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Sauropod and theropod dinosaur tracks from the Upper Cretaceous of Mendoza (Argentina): Trackmakers and anatomical evidences

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ABSTRACT

New findings of dinosaur ichnites from Agua del Choique section (Mendoza Province, Argentina) provides ichnological and anatomical information about the Cretaceous sauropods and theropods. Around 330 tracks distributed in six footprint levels were identified in this area, one of most important of South America. Two ichnocenoses are located in different paleoenvironmental contexts. In the Anacleto Formation (early Campanian) around 20 titanosaurian tracks were found in floodplain and ephemeral channel deposits. Herein, one pes track shows three claw impressions and this is congruent to two new titanosaur specimens recently discovered in Mendoza Province that have articulated and complete pedes. In this context, for the first time to titanosaurs, ichnological evidences are supported by skeletal elements. In the Loncoche Formation (late Campanian-early Maastrichtian) titanosaurian tracks of *Titanopodus mendozensis* are abundant (around 310 tracks) and were produced by titanosaurs that walked in a very wet substrate of tidally dominated deltas related with the first Atlantic transgression for northern Patagonia. In this facies association, three different trydactl tracks indicate the presence of small theropods (1–2 m long), expanding the knowledge about the faunistic components that lived in these marine marginal environments.

1. Introduction

Ichnological studies are essential for understanding the locomotion and behavior of dinosaurs. Important dinosaur track sites have been described in South America, particularly in Chile (Casamiquela and Fasola, 1968; Moreno and Pino, 2002; Moreno et al., 2004; Moreno and Benton, 2005), Bolivia and Brazil (Leonardi, 1989; Meyer et al., 2001; Lockley et al., 2002; Souza et al., 2010; Carvalho, 2004; Tavares et al., 2014). In Argentina, dinosaur track sites are known from Salta, Neuquén, and Mendoza Provinces. In Salta Province, Eastern Puna, theropod and ornithopod tracks were discovered in littoral and continental deposits of the Yacoraite Formation, Maastrichtian in age (Alonso, 1980; Alonso and Marquillas, 1986). In Neuquén Province, northern Patagonia, dinosaur tracks have been found in the Picún Leufú and El Chocón sites. These tracks were found in outcrops of the Candeleros Formation (early Cenomanian), a unit characterized by meandering rivers, poorly channeled ephemeral flows and playa lakes deposits. Titanosaurian tracks from this formation were named *Sauropodichnus giganteus* Calvo 1991.

Recently, a new track site, the first to be described from Mendoza Province and one of the most important of South America, was discovered in the upper Campanian-lower Maastrichtian strata of the Loncoche Formation. Around 310 sauropod footprints were identified. These sauropod tracks were assigned to a new ichnotaxon named *Titanopodus mendozensis* González Riga and Calvo, 2009. These tracks are an excellent example of wide-gauge style of locomotion. These features and the fossil record of the Loncoche Formation and equivalent units of Patagonia (Allen Formation)

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suggest that the *Titanopodus* trackmakers were titanosaurs of middle-size. González Riga (2011) studied the speed developed by the *Titanopodus* trackmakers based on comparative analyses of track sites and one articulated skeleton of "La Invernada" titanosaur specimen discovered in the Allen Formation, northern Patagonia. After this paper, the *Titanopodus* trakmaker has a hip height of 2.29 m and a total length of 12–14 m.

Up to now, all dinosaur tracks from Loncoche Formation correspond to titanosaur sauropods; however we discovered three different morphotypes of theropod tracks which give evidence of a broad ecological diversity in the marine marginal environments of the Upper Cretaceous on the region. Moreover, in the same geological section, 600 m of distance to the *Titanopodus* tracks, we found about 20 ichnites in a new site located in the early Campanian Anacleto Formation. One of the pes track is well preserved and shows three claw impressions. This morphology is compared with articulated and complete pedes recently discovered in Mendoza (specimens UNCUYO-LD-302 and 313) and Neuquén Provinces (MUCPv-1533). Articulated pedes of titanosaurs are extremely scarce in the fossil record; in this context, this study is important in light of its ichnological and anatomical data.

The aim of this paper is to describe, a new case study of titanosaurian tracks with claw impressions and their compassion, for the first time, with articulated pedes recently discovered. We also describe the first theropod tracks findings from Agua del Choique geological section, south of Mendoza Province, Argentina. This new ichnological record enlarges our knowledge of the faunistic components of the latest times of the Cretaceous.

2. Geological setting

Agua del Choique track site is located 14 km west of the Malargüe town in Mendoza Province, Argentina (Fig. 1A). In this area, the senior author discovered multiple track-bearing levels both in the Anacleto and Loncoche Formations. First, in the upper section of the Anacleto Formation (early Campanian) three track levels with sauropod tracks (named herein An-1, An-2 and An-3) were located (Fig. 1B). This formation comprises a fining- and thinning-upward fluvial succession. Facies associations include deep red to purplish massive and laminate mudstones and siltstones interbedded with thin gray to brown lenticular and tabular sandstones that exhibit massive, laminated or cross-lamination. Within the mudstones intervals, intense disruption of original sedimentary structures and fabrics occur by tubular burrowing. The best preserved tracks are located in the An-1 level that is composed by a lenticular medium to fine-grained sandstone bed (~2–10 cm) associated with deep red laminated mudstones. This is interpreted as a floodplain deposits with ephemeral channels.

