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Biostratigraphic significance of a new early sauropodomorph specimen from the Upper Triassic of southern Brazil

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ABSTRACT

The Wachholz site (Caturrita Formation, Late Triassic), in Agudo, Rio Grande do Sul (RS), southern Brazil, has yielded several sauropodomorphs. This includes CAPP/UFMS 0002, described here based on associated elements from the basalmost portion of the site. The specimen possesses a set of traits shared with typical 'prosauropods': a concave caudal margin of the trunk neural spines and a broadly convex proximal end of metacarpal V. However, it also retains some plesiomorphic features, for instance, the slender pedal digit I. Some bones closely resemble those of *Unaysaurus tolentinoi*, the other definitive sauropodomorph from the Caturrita Formation, an affinity corroborated by a new phylogenetic analysis. An updated biostratigraphic framework correlates the Wachholz, Água Negra (São Martinho da Serra/RS) and Botucaraí Hill (Candelária/RS) sites based on their sample of sauropodomorphs. In addition, the record of *Jachaleria* in the Botucaraí Hill site, a dicynodont also known from early Norian deposits of Argentina, indicates an equivalent age to deposits bearing *U. tolentinoi*. Accordingly, a more constrained age is proposed for the Água Negra site. This is important as the early Norian marks the transition from an epoch of low sauropodomorphs representativeness to a period of extreme abundance of the group in Early-to-Middle Mesozoic ecosystems.

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Plateosauria; Norian;
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Introduction

Sauropodomorpha and Theropoda are the two major saurischian clades. Theropoda mostly comprises carnivorous animals and includes the bird lineage (Gauthier 1986), whereas Sauropodomorpha were predominantly herbivorous, including the largest land animals that ever lived. In addition to colossal size, the sauropodomorph *bauplan* is also generally characterised by a small head, long neck, barrel-shaped body and columnar limbs (Upchurch et al. 2004). Depending upon taxonomic definitions (node- or stem-based) and the phylogenetic position of some taxa, the group origin goes back to the Late Triassic (Yates et al. 2010; Otero and Pol 2013) or Early Jurassic (McPhee, Bonnan, et al. 2015), extending until their final demise in the Cretaceous–Paleogene extinction. Sauropodomorphs were successful and diverse (Mannion et al. 2011) during this time range, achieving a worldwide geographical distribution (Upchurch et al. 2004; Cerda et al. 2012). However, before the rise of sauropods, a wide range of 'basal' sauropodomorphs exercised a similar dominance over Mesozoic terrestrial ecosystems (Galton and Upchurch 2004).

The term 'basal' sauropodomorph typically refers to non-sauropod sauropodomorphs (Yates 2012). A small head with coarse serrated teeth, a moderately long neck, relatively robust limbs and a hypertrophied manual digit I with a large and sharp claw

characterises their overall morphology (Galton and Upchurch 2004). Earliest forms, such as *Saturnalia tupiniquim* were small (about 1.5 m in length, Langer et al. 1999), whereas later non-sauropod sauropodomorphs reach about nine metres in length, e.g. *Jingshanosaurus xinwaensis* (Zhang and Yang 1995). The oldest non-sauropod sauropodomorph records are from the Carnian of South America (Sereno et al. 1993, 2012; Langer et al. 1999; Martinez and Alcober 2009; Ezcurra 2010; Cabreira et al. 2011), extending until the Early Jurassic (Allain and Aquesbi 2008).

Early sauropodomorphs reached a wide geographical distribution during their evolutionary history (Galton and Upchurch 2004), with records in Europe, Africa, Asia, South America, North America and Antarctica (Langer et al. 2010). However, distribution patterns of some less inclusive groups are unclear (Bittencourt et al. 2012) and their phylogenetic relationships are controversial (Peyre de Fabrègues et al. 2015), e.g. 'prosauropods' have been considered either monophyletic (Sereno 1989; Upchurch et al. 2007) or paraphyletic (Yates 2003a, 2007); phylogenetic relationships are ambiguous for most early taxa (Langer 2014); the inclusivity of Plateosauridae is unclear (Novas et al. 2011; Bittencourt et al. 2012; Apaldetti et al. 2013); and the phylogenetic status of some North American forms is problematic (Sertich and Loewen 2010; Rowe et al. 2011). In addition, the early Norian record of sauropodomorphs is scarce (Mannion et al. 2011). This moment was crucial for their radiation, as it

pinpoints the transition from a low representativeness period to a time of extreme abundance in terrestrial ecosystems. Therefore, new data regarding early Norian sauropodomorphs can help solving some of the aforementioned issues.

The Caturrita Formation (*sensu* Andreis et al. 1980), from southern Brazil, is an important window to early Norian land ecosystems. This geological unit has yielded several specimens ascribed to Sauropodomorpha (Leal et al. 2004; Bittencourt et al. 2012, 2013; Müller, Da-Rosa, et al. 2015). Yet, only one unambiguous species has been recognised so far, the putative plateosaurid *Unaysaurus tolentinoi* (Leal et al. 2004). In the present study, we describe a new sauropodomorph specimen from the Caturrita Formation and compare its morphology to that from other saurischians found in that stratigraphic unit. The affinity of this specimen is phylogenetically tested and the age of *U. tolentinoi* is discussed, based on data from three different localities with Norian sauropodomorph remains (Leal et al. 2004; Bittencourt et al. 2013; Müller, Da-Rosa, et al. 2015).

Institutional abbreviations

BM HR, National Museum of Natural History, Paris, France. MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, United States of America. MMACR, Museu Municipal Aristides Carlos Rodrigues, Candelária, Rio Grande do Sul, Brazil; CAPP/UFMS, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia, São João do Polésine, Rio Grande do Sul, Brazil; SAM-PK, Iziko-South African Museum, Cape Town, South Africa; UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; UFSM, Universidade Federal de Santa Maria, Santa Maria, Rio Grande do Sul, Brazil.

Anatomical abbreviations

caif, caudal infradiapophyseal fossa; cas, convex articular surface; ccdl, caudal centrodiapophyseal lamina; clg, collateral groove; clp, collateral ligament pit; clpr, craniolateral process; cmpr, craniomedial process; crd, central ridge; crif, cranial infradiapophyseal fossa; de, distal ischial expansion; ded, dorsal extensor depression; dfp, deflection point; dip, dorsal intercondylar process; dmr, dorsomedial ridge; dp, diapophysis; dpc, deltopectoral crest; dpr, depression; hh, humeral head; hucc, humeral ulnar condyle contact; hpa, hypapophysis; hy, hyosphene; hyp, hypantrum; iaf, ischial acetabular fossa; ilg, ischiadic longitudinal groove; ipd, iliac peduncle; ldc, lateral distal condyle; lrdg, lateral ridge; mdc, medial distal condyle; mif, middle infradiapophyseal fossa; mlg, medial longitudinal groove; mrd, medial ridge; mvl, mediventral lamina; nc, neural canal; ncs, neurocentral suture; ns, neural spine; ol, olecranon; pa, parapophysis; padl, paradiapophyseal lamina; pi, pit; podl, postzygodiapophyseal lamina; ppp, pubic peduncle; prdl, prezygodiapophyseal lamina; pz, prezygapophysis; rf, radial fossa; rla, radiale articulation; rlu, radial ligament of the ulna; spol, spinopostzygapophyseal lamina; srd, symphyseal ridge; tbr, tubercle; ua, ulnar articulation; vk, ventral keel.

Systematic palaeontology

Dinosauriformes Novas 1992

Dinosauria Owen 1842

Saurischia Seeley 1887

Sauropodomorpha Von Huene 1932

Material

CAPP/UFMS 0002 – associated postcranial elements of a single individual (Figure 1(B)), including eleven trunk vertebrae, partial left forelimb, right radius, right metacarpal V, right ischium and six pedal phalanges. Their direct association is justified by the lack of duplicated bones, proximity of elements in the field, presence of some articulated bones and equivalent size proportions.

Locality and horizon

CAPP/UFMS 0002 was excavated from massive fine sandstones at the base of a newly discovered outcrop known as Wachholz site (Müller, Da-Rosa, et al. 2015), Linha das Flores locality, Agudo municipality, Rio Grande do Sul (S29°36'46.42"; W53°15'54.06") (Figure 1(A)). The Wachholz site deposits belong to the Caturrita Formation, which is part of the Candelária Sequence of Horn et al. (2014 = Santa Maria 2 Sequence of Zeffass et al. [2003]). Based on biostratigraphic correlation, this site was tentatively dated as early Norian (Müller, Da-Rosa, et al. 2015).

Description and comparison

Trunk vertebrae

A continuous series of 11 elements was preserved, some of them represented only by centra (Figure 2). Compared to other early sauropodomorphs, details of both the laminae and the position of the parapophyses suggest that they range from the first to the 11th trunk element.

The vertebral bodies gradually increase in size from the more cranial to the more caudal vertebrae. Centra are spool-shaped and amphicoelous, with the cranial articular surface slightly higher than the caudal one (Figure 3). The lateral surfaces bear a shallow depression, which does not significantly invade the centrum (= acamerate condition of Wedel et al. 2000). As in many early sauropodomorphs, the ventral surface of the centra is constricted, with a longitudinal ventral keel in the first two trunk vertebrae (Figure 2(E) and (F)). In these two vertebrae, the contact between the ventral edge of the cranial articular surface and the ventral keel is marked by a well-developed hypapophysis (Figure 2(B)). As in *Efraasia minor*, *Massospondylus carinatus* and *Adeopapposaurus mognai* (Martínez 2009) the centra are elongated, rather than short and tall, as in massopodans such as *Riojasaurus incertus*, *Lufengosaurus huenei* and *Coloradisaurus brevis* (Apaldetti et al. 2013). The parapophysis is located near the shallow depression on the lateral surface of the centrum in the second trunk vertebra, but not exactly in the midpoint (dorsoventrally) of the vertebral body. In subsequent vertebrae, the parapophysis changes to the cranial end of the centrum and progressively moves upwards towards the neural arch. From the cranial to middle trunk vertebrae, the parapophysis becomes more excavated and bound by faint bone walls.

