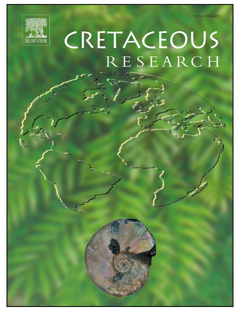

Vertebrate tracks from the Paso Córdoba fossiliferous site (Anacleto and Allen formations, Upper Cretaceous), Northern Patagonia, Argentina: Preservational, environmental and palaeobiological implications

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Vertebrate tracks from the Paso Córdoba fossiliferous site (Anacleto and Allen formations, Upper Cretaceous), Northern Patagonia, Argentina: preservational, environmental and palaeobiological implications

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Abstract. The Paso Córdoba fossiliferous site (Río Negro, Northern Patagonia) is one of the first Mesozoic fossiliferous localities studied in Argentina. There, turtle, crocodile and dinosaur remains as well as dinosaur and bird tracks have been recorded. Recently, a new locality with vertebrate tracks, the Cañadón del Desvío, has been discovered in Paso Córdoba. Six track-bearing layers were located in outcrops belonging to the Anacleto (lower to middle Campanian, Neuquén Group) and Allen (middle Campanian-lower Maastrichtian, Malargüe Group) formations. The Cañadón del Desvío locality reveals that vertebrate trace fossils are distributed in two distinct environments, floodplains of a meandering fluvial to shallow lacustrine system and a wet interdune deposit that is associated to an aeolian setting. Also, in the logged section several soft sediment deformation structures were found. In regard of this, a sedimentary facies analysis is provided in order to assess the palaeoenvironmetal implications of this new record. The analyzed tracks are preserved in cross-sections, on bedding-planes and as natural casts. When it is possible, the tracking surface, true tracks, undertracks and overtracks/natural casts have been identified and the track preservation and the formation history of the tracksite are discussed. Only two tracks preserve enough anatomical details to relate them with their trackmakers, in this case hadrosaurid dinosaurs. The stratigraphical, facial and palaeoenvironmental data of this study support the idea of a transitional passage between the Anacleto and Allen Formation in Paso Córdoba. The presence of hadrosaurid dinosaur tracks suggest that the upper part of the log, where this kind of tracks were found, likely belong to Allen Formation due to this dinosaurs appear in the Southern Hemisphere in this epoch. The sum of osteological and ichnological remains improve the Paso Córdoba paleofaunistic knowledge. The presence of six different levels in which the trackmakers walked reflects the abundance of vertebrates in the transition between Anacleto and Allen formations.

Keywords. Vertebrate ichnology; Sedimentary structures; Paleodiversity; Campanian-Maastrichtian; Argentina.

1. Introduction

The area of Paso Córdoba, situated on the southern margin of the Negro river, to the south of the city of General Roca (Northern Patagonia, Río Negro Province), was one of the first Mesozoic fossiliferous localities in being recognized in the Argentinean territory. In fact, the first discoveries of Mesozoic reptile fossils in that Rionegran locality were reported by Adolf Döering (1882), the German naturalist commissioned in the military expedition to that territory commanded by the General J. A. Roca in 1879 (Salgado, 2007).

The palaeontological potential of the Paso Córdoba area is well known since the discovery, at the beginning of the 20th century, of the partial skeleton of the sauropod dinosaur *Antarctosaurus wichmannianus* von Huene, 1929. These materials have been referred to the Anacleto Formation (Powell, 1986; Garrido, 2010), although some authors think that they come from the overlying Allen Formation (Calvo and Ortíz, 2011; Salgado and Bonaparte, 2007).

In the Paso Córdoba area, the Mesozoic is represented by three lithostratigraphic units, in ascending order, they are: the Bajo de la Carpa, Anacleto and Allen fortmations. The Bajo de la Carpa Formation, represents the lowest Cretaceous unit exposed there, being perhaps the richest one in fossil reptiles of the area. The remains of the small dinosaur *Achillesaurus manazzonei* Martinelli and Vera, 2007, the only theropod from Paso Córdoba recognized at genus level, comes from that unit, as well as the fragmentary materials of an undetermined abelisaur (Ezcurra and Méndez, 2009). The herpetological fossil record of the Bajo de la Carpa Formation in Paso Córdoba is completed with the mesoeucrocodylians *Notosuchus* Woodward, 1896, *Comahuesuchus* Bonaparte, 1991, and the booid snake *Dinilysia* Woodward, 1901 (e.g., Caldwell and Calvo, 2008; Martinelli, 2003; Pol, 2005).