Second, in the middle section of the Loncoche Formation (late Campanian-early Maastrichtian) three different tracks levels with

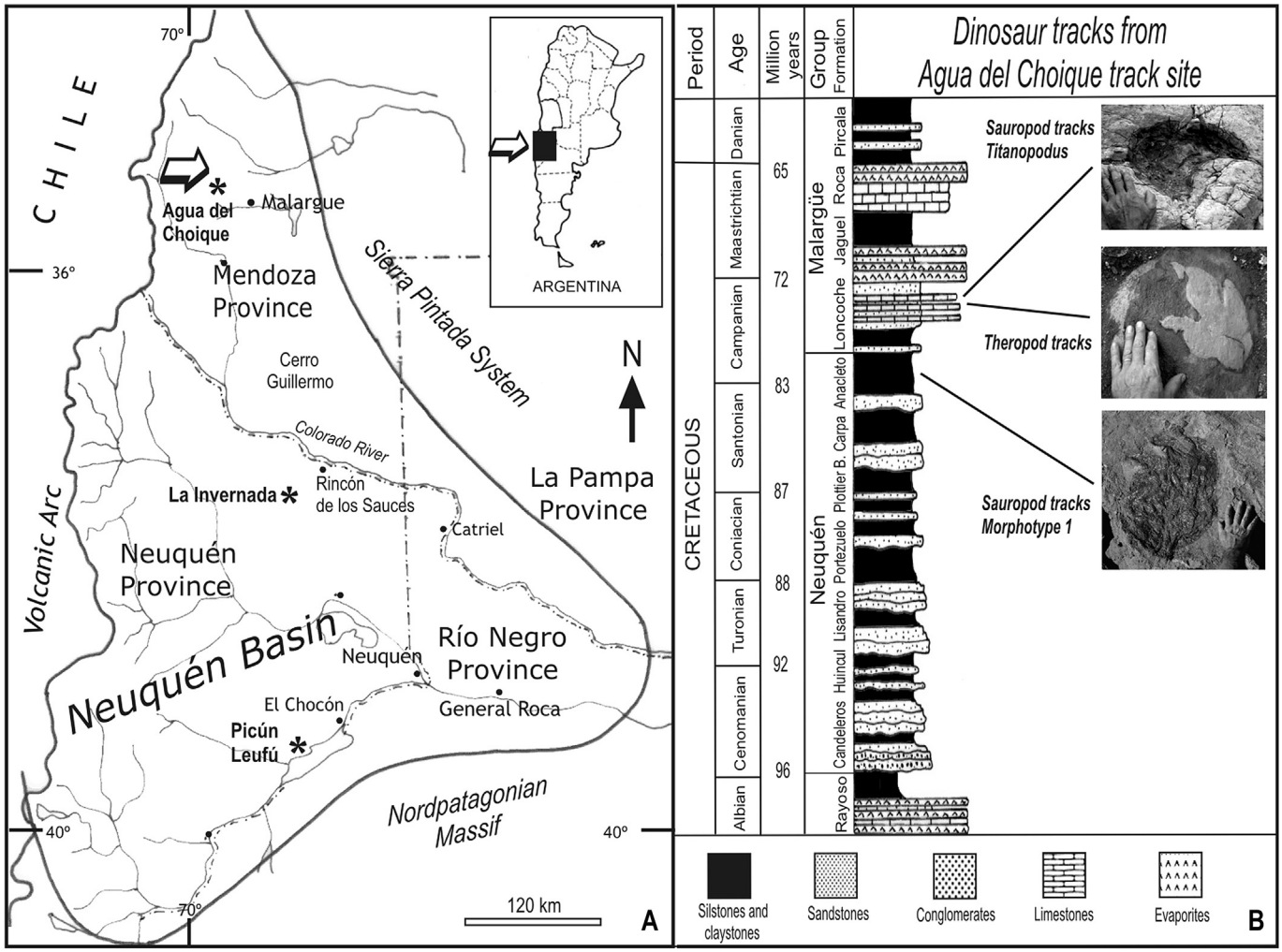

Fig. 1. A. Location map of the Neuquén Basin (Argentina) showing the Agua del Choique and Picún Laufú track sites. B. Stratigraphic column of the Neuquén Basin with indication of the footprint levels in Anacleto and Loncoche Formations.

dinosaur tracks (named herein Lo-1, Lo-2, and Lo-3) were found in marine marginal facies (Fig. 1). In the level Lo-3, the holotype of *Titanopodus mendozensis* is situated.

The Loncoche Formation is the lower unit of the Malargüe Group and unconformably overlies the Anacleto Formation (Neuquén Group). At different sites in Mendoza Province, this formation is comprised by lacustrine and marginal marine facies (e.g., tidal flats, lagoonal and sabkhas deposits) that were produced by a transgression of the Atlantic Ocean that covered central-northern Patagonia (González Riga and Parras, 1998). In the Ranquil-Có and Calmu-Co sections, the Loncoche Formation has yielded a varied association of fossil fishes and reptiles (González Riga, 1999; Previtera and González Riga et al., 2008). These vertebrate assemblages are associated with ancient tidally dominated deltaic deposits and include a mixture of terrestrial vertebrates (dinosaurs and snakes), together with freshwater taxa (e.g. turtles, fishes) as well as marine or littoral forms (plesiosaurs and rays). Parras et al. (1998) recognized two depositional environments in the Agua del Choique section. The first is attributed to a river-dominated delta and lake setting, and the second corresponds to a river-dominated delta that change to a tide-dominated delta. They represent a mosaic of dynamic coastal environments developed within a very low-gradient marginal-marine setting, known as the Neuquén embayment (Astini et al., 2014). The *Titanopodus* level as well as the other track horizons dip 12–15° toward the northeast (80°).

