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New dinosauriform (Ornithodira, Dinosauromorpha) record from the Upper Triassic of Southern Brazil

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Introduction

Dinosauriformes includes the most recent common ancestor of *Marasuchus lilloensis* and Dinosauria, and all taxa stemming from it (Novas, 1992). The origin of this group and its diversification have been the subject of extensive studies in recent years (Langer *et al.*, 2010; Langer *et al.*, 2013), especially because it includes the dinosaur lineage, one of the most diverse groups of Mesozoic tetrapods (Irmis, 2011; Novas *et al.*, 2011). The oldest Dinosauriformes came from the upper Anisian of Tanzania (Nesbitt *et al.*, 2010) and the Ladinian of Argentina (Romer, 1972a, b; Arcucci, 1987; Sereno and Arcucci, 1993) and recent studies demonstrated that non-dinosaur dinosauriforms shared environments with dinosaurs until the end of the Triassic (Novas and Ezcurra, 2005; Ezcurra, 2006; Nesbitt *et al.*, 2010; Langer *et al.*, 2013). Yet, the small number of available specimens regarded as early members or possible ancestors of Dinosauria still brings great uncertainty regarding both origins and phylogenetic relationships of the group.

In the present contribution, we report the occurrence of a new non-dinosaur dinosauriform specimen from the Santa Maria Formation, a stratigraphic unit that congregates the oldest unequivocal dinosauriform records from Brazil (Colbert, 1970; Langer *et al.*, 1999; Kischlat, 1999; Da-Rosa *et al.*, 2006; Cabreira *et al.*, 2011), all of which are included within Dinosauria. One exception is the problematic *Teyuwasu barberenai* (Kischlat, 1999), considered *nomen dubium* by Langer (2004) and revised recently by Ezcurra (2012), which tentatively suggests a

silesaurid affinity.

Institutional abbreviations.—UNIPAMPA, Universidade Federal do Pampa, São Gabriel, Brazil.

Systematic palaeontology

Archosauria Cope, 1869

Ornithodira Gauthier, 1986

Dinosauromorpha Benton, 1985

Dinosauriformes Novas, 1992

Figure 1

Material.—UNIPAMPA-0632, partial left femur.

Locality and Horizon.—Janner Site, 2 km west of Agudo, Rio Grande do Sul, Brazil. Upper portion of the *Hyperodapedon* Assemblage Zone (sensu Langer *et al.*, 2007), upper Carnian of the Paraná Basin.

Description.—The partial left femur is 110 mm long and sigmoid in cranial and lateral views. The proximal extremity is missing, and only the distal portion of the “crest-like” fourth trochanter is preserved (Figure 1B-C). The ‘lesser trochanter’ (*Musculus iliofemoralis cranialis* insertion) is seen on the lateral surface of the proximal half of the bone as a slight proximodistally elongated prominence that is completely connected to the shaft (Figure 1B and E). This condition differs from the knob-like ‘lesser trochanter’ of *Pampadromaeus barberenai* (Cabreira *et al.*, 2011), *Saturnalia tupiniquim* (Langer *et al.*, 1999), and *Sacisaurus agudoensis* (Ferigolo and Langer, 2007), in which the proximal portion is separated from the shaft by a cleft. The ‘trochanteric shelf’ is

