

New stem-sauropodomorph (Dinosauria, Saurischia) from the Triassic of Brazil

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Abstract Post-Triassic theropod, sauropodomorph, and ornithischian dinosaurs are readily recognized based on the set of traits that typically characterize each of these groups. On the contrary, most of the early members of those lineages lack such specializations, but share a range of generalized traits also seen in more basal dinosauriforms. Here, we report on a new Late Triassic dinosaur from the Santa Maria Formation of Rio Grande do Sul, southern Brazil. The specimen comprises the disarticulated partial

skeleton of a single individual, including most of the skull bones. Based on four phylogenetic analyses, the new dinosaur fits consistently on the sauropodomorph stem, but lacks several typical features of sauropodomorphs, showing dinosaur plesiomorphies together with some neo-theropod traits. This is not an exception among basal dinosaurs, the early radiation of which is characterized by a mosaic pattern of character acquisition, resulting in the uncertain phylogenetic placement of various early members of the group.

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Introduction

Previous to the discovery of *Saturnalia tupiniquim*, from the Santa Maria Formation of southern Brazil (Langer et al. 1999), the oldest known members of the sauropodomorph lineage were relatively massive, medium to large sized dinosaurs, recovered from Norian aged strata, mainly in Europe, Argentina, and South Africa (Galton 1990). Since then, an unsuspected diversity of smaller, more gracile stem-sauropodomorphs (sensu Langer 2003) was recovered from Carnian deposits of South America, especially from the Ischigualasto Formation, in Argentina. This includes *Panphagia protos* (Martinez and Alcober 2009), *Chromogisaurus novasi* (Ezcurra 2010), and possibly also *Eoraptor lunensis* (Martinez et al. 2011), formerly nested within Theropoda (Sereni et al. 1993). Here, we report on a disarticulated but otherwise well-preserved skeleton of a new stem-sauropodomorph from the Late Triassic of southern Brazil (Fig. 1), including most of the skull bones (Fig. 2).

