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Research paper

An articulated titanosaur from Patagonia (Argentina): New evidence of neosauropod pedal evolution

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Abstract

Most titanosaur dinosaurs are represented by incomplete skeletal elements lacking articulated pes. An exceptionally preserved specimen from the Late Campanian–Early Maastrichtian strata of Patagonia (Argentina) provides new data on pedal morphology and the evolutionary trends of these huge dinosaurs. This finding is one of the few articulated titanosaur pes known in the world, and shows a phalangeal formula of 2-2-2-2-0. The first three digits possess sickle-shaped claws and the articular facets of ungual phalanges, suggesting mobility in horizontal and vertical planes. A comparative analysis of available record suggests that titanosaurs had a progressive reduction of size and number of pedal phalanges in digits III and IV during the Late Cretaceous.

Keywords: Pes morphology; Sauropoda; Titanosauria; Cretaceous; Patagonia; Argentina

1. Introduction

The study of the pedal structure is essential for understanding the locomotion, evolutionary trends and the behavior of the sauropod dinosaurs. Sauropod pedes possess several unique features: an asymmetrical pes, extreme reduction of the tarsus, typically three large pedal claws, and expanded phalangeal articular surfaces (Bonnan, 2005). Sauropod titanoaurs have a similar morphology, but articulated records are scarce. Up to now, more than 40 taxa are known, but only 2 have complete and articulated pes: *Opisthocoelicaudia* Borsuk-Bialyncka, 1977 and *Epachthosaurus* Powell, 1990 (Martínez et al., 2004). In this context, the discovery of a new specimen herein described, with exceptionally preserved pedal structure, is relevant from a systematic viewpoint. This finding is, therefore, one of the few records of an articulated titanosaur pes known in the world.

The specimen was collected by the authors during a paleontological exploration at La Invernada area (Neuquén Province, Northern Patagonia) in 2005. The material came from the Allen Formation that corresponds to Late Campanian–Early Maastrichtian strata of the Neuquén Basin. The specimen comprises a partial skeleton with complete manus and pes (MUCPv-1533). In this paper, we only describe and analyze the complete and articulated pes (Fig. 1), and other skeletal elements will be described elsewhere.

2. Geological setting

The Neuquén Basin is located in northern Patagonia, Argentina, between 34°40′ and 40° south latitude and from 66° to 70°20′ west longitude (Fig. 2). This basin extends between the active margin magmatic arc along the Andes to the west, and the Sierra Pintada System and the North Patagonian Massif to the east, respectively (Vergani et al., 1995). The Neuquén Basin covers a surface of 137 000 km^2 and consists in a succes-

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Fig. 1. Field excavation of the titanosaur skeleton at La Invernada, Patagonia (MUCPv-1533).

sion of 7000 m of sedimentary rocks from Triassic to the Early Paleocene.

The basement rock of the Neuquén Basin is commonly known as the Choiyoi Group. It is composed by volcanic, piroclastic, and sedimentary complex of Permian–Triassic age (Cazau and Uliana, 1973). From the middle-later Triassic the basin was filled by sedimentary rocks composed mostly by continental clastics with tuff and volcanic intercalations. During the Jurassic and Cretaceous, transgressive and regressive episodes were developed, depositing continental, littoral and marine facies (Legarreta and Gulisano, 1989).

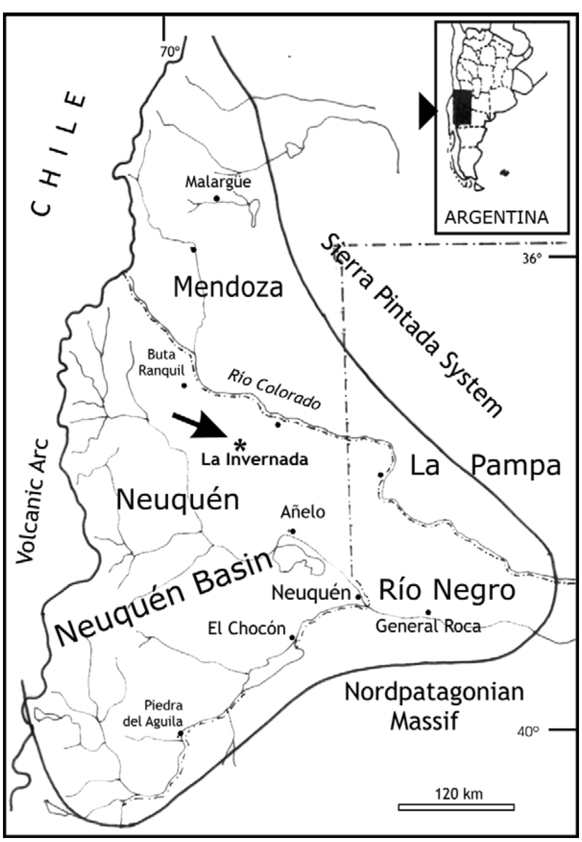

Fig. 2. Map of the Neuquén Basin (after Vergani et al., 1995) showing La Invernada site (asterisk).