3. Methods

For sauropod tracks we follow the terminology of Farlow et al. (1989) (Figure 2.A). The dimension of sauropod tracks were measured inside any mud rims, i.e., across the floor of the track that corresponds to the area where the foot registered (see Lockley et al., 2004). To study the relative wide of the trackway, we follow the indices proposed by Romano et al. (2007). These authors defined the manus trackway ratio (MTR) and pes trackway ratio (PTR) as the ratio of the track width measured transversely to the midline (side width, SW) relative to the total width of the trackway (overall width, OW) as follows: TR = SW/OW x 100.

The estimation of speed was made using the original paper of Alexander (1976). This author proposed this equation ($V = 0.25\ G^{0.5}\ S^{1.67}\ H^{-1.17}$) where V is the speed, G is the acceleration of free fall, H is the height of the hip joint from the ground and S is the stride (the distance between corresponding points on successive prints of the same foot).

The estimation of H is difficult because it is based on the length of the hind foot print (L). As refinements of previous studies, González Riga (2011) calculated that H is about 4.586 based on an articulated titanosaur specimen from Patagonia (González Riga et al., 2008), similar in size and age to the *Titanopodus* trackmaker. For theropod tracks we follow the parameter of Leonardi (1987) and Farlow et al. (1989) (Figure 2.B.). The measurements are explained in the Fig. 2.

Institutional Abreviations. UNCUYO-LD, Universidad Nacional de Cuyo, Facultad de Ciencias Exactas y Naturales, Laboratorio de Dinosaurios, Mendoza, Argentina. MUCPv, Universidad Nacional del Comahue, Museo de Geología y Paleontología, Neuquén, Argentina.

4. Results

4.1. Sauropod tracks

4.1.1. Morphotype 1

In the upper section of the Anacleto Formation three levels with sauropd tracks are located. In the level An-1, nine tracks are well exposed, three of them disposed in a trackway directed to the northwest (292°). They show a manus-pes distance of 105 cm. The manus tracks have crescent shapes with posterior concave contours, and are relatively symmetrical, wider than long (21 cm length; 35 cm width). The pes tracks have a subcircular contour, longer than wide (52 cn length; 38 cm width). The best preserved

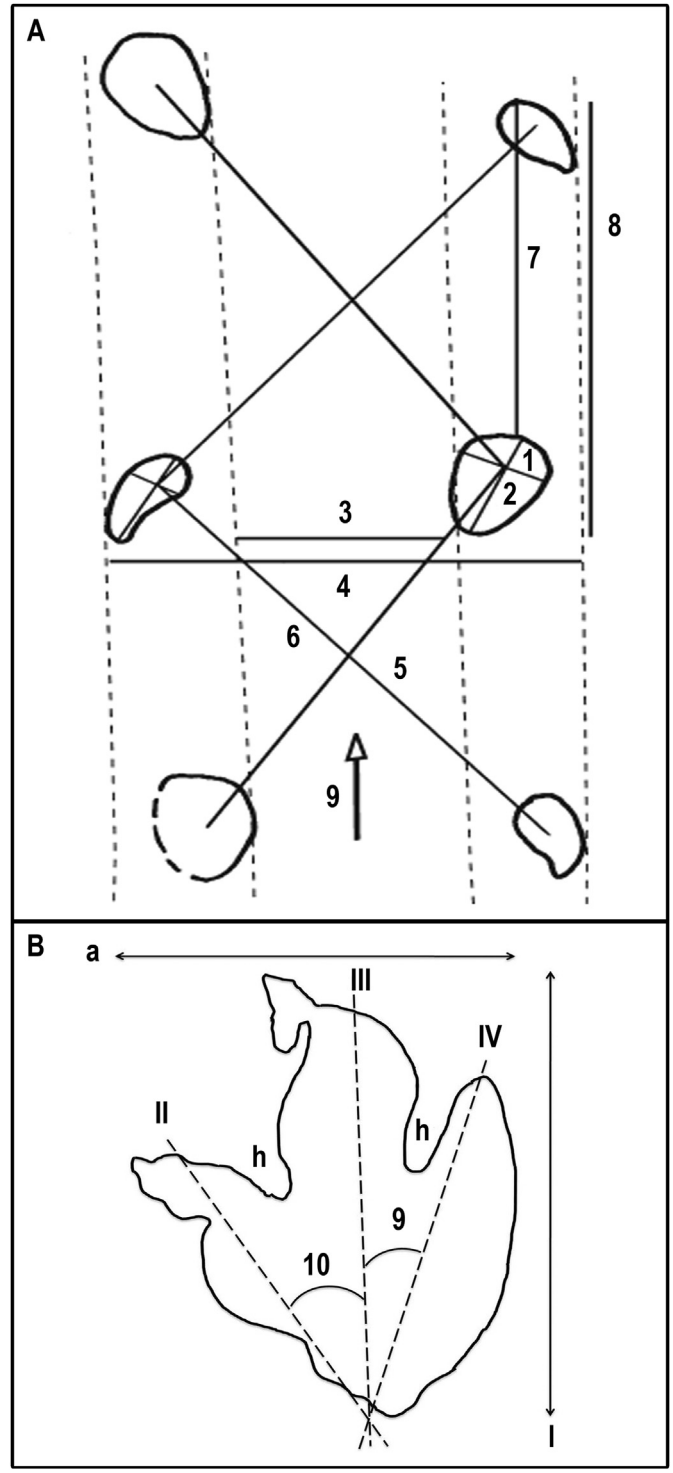

Fig. 2. Measurements of dinosaur tracks. A. Measurements of sauropod tracks based on Farlow et al. (1989). 1. Pes, footprint width, 2, pes footprint length. 3, inner trackway width. 4, outer trackway width, 5, manus pace. 6, pes pace. 7, manus-pes distance. 8, length of manus-pes set. 9, direction of the gait. B. Measurements of theropod tracks after Leonardi (1987) and Farlow et al. (1989). L, total length., W, total width, Ratio L/W; (h) Hypex; 9, angle between the digits III and IV; 10, angle between the digits II and III.