Five of the eleven recovered vertebrae preserve neural arches. As in *Unaysaurus tolentinoi*, these are not fused to their respective centrum, suggesting that the specimens did not reach their maximum size ([Brochu 1996]; but see Irmis [2007]). The neural arches (excluding the neural spines) of CAPP/UFMS 0002 are somewhat dorsoventrally lower than their respective centra (Figure 3(A)), differing from those of most sauropodomorphs

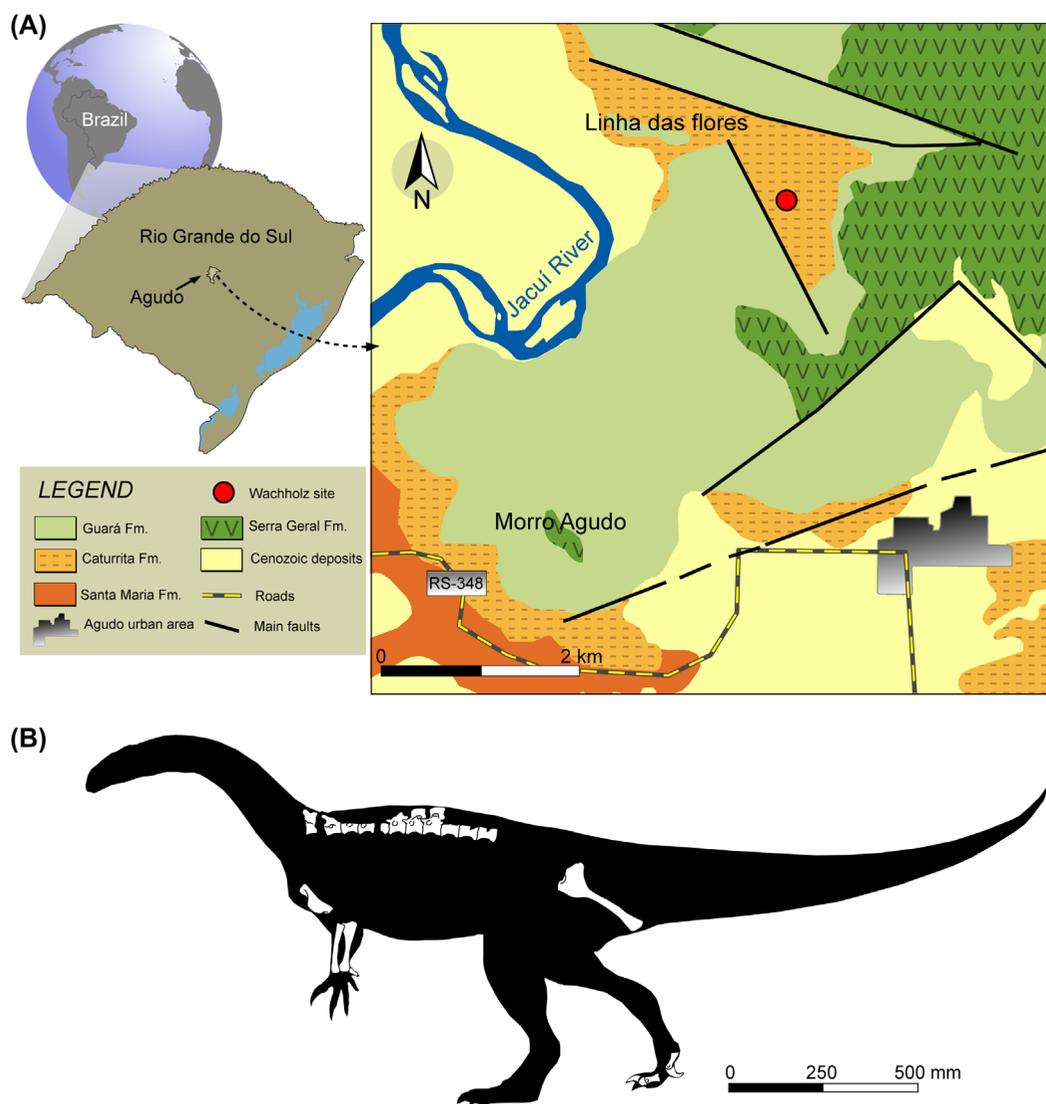


Figure 1. (Colour online) (A) map of the Agudo area, Rio Grande do Sul, Brazil, showing the location of the Wachholz site. Surface distribution of geological units according to Zerfass et al. (2007). (B) Outline of CAPP/UFMS 0002, showing the preserved bones.

(e.g. *Coloradisaurus brevis*, *Lufengosaurus huenei*), which are much shallower than the centra. Indeed, the condition of CAPP/UFMS 0002 approaches that of *Seitaad ruessi*, *Adeopapposaurus mognai* and *Unaysaurus toletinoi* (Leal et al. 2004; Martínez 2009; Sertich and Loewen 2010). However, the condition in the latter should be carefully re-evaluated, as its trunk vertebrae seem to have been affected by sedimentary compression. There is evident transverse deformation, producing elliptical cranial and caudal centrum articulations and strongly upwards directed transverse processes. The holotype of '*Ignavusaurus rachelis*' (BM HR 20, Knoll 2010) has a similar taphonomic pattern. The neural canal of the trunk vertebrae in CAPP/UFMS 0002 is subcircular.

The prezygapophysis slightly exceeds the cranial margin of its respective centrum. In the cranial trunk vertebrae, their tips are higher than the transverse processes and the articular facets are oblique in relation to the sagittal plane. In middle trunk vertebrae, the prezygapophyses are lower than the transverse processes and the articular facets form almost right angles to the sagittal plane. The prezygapophyses bear two distinct articular facets: the

dorsomedial that articulates with the postzygapophysis, and the hypantrum (Figure 3(G)), a small articular facet located in the medial surface of the prezygapophysis, which articulates with the hyposphene of the previous vertebral element. The hyposphene results from a downwards folding of the medial margins of the postzygapophysis. Different from later sauropodomorphs, such as *Melanorosaurus readi* (SAM-PK 3449) (Gauthier 1986; Yates 2007), the hyposphene of CAPP/UFMS 0002 is not as high as the neural canal.

In cranial view, the transverse processes of the cranial trunk vertebrae are horizontally oriented, whereas they are more dorsally directed in middle trunk elements. In dorsal view, the transverse processes of middle trunk vertebrae are gently directed caudally. There are several laminae connected to each transverse process. Their arrangement results in three distinct infradiapophyseal fossae (*sensu* Yates et al. 2012) in both cranial and middle trunk vertebrae. The cranial infradiapophyseal fossa is bound by the prezygodiapophyseal and paradiapophyseal laminae. This fossa is quite expanded in the cranial trunk vertebra but reduced in the eighth trunk element. The reduction of this fossa reflects changes in position of

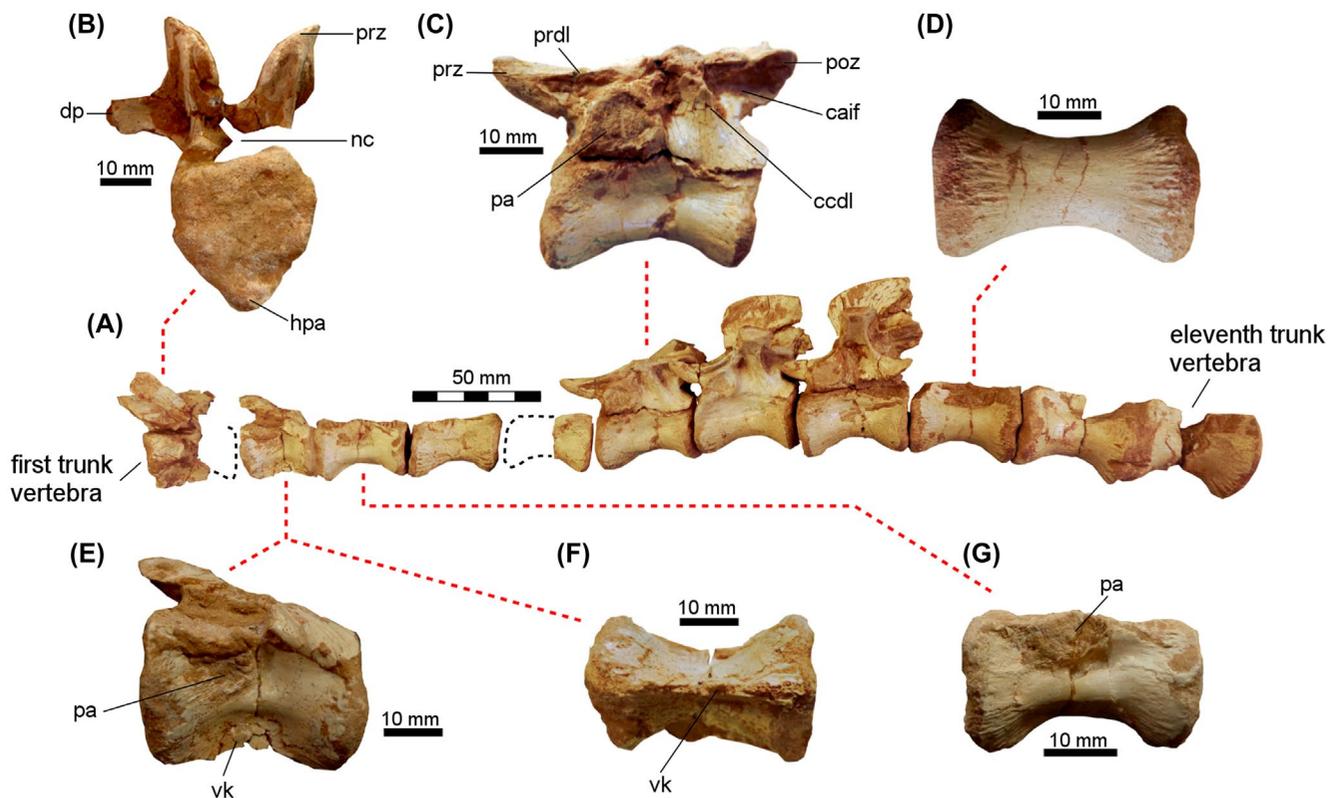


Figure 2. (Colour online) CAPP/UFMSM 0002, photographs of trunk vertebrae. (A) first to eleventh trunk vertebrae in lateral view. (B) First trunk vertebra in cranial view. (C) Sixth trunk vertebra in lateral view. (D) Ninth trunk vertebra in ventral view. E–F, second trunk vertebra in (E) lateral and (F) ventral views. (G) Third trunk vertebra in lateral view. Abbreviations in the text.

both the prezygapophysis and parapophysis, and also the retraction of the prezygodiapophyseal lamina, that does not reach the prezygapophysis in the eighth trunk vertebra. Possibly, that fossa was absent in more caudal elements. The middle infradiapophyseal fossa is bound by the paradiapophyseal and the caudal centrodiapophyseal laminae. Finally, the caudal infradiapophyseal fossa is bound by the caudal centrodiapophyseal and the postzygodiapophyseal laminae. A prezygoparapophyseal lamina, as seen in *Guaibasaurus candelariensis* (Bonaparte et al. 1999), is absent in the trunk vertebrae of CAPP/UFMSM 0002.

