern Gondwana were initiated (Lawver *et al.* 1998, MacDonald *et al.* 2003, Golonka 2007). In this scenario, the absence of plateosaurids in the Late Triassic–Early Jurassic strata of the Karoo Basin (Yates 2003b, Rubidge 2005), with its more southeastern position with respect to the Parana Basin, may also reflect a true biogeographic pattern.

On the other hand, coeval archosaur-bearing deposits in northern Gondwana are sparse and include only strata of the Argana Basin, Morocco (Gauffre 1993, Lucas 1998). So, the absence of the group from Africa as a whole might be explained by poor sampling. Alternatively, the biogeographic conundrum may be related to the phylogenetic hypothesis. Indeed, both phylogenetic frameworks of Yates (2007a, b) and Upchurch *et al.* (2007) are inconsistent with the currently known geographic distribution of the sauropodomorphs.

Recent works show that the phylogeny of the Sauropodomorpha is in state of flux. Pol *et al.* (2011), for instance, presented a different hypothesis for the phylogenetic position of the plateosaurids. This clade (*Unaysaurus* was not included) falls within a polytomy with *Ruehleia* and Massopoda. In addition, a preliminary comparison of *Unaysaurus* with *Sarhsaurus*, from the Kayenta Formation, USA, suggests that these genera share at least two potential synapomorphies: the prezygodiapophyseal laminae on cranial trunk vertebrae and the narrower proximal margin of the metacarpal I (Upchurch *et al.* 2007, Rowe *et al.* 2010), casting doubt on the plateosaurid affinity of *Unaysaurus*. Novas *et al.* (2011) recently described new sauropodomorphs from the Late Triassic of India, one of which (*Jaklapallisaurus*), has been positioned as a plateosaurid, because of the caudal flushing of the proximal condyles of the tibia. However, the tibiae of *Plateosaurus* (GPIT mounted skeletons, Galton 2001, Moser 2003) have a cranially offset lateral condyle. Thus, the position of *Jaklapallisaurus* as a plateosaurid is ambiguous and requires further investigation.

Additional material is needed to evaluate the affinities of the sauropodomorphs of the Caturrita Formation. However, the discovery of the fragmentary MN 1326-V corroborates the presence of basal sauropodomorphs in this unit and highlights the value of early fieldwork in the Upper Triassic outcrops of southern Brazil, as well as curation of incomplete specimens for long-term research (see Molnar 2011a, b).

## Acknowledgements

We are indebted to Alexander Hohloch (GPIT), Atila da Rosa (UFSM), Ana Maria Ribeiro and Jorge Ferigolo (MCN), Cesar Schultz (UFRGS), Claudia Malabarba (MCP), Jaime Powell (PVL), Rainer Schoch (SMNS), Ricardo Martínez (PVSJ), Alejandro Otero and Marcelo Reguero (La Plata, Argentina), Diego Pol and Eduardo Ruigomez (Trelew, Argentina) who allowed examination of specimens

under their care. Stephen McLoughlin, Peter Galton and Octávio Mateus are thanked for valuable suggestions that greatly improved the final version of this paper. This research was funded by FAPESP (Proc. 2010/08891-3, post-doctoral fellowship to JSB).

## References

- ABDALA, F. & RIBEIRO, A.M., 2010. Distribution and diversity patterns of Triassic cynodonts (Therapsida, Cynodontia) in Gondwana. *Palaeogeography, Palaeoclimatology, Palaeoecology* 286, 202–217.
- ANDREIS, R.R., BOSSI, G.E. & MONTARDO, D.K., 1980. O Grupo Rosário do Sul (Triássico) no Rio Grande do Sul. *Anais do 31º Congresso Brasileiro de Geologia* 2. Camboriú, 659–673.
- BELTRÃO, R., 1965. Paleontologia de Santa Maria e São Pedro do Sul, RS, Brasil. *Boletim do Instituto de Ciências Naturais da Universidade Federal de Santa Maria* 2, 1–151.