track is associated with a manus and exhibits the impression of claws in the digits I, II and III. Claw impressions are laterally deflected and their print is not deep (~4 cm) (Fig. 3). The other pes tracks have a deep of 5–8 cm and show a reduced slim.

The sauropod tracks of the level An-2 exhibit a subcircular to subtriangular pes tracks. They are longer than wide (30 cm width; 35 cm length). These ichites have a typical wide-gauge trackway, with an indice of PTR (pes trackway ratio) *sensu* Romano et al. (2007) of 25. The manus track are overprinted in the pes tracks, like have been described in some track sites of Spain (e.g. Casanovas et al., 1997). The level An-3 is only exposed in cross section.

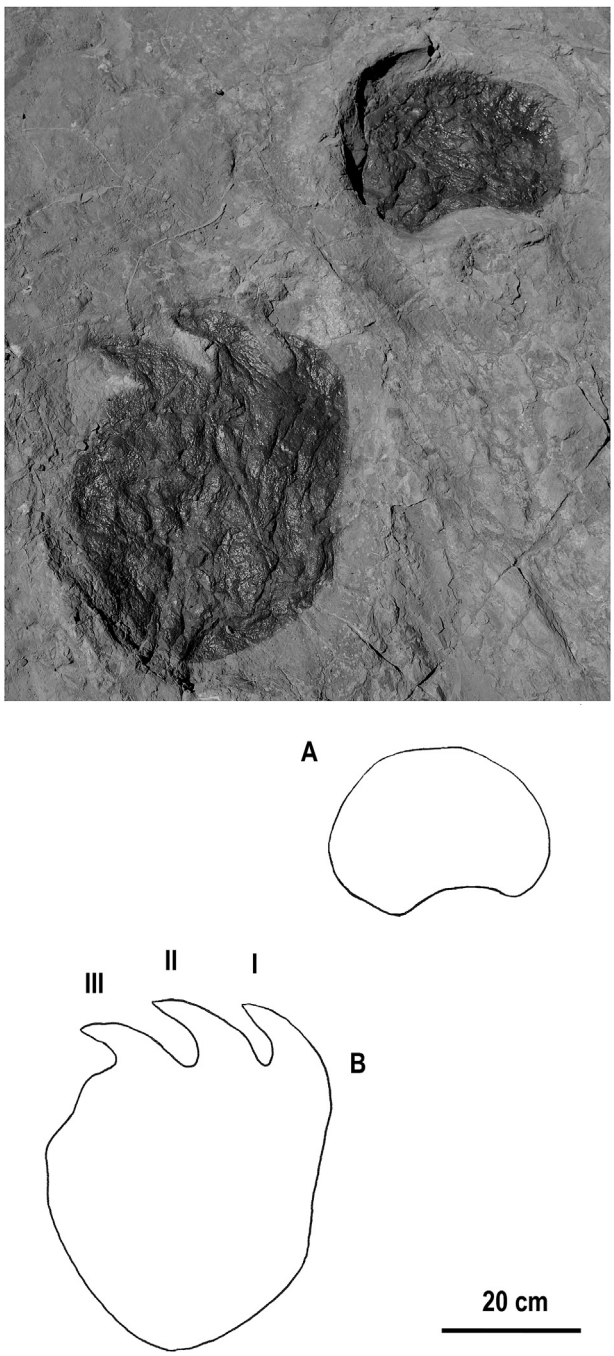

Fig. 3. Manus (A) and pes (B) tracks of the morphotype 1 from the Anacleto Formation. Note the claw impression on the pes track.