The Malargue Group (Campanian to Danian) includes the Allen, Jaguel and Roca formations (Fig. 3). The Allen Formation is integrated by fluvial, lacustrine and marginal marine facies (tidal flats, lagoon and sabkhas). These facies are related to a first marine ingression from the Atlantic sea that covered central-northern Patagonia toward the end of the Cretaceous Period (Andreis et al., 1974; Barrio, 1990; Parras et al., 1998; González Riga, 1999). The fossil described here was found in the middle section of the Allen Formation, in laminated grey-greenish pelites that are preliminarily assigned to a lacustrine environment deposited during Late Campanian–Early Maastrichtian. The taphonomic and sedimentological aspects of this quarry, including burial processes of the articulated specimen, will be analyzed elsewhere.

3. Paleontology

3.1. Phylogenetic criteria and material recovered

The phylogenetic relationships of Titanosauria taxa are not resolved yet, since most of taxa are represented by fragmentary and disarticulated remains. Moreover, the published cladistic analyses use different terminal taxa and are based on diverse criteria in naming the nodes (see Curry Rogers, 2005; Wilson, 2006). For example, the name Titanosauridae, a mostly traditional titanosaurian group, is used (Salgado, 2003) or avoided (Sereno, 1998; Wilson, 2002; Wilson and Upchurch, 2003) after

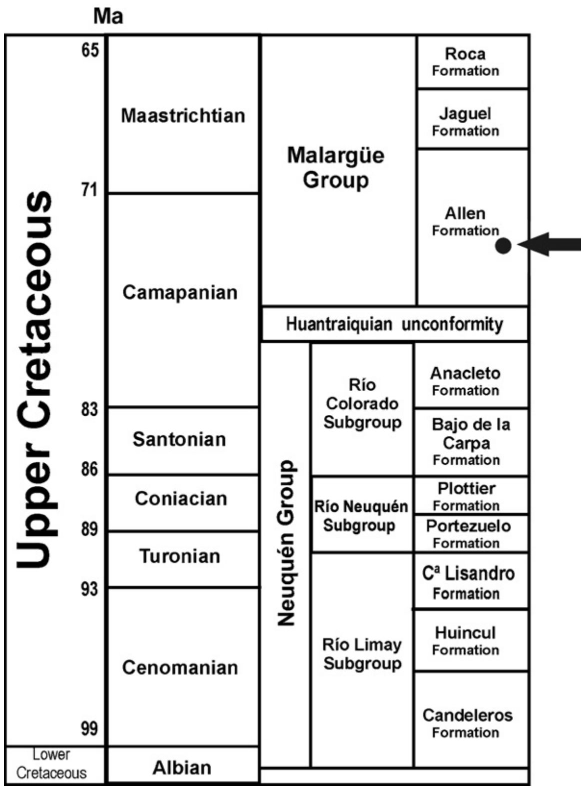

Fig. 3. Geologic column of the Neuquén and Malargue Groups. The arrow and dot show the finding of specimen MUCPv-1533.

different interpretations of the Phylogenetic Code. We think that titanosaurian clades need a detailed study including all species recently discovered, and a carefully revision of the numerous names, both in node-based and stem-based taxa. In this study we adopt Titanosauria and Titanosauridae names after definitions proposed by Salgado et al. (1997a) and Salgado (2003).

In this paper we follow the anatomical nomenclature proposed by Weishampel et al. (1990). These authors use cranial and cranially instead anterior and anteriorly, craniocaudally instead anteroposteriorly, and caudal and caudally instead posterior and posteriorly, respectively.

The specimen described herein (MUCPv-1533) includes a partial caudal series and the left portion of the skeleton lacking the skull and cervical vertebrae (Fig. 4). The left limbs are complete and articulated. The specimen is still in preparation; however, a preliminary observation indicates that is a derived titanosaurid sensu phylogenetic definition of Salgado (2003). It has strongly procoelous caudal vertebrae with prominent condyles, neural arches cranially located in middle and distal caudal centra, haemal arches articulations open proximally, metacarpals without distal articular facets, absence of manual phalanges and claws, and femora with a lateral bulge below the greater trochanter.

Institutional abbreviations. MUCPv-1533, Museo de Geología y Paleontología Universidad Nacional del Comahue, Argentina.

3.2. Description

The astragalus (Fig. 5) is the only ossified element of the tarsus, as in *Opisthocoelicaudia* (Borsuk-Bialyncka, 1977), *Epachthosaurus* (Martínez et al., 2004) and *Neuquensaurus* (Salgado et al., 2005). This bone is transversely reduced and has a slightly concave lateral face for the articulation of the fibula (Fig. 5B). The cranial face has a triangular contour; it shows a convex surface that articulates with the proximal end of the metatarsals (Fig. 5A). In dorsal view it has a triangular contour with a relatively small ascending process that articulates with a depression in the distal end of the tibia, as in *Epachthosaurus* (Martínez et al., 2004). The distal face is convex and strongly rugose (Fig. 5C). The tibial face is not strongly inclined as in *Aeolosaurus* sp. (Salgado et al., 1997b, p. 47).