- 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.
- BONAPARTE, J.F., 1971. Los tetrápodos del sector superior de la Formación Los Colorados, La Rioja, Argentina (Triásico Superior). I Parte. *Opera Lilloana* 22, 1–183.
- BONAPARTE, J.F., 1982. Faunal replacement in the Triassic of South America. *Journal of Vertebrate Paleontology* 2, 362–371.
- BONAPARTE, J.F., 1984. Locomotion in rauisuchid thecodonts. *Journal of Vertebrate Paleontology* 3, 210–218.
- BONAPARTE, J.F., FERIGOLO, J. & RIBEIRO, A.M., 1999. A new early Late Triassic saurischian dinosaur from Rio Grande do Sul State, Brazil. *National Science Museum Monographs* 15, 89–109.
- BONAPARTE, J.F., BREA, G., SCHULTZ, C.L. & MARTINELLI, A.G., 2007. A new specimen of *Guaibasaurus candelariensis* (basal Saurischia) from the Late Triassic Caturrita Formation of southern Brazil. *Historical Biology* 19, 73–82.
- BRUSATTE, S.L., NESBITT, S.J., IRMIS, R.B., BUTLER, R.J., BENTON, M.J. & NORELL, M.A., 2010. The origin and early radiation of dinosaurs. *Earth-Science Reviews* 101, 68–100.
- COLBERT, E.H., 1970. A saurischian dinosaur from the Triassic of Brazil. *American Museum Novitates* 2405, 1–39.
- COLBERT, E.H., 1989. The Triassic dinosaur *Coelophysis*. *Museum of Northern Arizona Bulletin* 57, 1–160.
- COLBERT, E.H. & MOOK, C.C., 1951. The ancestral crocodylian *Protosuchus*. *Bulletin of the American Museum of Natural History* 97, 145–182.
- CONEY, P.J., 1982. Plate tectonic constraints on the biogeography of middle America and the Caribbean region. *Annals of the Missouri Botanical Garden* 69, 432–443.
- DZIK, J., 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. *Journal of Vertebrate Paleontology* 23, 556–574.
- 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.
- FACCINI, U.F., 1989. *O Permo-Triássico do Rio Grande do Sul: uma análise sob o ponto de vista das seqüências deposicionais*. PhD thesis, Universidade Federal do Rio Grande do Sul, 212 pp. (unpublished)
- FERIGOLO, J., 2000. Esfenodontídeos do Neo-triássico/Jurássico do Estado do Rio Grande do Sul. In *Paleontologia do Rio Grande do Sul*. HOLZ, M. & DE ROS L.F., eds, CIGO/UFRGS, Porto Alegre, 236–245.

- FERIGOLO, J. & LANGER, M.C., 2007. A Late Triassic dinosauriform from south Brazil and the origin of the ornithischian prenatary bone. *Historical Biology* 19, 23–33.
- GALTON, P.M., 1973. On the anatomy and relationships of *Efraasia diagnostica* (HUENE) n. gen., a prosauropod dinosaur (Reptilia: Saurischia) from the Upper Triassic of Germany. *Paläontologische Zeitschrift* 47, 229–255.
- GALTON, P.M., 1984. An early prosauropod dinosaur from the Upper Triassic of Nordwürttemberg, West Germany. *Stuttgarter Beiträge zur Naturkunde B* 106, 1–25.
- GALTON, P.M., 2000. Are *Spondylosoma* and *Staurikosaurus* (Santa Maria Formation, Middle–Upper Triassic, Brazil) the oldest saurischian dinosaurs? *Paläontologische Zeitschrift* 74, 393–423.
- GALTON, P.M., 2001. The prosauropod dinosaur *Plateosaurus MEYER*, 1837 (Saurischia: Sauropodomorpha; Upper Triassic). II. Notes on the referred species. *Revue de Paleobiologie* 20, 435–502.