4.1.2. Morphotype 2: Titanopodus mendozensis

The *Titanopodus* tracks (described as morphotype 2 in this paper) were located in the level Lo-3, in the middle section of the Loncoche Formation. It corresponds to yellowish grey, calcareous sandstone facies interbedded with yellow oolitic limestones and green claystones. This association of facies corresponds to a tide-dominated delta. In this level around 310 titanosaur tracks and two different theropod tracks, the morphotypes 4 and 5 of this paper. The level Lo-2 is located 80 cm under the Lo-1 and corresponds to sauropod tracks preserved in cross-section. González Riga and Calvo (2009) published a detailed description of *Titanopodus* tracks, focused on the trackways AC-1 (27 ichnites) and AC-2 (71 ichnites). Manus tracks of AC-1 trackway are lateromedially elongated (32.2 cm width and 19.6 cm length) and have a typical crescent shape but with a peculiar morphology: a very asymmetrical contour with an acuminated and thinner external border, unlike the manus of the morphotype 1 (Anacleto Formation, this paper) and the manus of *Sauropodichnus giganteus* from Northern Patagonia (Calvo, 1991, 1999). In Titanopodus manus there are no indications of digits or claw impressions. Pes tracks are subtriangular to subcircular in shape (34 cm width and 46 cm length) (Table 1). Pedal claw impressions are not preserved. The ichnological features of *Titanopodus* indicated that its trackmakers were sauropods of wide-gauge stance where both manus and pes prints were well separated from the midline, as is described in titanosauriforms (Wilson and Carrano, 1999) (Fig. 4). In trackway AC-1 (holotype of *Titanopodus*), the total width of the trackway is about 133 cm, and the inner trackways width is about 40 cm. In this case, the trackway shows a MTR and PTR values of 24.2 and 25.5 per cent, respectively. These values indicate that *Titanopodus* has a very wide-gauge trackway in comparison with other trackways known. According to the speed study of González Riga (2011) the *Titanopodus* tracks were produced by medium-sized titanosaurs that had a hip height of 2.10 and 2.29 m in the AC-1 and AC-2, respectively. In trackway AC-1 (18.5 m long) one titanosaurian individual walked at 1.361 m/s (4.9 km/h) toward the southwest (193–224). In trackway AC-4 (46.2 m long) another titanosaur of similar size walked at 1.323 m/s (4.7 km/h) following a sinuous pathway. In both trackways, some pes tracks reach a depth of 20–30 cm and exhibit a distorted contour. Some of them are elongated (about 50–60 cm length) in comparison with the best preserved prints. In these tracks the presence of prominent rims indicates high water content in the substrate and some degree of sliding of the pedes during locomotion. The *Titanopodus* trackmakers moved at moderate speed, indicating their capacity to effectively walk in very humid substrates.

4.2. Theropod tracks

In the middle section of the Loncoche Formation, the print levels Lo-1 and Lo-3 preserves theropods tracks. They show some features that are common in theropod tracks like tridactyl impression longer than wide, digits with high length/width ratio, low interdigital angles, asymmetrical posterior border (heel), presence of well defined digital pads and a notch on the posterior medial border of the heel (García-Ramos et al., 2001; Lockley, 2009).

4.2.1. Morphotype 3

Only one tridactyl track is preserved on a thin grey mudstone located in the level Lo-1, under 144 cm to the level Lo-3 of *Titanopodus.* In the level Lo-1, 7 m of distance to the tridactyl track, we found an isolated vertebral centrum of Elasmosauridae. Tridactyl track corresponds to a right pes (22.5 cm length and 19 cm width) and exhibits a well preserved impression of claws and digits. The digits are relatively thick, being the digit III longer than the other

Table 1
Data of the AC-1 and AC-4 trackways showing the field measurements and tue ichnological indices.

Trackway	Manus		Pes		External width of the track(cm)	Internal width of the track (cm)	Romano's index		Direction of the gait	Height (cm)	Stride (cm)	Estimated speeds
	Length (cm)	Width (cm)	Length(cm)	Width (cm)			PTR (%)	MTR (%)				
AC-1	19.6	32.2	46	34	133	40	25.5	24.2	208°	210.9	235	1.361 m/s 4.901 km/h
AC-4	17	34	50	36.6	150	55	24.4	22.6	176°	229.3	245	1.323 m/s 4.765 km/h

ones. The claws of digits II and III are displaced medially. The heel had an acuminate edge and a posterior notch on the left border. In the Table 2 are described the angles between digits and ratio length/width of digits. Morphotype 4 is partially similar to *Abelichnus astigarrae* Calvo 1991 from the Canderos Formation (Early Cenomanian, Neuquén Province, Patagonia), but it is smaller and had finders relatively shorter than *Abelichnus*. (Fig. 5A.)

4.2.2. Morphotype 4

A left tridactyl track, longer than wide, is preserved in the level Lo-3. Digits are relatively thick and long. The digit III is longer than the other ones, and the digit II is shorter than the digit III. The heel had a rounded and expanded contour, unlike to the morphotype 3. The pads of the digits are well defined. The interdigital angles are very low (see Table 2) and the track shows a subparallel fingers. The noch of the heel is poorly developed and is located on the right side. The morphotype 4 is partially similar to an indeterminate theropod track from the Candeleros Formation, Early Cenomanian, Neuquén Province, Patagonia (Calvo, 1991) although the digit III is longer than the digit II and exhibits an asymmetrical contour. (Fig. 5B.)