Only the seventh and eighth trunk vertebrae preserved neural spines (Figure 3). They are transversally thin (plate-like), subrectangular in lateral view and lack laterally expanded tables. They differ from the tall neural spines of early diverging sauropodiforms (e.g. *Aardonyx celestae*, *Antetonitrus ingenipes*, *Lessemsaurus sauropoides*, *Tazoudasaurus naimi*) and are longer than high. The eighth trunk vertebra has the caudal margin of the neural spine better preserved. It is gently concave (Figure 3(E)), as in *Plateosaurus engelhardti*, *Mussaurus patagonicus* and massospondylids, whereas other sauropodomorphs has this margin straight (Yates 2003b; Otero and Pol 2013). On the caudal margin of the neural spines, there is a pair of spinopostzygapophyseal laminae bounding the sides of a spindle-like spinopostzygapophyseal fossa (Figure 3(H)).

Humerus

A partial left humerus includes the proximal half of the shaft and part of the lateral portion of the head (Figure 4). In proximal view,

the articulation becomes gradually thicker from lateral to its central portion, where part of the humeral head is preserved. Although incomplete, it is possible to see that the humeral head is somewhat less protruding than in *Adeopapposaurus magnai*. The preserved portion of the proximal surface does not show signs of a marked proximally convex margin, which is present in massospondylids and early diverging sauropodiforms, e.g. *Lessemsaurus sauropoides*, *Melanorosaurus reardi*, *Kotasaurus yamanpalliensis* (Pol and Powell 2007; Apaldetti et al. 2013; McPhee et al. 2014). Indeed, this proximal margin is straight in CAPP/UFMSM 0002, matching the morphology of several non-massopodan sauropodomorphs (Pol and Powell 2007), especially *Plateosaurus engelhardti* and *Unaysaurus tolentinoi*, which completely lack a doming of the humeral head according to Remes (2008).

The lateral corner of the proximal humeral end is deflected distally, forming the proximal part of the deltopectoral crest, which is subrectangular in lateral view, a common trait of dinosaurs (Langer et al. 2010). The main edge of the deltopectoral crest of CAPP/UFMSM 0002 is straight (Figure 4(A)). On the contrary, its proximal summit is medially inflected in various sauropodomorphs (e.g. *Coloradisaurus brevis*, *Lufengosaurus huenei*, *Plateosaurus cullingworthi*), forming a strongly sinuous proximal portion of the crest (Yates 2003a). *Adeopapposaurus magnai* is the only massospondylid that possesses a non-sinuous morphology (Martínez 2009), which is also seen in several other non-massospondylid sauropodomorphs, e.g. *Efraasia minor*, *Plateosaurus engelhardti*, and *Unaysaurus tolentinoi*. However, the role of taphonomy should be carefully considered on the morphology of some specimens.

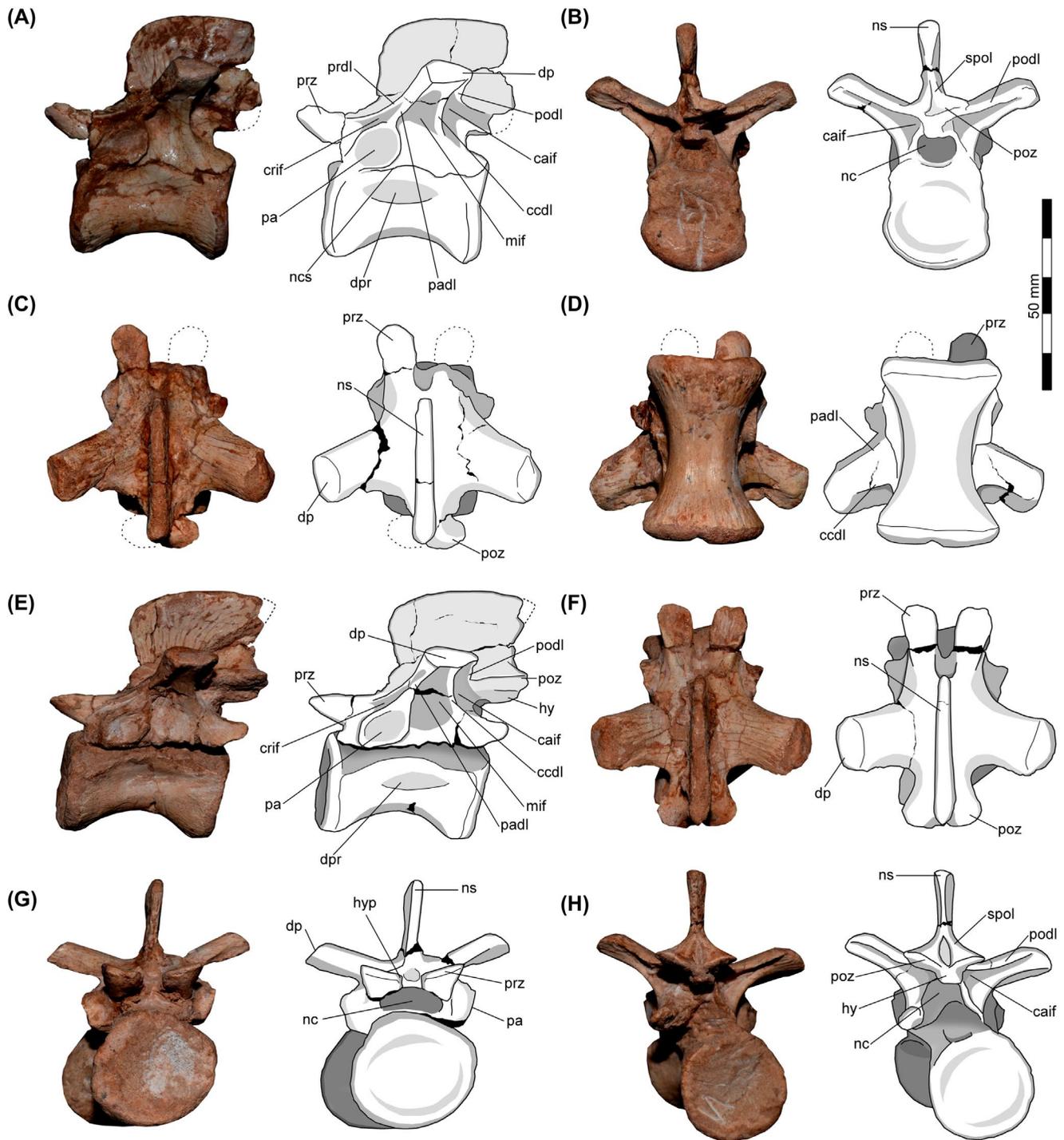


Figure 3. (Colour online) CAPPA/UFMS 0002, photographs and drawings of trunk vertebrae. (A)–(D) Seventh vertebra in (A) lateral, (B) caudal, (C) dorsal and (D), ventral views. (E)–(H) Eighth vertebra in (E) lateral, (F) dorsal, (G) cranial and (H), caudal views. Abbreviations in the text.

A proximodistally oriented and elongated ridge extends along the lateral surface of the deltopectoral crest (Figure 4(C)). This closely resembles the ridge present in *Seitaad ruessi* (Sertich and Loewen 2010) and *Unaysaurus tolentinoi* (Leal et al. 2004). Conversely, a less-developed ridge is present in several other early sauropodomorphs (e.g. *Saturnalia tupiniquim*, *Massospondylus carinatus*, *Riojasaurus incertus*). Distal to the end of this ridge, just as in *U. tolentinoi* (Leal et al. 2004) and *S. tupiniquim* (Langer et al. 2007), there is a small pit (Figure 4(C)). In *Lufengosaurus huenei*, *Jingshanosaurus xinwaensis* and *M. carinatus*, a similar

pit (Yates 2007) is located in the centre of the lateral surface of the deltopectoral crest. The equivalence of both pits is uncertain, but Remes (2008) considered them as the insertion point for *Musculus latissimus dorsi*.

Ulna

A nearly complete left ulna is preserved (Figure 5(A)–(D)), but the mid shaft is missing. Its proximal outline is subtriangular (as in most early sauropodomorphs) rather than triradiate