While the fossiliferous content of the overlying Anacleto Formation is scant in reptiles –with the probable exception of *Antarctosaurus whichmannianus*–, the Allen Formation, at the top of the Mesozoic sequence in Paso Córdoba, is rich in these vertebrates. In fact, the record of the bones of turtles, crocodiles and dinosaurs is relatively common (Calvo and Ortíz, 2011). Recently, a very complete skeleton of a titanosaur has been collected from that unit in that place (Álvarez et al., 2015; Díaz-Martínez et al., 2015a). Near this skeleton, currently under study, at least twelve isolated theropod teeth have been also found (Meso et al., 2015). With respect to the vertebrate tracks, some few records have been mentioned both from the Anacleto and Allen formations (Calvo and Ortíz, 2011, 2013; Ortíz and Calvo, 2016; Ortíz et al., 2013; Paz et al., 2014).

The present contribution is focused on a new ichnological site within the locality of Paso Córdoba (Fig. 1), which comprises fossils from both the Anacleto (lower Campanian, Neuquén Group) and Allen (late Campanian-lower Maastrichtian, Malargüe Group) formations. Specifically, the aims of this study are: 1) to describe the new vertebrate ichnological remains taking into account their preservation, 2) to relate these vertebrate tracks with their depositional paleoenvironments, and 3) to value the importance of these ichnological associations in the context of the Cretaceous faunas recorded in the area.

2. Geological setting

The Neuquén Basin is located in the central west Argentina, covering an area of over 200.000 km^2 (Yrigoyen, 1991). The basin was active since the Late Triassic up to the Cenozoic, being filled with 7000 m of cyclical succession of marine and continental sediments (Arregui et al., 2011; Howell et al., 2005).

The Neuquén Basin is characterized by three filling episodes: in ascending order, 1) Precuyano Group: volcaniclastic and volcanic deposits with variable distribution and thickness from Upper Triassic to Lower Jurassic (e.g., Franzese and Spalletti, 2001; Gulisano and Gutiérrez Pleimling, 1995), 2) Cuyo and Lotena groups, with marine and continental deposits, from the Lower Jurassic-Upper Jurassic (e.g., Bechis et al., 2010; Zavala and González, 2001), and 3) Mendoza, Rayoso, Neuquén and Malargüe groups, that present carbonatic, evaporitic and clastic marine and continental rocks from the Upper Jurassic-Paleocene (e.g., Leanza and Hugo 2001; Leanza et al., 2004; Legarreta et al., 1989).

The Neuquén Basin accumulates mainly continental successions belonging to the Neuquén (lower Cenomanian-middle Campanian) and Malargüe (Late Campanian-Danian) groups (Vergani et al., 1995; Tunik et al., 2010). In the Paso Córdoba area, the Neuquén Group is represented by the Bajo de la Carpa and Anacleto formations (Río Colorado Subgroup) (Hugo and Leanza, 2001), while the Malargüe Group, which represents the last depositional episode of the Neuquén Basin (sensu Legarreta et al., 1999) and the first Atlantic transgression (Weaver, 1931), comprises the Allen Formation (Hugo and Leanza, 2001; Leanza et al., 2004; Page et al., 1999).

At the top of the Neuquén Group, the Anacleto Formation (lower to middle Campanian on the base of paleomagnetic data; Dingus et al., 2000) conformably overlies the Bajo de la Carpa Formation (Santonian, according to Garrido, 2010) and underlies the Allen Formation (Leanza et al., 2004). It has been generally related with low energy fluvial environments with stream courses along alluvial plains and abundant paleosols, and aeolian deposits (e.g., Heredia and Calvo, 2002; Hugo and Leanza, 2001; Leanza et al., 2004; Sánchez et al., 2006). In Paso Córdoba, the Anacleto Formation has been recently related with a lacustrine system represented by offshore and shoreface deposits, with associated deltaic systems (Paz et al., 2014).

The Allen Formation (middle Campanian-early Maastrichtian in age, based on its fossil record, Ballent, 1980) is conformably overlaid by the Jagüel Formation. It has been related with diverse palaeoenvironments, such as estuaries and tidal flats (Andreis et al., 1974; Armas and Sánchez, 2011; Barrio, 1990), brackish lakes (Salgado et al., 2007), braided fluvial (Hugo and Leanza, 2001) and aeolian fields (Armas and Sánchez, 2013, 2015; Paz et al., 2014). In the Paso Córdoba area, the Allen Formation represents an aeolian system related with coastal dunes (Armas and Sánchez, 2013, 2015; Paz et al., 2014).

The boundary between the Anacleto and Allen formations has been related with a discordance: the Huantraiquican unconformity (e.g., Hugo and Leanza, 2001; Leanza et al., 2004; Leanza, 2009; Garrido, 2010). However, there is no uniformity of criteria regarding this limit in the Paso Córdoba area, so both a transitional (see Paz et al., 2014; Armas and Sánchez, 2015) and an erosive discordance (Hugo and Leanza, 2001) have been suggested.