The pes, as in all sauropods, is typically asymmetrical. It has five metatarsals, where the metatarsals III and IV are the longest elements. In proximal view the articular faces of the metatarsals II–IV have a subrectangular shape; therefore, they form a very flat arch when articulated. A similar condition is seen in *Opisthocoelicaudia* (Borsuk-Bialyncka, 1977, p. 49). In the specimen herein described, the metatarsal V is in a laterocaudal position, showing a strongly convex contour (Fig. 6). This morphology is different to those described for all other neosauropods, which

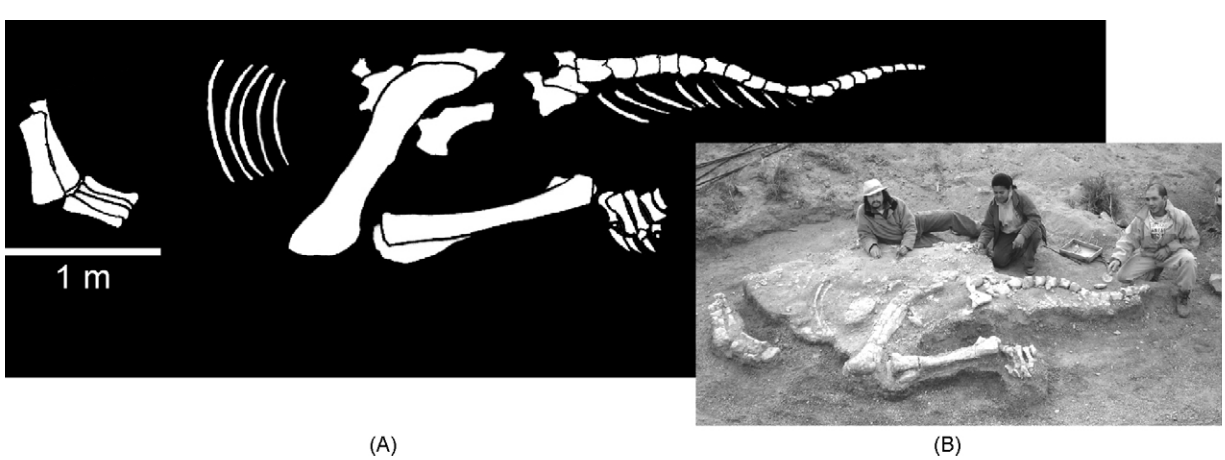

Fig. 4. Skeletal disposition of bone in La Invernada site (Patagonia, Argentina): (A) map of the quarry; (B) excavation of the specimen.

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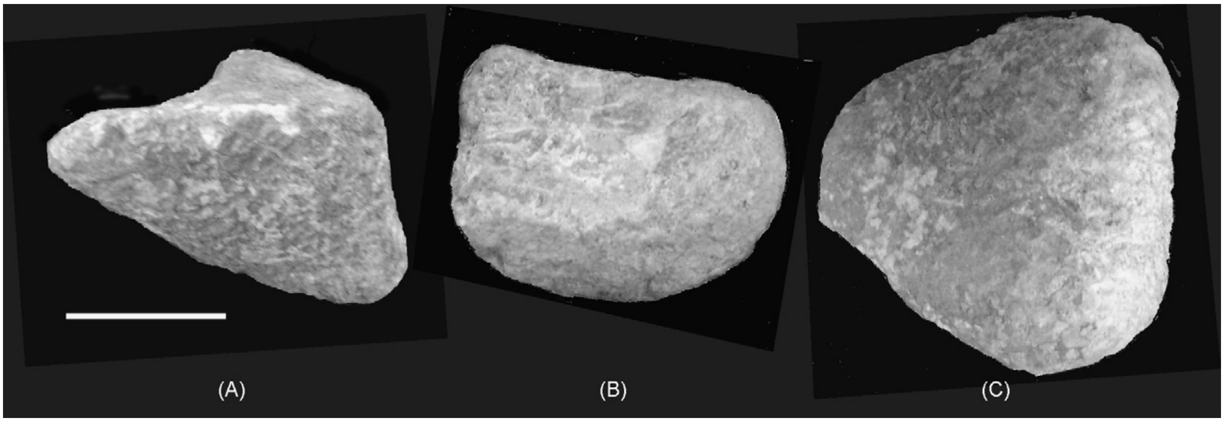

Fig. 5. Left astragalus in anterior (A), lateral (B), and caudal (C) views. Scale bar = 5 cm.

have a more linear configuration (see Bonnan, 2005, p. 356).

The length of metatarsals increases from I to IV (Fig. 7; Table 1). Both the original position of the pes in the field and the study of the articular surfaces have allowed documenting the general disposition of metatarsals and phalanges. The unguals are inclined 40–60° with respect to the vertical. This special disposition is also described in the titanosauriform *Pleurocoelous* (Gallup, 1989) and *Opisthocoelicaudia* (Borsuk-Bialyncka, 1977).