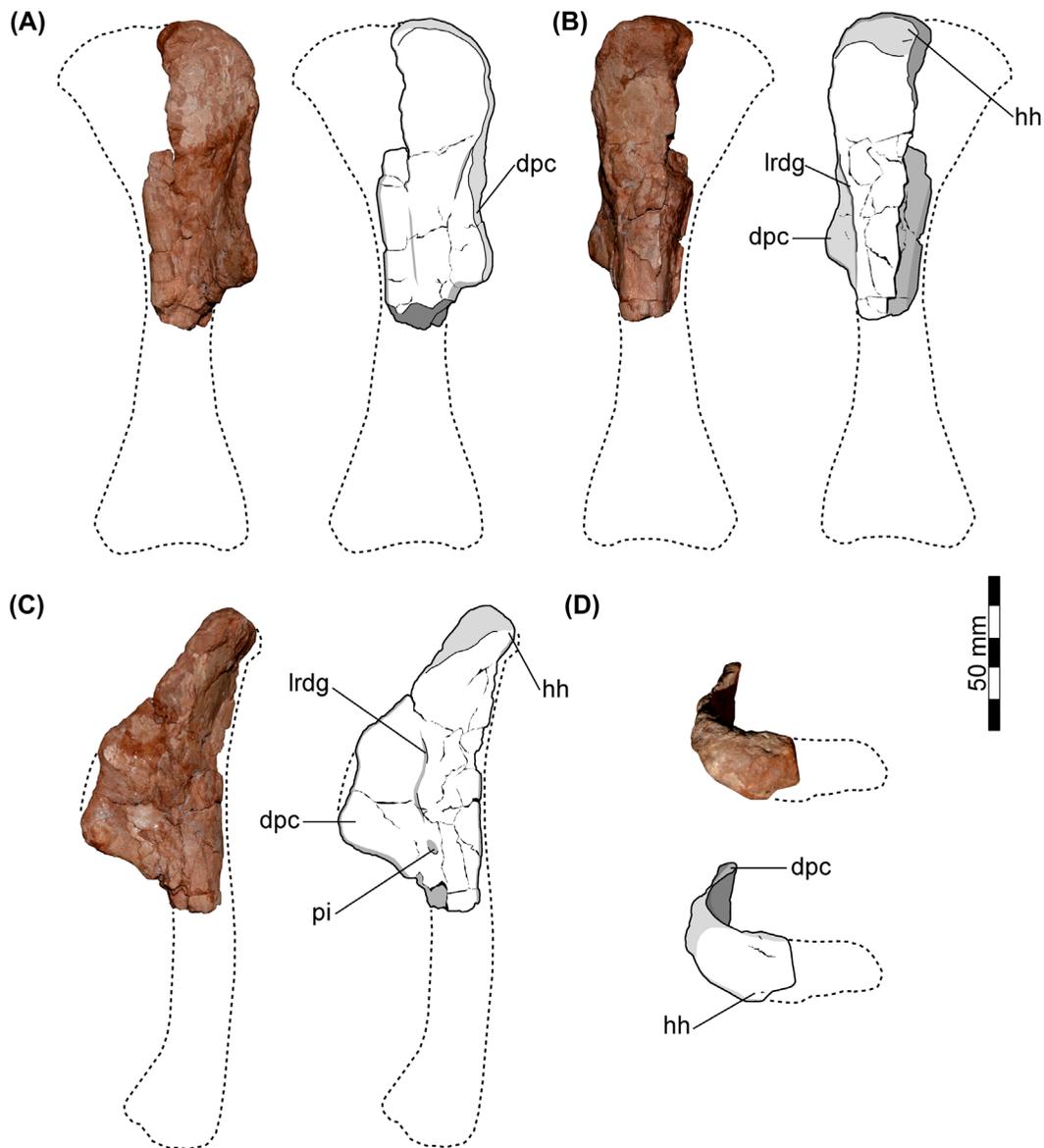


Figure 4. (Colour online) CAPP/UFM 0002, photographs and drawings of the left humerus in (A) cranial, (B) caudal, (C) lateral and (D) proximal views. Dash lines reconstruct the hypothetical bone shape. Abbreviations in the text.

(= Y-shaped) of eusauropods (McPhee et al. 2014) and some early diverging sauropodiforms (e.g. *Antetonitrus ingenipes*, *Sefapanosaurus zastronensis*). The craniomedial process is less developed than in *Lufengosaurus huenei* and *Yunnanosaurus xinwaensis*. A slight concavity occurs in the contact between the craniomedial process and the humeral ulnar condyle (Figure 5(A)). Distinct from sauropodomorphs more closely related to sauropods than *Melanorosaurus readi*, the ulnar craniolateral process is rounded and weakly developed, which results in the absence of a deep radial fossa bound by this process (Figure 5(C)). A convex olecranon process is present at the proximal end of the bone, which gives a sigmoid shape to its proximal margin, in lateral and medial views.

The ulnar shaft is quite slender, contrasting with those more robust seen in *Yunnanosaurus xinwaensis* and *Riojasaurus incertus*. On the craniomedial surface of the distal half of the bone, a tubercle for the radial-ulnar ligament is present (Figure 5(A)). In *Massospondylus carinatus* and *Antetonitrus ingenipes* that

structure is very prominent (Cooper 1981; MCPhee et al. 2014), but this is not the case in CAPP/UFM 0002. The distal articular surface of the ulna is convex and covered by rugose areas, indicating *in vivo* cartilage covered portions (Remes 2008).

Radius

Both preserved radii are gracile and straight bones with expanded extremities (Figure 5(E)–(H)). Their general morphology resembles that of other early sauropodomorphs. The proximal articular surface is concave and craniocaudally enlarged. Its caudal corner is proximally larger than the cranial. In proximal view, the medial edge is slightly concave, whereas the lateral is convex, resulting in a subovoid shape. As parts of the cylindrical shaft of both radii are damaged, the cranial radial tubercle was not identified. The radial shaft is perpendicular to the plane of the proximal articulation, differing from the cranially projected shafts of *Antetonitrus ingenipes*, *Massospondylus carinatus*, and

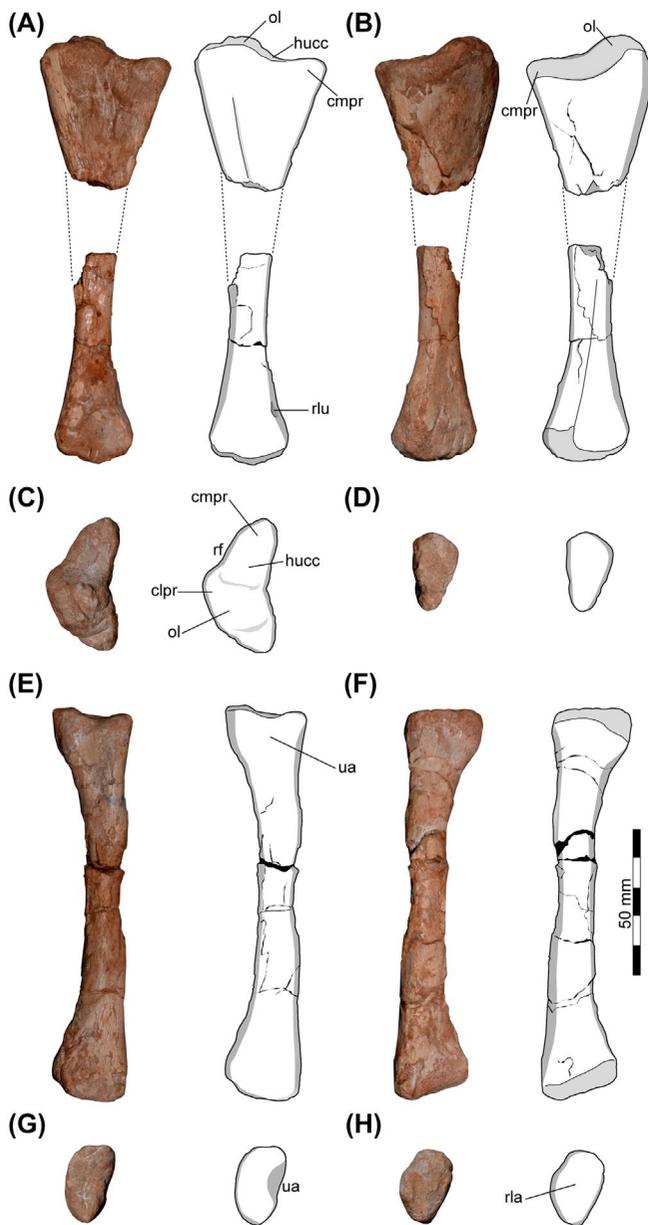


Figure 5. (Colour online) CAPP/UFMS 0002, photographs and drawings of the left forearm. (A)–(D) Ulna in (A) medial, (B) lateral, (C) proximal and (D) distal views. (E)–(H) Radius in (E) medial, (F) lateral, (G) proximal and (H) distal views. Dash lines reconstruct the hypothetical bone shape. Abbreviations in the text.

Lufengosaurus huenei (Remes 2008). In contrast with *Mussaurus patagonicus*, *Sefapanosaurus zastronensis*, *Aardonyx celestae*, (Otero et al. 2015) and some other sauropodomorphs, the radius lacks a proximodistally oriented ridge on the caudal margin of its distal end. The distal condyle is rounded in distal view and subequal (craniocaudally) in length to the proximal end. As in the ulna, a rugose surface covers the distal end of both radii.

Metacarpal V

This element is preserved from the right manus (Figure 6). Its proximal end is transversely expanded, accounting for about 62% the length of the bone. This differs from the condition of several early sauropodomorphs, such as *Eoraptor lunensis*, *Thecodontosaurus antiquus*, *Efraasia minor* and *Ruehleia*

bedheimensis, where the proximal end of that metacarpal is considerably less expanded transversely. Metacarpal V of CAPP/UFMS 0002 is also transversely wider than deep in proximal view. The articular surface of the proximal end is broadly convex (Figure 6(A) and (B)) and, in proximal view, has a triangular shape. This is the typical pattern of the sauropodomorphs generally called ‘prosauropods’ (Upchurch et al. 2007), as seen in *Plateosaurus englharti*, *Massospondylus carinatus* and *Lufengosaurus huenei*. On the other hand, several other sauropodomorphs (e.g. *Thecodontosaurus antiquus*, *Ruehleia bedheimensis*, *Seitaad ruessi*, *Sefapanosaurus zastronensis*) bear a flat proximal articular surface of metacarpal V.

A ridge, less evident than that of *Massospondylus carinatus* (Cooper 1981), is located on the dorsomedial surface of the proximal half of metacarpal V (Figure 6(A)). In medial and lateral view, the bone shows a dorsally concave and ventrally straight outline. In cross section, the shaft is elliptical. There are no well-defined collateral ligament pits on the distal portion of the bone. However, a small tubercle is present on the dorsomedial surface of its distal portion (Figure 6(C)). The distal end is moderately expanded in relation to the shaft, with a width of 37% the length of the bone. As for the proximal end, the distal end is convex, wider than deep and circular in outline.

Ischium

The right ischium of CAPP/UFMS 0002 is partially preserved (Figure 7) and divided into two distinct portions (e.g. Otero and Pol 2013): a proximal dorsoventrally expanded plate, which comprises the medioventral lamina, iliac and pubic peduncles, and a long and slender shaft that expands in the distal end.

The proximal surface of the iliac peduncle is subovoid and transversally larger than the triangular proximal surface of the pubic peduncle. Between them, there is a concave ischial acetabular fossa medially bound by a fractured bone wall (Figure 7(A)). In contrast to *Saturnalia tupiniquim* (Langer 2003), a strongly expanded acetabular margin is absent on the lateral surface of the iliac peduncle. A well-developed thin lamina starts from the ventral surface of the pubic peduncle and extends over the proximal third of the ischial shaft, forming the obturator plate, as in other saurischians (Langer and Benton 2006). The presence or absence of a notch separating the caudoventral end of that lamina from the ischial shaft is uncertain given its fractured condition (see Yates 2003c).