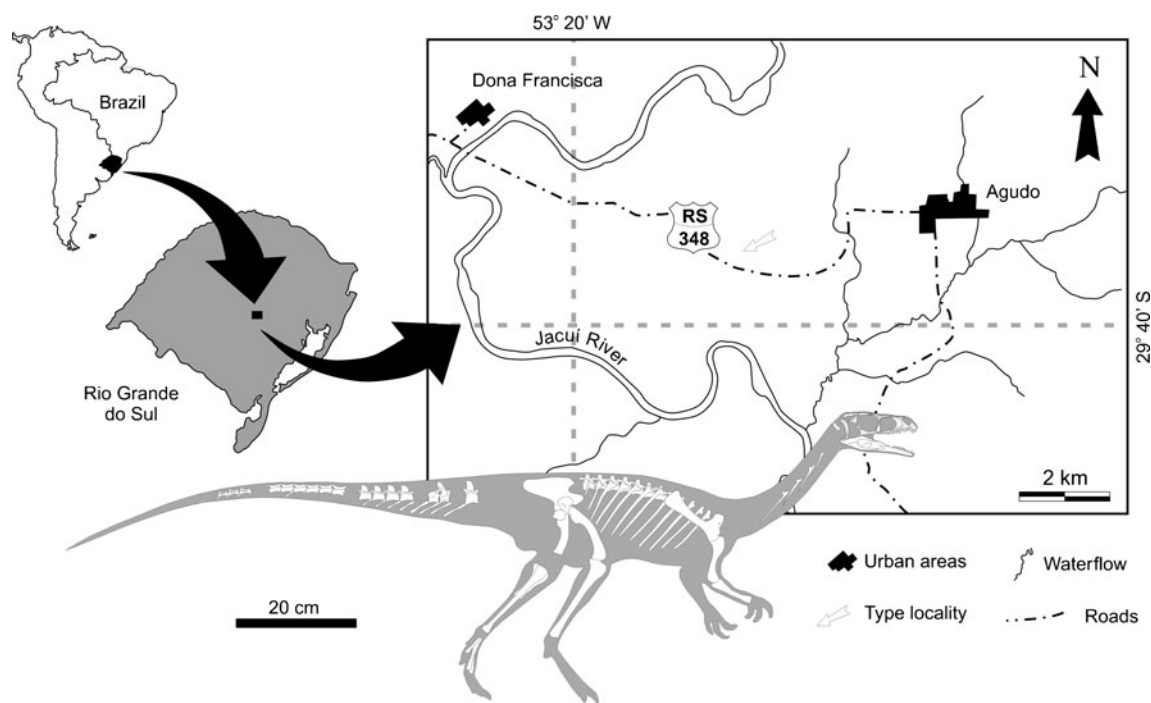


Fig. 1 *Pampadromaeus barberenai*, locality map and skeletal silhouette, showing preserved elements of the holotype (ULBRA-PVT016)

Systematic palaeontology

Dinosauria Owen 1842 sensu Padian and May (1993)

Saurischia Seeley 1887 sensu Gauthier (1986)

Eusaurischia Padian, Hutchinson & Holtz 1999 sensu Langer (2004)

stem-Sauropodomorpha Huene 1932 sensu Salgado et al. (1997; see Langer 2003)

Pampadromaeus barberenai new genus and species

Etymology The generic name is derived from the Quechua word *pampa* (=plain), in reference to the grassland landscape that covers parts of Rio Grande do Sul, and *dromaeus*, variant of Greek *δρομεύς* (=runner), in reference to the probable cursoriality of the animal. The specific epithet honors the Brazilian palaeontologist Mário C. Barberena.

Holotype ULBRA-PVT016 (Museu de Ciências Naturais, Universidade Luterana do Brasil, Canoas), disarticulated partial skeleton preserved in a single mudstone block (Figs. 1 and 2), including most skull bones, parts of the mandible, incomplete vertebral column, and appendicular skeleton (see details of the preserved elements in the [Electronic Supplementary Material](#)). Some of the elements were extracted, but most were only superficially exposed, retaining their original position in the block.

Type locality and horizon Reddish mudstones of the Alemoa Member, Santa Maria Formation, Rosário do Sul

Group (Zerfass et al. 2003), exposed at the site known as “Janner” or “Várzea do Agudo” ($53^{\circ}17'34.20''$ W, $29^{\circ}39'10.89''$ S), located about 2 km west of the town of Agudo, Rio Grande do Sul, Brazil (Fig. 1). Based on the co-occurrence of index fossils such as *Exaeretodon* and *Hyperodapedon*, the site can be assigned to the upper portions of the *Hyperodapedon* Assemblage Zone (Langer et al. 2007). Correlation to the better constrained Ischigualasto Formation, northwestern Argentina (Martinez et al. 2011), suggests a late Carnian age; ca. 230–228 Ma.

Diagnosis It is distinguished from all other well-known Triassic dinosauriforms by the following unique combination of character states (see extended diagnosis in the [Electronic Supplementary Material](#)): head longer than two thirds of the femoral length, premaxilla with short subnarial process, concave ventral margin of the premaxilla–maxilla articulation, no inset of first premaxillary or dentary tooth, premaxilla and dentary with unserrated mesial-most tooth crowns, most teeth lanceolate with coarse denticles along the carinae, sacral vertebrae with dorsoventrally expanded ribs, femur with reduced medial tuberosity (“t” in Novas 1996; Fig. 3) in the head and well-developed trochanteric shelf, epipodium significantly longer than femur.