- GALTON, P.M. & UPCHURCH, P., 2004. Prosauropoda. In *The Dinosauria*. WEISHAMPEL, D.B., DODSON, P. & OSMÓLSKA, H., eds, University of California Press, Berkeley, 232–258.
- GAUFFRE, F.-X., 1993. The prosauropod dinosaur *Azendohsaurus laaroussii* from the Upper Triassic of Morocco. *Palaeontology* 36, 897–908.
- GAUTHIER, J., 1986. Saurischian monophyly and the origin of birds. In *The Origin of Birds and the Evolution of Flight*. PADIAN, K., ed., *Memoirs of the California Academy of Sciences* 8, 1–55.
- GEBAUER, E.V.I., 2004. Redescription of *Stagonosuchus nyassicus* v. HUENE, 1938 (Thecodontia, Rauisuchia) from the Manda Formation (Middle Triassic) of Southwest Tanzania. *Neues Jahrbuch für Geologie und Paläontologie—Abhandlungen* 231, 1–35.
- GOLONKA, J., 2007. Late Triassic and Early Jurassic palaeogeography of the world. *Palaeogeography, Palaeoclimatology, Palaeoecology* 244, 297–307.
- GORDON Jr, M., 1947. Classificação das formações gondwânicas do Paraná, Santa Catarina e Rio Grande do Sul. *Notas Preliminares e Estudos, DNPM/DGM* 38, 1–20.
- GOWER, D.J. & SCHOCH, R.R., 2009. Postcranial anatomy of the rauisuchian archosaur *Batrachotomus kupferzellensis*. *Journal of Vertebrate Paleontology* 29, 103–122.
- HOLTZ, T.R., Jr, MOLNAR, R.E. & CURRIE, P.J., 2004. Basal Tetanurae. In *The Dinosauria*. WEISHAMPEL, D.B., DODSON, P. & OSMÓLSKA, H., eds, University of California Press, Berkeley, 71–110.
- HUENE, F. VON, 1929. Über Rhyncosauries und andere Reptilien aus den Gondwana-Ablagerungen Sudamerikas. *Geologische und Paläontologische Abhandlungen* 17, 1–61.
- HUENE, F. VON, 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographien zur Geologie und Paläontologie (series 1)* 4, 1–361.
- HUENE, F. VON, 1938. Die fossilen Reptilien des südamerikanischen Gondwanalandes. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Referate* 1938, 142–151.
- KISCHLAT, E.E., 1999. A new dinosaurian 'rescued' from the Brazilian Triassic: *Teywasu barberenai*, new taxon. *Paleontologia em Destaque* 14, 58.
- KISCHLAT, E.E. & BARBERENA, M.C., 1999. Triassic Brazilian dinosaurs: new data. *Paleontologia em Destaque* 14, 56.
- KREBS, B., 1977. Pseudosuchia. In *Thecodontia*. KUHN, O., ed., *Handbuch der Paläoherpetologie* 13, Gustav-Fischer, Stuttgart, 40–98.
- LANGER, M.C., 2003. The pelvic and hind limb anatomy of the stem-sauropodomorph *Saturnalia tupiniquim* (Later Triassic, Brazil). *Paleobios* 23(2), 1–40.
- LANGER, M.C., 2004. Basal Saurischia. In *The Dinosauria*. WEISHAMPEL, D.B., DODSON, P. & OSMÓLSKA, H., eds, University of California Press, Berkeley, 25–46.
- LANGER, M.C., 2005. Studies on continental Late Triassic tetrapod biochronology. I. The type locality of *Saturnalia tupiniquim* and the faunal succession in south Brazil. *Journal of South American Earth Sciences* 19, 205–218.
- LANGER, M.C. & BENTON, M.J., 2006. Early dinosaurs: A phylogenetic study. *Journal of Systematic Palaeontology* 4, 309–358.
- 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 IIA* 329, 511–517.