3. Materials and Methods

For this study, we have logged a detailed stratigraphic section (Fig. 2) in the Cañadón del Desvío, from 39°7'24.90"S, 67°41'42.34"W to 39°7'43.03"S, 67°41'49.90"W (Fig. 1). Almost all the fossiliferous materials are *in situ* but three slabs are housed in the Museo Patagónico de Ciencias Naturales collection under the acronym MPCN. Each slab has a track preserved as positive hypichnial (positive relief), currently with collection numbers in process, so in this contribution they have provisional field numbers: PC-1-A, PC-1-B and PC-1-C.

The vertebrate track and sedimentological structure-bearing layers studied in this work have been named according to their metrical position in the log. For instance, PC-1-10.2 means that is a layer from Paso Córdoba, the first log studied by us, located in the 10.2 m of height in the log.

For definitions and sedimentological analysis, we follow the criteria by Miall (1978, 2006). The terminology used for describing the vertebrate tracks is synthetized and discussed in Milàn et al. (2004), Marty (2008), Díaz-Martínez et al. (2009) and Marty et al. (2009). The sediment surface where the trackmaker walked is termed the “tracking surface” (Fornós et al., 2002), and the imprint emplaced on the tracking surface is named “true track” (Lockley, 1991). “Natural cast” is the homogeneous sediment that fills the true track (Lockley, 1991). When the true track is filled by several sedimentological layers, they are called as "overtracks" (Paik et al., 2001). The layers deformed by the trackmaker that are below the true track are the "undertracks" (Thulborn, 1990). The track that is preserved in a view perpendicular to the bedding plane is termed as "cross-section track". The "track penetration depth" is the maximum depth measured from the tracking surface to the undertracks or deformation of the sediment is still discernable in a cross-section track (Marty, 2008; Marty et al., 2016).

4. Results

4.1. Facies and facies assemblages

The overall pattern of facies variations is indicative of a meandering fluvial to shallow lacustrine system that is associated upward to an aeolian setting. A summary of facies and fossil content is provided in Table 1 and the logged section in Figure 2.

4.1.1. Floodplain

4.1.1.1. Description. The floodplain deposits are composed of the facies Fm, Sc, Sh, Sl, and rudstone–floatstone (Table 1). In these facies, three stacking patterns are observed. They are: I- Floodplain 1 type: it is related to massive reddish shales and fine reddish sandstones with horizontal lamination (facies Fm, Sc and Sh) and some bone fragments, vertebrate tracks and microbial wrinkle structures are preserved (Fig. 2); II- Floodplain 2 type: it is composed of fine to medium whitish sandstones with horizontal lamination and low angle cross bedding, with frequent convolute structures (facies Sh, Sl, Sc) and vertebrate tracks; and, III- Floodplain 3 type: this stacking pattern of facies is the less frequent, with a single level represented, and it is represented by limestones (rudstone–floatstone) with bivalve moulds (Fig. 2).

In the lower part of the section (Fig. 2) there are frequent convolute structures belonging to floodplain 1 and 2 facies (Figs. 3A-D). Convolute laminae are ranging around centimetric scale, with asymmetric distribution along the strata (Figs. 3A-D). The substrate soft deformation is irregular in shape, exhibiting abrupt changes in a few centimeters along each bed (e.g., Figs. 3C-D). Regarding convolute structures of the middle section of the logged outcrop, all deformation occurs in fine sandstones that are overlying shales of floodplain 2 facies (Figs. 3E-F). In this case, the deformation is not restricted in a single level as in lower sections. The deformation is involving around of 20 cm within the strata (Figs. 3E-F).

4.1.1.2. Interpretation. The Floodplain 1 type association is interpreted as a product of a lacustrine deposit, probably a floodplain pond (e.g., Nadon, 1993). The reddish massive shales are probably deposited in ponds settings. This origin is inferred based on the absence of roots traces and ped structures, being the reddish color probably the result of the oxidization of iron compounds (Nadon, 1993). The establishment of coherent microbial mats in the substrate enabled tracks preservation, as has been observed in analogous trampled environments, as floodplain of meandering fluvial and marginal lake areas (e.g., de Souza Carvalho et al., 2013; Melchor et al., 2006). As we mentioned before, convolute structures are less frequent than in the Floodplain 2 setting, maybe suggesting a transition between these two facies. The explanation on convolute structures is provided in the interpretation of Floodplain 2 type facies. It is envisaged as the result of a transition between flooding conditions of rapid flow (horizontal lamination) to a decrease in velocity (low angle cross stratification and convolute bedding) (McKee et al., 1967). With respect to the convolute bedding levels, these structures seem to be a common feature in many river floodplain deposits (McKee et al., 1967). Field relations suggest that the convolute structures were developed during a late stage of the flood when current velocities had slowed down materially and sediment was in the condition of quicksand (McKee et al., 1967). Convolute bedding and lamination are indicative of internal foundering of liquefied sediment layers upon themselves, commonly in conjunction with active upward escape of pore water (Collinson, 1994). The Floodplain 3 type is composed of facies of a bioclastic rudstone–floatstone. There are molds of bivalves, possibly belonging to the genus *Corbicula*, sensu Paz et al. (2014). This level is related to the establishment of a shallow pond that allowed the colonization of freshwater bivalves, in a setting analogous with the offshore lacustrine facies described in Paz et al. (2014).