Description

The premaxilla has a shallow narial fossa, four alveoli, and a subnarial process that does not reach the nasal. On the

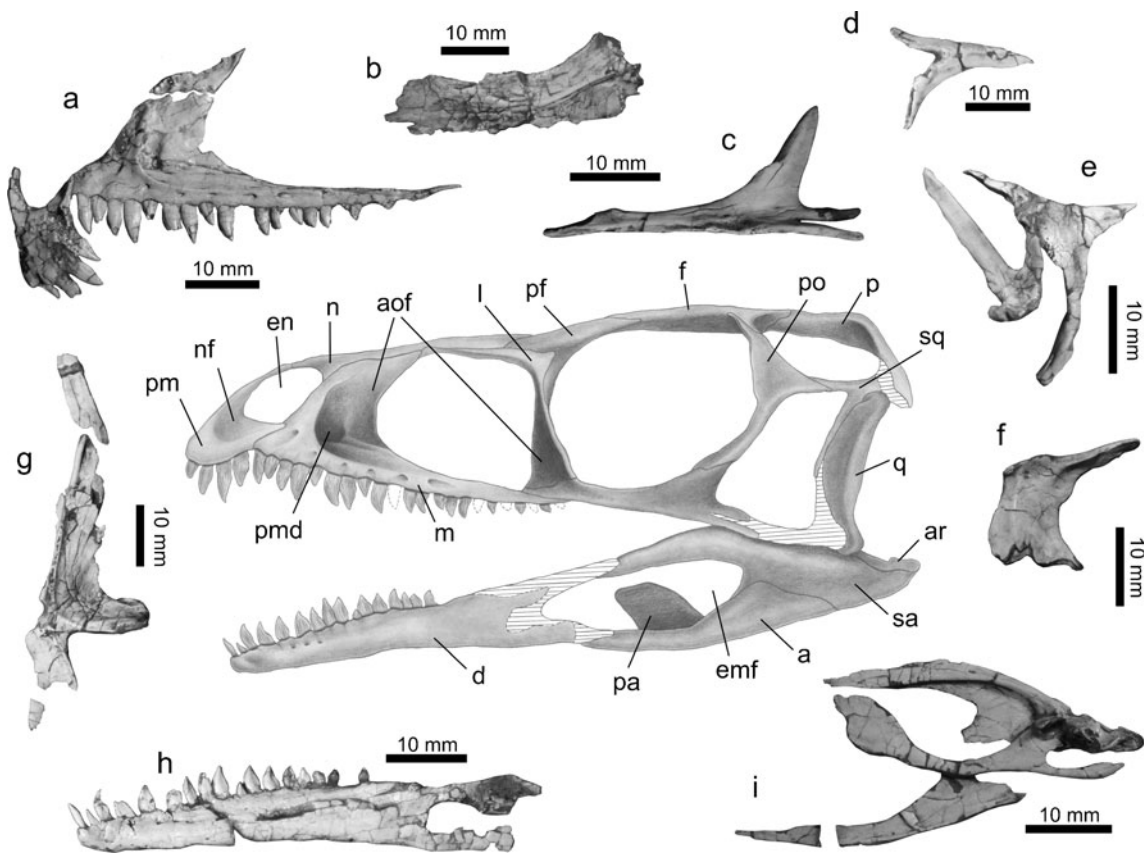


Fig. 2 *Pampadromaeus barberenai*, ULBRA-PVT016 (holotype), skull elements reversed as needed to left lateral (total skull length slightly over 10 cm). **a** Right premaxilla and maxilla. **b** Right frontal in ventral view. **c** Right jugal. **d** Right prefrontal. **e** Right postorbital and left squamosal. **f** Left parietal in ventral view. **g** Left pterygoid in ventral view. **h** Left dentary. **i** Right surangular, angular, articular, and