- LANGER, M.C., RIBEIRO, A.M., SCHULTZ, C.L. & FERIGOLO, J., 2007. The continental tetrapod-bearing Triassic of South Brazil. In *The Global Triassic*. LUCAS, S.G. & SPIELMANN, J.A., eds, *New Mexico Museum of Natural History and Science Bulletin* 41, 201–218.
- LANGER, M.C., EZCURRA, M.D., BITTENCOURT, J.S. & NOVAS, F.E., 2010. The origin and early evolution of dinosaurs. *Biological Reviews* 85, 55–110.
- LANGER, M.C., BITTENCOURT, J.S. & SCHULTZ, C.L., 2011. A reassessment of the basal dinosaur *Guaibasaurus candelariensis*, from the Late Triassic Caturrita Formation of south Brazil. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 101, 301–332.
- LAWVER, L.A., GAHAGAN, L.M. & DALZIEL, I.W.D., 1998. A tight fit—early Mesozoic Gondwana, a plate reconstruction perspective. *Memoirs of National Institute of Polar Research C* 53, 214–229.
- LEAL, L.A., AZEVEDO, S.A.K., KELLNER, A.W.A. & DA ROSA, A.A.S., 2004. A new early dinosaur (Sauropodomorpha) from the Caturrita Formation (Late Triassic), Parana Basin, Brazil. *Zootaxa* 690, 1–24.
- LUCAS, S.G., 1998. The aetosaur *Longosuchus* from the Triassic of Morocco and its biochronological significance. *Comptes Rendus De L'Academie Des Sciences Serie IIA* 326, 589–594.
- LYRIO, M.C., BITTENCOURT, J., LEAL, L.A. & AZEVEDO, S.A., 2003. Saurischian remains from Caturrita Formation (Upper Triassic, Southern Brazil) and the Triassic dinosaur fauna from Brazil. *Anais do 4º Simpósio Brasileiro de Paleontologia de Vertebrados*, Rio Claro, 41–42.
- MACDONALD, D., GOMEZ-PEREZA, I., FRANZESE, J., SPALLETI, L., LAWVER, L., GAHAGAN, L., DALZIEL, I., THOMAS, C., TREWIN, N., HOLE, M. & PATON, D., 2003. Mesozoic break-up of SW Gondwana: implications for regional hydrocarbon potential of the southern South Atlantic. *Marine and Petroleum Geology* 20, 287–308.
- MADSEN, J.H., 1976. *Allosaurus fragilis*: a revised osteology. *Utah Geological and Mineral Survey Bulletin* 109, 1–163.
- MARTÍNEZ, R.N., 2009. *Adeopapposaurus mognai*, gen. et sp. nov. (Dinosauria: Sauropodomorpha), with comments on adaptations of basal Sauropodomorpha. *Journal of Vertebrate Paleontology* 29, 142–164.
- MARTÍNEZ, R.N. & ALCOBER, O.A., 2009. A basal sauropodomorph (Dinosauria: Saurischia) from the Ischigualasto Formation (Triassic, Carnian) and the early evolution of Sauropodomorpha. *PLoS ONE* 4, 1–12.
- MOLNAR, R., 2011a. Sauropod (Saurischia: Dinosauria) material from the Early Cretaceous Griman Creek Formation of the Surat Basin, Queensland, Australia. *Alcheringa* 35, 303–307.
- MOLNAR, R., 2011b. New morphological information about Cretaceous sauropod dinosaurs from the Eromanga Basin, Queensland, Australia. *Alcheringa* 35, 329–339.
- MOSER, M., 2003. *Plateosaurus engelhardti* Meyer, 1837 (Dinosauria: Sauropodomorpha) aus dem Feuerletten (Mittelkeuper; Obertrias) von Bavaria. *Zitteliana* 24, 3–186.
- NESBITT, S.J., IRMIS, R.B. & PARKER, W.G., 2007. A critical re-evaluation of the Late Triassic dinosaur taxa of North America. *Journal of Systematic Palaeontology* 5, 209–243.