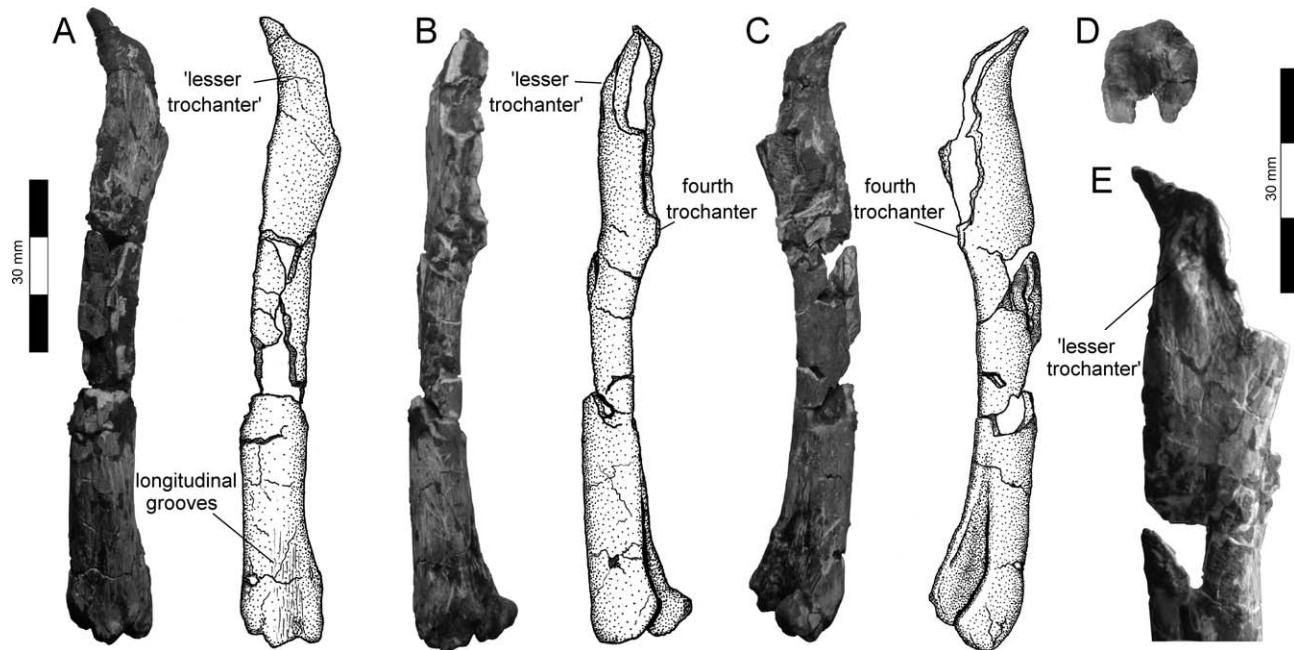


Figure 1. Photographs and illustrations of specimen UNIPAMPA-0632. **A**, cranial view; **B**, lateral view; **C**, caudomedial view; **D**, distal view, and **E**, caudolateral view.

absent (Figure 1E), as in *Sacisaurus* and differently from *Pampadromaeus* and *Saturnalia*. The popliteal fossa extends for one-fourth to one-third of the shaft length (Figure 1C), as in *Asilisaurus kongwe* (Nesbitt *et al.*, 2010), *Eucoelophysoides baldwini* (Sullivan and Lucas, 1999), *Silesaurus opolensis* (Dzik, 2003), *Sacisaurus* and *Diodorus scytobrachion* (Kammerer *et al.*, 2012). Some longitudinal grooves can be observed along the cranial surface of the distal portion of the femur, which may correspond to points of insertion for the *Musculus femorotibialis externus* (Figure 1A).

Discussion and conclusion

UNIPAMPA-0632 is assigned to Dinosauriformes due to the presence of a ‘lesser trochanter’ and a “crest-like” fourth trochanter. It does not bear any clear autapomorphic character, but differs from all previously known dinosauromorphs from the Santa Maria Formation due to the combination of a ‘lesser trochanter’ completely connected to the shaft and a longitudinally extensive popliteal fossa. Therefore, it might represent a still unknown taxon from the upper portion of the *Hyperodapedon* Assemblage Zone in Southern Brazil.

Nesbitt *et al.* (2010) recognized an unnamed clade within Silesauridae, containing *Asilisaurus*, *Eucoelophysoides*, *Sacisaurus*, and *Silesaurus* supported by about five

synapomorphies, including a popliteal fossa extending for proximally one-fourth to one-third the length of the femur, as observed in UNIPAMPA-0632. However, both the composition and phylogenetic position of Silesauridae have been recently considered uncertain (Langer and Ferigolo, 2013), hampering the precise taxonomic attribution of this specimen. Still, the absence of a protruding ‘lesser trochanter’ suggests a closer affinity to non-dinosaur Dinosauriformes, given that all well known Triassic dinosaurs have that structure (Nesbitt, 2011; Langer and Ferigolo, 2013).

The faunal content of the Janner, or Várzea do Agudo, site resembles that of the Ischigualasto Formation, in northwestern Argentina, which shows a predominance of both *Exaeretodon* (Cabrera, 1943) and *Hyperodapedon* (Huxley in Murchison, 1859; p. 435, 436; Huxley, 1869). [Note: The genus and species name *Hyperodapedon gordoni* was introduced by Sir Roderick I. Murchison in 1859, in a postscript added in press (see References in the present paper), the fossil having been sent by Murchison to T. H. Huxley for identification. Murchison therein attributed the name to Huxley. Consequently the genus should be cited as *Hyperodapedon* Huxley in Murchison, 1859, and likewise the type species *H. gordoni*.] This allows a direct biostratigraphic correlation and the proposition of a late Carnian age for the Janner Site (Martinez *et al.*, 2011). Because of the predominance of *Exaeret-*

odon specimens, Langer *et al.* (2007) assigned that locality to the upper portions of the *Hyperodapedon* Assemblage Zone, whereas the *Sacisaurus agudoensis* locality (also in the municipality of Agudo) belongs to the lower (upper Carnian/lower Norian) *Riograndia* Assemblage Zone (Soares *et al.*, 2011), within the Caturrita Formation. Accordingly, UNIPAMPA-0632 is probably older than *Sacisaurus agudoensis*. Indeed, if UNIPAMPA-0632 corresponds to a Silesauridae, it extends the occurrence of this clade to the Carnian of Brazil. In global terms, the only two other putatively Carnian silesaurids are *Diodorus scytobrachion* from the Timezgadiouine Formation, Morocco, and *Ignotosaurus fragilis* (Martínez *et al.*, 2013) from the Ichigualasto Formation, Argentina.

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