4.1.2. Point bar deposits

4.1.2.1. Description. Point bar deposits comprise facies of Gmm, Sh, Sl, St (Table 1). This facies is encompassing medium to coarse yellowish sandstones, with some shale lenses and massive gravels. The observed point bar sequence pattern is composed of low angle cross beds of sandstones at the base with some shale lenses, followed by matrix supported massive gravels. At the top of the sequence there are horizontal to low angle cross beds of sandstones. This sequence resembles the pattern of the transition between lower to upper point bar deposits discussed by McGowen and Garner (1970) and Walker (1979).

4.1.2.2. Interpretation. This facies is indicative of point bar accretion in a meandering dominated fine-grained fluvial system, and the sequence is suggesting accumulation from slightly below mean low-water level to upper point bar, with channel-lag deposits not exposed (McGowen and Garner, 1970).

4.1.3. Wet interdune

4.1.3.1. Description. The wet interdune facies is composed of facies Fm/Sa/Sc, Sh, Sp and Sr (Table 1). This facies is encompassing fine reddish sandstones intercalated with shale lenses, exhibiting horizontal lamination and sand diapirs structures, and medium to coarse whitish sandstones with current ripples, convolute bedding and planar crossbedding, with vertebrate tracks (Figs. 3G-J). There are also frequent rizoliths. This facies is homologous with the interdune facies described by Armas and Sánchez (2013) and Paz et al. (2014).

4.1.3.2. Interpretation. These wet interdune deposits are indicative of current activity that is represented by horizontal lamination and ripples, and the presence of standing water as ponds, and aeolian activity denoted by aeolian cross strata. Rizoliths are indicative of substrate stabilization and some level of pedogenesis processes. Convolute bedding represents of post-depositional soft sediment deformation (McKee et al., 1967).

Sand diapirs structures are located between the contact of sandstones and sandstones with shales interbedded (Figs. 3G-J). These structures are interpreted as a soft substrate syn-depositional to post-depositational deformation that is result of the lesser effective viscosity of the upper as compared with the lower layer (Allen, 1982). A further discussion on these soft deformation structures is provided in sections 5.2 and 5.3.

This facies is inferred as the product of alluvial overbank flooding into these low-lying interdune depressions (Mountney and Thomson, 2002). Armas and Sánchez (2013) in regard of this facies inferred a climatic alternance between arid and wet conditions, which implies as result a seasonal variation of the water table position (Mountney and Thomson, 2002).

4.2. Vertebrate tracks: description and preservation

4.2.1. PC-1-10.2 (Fig. 4). The tracks are on a bedding-plane at the top of a centimetric laminated fine sandstones, preserved mainly as negative epichnial (negative relief, sensu Martinsson, 1970). They are at least eleven semicircular to circular concave depressions of about 30-50 cm diameter and up to 5 cm depth (Fig. 4A). Two of the tracks are preserved in cross-section as well (Figs. 4B-C). They have no clear evidences of anatomical structures. The displacement rims are very shallow. The tracks are preserved as true tracks, overtracks and undertracks (Figs. 4D-E, G). The tracking surface is a 1 cm layer and shows five true tracks and some invertebrate trace fossils. This surface is infilled by thin laminated fine sandstones that preserved the overtracks. Bellow the true track, there are other deformed layers that correspond to undertracks. The true tracks with all the undertracks represent more than 20 cm of track penetration depth. The pinky sand-silt surface of the first undertrack have abundant wrinkle structures, elliptic, elongated, and hemispherical bulges preserved as positive epirelief, interpreted as evidence of a continuous microbial mat (Fig. 4F). The high density of the tracks suggests a high trampled tracking surface.

4.2.2. Layer PC-1-15.9 (Fig. 5). The specimens are concave structures caused by deformation, with their bases horizontal or slightly curved downward respect to bedding. They are interpreted as cross-section tracks (Figs. 5A-B). The tracking surface is a reddish mudstone. This surface is covered by homogeneous decametric yellowish fine sandstone that forms natural casts of about 20 cm depth (Fig. 5C). The displacement rims are not well-developed. The preserved section of the true tracks measure horizontally about 40 cm. The true tracks lack of any clear anatomical features. Below the true track, there are at least eight mudstone-sandstone deformed heterolitic layers. They are the undertracks and all together represent more than 20 cm of track penetration depth. As can be seen in Fig. 5A, the tracking surface is few trampled, with discrete vertebrate tracks.

4.2.3. PC-1-20.5 (Figs. 6A-B). The tracks are on a bedding-plane at the top of a centimetric laminated fine sandstones, preserved as negative epichnial. They are several circular to subcircular depressions of about 20-30 cm diameter and up to 5 cm depth (Fig. 6A). Besides the bad preservational condition, the tracks specimens lack the features to know whether they are true tracks, undertracks or overtracks. The high density of the tracks is reflecting a trampled area.