The twisted metatarsal I is the thickest and shortest of all metatarsals. The proximal end has a subcircular contour, and shows a rugose and slightly convex surface. It is inclined with respect to the axis of the shaft. The shaft has a concave surface for the contact with the metatarsal II. The distal end has a sub-

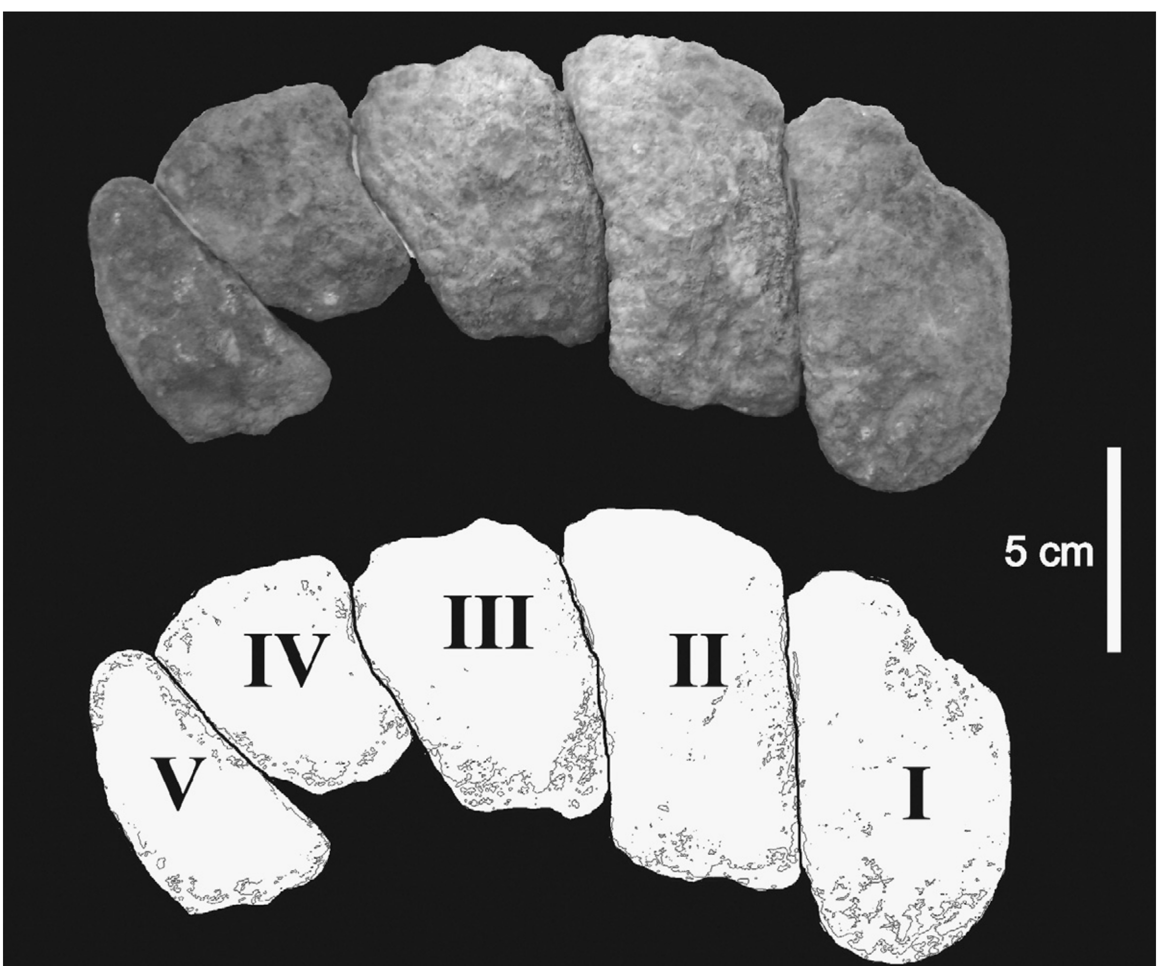

Fig. 6. Metatarsals of the titanosaur MUCPv-1533 in proximal view (roman numbers show digit numbers). Scale bar = 5 cm.

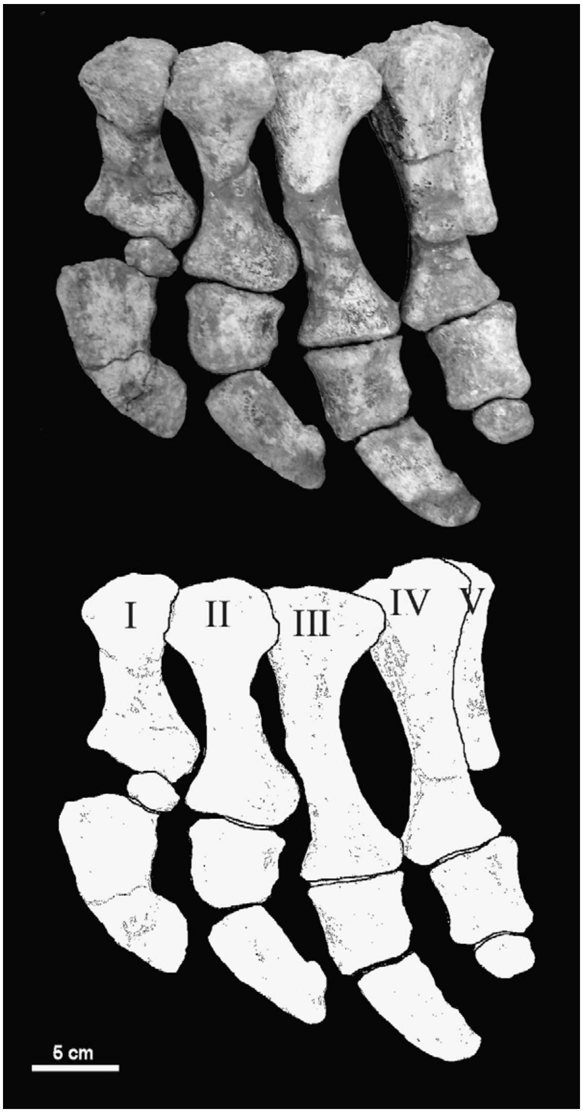

Fig. 7. Pes of the titanosaur MUCPv-1533 in dorsal view (roman numbers show digit numbers). Scale bar = 5 cm.