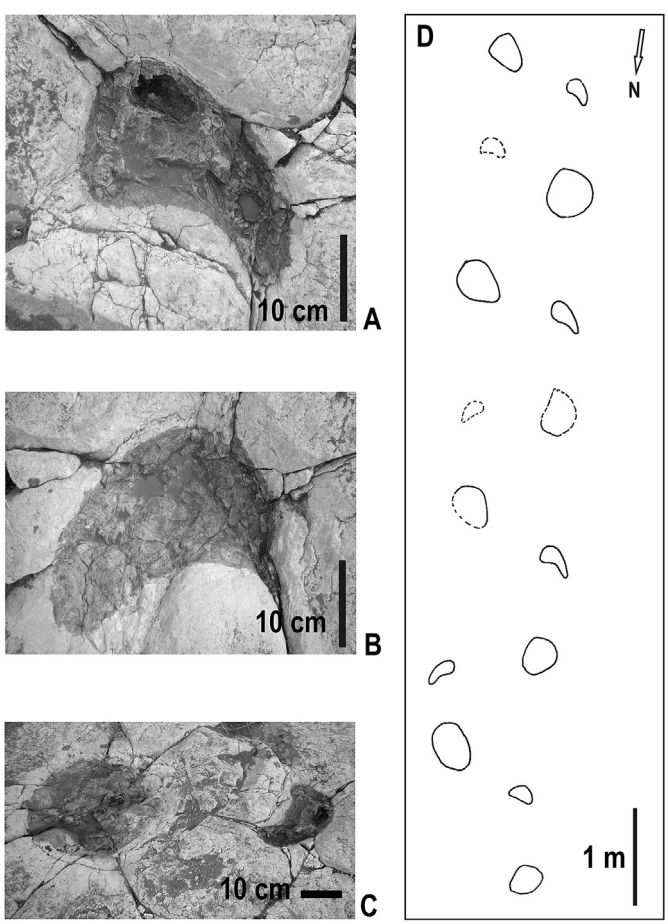

Fig. 4. *Titanopodus mendozensis* tracks. A, right manus. B, left manus. C, manus-pes track set. D, map of the trackway AC-1 (modified from González Riga and Calvo, 2009).

4.2.3. Morphotype 5

A small left tridactyl track (10.3 cm length and 8 cm width) is preserved in the level Lo-3, 33 m to the morphotype 4. The digit III is the longest and the digit IV shows the impression of the claw laterally displaced (see Table 2). Impressions of digits are relatively short and thick. The digit IV is longer than the digit II. Heel exhibits an acuminate posterior border and posterior notch on the right left side is well defined. (Fig. 5C.)

5. Discussion

5.1. Trackmackers of sauropod ichnites

In South America, the only sauropod that lived since the Coniacian age are titanosaurs (e.g. Leanza et al., 2004; González Riga, 2011). This is congruent with the ichnological record described in this paper. In the Anacleto Formation (early Campanian) both the wide gauge style of locomotion and the morphology of the tracks confirm that the trackmakers were titanosaurs. The most conspicuous of the morphotype 1 of the Anacleto Formation is the preservation of claw impressions. Although other studies have documented impressions of digits or claws in titanosaurs, they are poorly defined and do not provide relevant anatomical information. For example, in Bolivia Lockley et al. (2002) described titanosaur tracks with three poorly defined digital prints. Moreover, in Fumanya (Spain) Le Loeuff and Martínez-Rius (1997); Schulp and Brokx (1999) and Vila et al. (2008) mentioned the presence of four pedal ungeals in sauropod tracks. Both sites correspond to the Maastrichthian and were made by titanosaurs.

Anatomically, the record of articulated and complete pes is really scarce in titanosaurs. Up to now, from around 65 titanosaur species recognized across the world, only three taxa exhibit complete pedes: *Opisthocoelicaudia* Borsuk-Bialynicka 1977 from the Maastrichthian of Mongolia, *Epachthosaurus sciuttoi* Powell, 1990 (Martínez et al., 2004) from the Chubut Province, Patagonia, Argentina, and La Invernada titanosaur specimen (MUCpv-1533, González Riga et al., 2008) from Neuquén Province, Patagonia, Argentina. In the last years, we discovered in the South of Mendoza province, two new titanosaur specimens that preserve articulated pedes from the late Coniacian-early Santonian Plottier Formation. One of them correspond to a large titanosaur (UNCUYO-LD 301 and 302) represented by an anterior dorsal vertebra, an anterior caudal vertebra, some middle caudal vertebrae, the right humerus, a fragment of left pubis, and an articulated right pes. This pes is

Table 2
Measurements (in cm) of theropod tracks.

	Length (L)	Width (W)	Length/ Width ratio	Hypex (h)		Interdigital angles		Length/ width ratio of the digit
				h II-III	h III-IV	II-III	III-IV	
Morphotype 3	22.5	19.2	1.17	3.7	2.5	39°	27°	2.74
Morphotype 4	22.4	13.3	1.68	0.2	0.2	20°	19°	3.64
Morphotype 5	10.3	8	1.28	1.1	1.4	23°	27°	4.45