The studied surface bears wrinkle structures with a similar morphology of those in the layer PC-1-10.2, evidencing microbial mats (Fig. 6B).

4.2.4. PC-1-23.2 (Figs. 6C-E). The specimens are three vertebrate tracks preserved as positive hypichnial or natural casts, in a homogeneous, centimetric and fine grain sandstone (Fig. 6C). Two of the tracks have the same main features. They are tridactyl, mesaxonic, subsymmetrical pes tracks that are slightly longer than wide (PC-1-A: 25 cm long, 28 cm wide; PC-1-B: 27 cm long, 29 cm wide) (Fig. 6D). The digit impressions are short and wide, with blunt ends, and the heel impression is large and rounded. They have no evidences of digital-metatarsophalangeal pad impressions or claw marks. The posterior part of the track has less depth (2 cm) than the anterior one (up to 9.5 cm). PC-1-B has a relative homogeneous depth of about 7 cm depth. The tracking surface is a reddish decametric very fine sandstone, although the true track or undertracks have not been preserved. The third footprint is PC-1-C (Fig. 6E). Even though it is not clear the exact contour of the track, it seems to be laterally symmetrical, wider than long (33 cm long and 28 cm wide), possibly pentadactyl with very short digit imprints. It has a maximum depth of about 12 cm.

The tracks are preserved as isolated natural casts, so it is not possible to affirm if the tracking surface is well or poorly trampled.

4.2.5. PC-1-23.7 (Figs. 6F-G). The specimens are preserved as cross-section tracks, in two different layers, both as true and natural casts. In both cases, the tracking surfaces are at the top of homogeneous reddish very fine sandstones, which were infilled by fine grained whitish sandstones. In some sectors both true tracks and natural casts are present, while in others only the natural casts are preserved because the less coarse reddish sandstones have been eroded.

The clearest and more interesting specimen is a natural cast in the upper layer, of about 12 cm in depth (Fig. 6F). It lacks anatomical features, such as digits impressions, but displays large, parallel grooves of up to 4 mm width (Fig. 6G). They are interpreted here as exceptional skin traces produced by the pedal integument when the autopod was moving into the substrate.

The rest of tracks are poorly preserved, but the high density indicates an intense trampling.

4.2.6. PC-1-24.3 (Fig. 7). The tracks are located on a bedding plane at the top of a centimetric laminated fine sandstones (Fig. 7A); some of them are preserved as cross-section tracks as well (Figs. 7B-C). They lack of any clear anatomical features. In the tracking surface, the true tracks are shallow concave depressions (about 25 cm diameter). Covering this surface, some fine laminated layers filled the tracks conforming overtracks. The first overtracks are concave adapting to the track shape, while the last overtracks are almost horizontal. Vertically bellow the true track, there are others deformed layers that correspond to undertracks. They have few centimeters of track penetration depth. The outcrop is quite trampled in view that in almost all the visible surface there is evidence of vertebrate tracks.

This kind of tracks as well as true tracks have also wrinkle structures, elliptic and elongated bulges or even interconnected, cohesive bridges, interpreted as microbial mat, mainly formed in the center of the tracks (Figs. 7D-E).

5. Discussion

5.1. Preservation and characterization of the vertebrate tracks from the Cañadón del Desvío

Because the vertebrate track morphology is determined by the limb motion, autopod anatomy and substrate consistency, studies about fossil tracks provide information about trackmaker, behaviour and palaeoenvironment (see Falkingham, 2014). Therefore, when vertebrate tracks and trackways are well-preserved, it is possible to obtain more valuable information about the autopod morphology and the trackmaker mode of locomotion

(Castanera et al., 2013a,b; Gatesy, 2001; Razzolini et al., 2016). Nevertheless, many times the specimens are poorly preserved, being barely recognizable as tracks (Milàn and Loope, 2007).

For many authors (e.g., Falkingham et al., 2011; Gatesy et al, 1999; Milàn and Bromley, 2008; Razzolini et al., 2014), the substrate is the major control in determining the final track morphology, thus the tracks are excellent structures to analyze the environmental conditions where the animal have walked. As it has been commented above, the vertebrate tracks found in the Cañadón del Desvío display different condition of preservation.