A longitudinal groove, medially bound by a transversely broad symphyseal ridge, extends from the dorsal surface of the iliac peduncle, and nearly reaches the midpoint of the ischial shaft. At this point, the groove becomes shallow and then disappears. In *Guaibasaurus candelariensis*, this groove extends until close to the distal third of the shaft, and is medially delimited by a sharp, rather than transversely broad, symphyseal ridge (Langer et al. 2011). A lateral ridge (*sensu* Langer 2003) divides the dorsal from the lateral surfaces of the shaft, resulting in the characteristic triangular cross section of this element in sauropodomorphs. The depth of the medial surface of the shaft is larger than the width of its dorsal surface (Figure 7(C)), whereas the opposite is observed in *Saturnalia tupiniquim*. The aforementioned lateral ridge extends longitudinally along the shaft, but deflects dorsally in its caudal portion, contributing to the dorsocaudal expansion

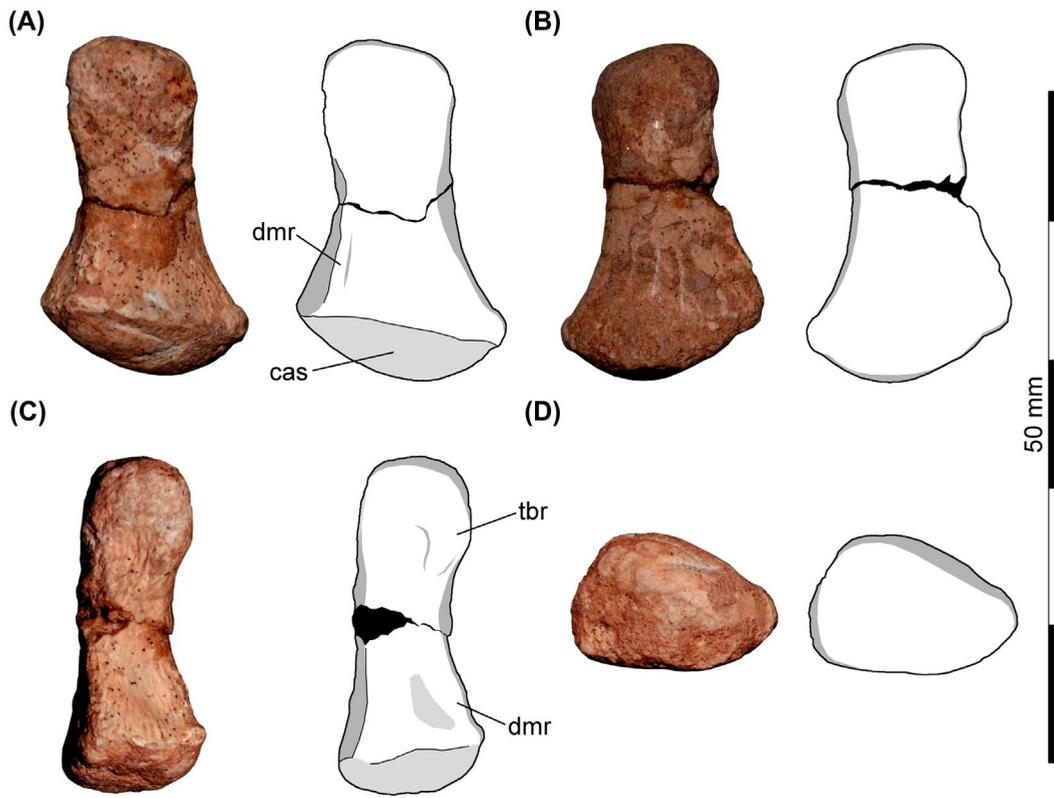


Figure 6. (Colour online) CAPP/UFM 0002, photographs and drawings of right metacarpal V in (A) dorsal (B) ventral, (C) medial and (D) proximal views. Abbreviations in the text.

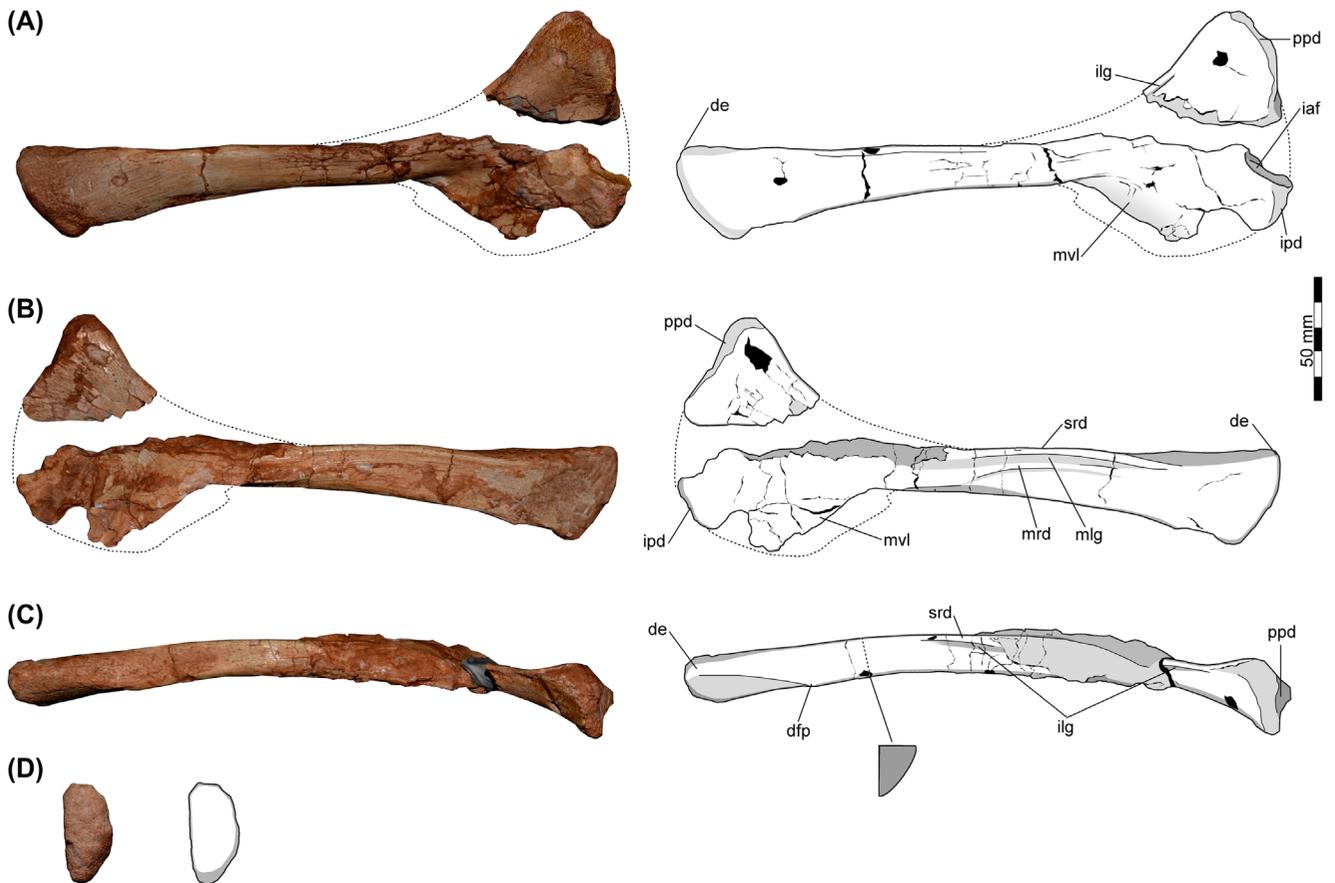


Figure 7. (Colour online) CAPP/UFM 0002, photographs and drawings of right ischium in (A) lateral, (B) medial, (C) dorsal and (D) distal views. Dash lines reconstruct the hypothetical bone shape. Abbreviations in the text.

of the distal end (Figure 7(C)). This deflection point is marked by a slight reduction of the dorsal width of the shaft. This pattern is also present in *Herrerasaurus ischigualastensis*, *G. candelariensis*, *S. tupiniquim* and 'core' early sauropodomorphs (Langer 2003). On the flat medial surface, there are two ridges bounding a longitudinal groove, the stronger one extending more distally (Figure 7(B)). According to Bittencourt et al. (2013), a similar arrangement is also present in the ischia of two indeterminate Triassic sauropodomorphs found in the municipality of Candelária (Rio Grande do Sul, Brazil), in the early sauropodomorph *Panphagia protos*, and in the massospondylid *Adeopapposaurus mognai*.

The ischial shaft expands gradually in depth from the middle to the distal end. However, the dorsal corner of the distal end differs from those more dorsally projected of *Guaibasaurus candelariensis* (Bonaparte et al. 1999), *Mussaurus patagonicus* (Otero and Pol 2013) and *Saturnalia tupiniquim* (Langer 2003), resembling more the straight condition present in *Eucnemesaurus entaxonis* (McPhee, Choiniere, et al. 2015). The ventral margin of the distal end is slightly expanded but not markedly concave as in *Eucnemesaurus entaxonis* (McPhee, Choiniere, et al. 2015) and *Coloradisaurus brevis* (Apaldetti et al. 2013). In distal view, the ischium is subovoid, with a flat medial and a convex lateral margin, with the dorsoventral height more than twice the lateromedial width (Figure 7(D)). This resembles the condition of *C. brevis*, *Massospondylus carinatus* and *Plateosaurus engelhardti* (Yates 2003a; Apaldetti et al. 2013). In contrast, the distal ischial depth for the South American sauropodomorphs *Riojasaurus incertus*, *Adeopapposaurus mognai*, *Lessemsaurus sauropoides* and *Mussaurus patagonicus* is less than twice the transverse width (Yates 2003c; Pol and Powell 2007; Martínez 2009; Otero and Pol 2013).

Pes

Only phalanges were recovered from the *pes* (Figure 8), including one proximal, two non-terminal and three ungual elements from the left side. On the field, these phalanges were mostly disarticulated and not closely associated to the forelimb elements. Just one non-terminal phalanx was found articulated with its corresponding ungual. The dorsal margin of the proximal end of this non-terminal phalanx is convex (Figure 8(A)), lacking a dorsal process, suggesting its articulation with a metatarsal (or metacarpal in the case of manual elements). Thus, these two phalanges correspond to a digit with a single non-terminal phalanx, matching digit I, most likely from the *pes* due to the poorly developed flexor tubercle of the ungual (a condition also present in the other two indeterminate unguals) and their large size in comparison with the forelimb elements. In addition, the ungual articulated to the non-terminal phalanx is transversely compressed (Figure 8(J)), whereas the other two ungual are lateromedially expanded (Figure 8(L)). This discrepancy between the ungual of digit I and the other unguals is a common pattern of the foot among sauropodomorphs. The elements are assigned to the left *pes* due the larger proximal articular facet on the left side of the phalanges and the ventromedial sharp margin on the right side of the unguals (see Martínez 2009). This asymmetry reinforces their assignation to pedal elements, as manual unguals are more symmetrical.