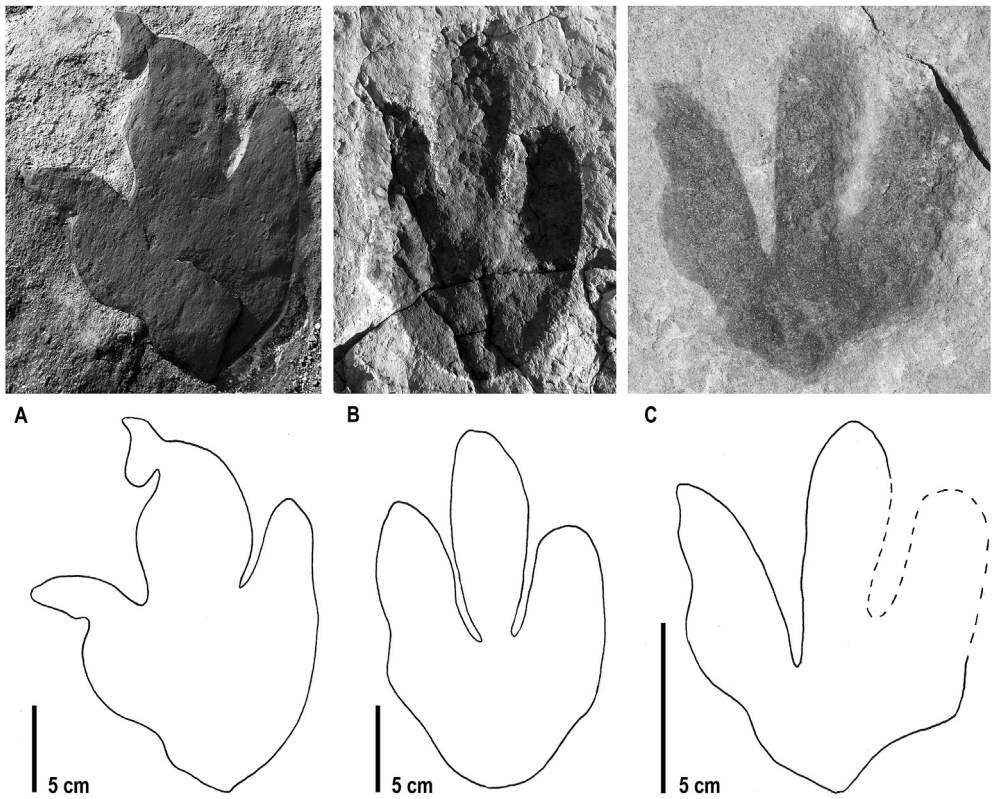

Fig. 5. Theropod tracks from the Loncoche Formation. A, morphotype 3. B, morphotype 4. C, morphotype 5.

relatively robust and had short metatarsals (Fig. 8C). The other titanosaur specimen correspond to a slender titanosaur (UNCUYO-LD 313) represented by a complete pes and some appendicular bones (Fig. 8A.). Anatomically, both titanosaur specimens from Mendoza, as well as the La invernada specimen from Neuquén, have the same phalangeal formula (2-2-2-2-0) and exhibit three sickle-shaped ungeals (claws) that were laterally deflected in the field (Fig. 8B.). The fourth digit has a very small and rounded ungeal phalanx. This anatomical structure is perfectly consistent with the pes track of the Anacleto Formation which shows only three claw impressions laterally deflected (Figs. 6 and 7).

In the case of *Titanopodus mendozensis* tracks from the Loncoche Formation (late Campanian-early Maastrichtian), trackmakers are also titanosaurs. This point was widely justified in previous papers (González Riga and Calvo, 2009; González Riga, 2011). Trakmaker of *Titanopodus* was different than those of the titanosaurian tracks of the Anacleto Formation (morphotype 1, this paper). They lived in different times and shows differences in the manus shape. The manus track is symmetrical in the morphotype 1 indicating a semi-tubular and U-shaped structure of metatarsals, as in most titanosaurs (e.g. *Epachthosaurus*, *Opisthocoelicaudia*). In contrast, the asymmetry of the manus track *Titanopodus* is probably related with

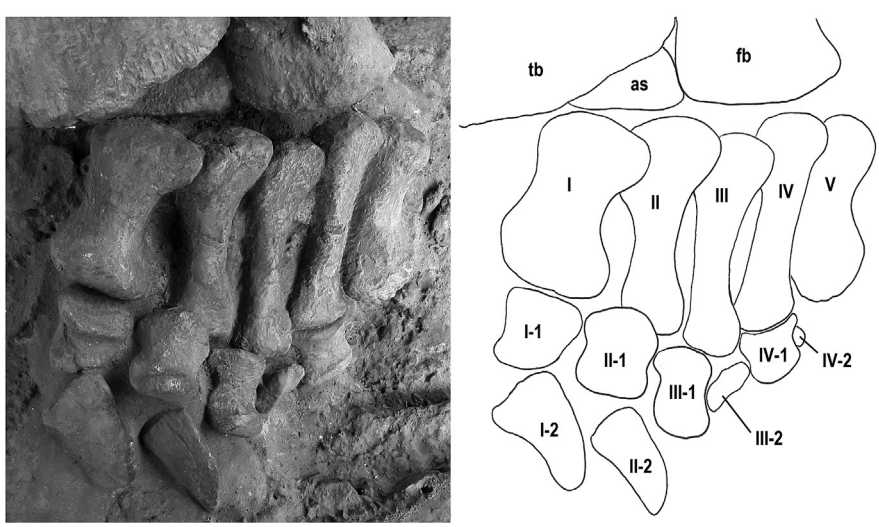

Fig. 6. Articulated and complete left pes of a new titanosaur exceptionally preserved from. the Neuquén Group, Plottier Formation (Specimen UNCUYO-LD-313). Note almost all bones are preserved in their original anatomical position. It has a phalangheal formula of 2-2-2-2-0 with three sickle-shaped ungeals (claws I-2, II-2 and III-2).

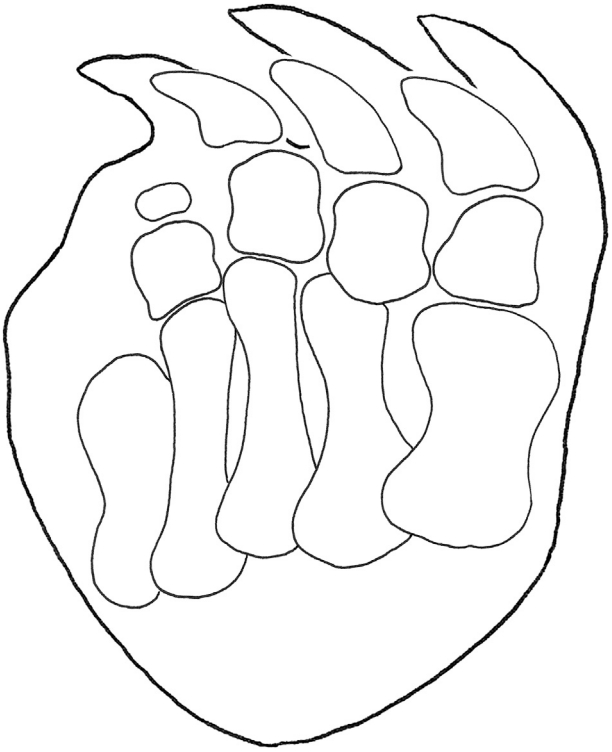

Fig. 7. Pes track (morphotype 1) with the impression of claws (Anacleto Formation) in comparison with the articulated pes of a new titanosaur species (UNCUYO-LD-313, Plottier Formation). Both from the Neuquén Group of Mendoza.