quadrangular shape and a craniomedial small concavity for the articulation with the first phalanx.

The metatarsal II is longer than metatarsal I. It has a craniocaudally expanded proximal end with an elongated and rectangular rugose surface. The distal end is quadrangular, rugose and slightly convex.

The metatarsal III is as long as metatarsal IV. It is a slender bone with expanded ends. The rugose proximal end has a subquadrangular outline. The lateral border of the proximal end is slightly convex cranially, but it is straight caudally. This border is the contact area for the metatarsal IV. The distal end is subquadrangular, wider transversely than craniocaudally.

Table 2
Proximodistal lengths (cm) of phalanges of the left pes of MUCPv-1533

	Digit I	Digit II	Digit III	Digit IV
Phalanx I	21	57	51	57
Phalanx II	113	82	76	24

The metatarsal IV is a slender bone, expanded distally and proximally. Both articular surfaces are rugose. The proximal end has a trapezoidal outline, wider cranially than caudally. The shaft has a triangular section with a flat dorsal (palmar) face and pointed ventral (plantar) one. The convex distal end has a suboval outline, transversely wider than craniocaudally.

The metatarsal V has a subtriangular outline in proximal view, with a more acute cranial border. It is the shortest metatarsal of the pes. Metatarsal V possesses an extremely craniocaudally broadened fan-shaped proximal end. The distal end is reduced to almost the half of the proximal end. The medial surface is flat on the half proximal portion, and has a straight outline in proximal view.

The phalangeal formula is 2-2-2-2-0 (Fig. 7). The first phalanges increase in length from digit I to IV (Table 1); in contrast, the second phalanges (ungueals), reduce their size from digit I to IV (Table 2).

The phalanx I of digit I is very reduced in relation to the others. It has a hemi-spheric shape. This structure is very different from the titanosaurid *Epachthosaurus* (Martínez et al., 2004), in which it is a more robust element.

The first phalanx of digits II–IV are wedge-shaped and have a trapezoidal shape in dorsal view. This surface is convex lateromedially and concave craniocaudally. In proximal view, an asymmetry is developed in these phalanges and they are deeper medially than laterally. In dorsal view, the medial border is longer than the lateral one.

The phalanx I of digit II is similar in shape to that of digit III, but it is thicker and shorter. By contrast, the phalanx I of digit IV is thinner and has a flat ventral face. Their distal ends have a convex surface, more pronounced in the borders than in the middle for articulation with a phalanx II.

Phalanx II forms the ungual in the digits I–III (Fig. 7; Table 2). By contrast, in *Epachtosaurus* the ungueal in digit III is the phalanx III (Martínez et al., 2004). Unguals I–III are flattened lateromedially, and has a typical "sickle" shape, as in *Mendozasaurus neguyelap* (González Riga, 2003; Fig. 6).

The phalanx II of digit IV has a structure similar to phalanx I of digits I–III, but it is smaller, and wider lateromedially.

Table 1
Measurements (cm) of metatarsals of MUCPv-1533

	Metatarsal I	Metatarsal II	Metatarsal III	Metatarsal IV	Metatarsal V
Length	120	137	168	172	127
Proximal width	104	104	80	67	78
Distal width	72	61	60	61	40

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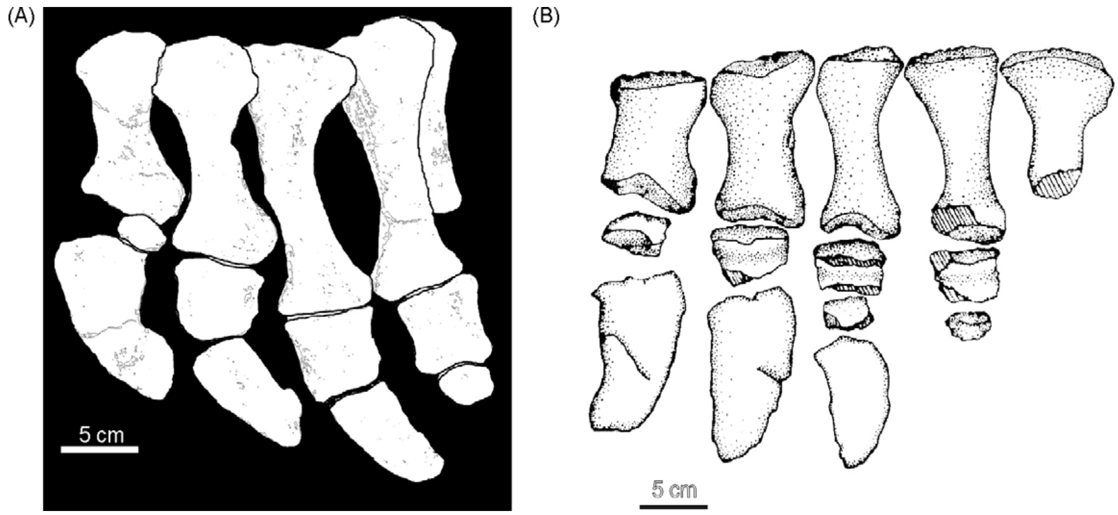