The first phalanx of digit I is proximodistally elongated and quite slender (Figure 8(A)) as in *Pantydraco caducus*, *Unaysaurus toletinoi* and *Jaklapallisaurus asymmetrica* (Novas et al. 2011) differing from those of sauropodomorphs such as *Plateosaurus engelhardti*, *Adeopapposaurus mognai* and *Coloradisaurus brevis*, which are stouter. The slender morphology is also present in *Guaibasaurus candelariensis*, *Eoraptor lunensis* and *Herrerasaurus ischigualastensis* (Novas 1994; Langer et al. 2010; Sereno et al. 2012), corresponding to the plesiomorphic condition for sauropodomorphs. Its distal end has an expanded plantar surface, with the lateral condyle slightly larger than the medial. Together, those condyles are wider at the plantar margin than dorsally. Well-defined and deep collateral ligament pits are present on the medial and lateral surfaces of the distal portion of the phalanx.

The position in the foot of the other two non-terminal phalanges is ambiguous. Their proximal articular surfaces are broader than those of the first phalanx of digit I. A proximal dorsal process is present in both elements (Figure 8(E)–(G)). Therefore, they do not correspond to the first phalanx of the respective digit. In proximal view, they have a subtriangular shape, with two distinct articular surfaces divided by a central ridge. The articular surface of the lateral distal condyle is larger than that of the medial distal condyle (Figure 8(F)). One of these non-terminal phalanges is incomplete, with only its proximal half preserved. The other complete phalanx is longer than broad and constricted at the mid-shaft (Figure 8(E)). The dorsal surface of its distal half bears an extensor depression and both proximal and distal ends are similar in width.

The ungual phalanx of digit I is extremely curved (Figure 8(I)), with almost the same length of the first phalanx of the same digit. In *Eoraptor lunensis* and *Pantydraco caducus*, the ungual element is shorter in length than the first phalanx of digit I (Galton and Kermack 2010; Sereno et al. 2012), whereas the inverse condition is present in other sauropodomorphs (Yates and Kitching 2003). The extremely curved shape of this element results in a distal plantar surface that is almost parallel to the articular facets. This resembles the condition found, to a lesser extent, in *Adeopapposaurus mognai*, differing from that of *Coloradisaurus brevis* and *Guaibasaurus candelariensis*, both of which have a less curved ungual of pedal digit I. Only the proximal half of this bone is present in *Unaysaurus toletinoi*, and its degree of curvature is unknown. The proximal end of ungual I is more transversely compressed than those of the other two preserved unguals. This morphology is observed in a number of other sauropodomorphs (e.g. *Unaysaurus toletinoi*, *Plateosaurus engelhardti*, *Adeopapposaurus mognai*). A faint central ridge divides two articular facets in the proximal end (Figure 8(J)). The lateral is transversely and dorsoplantarly larger than the medial. Both lateral and medial surfaces bear deep longitudinal collateral grooves, which extend from the ventral border of the proximal end, reaching the distal tip of the bone, but lack the proximal bifurcation seen in several other sauropodomorphs (Pol and Powell 2007). The plantar surface of the two indeterminate unguals are transversely broader than that of ungual I. The latter also differs from the complete indeterminate unguals in the shape of the distal tip, which is pointed in digit I and slightly rounded in the complete indeterminate ungual.

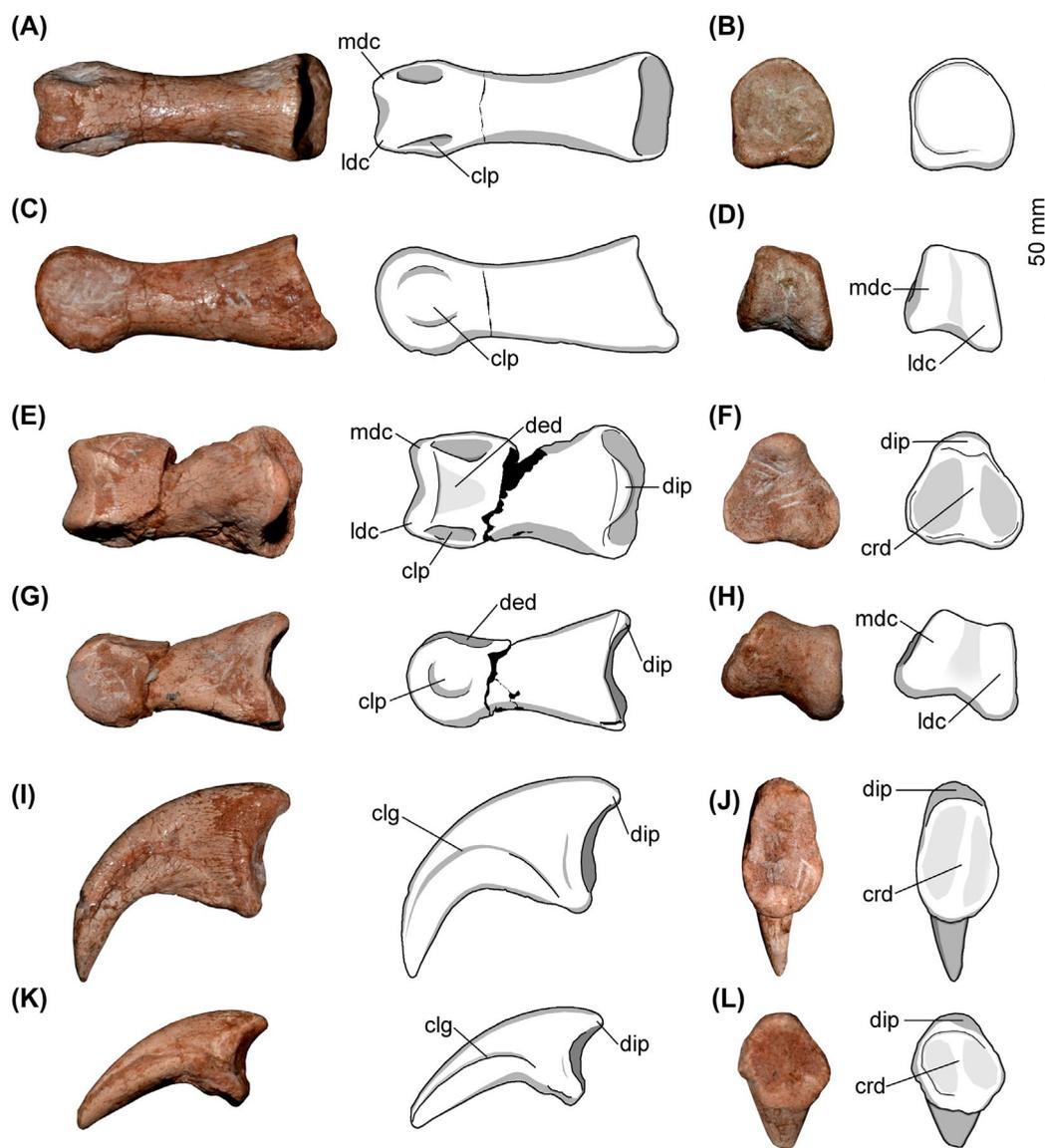


Figure 8. (Colour online) CAPP/UFM 0002, photographs and drawings of left pedal phalanges. (A)–(D) First phalanx of digit I in (A) dorsal, (B) proximal, (C) lateral and (D) distal views. (E)–(H) Indeterminate phalanx in (E) dorsal, (F) proximal, (G) lateral and (H) distal views. (I)–(J) Ungual phalanx of digit I in (I) lateral and (J) proximal views. (K)–(L) Indeterminate ungual phalanx in (K) lateral and (L) proximal views. Abbreviations in the text.

Phylogenetic analysis

Data-set and procedure

The present phylogenetic analyses aims to access the affinities of CAPP/UFM 0002 in relation to other early sauropodomorphs, based on a modified version of the data matrix of McPhee, Bonnan, et al. (2015). A new state was added to character 212, which refers to the presence of a rugose pit centrally located on the lateral surface of the deltopectoral crest of the humerus. It was originally proposed (Yates 2007), with two states: absent (0) or present (1); and a third subordinate state was added: present and distally located (2). This corresponds to the condition found in *Unaysaurus toletinoi*, *Saturnalia tupiniquim* and CAPP/UFM 0002. The four characters proposed by Otero et al. (2015) were included and numbered 366, 367, 368 and 369. In addition, we included a new character (370), relative to the proportions of the first phalanx of pedal digit I. This correlates the phalanx length (at midpoint) in lateral view by its maximum height at

the proximal end (also in lateral view). Specimens in which the ratio is near or above 2.4 were scored as (0), corresponding to the slender condition of early sauropodomorphs. A more robust condition (1) results from a ratio of 2.3 or less. Therefore, the present data matrix includes 370 characters and 55 operational taxonomic units (OTUs). An additional data-set with the inclusion of an isolated sauropodomorph ischium (MMACR PV 037-T) from the Botucaraí Hill site (municipality of Candelária-RS, Brazil) was also analysed.