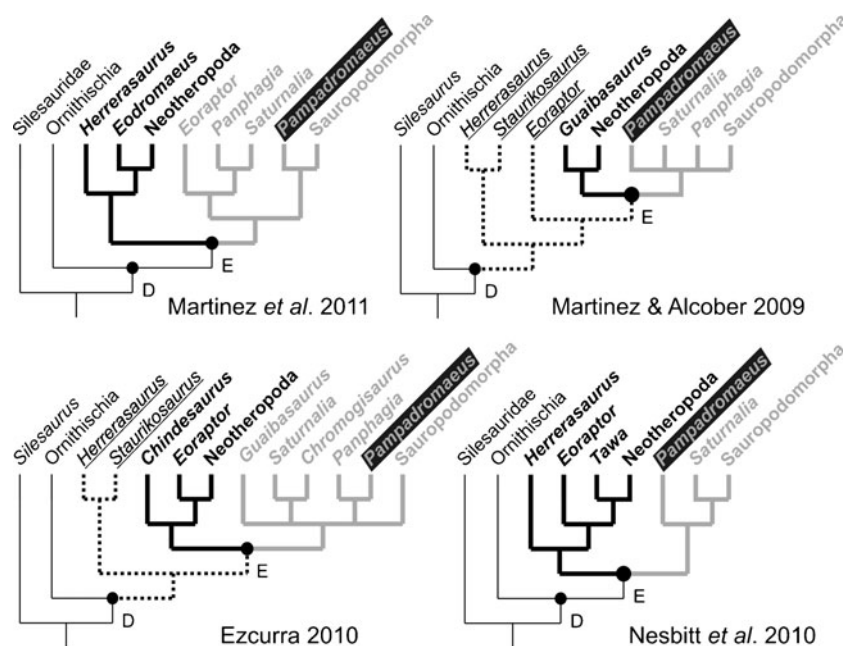
prearticular in medial view. *a* Angular; *aof* antorbital fossa; *ar* articular; *d* dentary; *emf* external mandibular fenestra; *en* external naris; *f* frontal; *l* lacrimal; *m* maxilla; *n* nasal; *nf* narial fossa; *p* parietal; *pa* prearticular; *pf* prefrontal; *pm* premaxilla; *pmd* “promaxillary” depression; *po* postorbital; *q* quadrate; *sa* surangular; *sq* squamosal

medial side, the maxillary process of the premaxilla forms a horizontal shelf below the palatal process of the maxilla. The dorsal and rostral rami of the maxilla meet forming a low, but well-defined angle at the rostral margin of the bone. Reconstruction of the premaxilla–maxilla articulation suggests that the former is ventrally projected. This is reminiscent of the subnarial gap of theropods, in the sense that the alveolar margin is bent upwards (Rauhut 2003), but no diastema is evident. The antorbital fossa has a deep rostral depression in a position equivalent to that of the promaxillary fenestra/foramen described for *Zupaysaurus rougieri* (Ezcurra 2007), “*Syntarsus kayentakatae* (Tykoski 1995), and cf. *Dracovenator regenti* (Yates 2005). This leads to a rostral furrow that apparently opens onto the medial surface of the bone, but no aperture is laterally visible. There are about 20 maxillary tooth positions and six large foramina around the antorbital fossa, the latter of which opens caudally. The lacrimal has a long, nearly vertical ventral ramus, the ventral portion of which is excavated by the antorbital fossa. The prefrontal lacks a

sheet of bone covering the lacrimal, which is present in various basal sauropodomorphs, but not in *P. protos* (Martinez and Alcober 2009). The postorbital forms a pendant eminence over the dorsocaudal border of the orbit, as seen in other basal dinosaurs (Sereno and Novas 1994; Martinez et al. 2011). The squamosal has a strap-shaped ventral process, as typical of early sauropodomorphs (Yates 2003). The caudal ramus of the jugal is forked and not ventrally arched. A medial ridge on the ventral surface of the pterygoid holds a row of about 15 positions for small rudimentary teeth, as previously recognized only in *E. lunensis* and *Eodromaeus murphi* among dinosaurs (Martinez et al. 2011; Nesbitt 2011).