In the layers PC-1-15 and PC-1-23.7 the tracks are only preserved in cross-section (Fig. 5, 6G-H). The PC-1-15 tracks lack clear anatomical details and information of trackway patterns. The assignment of this kind of tracks with particular taxa of trackmakers or try a biomechanical interpretation becomes hazardous. Usually, cross-section tracks provide evidence about the history of the substrate before, during and after the track formation. In this case, the timing and formation of true tracks, undertracks, and natural cast can be reconstructed with confidence. The tracking surface and deeper layers have been deformed by the autopod forming the true track and the undertracks. The pressure have modified about 20 cm thickness of heterolitic layers plastically (no fractures are present), suggesting sediment conditions of mainly soft to moderately stiff mud (see Allen, 1997; Melchor, 2015). Normally, undertracks are common in thin laminated layers (Thulborn, 1990). These tracking surfaces have no evidence of large exposure event, such as paleosoils and mud cracks, thus likely the true track was filled (natural cast) shortly after forming. With respect to the PC-1-23.7 tracks, they are true tracks and natural casts. The animal walked in a sandy homogeneous and decametric fine layer, where undertracks are difficult to preserve. A sandy flow eroded partially the tracking surface and fills the true tracks. At least one track has preserved skin impressions in one of the tracks. Very few vertebrate tracks preserve the finest level of detail as marks of integument structures (Lockley, 1989). The skin impressions were only created as the integument registered on a receptive substrate such as the firm mud retains with sufficient moisture that it can be molded by the autopod but without adhering (Allen, 1997). In this case, the skin traces are parallel skin grooves. These structures can reflect the direction of autopods movement in the substrate when entry and exit striations are preserved. In this track, only one direction grooves is present and this inference is not possible.

Other tracksites in Paso Córdoba have been found at the top of bedding planes: PC-1-10.2, PC-1-20.5 and PC-1-24.3. The PC-1-10.2 has about 11 poorly-preserved tracks with any clear anatomical features or trackway patterns. In the studied surface, some different centimetric layers are preserved. In addition, some tracks are also preserved in cross-section, and allow proposing the history of this tracksite: 1- sedimentation of several centimetric sandstone layers and at least one of them has developed wrinkle marks at the top; 2- the animals walked and deformed the tracking surface and some layers below, forming the true tracks and undertracks; 3- thin sandstone layers, without evidence of erosion, filled passively the true tracks.

The PC-1-20.5 tracks are poorly preserved and lack anatomical features and locomotion patterns. The general form of the structures (shallow and subcircular) and the thickness of the preserved layers makes difficult to identify them as true tracks, undertracks or overtracks with confidence. However, the presence of wrinkle structures inside some tracks suggests that they could form in a concavity with moisture sediment.

PC-1-24.3 tracks are preserved as semicircular shallow depressions without any anatomical and biomechanical evidences. In a small area, true tracks, undertracks and overtracks have been identified. True tracks and undertracks have concentric structures inside produced by the pressure when the trackmaker stepped (see Allen, 1997). In addition, wrinkle marks are present in the true tracks surface. They are deformed, so they were formed before passing the animal. The pressure modifies few centimeters thickness of laminated fine sandstones and produced the concentric structures. This fact suggests that the sediment condition is a little stiff mud (see Allen, 1997). Finally other thin layers are covering the true tracks that correspond to overtracks.

Finally, one tracksite preserved the tracks as natural casts. The PC-1-A and B, from the PC-1-23.2, are natural casts and display general anatomical details (e.g., tridactyl, mesaxonic, subsymmetrical pes tracks) which make them to resemble to the ichnofamily Iguanodontipodidae Vialov, 1988 (see Díaz-Martínez et al., 2015b; Lockley et al., 2014). However, the phalangeal and metatarsophalangeal pad impressions, which are important ichnotaxobases from this ichnofamily, are not preserved. Thus, we classify these specimens as cf. Iguanodontopodidae. This kind of tracks, called informally as large ornithopod tracks, has been previously related with large iguanodontian trackmakers (see Díaz-Martínez et al., 2015b). In the Latermost Cretaceous, the unique large representatives of the Iguanodontia clade are the hadrosaurids (see Díaz-Martínez et al., 2016), so we propose these last dinosaurs as the trackmakers of PC-1-A and B. The third track, PC-1-C, is poorly-preserved, thus we consider it as an indeterminate vertebrate track.