The phylogenetic analyses were performed with TNT v1.1 (Goloboff et al. 2008). All characters were equally weighted and 40 (8, 13, 19, 23, 40, 57, 69, 92, 102, 117, 121, 131, 144, 147, 149, 150, 157, 162, 167, 170, 177, 205, 207, 225, 230, 237, 245, 254, 257, 270, 283, 304, 310, 318, 338, 351, 354, 356, 361 and 365) were treated as additive (ordered) following the analysis of McPhee, Bonnan, et al. (2015). The most parsimonious trees (MPTs) were obtained via heuristic searches ('traditional search' mechanism). The applied parameters include 1000 replicates of

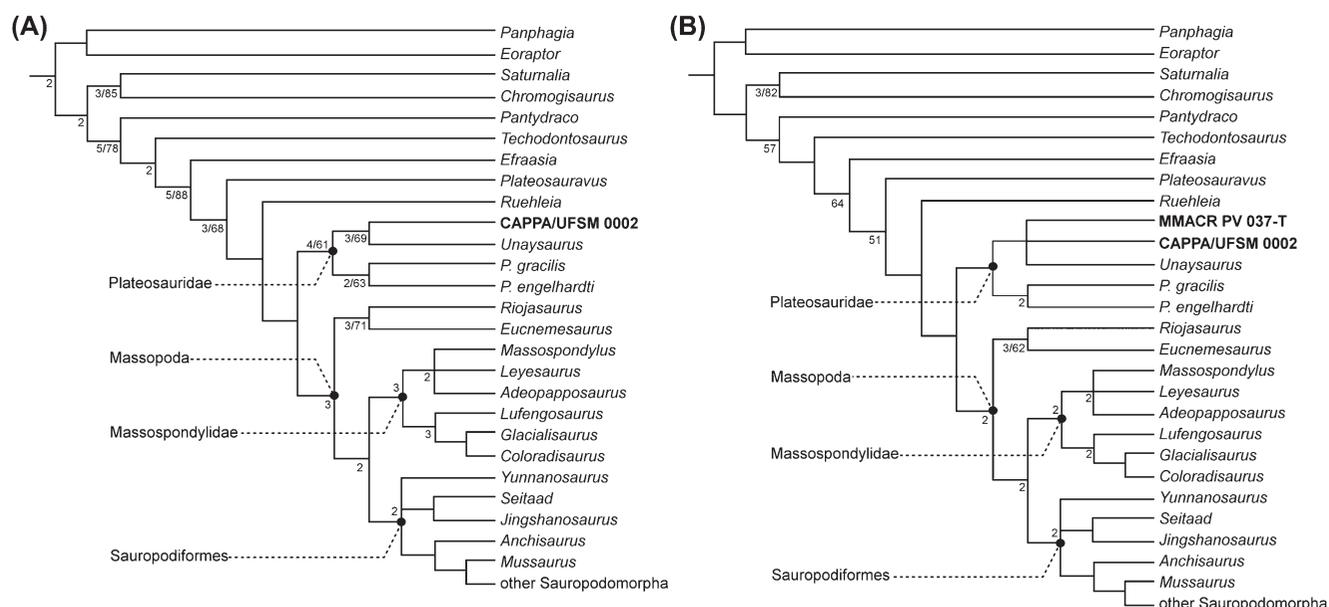


Figure 9. (Colour online) Results of phylogenetic analyses. A, abbreviated strict consensus tree of the first analysis depicting the phylogenetic position of CAPPA/UFSM 0002. B, abbreviated strict consensus tree of the second analysis depicting the phylogenetic position of CAPPA/UFSM 0002 and MMACR PV 037-T. Numbers below nodes represent Bremer support values (left) higher than 1 and Bootstrap values (right) higher than 50%. Clade names follow McPhee, Bonnan, et al. (2015).

Wagner trees (with random addition sequence), tree bisection reconnection (TBR) and branch swapping (holding 10 trees save per replicate). Decay indices (Bremer support values) and bootstrap values (1000 replicates) were also obtained with TNT v1.1 (Goloboff et al. 2008).

Results

The first analysis (without MMACR PV 037-T) recovered 24 MPTs of 1285 steps each (CI = 0.340; RI = 0.688) (Figure 9(A)). In all recovered MPTs, CAPPA/UFSM 0002 is the sister-group of *Unaysaurus toletinoi*, and both are nested within Plateosauridae, as the sister-group of the genus *Plateosaurus*. The former relation is supported by state 2 of character 212 (presence of a pit on the distal portion of the lateral surface of the deltopectoral crest of the humerus) and state 1 of character 365 (femoral length between 200 and 399 mm). As the femora were not recovered in CAPPA/UFSM 0002, the state of character 365 is tentatively inferred following the proportions of the preserved bones. There are six character states supporting Plateosauridae, but only one (character 281) could be scored for CAPPA/UFSM 0002. Character 281 was proposed by Yates (2003c) as the transverse width of the conjoined distal ischial expansion in relation to their sagittal depth. In Plateosauridae, the transverse width is smaller than the sagittal depth, but the same condition is also found in some massopodans (*Yunnanosaurus huangi*, *Coloradisaurus brevis*). The present results differ from those of McPhee, Bonnan, et al. (2015) in that *Ruehleia bedheimensis*, Plateosauridae and Massopoda do not form a trichotomy in the consensus tree, as *R. bedheimensis* is consistently placed outside of Plateosauria, as in some other previous studies (e.g. Yates 2007; Apaldetti et al. 2011). Also, Massospondylidae forms the sister-group of a trichotomy that includes *Y. huangi*, a node holding *Seitaad ruessi* plus *Jingshanosaurus xinwaensis*, and Anchisauria, and *Anchisaurus polyzelus* is basal to *Mussaurus patagonicus* and

‘other sauropodomorphs’, instead of forming a unresolved trichotomy as in McPhee, Bonnan, et al. (2015).

The second analysis (including MMACR PV 037-T), also recovered 24 MPTs of 1285 steps each (CI = 0.340; RI = 0.688). In the consensus tree (Figure 9(B)), MMACR PV 037-T is placed in a trichotomy with *Unaysaurus toletinoi* and CAPPA/UFSM 0002. The same two characters that support the node with *U. toletinoi* and CAPPA/UFSM 0002 in the first analysis also support this node. However, only character state 365 is coded to MMACR PV 037-T, based on the estimated size of its femur.

The new character (370) has a congruent distribution among OTUs of the two strict consensus trees. State ‘0’ (slender first phalanx of the digit one of the pes) is plesiomorphic and present in *Unaysaurus toletinoi*, CAPPA/UFSM 0002, and all non-plateosaurian taxa, among sauropodomorphs. The more robust shape (state ‘1’) occurs in *Plateosaurus* and massopodans. Considering that the increase in the robustness of this digit could be linked to the increase in body size, this is not a surprising result. Indeed, the small anchisaurian *Anchisaurus polyzelus* apparently has a relatively slender first phalanx of pedal digit I, but this was not coded in our analysis as this phalanx is partially covered by matrix, precluding a precise measurement. Yet, the robust condition is evident in closely related taxa.

Discussion

Biostatigraphic significance

During the late Norian, sauropodomorphs became far more abundant than any other large herbivores in terrestrial faunas (Benton 1983; Benton et al. 2014). However, the evolutionary period between that scenario and the earliest sauropodomorphs from the late Carnian is still poorly understood (Benton 1983; Ezcurra 2010). This scarcity of knowledge is mainly related to the meagre sauropodomorph record in this time interval

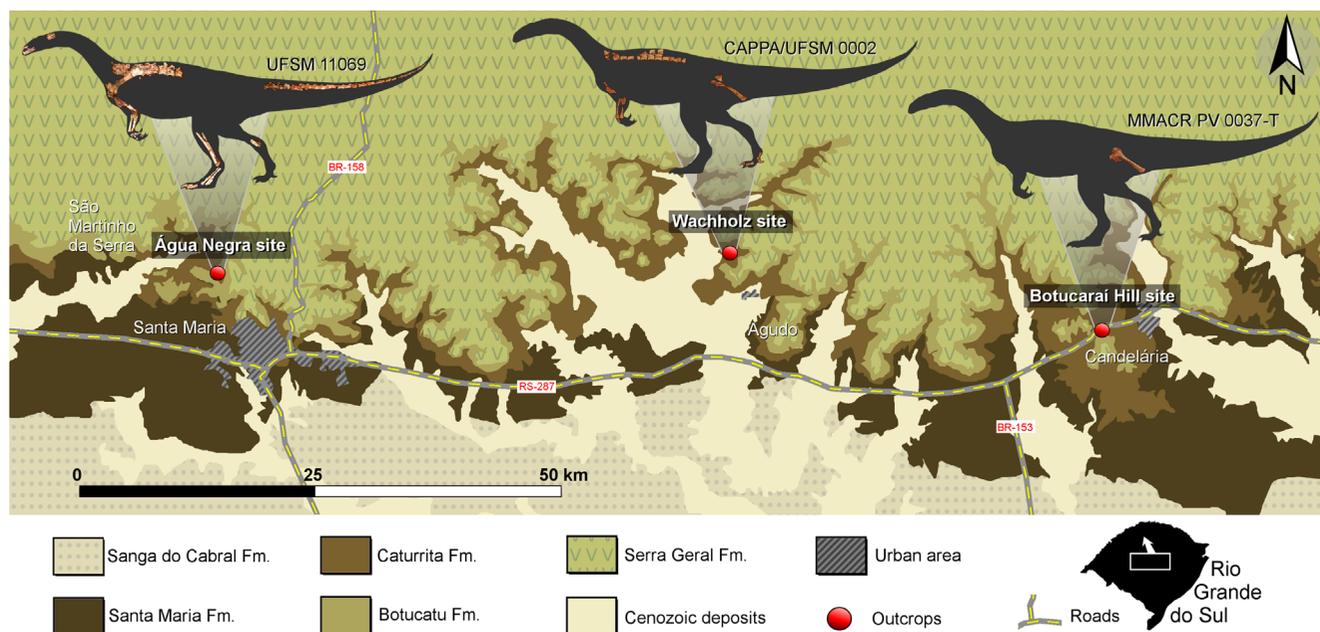


Figure 10. (Colour online) Map of the central Rio Grande do Sul, Brazil, showing the sauropodomorph-bearing localities of the Caturrita Formation. Surface distribution of geological units follows Wildner et al. (2006).

(corresponding to the early Norian), so far only comprising the European *Plateosaurus gracilis* (Von Huene 1908; Yates 2003c) and possibly the South American *Unaysaurus toletinoi* (Leal et al. 2004), both members of Plateosauridae.

Although the early Norian age of *U. toletinoi* it is usually accepted (Novas 2009; Ezcurra 2010; Irmis 2011; Langer 2014), a number of aspects need further consideration. Its holotype and unique specimen (UFSM 11069) comes from the Água Negra site, São Martinho da Serra-RS, Brazil. Leal et al. (2004) attributed this outcrop to the Caturrita Formation, but in the absence of absolute dating, the age of this unit is based on biostratigraphic data alone. At the Botucará Hill site, the Caturrita Formation bears the dicynodont genus *Jachaleria* (Schultz et al. 2000; Langer et al. 2007), which also occurs in the La Chilca Locality at the base of the Los Colorados Formation, Argentina (Bonaparte 1966, 1997). Martínez et al. (2011) dated the base of the *Jachaleria* Biozone in Argentina as 225.9 ± 0.9 Ma, and magnetostratigraphy dating of the Los Colorados Formation (Kent et al. 2014) yielded an age span of 227 to 213 Ma. Considering that only the basal portion of the Los Colorados Formation has yielded record of *Jachaleria* (Bonaparte 1997), it is possible that the *Jachaleria* biozone is early Norian in age. However, the problem of correlating the type-locality of *U. toletinoi* to the *Jachaleria*-bearing Botucará Hill (or to any other site of the Caturrita Formation) is that it is yet to yield any additional fossil vertebrates. This scenario is further complicated by other lines of evidence favoring a younger age for some sites of the Caturrita Formation. Abdala and Ribeiro (2010) suggest a late Norian-Rhaetian age for the *Riogradia* Assemblage-Zone, due to the presence of derived triheledontid and brasilodontid cynodonts (Bonaparte et al. 2001, 2003). In addition, the upper levels of the Linha São Luiz site (an outcrop ascribed to the Caturrita Formation) were recently considered as Raethian or Lower Jurassic in age, based on new data from fossil plants, paleoinvertebrates, and ichnofossils (Silva

et al. 2012; Barboni and Dutra 2013; Rohn et al. 2014). Thus, the Caturrita Formation may include sites with different ages across a relatively broad (early Norian to Early Jurassic) temporal range, so that the age of *U. toletinoi* is, in fact, poorly constrained.