Fig. 8. Articulated titanosaur pes in dorsal view. (A) Titanosaur MUCPv-1533 from La Invernada site, Northern Patagonia; (B) *Epachthosaurus* from Central Patagonia, after Martínez et al. (2004). Scale bar = 5 cm.

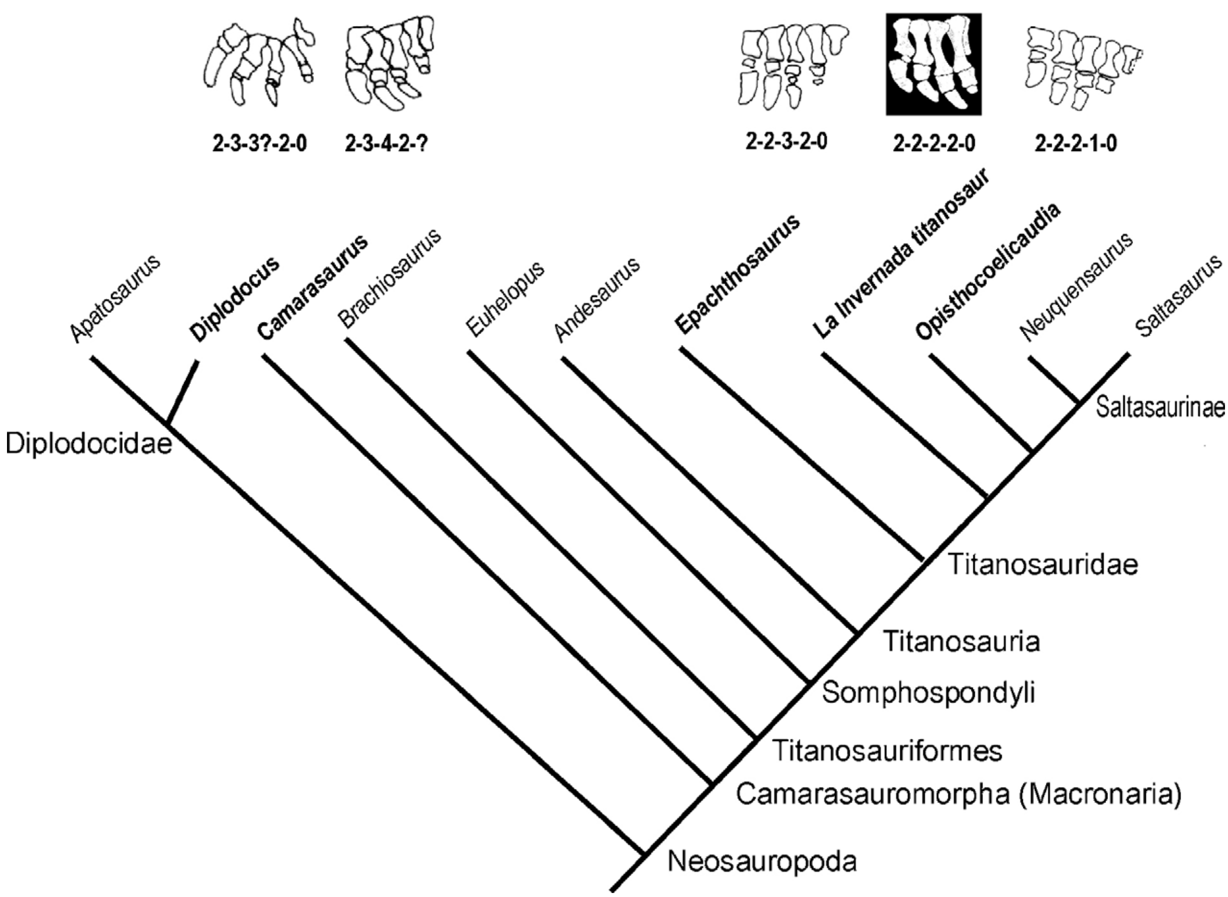

Fig. 9. Schematic cladogram of the neosauropods (modified from Salgado et al. (1997a), Wilson and Sereno (1998), Wilson (2006)) showing selected taxa, pedal structures and phalangeal formulae: *Diplodocus* and *Camarasaurus* (after Farlow, 1992), *Epachthosaurus* (after Martínez et al., 2004), 'La Invernada titanosaur' (this paper, specimen MUCPv-1533 from Argentina) and *Opisthocoelicaudia* (based on Borsuk-Bialyncka, 1977). The phylogenetic position of 'La Invernada titanosaur', based on axial characters, is hypothetic. *Observations*: The Macronaria clade (Wilson and Sereno, 1998) has not the same phylogenetic definition of Camarasauromorpha (sensu Salgado et al., 1997a).