5.2. Tracks against soft substrate deformation structures: features for recognition cross section tracks

In the field, the recognition of vertebrate tracks and its differentiation from soft substrate deformation structures is a significant issue. Such a topic has been discussed since several years ago, with contributions focused on experimental approaches (see reviews in Manning, 2004; Melchor et al., 2015). There is an important background about the formation of cross section tracks in laboratory tests (Allen, 1989, 1997; Jackson et al., 2010; Manning, 2004). In the same sense, Melchor (2015) reviewed and summarized key aspects which are important in the formation and preservation of vertebrate tracks, taking into account the substrate properties in different palaeoenvironments, with emphasis on the record of cross section tracks. In regard of this, we consider useful a brief mention of the tips that allow to recognize vertebrate tracks in cross sections. Although these issues have been already reviewed in previous contributions (e.g., Lea, 1996; Loope, 1986; Melchor, 2015), a short summary of the main points is: (a)- Presence of deformation in layers and/or strata along a cross section. Although it can be an obvious subject, the first approach to tracks recognition is the observation of structures that are modifying the shape and continuity of layers and strata; (b)- Continuity/discontinuity of structures laterally. Sedimentary structures like convolute bedding and load casts commonly are repetitive along an outcrop, instead biogenic structures such as footprints are discontinuously distributed (Lea, 1996; Loope, 1986; Melchor, 2015); (c)- Displacement/deformation of layers dominantly in downside direction. In vertebrate tracks, it is expected, when substrate conditions are suitable, that the dominant deformation vector are downward (Allen, 1989; Jackson et al., 2010; Manning, 2004); (d)- Tracks tend to preserve a quite uniform size. If substrate moisture conditions is suitable, the size of footprints in cross section is quite uniform laterally (Lea, 1996; Loope, 1986; Melchor, 2015); (e)- Preservation of some anatomical features. Sometimes, it is possible to recognize some extremities features, such as digit impressions, claw traces and skin impressions (e.g., Milàn et al., 2004; Xing et al., 2015); and (f)- Filling nature of structures. In tracks, the filling of the cavities is commonly of different texture and composition than the underlying and overlying rocks. This situation is usually different in convolute structures and other soft substrate deformation structures, where the lithology is pretty more uniform (Lea, 1996; Loope, 1986; Melchor, 2015).

5.3. Sedimentary structures and vertebrate tracks in their environmental context

Soft deformation structures such as convolute bedding and sand diapers are inferred as a product of substrate response to environmental conditions. Convolute structures (Figs. 3A-

F) are a common feature in fluvial settings, mainly in floodplain deposits (McKee et al., 1967). The most parsimonious criterion is considering sand diapirs (Fig. 3G-J) because of a sedimentological process product of a geomechanical differential response between strata (Allen, 1982, Owen, 1987). Other interpretations of this kind of structures are related with regional geological processes like seismic activity (Owen, 1987). However, the structures presented here lack in necessary conditions described by Owen and Moretti (2011) to be considered as product of seismicity; mainly lateral continuity, vertical repetition and proximity to fault(s) likely to have been active during sedimentation. Further discussion on these soft deformation structures is beyond the scope of this paper.

Regarding the distribution of vertebrate tracks is appropriate a brief discussion on their environmental distribution. As we presented before, sedimentary facies along the transition between the Anacleto and Allen formations are indicative of a fluvial to shallow lacustrine setting that is associated stratigrapically upward to an aeolian setting. Track-bearing strata belong to floodplain facies (Floodplain 1 and 2 types) and wet interdune facies with some level of pedogenization. Melchor et al. (2012) reviewed such kind of depositional environments, discussing several trace fossils occurrences in the geological record and even in neoichnological analogous. They found that trace fossils display a better preservation potential in overbank areas, particularly in pond and crevasse-splay facies (Melchor et al., 2012). In this sense, Uchman et al. (2004) described a comparable study case of invertebrate and vertebrate trace fossils ascribed to an Oligocene fluvial pond on a fluvial plain of a braided river in Switzerland. The association described by Uchman et al. (2004) is composed of invertebrate trace fossils (*Cochlichnus*, *Helminthoidichnites*, *Planolites*, *Steinsfjordichnus*, *Treptichnus*) and vertebrate tracks (*Pecoripeda*), that in association with the sedimentary structures, especially raindrop imprints and mudcracks, as well as the overall lithology, suggest that the trace fossils were produced in muddy bottom ponds characterized by shallow,

low-energy water and temporal desiccation. In the same sense, Melchor et al. (2006) described an interesting study case regarding the distribution of trace fossils along a fluvial to lacustrine system in the Santo Domingo Formation (Eocene in age after Melchor et al., 2013). Among several records in such environments, these authors described vertebrate and invertebrate trace fossils found in floodplain deposits that comprise fluvial shallow ponds frequently desiccated and associated crevasse-splay or proximal sheetflood deposits. In such sub-environments Melchor et al. (2006) mentioned the presence of invertebrate trace fossils (*Palaeophycus*, *Taenidium*, and more rarely *Diplichnites* sp., *Helminthoidichnites*, *Rusophycus*, *Skolithos* and *Spongeliomorpha*), and vertebrate trace fossils (bird-like footprints, small epichnial rounded pits, other tridactyl footprints and also some footprints preserved in cross-section). As concluding remark, Melchor et al. (2006) mentioned that the floodplain pond assemblage is characterized by the largest diversity of trace fossils.

The main difference between these analogous cases and the record presented here is the lack of invertebrate trace fossils in the Anacleto-Allen floodplain ponds deposits, possible related with a taphonomic bias. The establishment of coherent microbial mats (Figs. 4F, 6B) allowed the preservation of humidity and consequently the conservation of tracks. Furthermore these association between tracks and microbial mats in ponds facies indicates a cessation in water discharge of the river (Melchor et al., 2012) and the stabilization of substrate, in moist or slightly damp conditions (Melchor, 2015). Concerning the transition between fluvial to interdune conditions observed in this case, Krapovickas et al. (2016) analyzed several analogous along the geological record. Typical recurrent patterns suggest that a high water table is necessary to allow the track preservation and the pedogenization (Krapovickas et al., 2016). We observed the same situation in the stablishment of the wet interdune facies presented here. Stratigraphically this is relevant along the transition between the Allen and Anacleto formations, because is suggesting no hiatuses, and only a climatic alternance between arid and wet conditions.