The present phylogenetic results and the compatible morphology of CAPP/UFMS 0002 and *Unaysaurus toletinoi*, support the correlation between the Wachholz and Água Negra sites. Recently, the Wachholz site was correlated to the Botucará Hill site based on the congruent morphology of two ischia from those localities (Müller, Da-Rosa, et al. 2015). As the Botucará Hill site has yielded *Jachaleria* (Araújo and Gonzaga 1980) from the same level that produced the sauropodomorph specimens (MMACR PV 037-T; UFRGS-PV-0761-T) (Bittencourt et al. 2013), Müller, Da-Rosa, et al. (2015) suggested an early Norian age to the Wachholz site. In this context, CAPP/UFMS 0002 provides the first reliable connection between the Água Negra and the Botucará Hill sites (Figure 10). Indeed, the second phylogenetic analysis performed here bounds *U. toletinoi*, CAPP/UFMS 0002, and MMACR PV 037-T into a trichotomy. This is enhanced by the presence of a notch between the medioventral lamina and the ventral margin of the ischial shaft of MMACR PV 037-T (Bittencourt et al. 2013), that may represent a plateosaurid trait.

The biostratigraphic framework (Figure 10) presented above is the first to include the Água Negra site, and supports previous works favoring an early Norian age for *U. toletinoi* (Novas 2009; Ezcurra 2010; Irmis 2011; Langer 2014). This age means that *U. toletinoi* lived just before the first (late Norian–Raethian) global radiation of dinosaurs (Figure 11). After that, sauropodomorphs became much more abundant (Figure 11), reached a wide geographical distribution, and substantially increased their body size (Galton and Upchurch 2004; Upchurch et al. 2004; Irmis 2011). Indeed, the estimated femoral length of *U. toletinoi* (UFSM 11069) and CAPP/UFMS 0002 is between 300

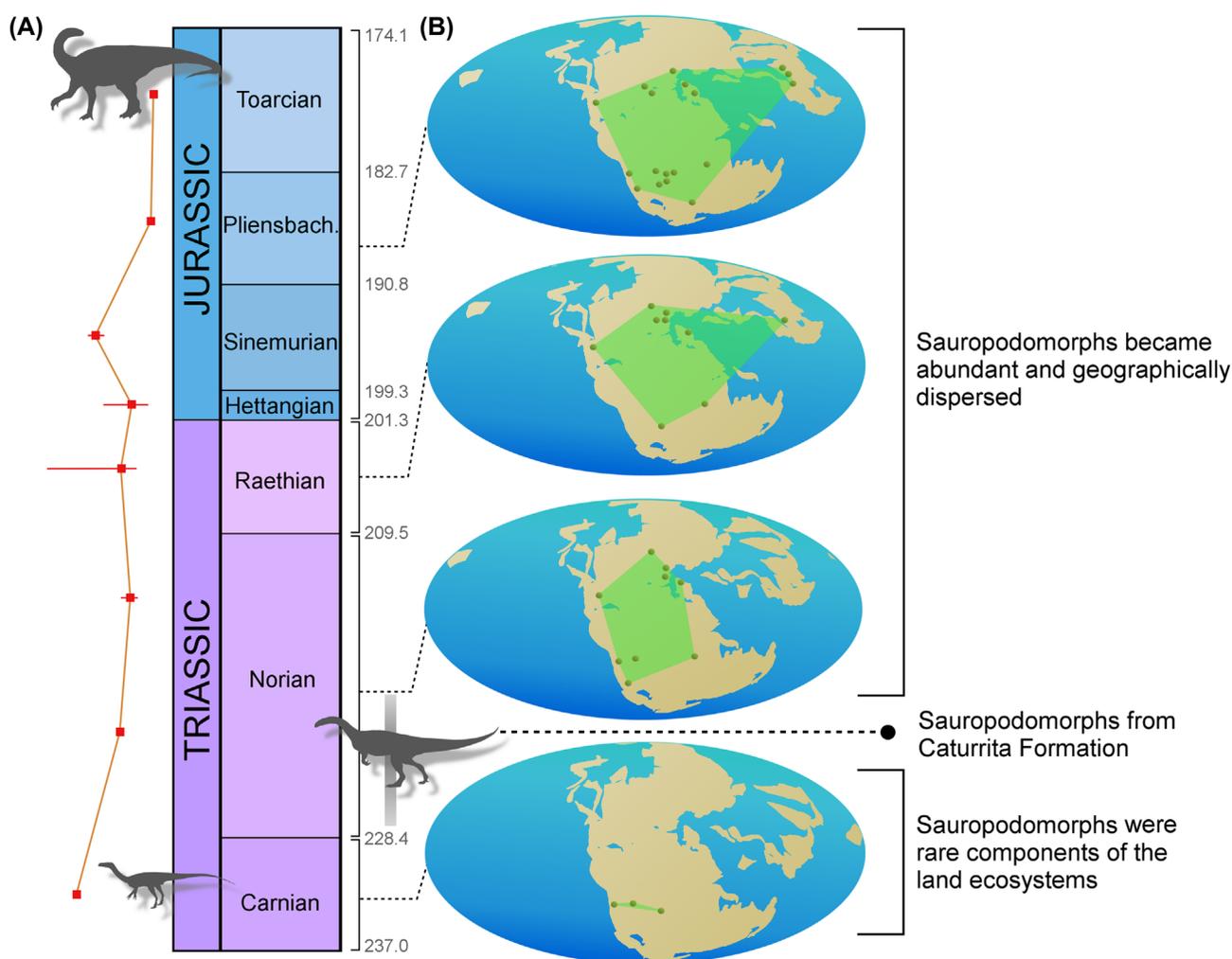


Figure 11. Age of Caturrita Formation sauropodomorphs and evolutionary patterns of the group through Late Triassic and Early Jurassic (Timescale from Gradstein et al. 2012). (A) Sauropodomorphs body size evolution (from Irmis 2011). (B) Convex hull geographic range maps for sauropodomorphs (data from the *Paleobiology Database*).

and 350 mm. Carnian forms have smaller femora: *Saturnalia tupiniquim* = 157 mm (Langer 2003) and *Pampadromaeus barberenai* = 142 mm (Müller, Langer, et al. 2015); whereas sauropodomorphs from the late Norian upper portions of the Los Colorados Formation (Kent et al. 2014) bear larger femora: *Coloradisaurus brevis* = 500 mm (Apaldetti et al. 2013) and *Riojasaurus incertus* = 608 mm (Carrano 2006). Therefore, the body size of *U. tolentinoi* and CAPP/UFM 0002 is also intermediate between those of Carnian and late Norian sauropodomorphs (Figure 11(A)).

CAPP/UFM 0002 and *Unaysaurus tolentinoi*

Some skeletal parts are preserved both in CAPP/UFM 0002 and in the holotype of *Unaysaurus tolentinoi* (UFM 11069). These include parts of the trunk vertebrae, forelimb and pedal phalanges. The bone elements of CAPP/UFM 0002 are 30% larger than those of UFM 11069, but there are few clear differences between both specimens. The centra of the trunk vertebrae of UFM 11069 are more lateromedially compressed than those of CAPP/UFM 0002, but (as mentioned above) this seems more likely the result of different taphonomic processes. Another putative difference is the form of the medial margin of

the proximal end of the ulna. The sigmoid crest seen in UFM 11069 is absent in CAPP/UFM 0002. In addition, the proximal articulation of the ulna is transversally convex in UFM 11069, but concave in CAPP/UFM 0002. This produces a larger articular area with the ulnar condyle of the humerus in UFM 11069. However, the proximal end of the ulna is crushed in UFM 11069, and such differences should also be treated with caution.

There are also peculiar similarities between the specimens. Both share a marked flat humeral head in cranial/caudal views, a trait also present in *Plateosaurus* spp and *Saturnalia tupiniquim* (Remes 2008; McPhee, Bonnan, et al. 2015). Also, the position of the pit distal to the deltopectoral crest on the lateral surface of the humerus is shared only with *S. tupiniquim*. Among plateosaurids, both specimens are the only with a quite slender first phalanx of pedal digit I.

The sharing of several morphological traits clearly points towards the referral of CAPP/UFM 0002 to *Unaysaurus tolentinoi*. However, we refrain for formally suggesting so because there are, indeed, few comparable elements. Moreover, more complete specimens (CAPP/UFM 0001) collected from the Wachholz site are still to be prepared and described. These may correspond to the same taxon as CAPP/UFM 0001 and will surely provide a better basis for comparison with *U. tolentinoi*.

Conclusions

The specimen described here possesses a set of morphological characters shared with typical 'prosauropods', such as a concave caudal margin of the dorsal neural spines, a broadly convex proximal articular surface of the metacarpal V, and the distal end of the ischium twice deeper than wider. However, it also retains some plesiomorphic features, such as the slender digit I of the foot. The performed phylogenetic analysis suggests that CAPP/UFMSM 0002 is closely related to the south Brazilian plateosaurid *Unaysaurus toleitinoi*. Such affinity supports a biostratigraphic framework that assigns an early Norian age to the type locality of *U. toleitinoi*, placing *U. toleitinoi* in a unique position on the evolutionary history of sauropodomorphs. Future studies of more complete specimens (CAPP/UFMSM 0001) from the Wachholz site (Müller, Da-Rosa, et al. 2015) will surely clarify the relationships between CAPP/UFMSM 0002 and *U. toleitinoi*, as there are a modest number of comparable elements between them.

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Disclosure statement

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