The dentary bears about 20 tooth positions, extending from the rostral tip of the bone. Medial to the glenoid, the articular is pierced by the foramen for the chorda tympani, as in *Silesaurus opolensis* (MCL, personal observation, 2007), some dinosaurs (Yates 2005; Nesbitt 2011), and various pseudosuchians (Gower 1999). Most tooth crowns in the central portion of the upper and lower rows are

Fig. 3 Simplified phylogenetic relations of *Pampadromaeus barberenai* among basal dinosaurs, based on the analyses of the cited matrices (see [Electronic Supplementary Material](#)). Dotted lines and underlined lettering indicate non-Eusaurischia saurischian grade; gray lines and lettering indicate sauropodomorph lineage; full black lines and lettering indicate theropod lineage. Sauropodomorpha applied *sensu* Langer (2003). *D* Dinosauria, *E* Eusaurischia



lanceolate, with an expanded base, a convex mesial margin, and a sigmoidal (convex at the base and concave apically) or nearly straight distal margin. More distal teeth are shorter, but retain this general shape that is typical of various basal dinosaurs (Barrett et al. 2011). There is some imbrication between adjacent crowns, with the mesial edge of the crowns medially overlapping the distal edge of the tooth mesial to it. Carinae are coarsely serrated, their denticles forming oblique angles with the crown margin. The most mesial teeth on both premaxilla and dentary are narrower and bear less evident serrations, as seen in coelophysid theropods (Tykoski and Rowe 2004). Mesial dentary teeth of other stem-sauropodomorphs such as *S. tupiniquim* (Langer et al. 1999) and *P. protos* (Martinez et al. 2011) are broader and bear serrated carinae, but the preserved elements may not belong to the very tip of the jaw.

The atlantal neurapophysis has a plate-like, dorsally expanding epiphysis that does not extend caudal to the postzygapophysis. Cervical ribs have elongated and straight shafts. As typical of saurischians (Langer and Benton 2006), trunk vertebrae have well developed laminations surrounding the diapophysis, and hyposphene–hypantrum auxiliary articulations. As in many basal dinosaurs (Langer 2003; Langer et al. 2011), two vertebrae form the entire sacrum, with ribs attached to the cranial half of the respective centrum. The ribs are dorsoventrally expanded and ventrally connected to one another. The circumscribed intercostal space has a small ventral aperture, medial to the caudal half of the first centrum, and a large dorsal opening bordered by unexpanded transverse processes. The scapular blade is cranially inclined, and the humerus has a broad

distal end, as typical of sauropodomorphs (Langer and Benton 2006). The ilium has a deep dorsal lamina, but the preacetabular ala is short and pointed. The long postacetabular ala bears an evident brevis fossa. The acetabular wall has a nearly straight ventral margin, as seen in *S. tupiniquim*, *Guaibasaurus candelariensis*, and *P. protos*. The femoral head is offset and inturned, with the long axis forming an angle of 40° to the intercondylar line. It has a flat cranio-lateral surface and subtle medial tubera (Nesbitt et al. 2009). The articular surface has well-developed transverse groove and *facies articularis antitrochanterica* (Langer 2003). The lateral surface of the proximal portion of the femur has a crescent-shaped dorsolateral trochanter, a knob-like lesser trochanter, and a well-developed trochanteric shelf. The fourth trochanter expands as an asymmetrical, sharp flange. The epipodium is nearly 20% longer than the femur. The cnemial crest of the tibia is cranially projected and the lateral condyle is set at the center of the lateral margin of the proximal articulation. Metatarsal I is significantly shorter than metatarsals II and III.