- NESBITT, S.J., SMITH, N.D., IRMIS, R.B., TURNER, A.H., DOWNS, A. & NORELL, M.A., 2009. A complete skeleton of a Late Triassic saurischian and the early evolution of dinosaurs. *Science* 326, 1530–1533.
- NORMAN, D.B., WITMER, L.M. & WEISHAMPEL, D.B., 2004. Basal Ornithischia. In *The Dinosauria*. WEISHAMPEL, D.B., DODSON, P. & OSMÓLSKA, H., eds, University of California Press, Berkeley, 325–334.
- NOVAS, F.E., 1994. 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.
- NOVAS, F.E., EZCURRA, M.D., CHATTERJEE, S. & KUTTY, T.S., 2011. New dinosaur species from the Upper Triassic upper Maleri and lower Dharmaram formations of Central India. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 101, 333–349.
- OWEN, R., 1842. Report on British fossil reptiles. Part II. *Reports of the British Association for the Advancement of Science* 11, 60–204.
- PADIAN, K. & MAY, C.L., 1993. The earliest dinosaurs. In *The Nonmarine Triassic*. LUCAS, S.G. & MORALES, M., eds, *Bulletin of the New Mexico Museum of Natural History and Science* 3, 379–381.
- POL, D., GARRIDO, A. & CERDA, I.A., 2011. A new sauropodomorph dinosaur from the Early Jurassic of Patagonia and the origin and evolution of the sauropod-type sacrum. *PLoS ONE* 6, 1–24.
- RAUHUT, O.W.M., 2003. The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology* 69, 1–213.
- ROWE, T.B., SUES, H.D. & REISZ, R.R., 2010. Dispersal and diversity in the earliest North American sauropodomorph dinosaurs, with a description of a new taxon. *Proceedings of the Royal Society B* 278, 1044–1053.
- RUBERT, R.R. & SCHULTZ, C.L., 2004. Um novo horizonte de correlação para o Triássico Superior do Rio Grande do Sul. *Pesquisas em Geociências* 31, 71–88.
- RUBIDGE, B.S., 2005. Re-uniting lost continents—Fossil reptiles from the ancient Karoo and their wanderlust. *South African Journal of Geology* 108, 135–172.
- SANTA LUCA, A.P., 1980. The postcranial skeleton of *Heterodontosaurus tucki* (Reptilia, Ornithischia) from the Stormberg of South Africa. *Annals of the South African Museum* 79, 159–211.
- SCALERA, G., 2001. The global paleogeographical reconstruction of the Triassic in the Earth's dilatation framework and the paleoposition of India. *Annali di Geofisica* 44, 13–32.
- SCHERER, C.M.S., FACCINI, U.F. & LAVINA, E.L., 2000. Arcabouço Estratigráfico do Mesozóico da Bacia do Paraná. In *Geologia do Rio Grande do Sul*. ROS, L.F. & HOLZ, M., eds, Universidade Federal do Rio Grande do Sul, Porto Alegre, 335–354.
- SCHULTZ, C.L., SCHERER, C.M.S. & BARBERENA, M.C., 2000. Biostratigraphy of southern Brazilian Middle–Upper Triassic. *Revista Brasileira de Geociências* 30, 495–498.
- SCOTese, C.R., 2002. *Paleomap Project*. Available online at: <http://www.scotese.com> (accessed 30 May 2011).
- SEELEY, H.G., 1888. On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London* 43, 165–171.
- SERENO, P.C., 1991. Basal archosaurs: phylogenetic relationships and functional implications. *Journal of Vertebrate Paleontology* 11, 1–53.
- SERENO, P.C., 1994. The pectoral girdle and forelimb of the basal theropod *Herrerasaurus ischigualastensis*. *Journal of Vertebrate Paleontology* 13, 425–450.
- SERENO, P.C., 1999. The evolution of dinosaurs. *Science* 284, 2137–2147.