This phalanx has a convex proximal end that articulates with the concave face of the distal end of the phalanx I of digit IV.

4. Discussion

The fossil preservation of titanosaurian pedes is very rare due to taphonomic processes of disarticulation. For this reason, most pes reconstructions are made with certain degree of uncertainty. For instance: *Janenshia robusta* Fraas, 1908 has a complete right pes (Fraas, 1908, plate XII) with a phalangeal formula 2-3-3-2-1; however, Bonaparte et al. (2000, p. 38) stated that "digit IV and V either lack ungual phalanges, or they could have been lost due to taphonomic factors" but they draw the complete pes (Bonaparte et al., 2000; Fig. 8A). Another example is the pes of a titanosauriform from Russia (Averianov et al., 2002) reconstructed with few bones.

A complete titanosauriform pes belongs to *Gobititan* (You et al., 2003) from the Albian of China. The phalangeal formula is 2-2-2-2-2, and it has a phalanx in the digit V, absent in all titanosaurs recorded. Although it was assigned to a Titanosauria, it does not have synapomorphies of this group of sauropods. Therefore, and based on the diagnosis of *Gobititan*, we can only consider it as a titanosauriform, not as a titanosaur.

The calcaneum is present in titanosauriforms such as *Brachiosaurus* and *Gobititan*; however it is absent in the specimen herein described and in other known titanosaurids.

Up to now, just two taxa have provided information about the pes structure in titanosaurids: *Opisthocoelicaudia skarzynskii* from Mongolia and *Epachtosaurus sciutoi* (Martínez et al., 2004) from Chubut Province.

The specimen described (MUCPv-1533) includes a partial caudal series and the left portion of the skeleton but lacks the skull and cervical vertebrae. The pes has five metatarsal and the phalangeal formula is 2-2-2-2-0. The first three digits possess sickle-shaped claws and the articular faces of ungual phalanges suggesting mobility in horizontal and vertical planes. In particular the first phalanx of the digit I is a much reduced structure (Fig. 7). In contrast, with this pedal structure, *Epachthosaurus* has a phalangeal formula 2-2-3-2-0 (Fig. 8) and *Opisthocoelicaudia* has 2-2-2-1-0. It is showing a wide diversity of pedal morphology in titanosaurid sauropods.

In general, the evolution of the sauropod pes shows a phalangeal reduction trend (Carrano, 2005), but this aspect has not been well documented in titanosaurs. In this context, phylogenetic analyses of titanosaurs indicate that *Epachthosaurus* is a basal taxon, and *Opisthoceolicaudia* is a derived genus closely related to *Saltasaurus* (Salgado et al., 1997a; Wilson, 2006). This record suggests that titanosaurs had a progressive reduction in the size and number of pedal phalanges in digits III and IV toward the end of the Cretaceous (Fig. 9). The new material from Patagonia herein described could be considered as a titanosaurid more derived than *Epachthosaurus*, based on its pedal structure. This preliminary hypothesis may be confirmed with a detailed study of the rest of skeleton.

5. Conclusions

An exceptionally preserved titanosaurid specimen from the late Campanian–Early Maastrichtian strata of Argentina provides new evidence of pedal morphology in these dinosaurs. As far as we know, this is the third record of a titanosaur articulated pes, and shows a phalangeal formula of 2-2-2-2-0. Morphological analysis of this structure suggests that titanosaurs had a progressive reduction in the size and number of pedal phalanges in digits III and IV, from the Late Cenomanian–Early Turonian to the Late Campanian–Early Maastrichthian in age.

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References

Andreis, R.R., Iñíguez Rodríguez, A.M., Lluch, J.J., Sabio, D.A., 1974. Estudio sedimentológico de las Formaciones del Cretácico Superior del área del Lago Pellegrini (provincia de Río Negro, República Argentina). Rev. Asoc. Geol. Argent. 29, 85–104.

Averianov, A.O., Voronkevich, A.V., Maschenko, E.N., Leshchinskiy, S.V., Fayngertz, A.V., 2002. A sauropod foot from the Early Cretaceous of Western Siberia, Russia. Acta Palaeontol. Polon. 47 (1), 117–124.

Barrio, C.A., 1990. Late Cretaceous–Early Tertiary sedimentation in a semiarid foreland basin (Neuquén Basin, western Argentina). Sediment. Geol. 66, 255–275.

Bonaparte, J.F., Heinrich, W.D., Wild, R., 2000. Review of *Janenschia* Wild, with the description of a new sauropod from the Tendaguru beds of Tanzania and a discussion on the systematic value of procoelous caudal vertebrae in the Sauropoda. Palaeontographica 256, 25–76.

Bonnan, M.F., 2005. Pes anatomy in sauropod dinosaurs: implications for functional morphology, evolution, and phylogeny. In: Carpenter, K., Tidwell, V. (Eds.), Thunder-Lizards: The Sauropodomorph Dinosaurs. Indiana University Press, Bloomington, pp. 346–380.