an asymmetry of the metacarpals, like we can observe in the La Invernada titanosaur from the Allen Formation of the Neuquén Province (specimen MUCPv-1533; González Riga et al., 2008). The Allen Formation is a lateral equivalent of the Loncoche Formation and both are deposited in the Neuquén Basin. In La Invernada titanosaur the metacarpals I and II are very robust elements in comparison with more laterally-positioned metacarpals (see González Riga, 2011). Other characters related with the bone structure of the foot are not preserved in the ichnological record of *Ttitanopodus*.

5.2. Trackmackers of theropod ichnites

The analysis of theropod tracks is based on the fossil record from Argentina and the anatomy of the hindlimb of this taxa. Argentina has the most relevant record of Cretaceous theropods from the Southern Hemisphere. It includes over 30 genera grouped into six clades: Abelisauridae, Noasauridae, Carcharodontosauridae, Megaraptoridae, Alvarezsauridae and Unenlagiidae. Abelisauroidea (Abelisauridae + Noasauridae) had a big radiation during the Cretaceous of Gondwana and their fossil remains have been found in Argentina, Brazil, Morocco, Nigeria, Libya, Madagascar, India and France (Carrano and Sampson, 2008; Novas, 2009). The theropod tracks described herein were made by small size theropods that lived during the latest times of the Cretaceous, like Alvarezssauridae, Megaraptoridae and Abelisauria. Is pretty sure Unenlagiidae taxa were not the trackmakers, since they are associated with tracks characterized by only two digits (Apesteguía et al., 2011; Li et al., 2007; Xing et al., 2013). Moreover, is also probable that Carcharodontosauridae taxa were not the trackmakers, since their fossil record is still questionable toward the end of the Cretaceous. We believe it is inappropriate to assign a particular theropod ichnotaxon to isolated tracks, like we describe in this paper. However, according to the anatomy of the footprints, the morphotype 4 presents similarities with *Jialingpus yuechiensis* Zhen et al., 1983 from the Lower Cretaceous of China, and the morphotype 5 has some likeness with *Paracorpulentapus zhangsanfengi* from the Upper Cretaceous of China (Lida Xing et al., 2014), although the latest it is smaller in size.

6. Conclusions

Agua del Choique geological section from the Late Cretaceous of Mendoza, Argentina, is one of most important ichnological areas of South America. It records two different ichnocenoses, one in the Anacleto Formation (early Campanian) and other in the Loncoche Formation (late Campanian-early Maastrichtian).

In the Anacleto Formation titanosaurian tracks are preserved in floodplain deposits and ephemeral channels. Both the morphology of tracks and the wide gauge style of locomotion confirm that the trackmakers were titanosaurs. One of tracks preserved claw impressions and their shape is congruent with articulated and complete pedes of two new titanosaurs discovered in the same red strata of the Neuquén Group (Plottier Formation) exposed in the Mendoza Province. Articulated pedes are extremely scarce in the titanosaur record; in this context, for the first time for Titanosauria, ichnological evidences are supported by articulated skeletal elements of the pes.

In the Loncoche Formation the ichnocenosis is dominated by titanosaur tracks assigned to *Titanopodus mendozensis* that correspond to wide-gauge trackways. The *Titanopodus* trackmakers were titanosaurs that walked in very humid substrates of marine marginal environment of the first Atlantic transgression of the region. Finally, new discoveries recognized three new morphotypes of tridactyl tracks assigned to non-Unenlagiidae theropods that walked in these marine marginal environments.

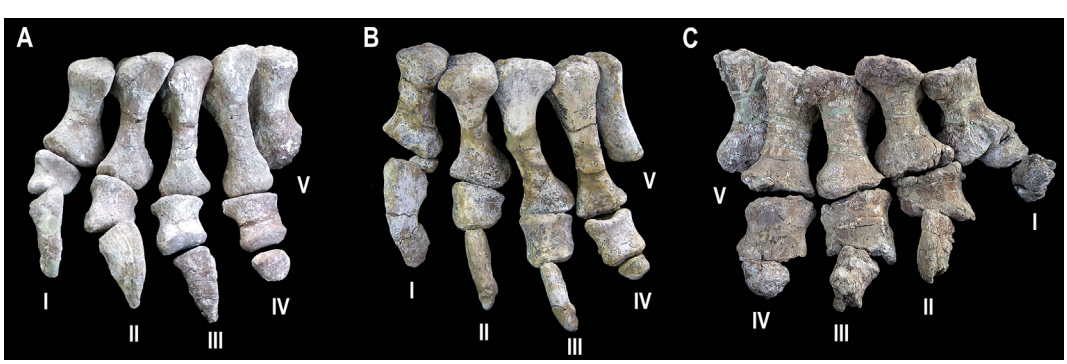

Fig. 8. Articulated and complete pedes of titanosaurs. A. Specimen UNCUYO-LD-313, B. Specimen MUC-Pv-1533; C. Specimen UNCUYO-LD-302.

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