- SERENO, P.C. & ARCUCCI, A.B., 1994a. Dinosaurian precursors from the Middle Triassic of Argentina: *Lagerpeton chanarensis*. *Journal of Vertebrate Paleontology* 13, 385–399.
- SERENO, P.C. & ARCUCCI, A.B., 1994b. Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, n. gen. *Journal of Vertebrate Paleontology* 14, 53–73.
- SERTICH, J.J.W. & LOEWEN, M.A., 2010. A new basal sauropodomorph dinosaur from the Lower Jurassic Navajo Sandstone of Southern Utah. *PLoS ONE* 5, 1–17.
- SMITH, N.D. & POL, D., 2007. Anatomy of a basal sauropodomorph dinosaur from the Early Jurassic Hanson Formation of Antarctica. *Acta Palaeontologica Polonica* 52, 657–674.
- SOARES, M.B., SCHULTZ, C.L. & HORN, B.L.D., 2011. New information on *Riograndia guaibensis* Bonaparte, Ferigolo & Ribeiro, 2001 (Eucynodontia, Tritheledontidae) from the Late Triassic of southern Brazil: anatomical and biostratigraphic implications. *Anais da Academia Brasileira de Ciências* 83, 329–354.
- TYKOSKI, R.S. & ROWE, T., 2004. Ceratosauria. In *The Dinosauria*. WEISHAMPEL, D.B., DODSON, P. & OSMÓLSKA, H., eds, University of California Press, Berkeley, 47–70.
- UPCHURCH, P., 1997. Prosauropoda. In *Encyclopedia of Dinosaurs*. CURRIE, P.J. & PADIAN, K., eds, Academic Press, San Diego, 599–607.
- UPCHURCH, P., BARRETT, P.M. & GALTON, P.M., 2007. A phylogenetic analysis of basal sauropodomorph relationships: Implications for the origin of sauropod dinosaurs. In *Evolution and Palaeobiology of Early Sauropodomorph Dinosaurs*. BARRETT, P.M. & BATTEN, D.J., eds, *Special Papers in Palaeontology* 77, 57–90.
- WELLES, S.P., 1984. *Dilophosaurus wetherilli* (Dinosauria, Theropoda). Osteology and comparisons. *Palaeontographica A* 185, 85–180.
- YATES, A.M., 2003a. A new species of the primitive dinosaur *Thecodontosaurus* (Saurischia: Sauropodomorpha) and its implications for the systematics of early dinosaurs. *Journal of Systematic Palaeontology* 1, 1–42.
- YATES, A.M., 2003b. A definite prosauropod dinosaur from the lower Elliot Formation (Norian: Upper Triassic) of South Africa. *Palaeontologia Africana* 39, 63–68.
- YATES, A.M., 2007a. Solving a dinosaurian puzzle: the identity of *Aliwalia rex* Galton. *Historical Biology* 19, 93–123.
- YATES, A.M., 2007b. The first complete skull of the Triassic dinosaur *Melanorosaurus* Haughton (Sauropodomorpha: Anchisauria). In *Evolution and Palaeobiology of Early Sauropodomorph Dinosaurs*. BARRETT, P.M. & BATTEN, D.J., eds, *Special Papers in Palaeontology* 77, 9–55.
- YATES, A.M., 2010. A revision of the problematic sauropodomorph dinosaurs from Manchester, Connecticut and the status of *Anchisaurus* Marsh. *Palaeontology* 53, 793–752.
- ZERFASS, H., LAVINA, E.L., SCHULTZ, C.L., GARCIA, A.G.V., FACCINI, U.F. & CHEMALE JR, F., 2003. Sequence stratigraphy of continental Triassic strata of southernmost Brazil, a contribution to southwestern Gondwana palaeogeography and palaeoclimate. *Sedimentary Geology* 161, 85–105.
- ZERFASS, H., CHEMALE JR, F., SCHULTZ, C.L. & LAVINA, E., 2004. Tectonics and sedimentation in southern South America during Triassic. *Sedimentary Geology* 166, 265–292.