Borsuk-Bialyncka, M., 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii*, gen. n. sp. n. from the Upper Cretaceous of Mongolia. Palaeontol. Polon. 37, 45–64.

Carrano, M.T., 2005. The evolution of Sauropod Locomotion. In: Curry Rogers, K.A., Wilson, J.A. (Eds.), The Sauropods, Evolution and Paleobiology. University of California Press, Berkeley, pp. 229–251.

Cazau, L.B., Uliana, M.A., 1973. El Cretácico Superior continental de la Cuenca Neuquina. 5° Congreso Geológico Argentino 3, pp. 131–163.

Curry Rogers, K., 2005. Titanosauria. In: Curry Rogers, K.A., Wilson, J.A. (Eds.), The Sauropods, Evolution and Paleobiology. University of California Press, Berkeley, pp. 50–103.

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Farlow, J.O., 1992. Sauropod tracks and trackmakers: integrating the ichnological and skeletal records. Zubia 10, 89–138.

Fraas, E., 1908. Ostafrikanische Dinosaurier. Palaeontographica 55, 105–144.

Gallup, M.R., 1989. Functional morphology of the hindfoot of the Texas sauropod *Pleurocoelus* sp. indet. Geological Society of America, Special Paper 238, 71–74.

González Riga, B.J., 1999. Hallazgo de vertebrados fósiles en la Formación Loncoche, Cretácico Superior de la provincia de Mendoza, Argentina. Ameghiniana 36, 401–410.

González Riga, B.J., 2003. A new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza, Argentina. Ameghiniana 40, 155–172.

Legarreta, L., Gulisano, C., 1989. Análisis estratigráfico secuencial de la cuenca Neuquina (Triásico superior–Terciario inferior). In: Chebli, G., Spalletti, L. (Eds.), Cuencas Sedimentarias Argentinas, Serie Correlación Geológica, vol. 6. Universidad Nacional de Tucumán, pp. 221–243.

Martínez, R.D., Jiménez, O., Rodríguez, J., Luna, M., Lamanna, M.C., 2004. An articulated specimen of the basal titanosaurian (Dinosauria: Sauropoda) *Epachthosaurus sciuttoi* from the Early Late Cretaceous Bajo Barreal Formation of Chubut Province, Argentina. J. Vertebr. Paleontol. 24 (1), 107–120.

Parras, A.M., Casadío S., Pires, M., 1998. Secuencias depositacionales del Grupo Malargüe y El límite Cretácico–Paleógeno, en el sur de la provincia de Mendoza, Argentina. Asociación Paleontológica Argentina, Publicación Especial 5 Paleógeno de América del Sur y Península Antártica, pp. 61–69.

Salgado, L., 2003. Should we abandon the name Titanosauridae? Some comments on the taxonomy of titanosaurian sauropod (Dinosauria). Rev. Espan. Paleontol. 18, 15–21.

Salgado, L., Coria, R.A., Calvo, J.O., 1997a. Evolution of titanosaurid sauropods. I. Phylogenetic analysis based on the postcraneal evidence. Ameghiniana 34, 3–32.

Salgado, L., Coria, R.A., Calvo, J.O., 1997b. Presencia del género *Aelosaurus* (Sauropoda, Titanosauridae) en la Formación Los Alamitos, Cretácico Superior de la Provincia de Río Negro, Argentina. Geociencias II (6), 44–49.

Salgado, L., Apesteguía, S., Heredia, S., 2005. A new specimen of *Neuquensaurus australis*, a Late Cretaceous saltasaurine titanosaur from north Patagonia. J. Vertebr. Paleontol. 25 (3), 623–634.

Sereno, P.C., 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. Neues Jahrb. Geol. Palaontol. Abh. 210, 41–83.

Vergani, G.D., Tankard, A.J., Belotti, H.J., Welsink, H.J., 1995. Tectonic evolution and Paleogeography of the Neuquén Basin, Argentina. In: Tankard, A.J., Suárez, S.R., Welsink, H.J. (Eds.), Petroleum Basin of South America, vol. 62. AAPG Memoir, pp. 383–402.

Weishampel, D.B., Dodson, P., Osmólska, H., 1990. Introduction. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. University of California Press, Berkeley, pp. 1–7.

Wilson, J.A., 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. Zool. J. Linn. Soc. 136, 217–276.

Wilson, J.A., 2006. An overview of titanosaur evolution and phylogeny. In: Colectivo Arqueológico–Paleontológico Salense (Ed.), Actas de las III Jornadas sobre Dinosaurios y su Entorn. Burgos, pp. 169–190.

Wilson, J.A., Sereno, P., 1998. Early evolution and higher level Phylogeny of sauropod dinosaurs. J. Vertebr. Paleontol. 18 (Supplement to number 2), 1–68.

Wilson, J.A., Upchurch, P., 2003. A revision of *Titanosaurus* Lydekker (Dinosauria–Sauropoda), the first dinosaur genus with a 'Gondwanan' distribution. J. System. Palaeontol. 1 (3), 125–160.

You, H., Tang, F., Luo, Z., 2003. A new basal Titanosaur (Dinosauria: Sauropoda) from the Early Cretaceous of China. Acta Geol. Sinica (English Edition) 77 (4), 424–429.

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