Phylogenetic analyses and discussion

Phylogenetic analyses (see details in the [Electronic Supplementary Material](#)) based on four recent studies on the early radiation of dinosaurs (Martinez and Alcober 2009; Ezcurra 2010; Nesbitt et al. 2010; Martinez et al. 2011) unambiguously place *P. barberenai* on the sauropodomorph stem (Fig. 3), with minor variations that include its sister-taxon relationship to either *P. protos*, Sauropodomorpha (sensu Langer 2003), or Sauropodomorpha plus *S. tupini-*

quim. However, despite this recurring position, the affinities of *P. barberenai* to sauropodomorphs are not supported by strong tree statistics, neither by many or uncontroversial anatomical traits. In conjunct, these include the following: (1) highly homoplastic characters (mean Consistency Index based on the four analyses indicated under brackets) as lanceolate tooth crowns (0.53) with expanded bases (0.30) that overlap one another (0.26), four premaxillary teeth (0.47), interpostzygapophyseal notch in proximal tail vertebrae (0.20), humerus longer than or subequal to 0.6 of the femoral length (0.43), supracetabular crest extensive to the pubic peduncle of the ilium (0.28), proximal femoral articulation with straight transverse groove (0.28), and proximal portion of the tibia with a cranially displaced fibular condyle (0.33); (2) characters codified as missing data for most fossil taxa, e.g., medial foramen on the articular (Nesbitt 2011); and (3) features with a seemingly more consistent distribution, such as strap-shaped ventral process of the squamosal, proximal tail vertebrae with long neural spines, humerus with broad distal end (relative to the length of the bone), and ilium with a subtriangular preacetabular ala and long pubic peduncle. However, *P. barberenai* lacks some typical sauropodomorph traits such as a small head and longer crowns on the rostral part of the tooth series (Martinez and Alcober 2009). The analyses also revealed numerous autapomorphies for *P. barberenai*, but most of them correspond to homoplastic traits more common to other dinosaur groups, and none is really unique to that taxon. Theropod features (Rauhut 2003; Tykoski 1995) include concave ventral margin of the premaxilla–maxilla articulation, unserrated teeth in the rostral tip of the upper and lower jaws, “promaxillary” depression, and deep dorsal iliac lamina. Other putative theropod traits of *P. barberenai*, such as a “forked” caudal process of premaxilla (Rauhut 2003) and a concave caudal margin of the iliac lamina in dorsal profile (Tykoski 1995), are also seen in sauropodomorphs and *S. opolensis*. Likewise, dinosaur plesiomorphies (Langer and Benton 2006) retained or reverted in *P. barberenai* include a deep acetabular medial wall with straight ventral margin and narrow sacral transverse processes that do not roof the intercostal space. This seems also to be the case of the palatal teeth, known in early members of the archosaurs lineage (Nesbitt 2011), putative basal pseudosuchians (Wu and Russell 2001), some pterosaurs (Kellner 2003), and basal dinosaur groups such as *Lewisuchus admixtus* (JSB, personal observation, 2011), although hitherto unrecognized in dinosaurs other than *E. lunensis* and *E. murphi*.

The outcomes of the phylogenetic analyses (Fig. 3) stress the uncertainties concerning the relationships of various basal dinosaurs. For example, *G. candelariensis*, *E. lunensis*, and herrerasaurs appear alternatively basal to the sauropodomorph–theropod dichotomy or at the base of

either lineage. This most likely results from the ambiguous distribution of traits, which became characteristic of certain dinosaur clades, among these and other basal dinosaur groups such as *S. opolensis*, *S. tupiniquim*, *P. protos*, *E. murphi*, and *Eocursor parvus*. Phylogenetic reconstructions of basal dinosaurs are further problematical because those features accumulated over a relatively short period of time (Irmis 2011), in forms with recurring body structure and inferred habits (i.e., medium-sized, bipedal, and omnivorous). In fact, the early dinosaur radiation may represent a segment of evolutionary history that is particularly hard to reconstruct, and its poor constraint is not surprising. Only additional finds and, especially, more detailed phylogenetic studies will facilitate development of a more stable evolutionary framework for the placement of many basal dinosaurs.

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