5.3. Contribution to the vertebrate diversity of the Anacleto and Allen formations in the Paso Córdoba area

Track record complements the skeletal record in order to a better understanding of the tetrapod diversity (e.g., Díaz-Martínez et al., 2015c, 2016; Leonardi, 1981).

As already mentioned (see Introduction), the vertebrate skeletal fossil record from the Anacleto and Allen formations is not abundant in the Paso Córdoba area (e.g., Garrido, 2010). Regarding specifically the ichnological record, the only data from the Anacleto Formation are the cross-section vertebrate tracks figured by Paz et al. (2014). From the Allen Formation, abundant tracks assigned to birds and different group of dinosaurs, such as titanosaurids and hadrosaurids, have been reported (Calvo and Ortíz, 2011, 2013; Ortíz and Calvo, 2016; Ortíz et al., 2013; Paz et al., 2014). The bird and bird-like tracks reported from Paso Córdoba are the only evidence assignable to the group in the area, although other localities where the Allen Formation is exposed have brought bird bones (see Clarke and Chiappe, 2001; Powell, 1986).

The record from the Cañadón del Desvío ichnosite consists of, at least, six track-bearing levels. Two tracksites have been found in the lower part of the log: PC-1-10.2 and PC-1-15.9. Particularly, PC-1-15.9 is similar to the tracks from the Anacleto Formation figured by Paz et al. (2014). In the upper part of the log, there are four tracksites. One of them, PC-1-23.2, has two tracks with anatomical details that allow relate them with hadrosaurids(Figs. 6C-E). The presence of these six tracksites, added at the osteological remains, located in different levels of the stratigraphical log, reflects the abundance of vertebrates in the Anacleto and Allen formations from the Cañadón del Desvío.

The sum of the osteological and ichnological remains improves the knowledge on the Paso Córdoba paleofaunas. Nevertheless, it is difficult to know the paleodiversity of each geological unit since that, as previously mentioned, the limit between the Anacleto and Allen formations is not clear in that area. Traditionally, the Huantraiquican unconformity has been considered as the boundary between the Neuquén Group (Anacleto Formation) from the Malargüe Group (Allen Formation). This unconformity resulted from the regional subsidence that caused the marine ingression from the east (e.g., Garrido, 2010; Hugo and Leanza, 2001; Leanza, 2009; Leanza et al., 2004). The Huantraiquican unconformity is well exposed in the area of Cinco Saltos and Lago Pellegrini, both in the Río Negro province (Leanza, 2009), but in Paso Córdoba its existence is discussed. Hugo and Leanza (2001) suggested that, in fact, there is an erosive discordance between the red/purple mudstone of the Anacleto Formation, and the yellowish sandstones of Allen Formation, but Paz et al. (2014) and Armas and Sánchez (2015) have recently studied some stratigraphical sections in that area and proposed a transitional passage between both formations, which would owe to the gradual evolution of the depository system. According to the stratigraphical, facial and paleoenvironmental analyses presented in this contribution, we observed no clear changes or unconformities in the Cañadón del Desvío, which would allow a reinforce the proposal of transitional passage between both formations . The pattern of facies succession suggests an alternation between two complementary sedimentary systems (e.g., Krapovickas et al., 2010, 2016), supporting the idea of a transitional passage between the Anacleto and Allen formations in Paso Córdoba.

On the other hand, some facial and paleontological particularities have been observed along the Cañadón del Desvío stratigraphical section. Paleontologically, Leanza et al. (2004) analyzed the general tetrapod record from the Neuquén Basin and identified six tetrapod assemblages, in ascending order: Amargan, Lohancuran, Limayan, Neuquenian, Coloradoan, and Allenian assemblages. The Coloradoan tetrapod assemblage (= Greater Gondwanan

Endemic Dinosaur Domain, sensu Apesteguía, 2002), characteristic from the Río Colorado Subgroup (Bajo de la Carpa and Anacleto formations), is mainly composed of titanosaur and abelisaurid dinosaurs, although alvaresaurid, enantiornithine birds and basal euiguanodontian ornithopods are also present (see Leanza et al., 2004, and references therein; Martinelli and Vera, 2007). The Allenian tetrapod assemblage (= Alamitense, sensu Bonaparte, 1991; = Alamitian SALMA, sensu Flynn and Swisher, 1995), from the basal unit of the Malargüe Group, the Allen Formation, is characterized by the co-occurrence of highly derived members of typical Gondwanan lineages and probable immigrants from the Northern Hemisphere (see Leanza et al., 2004, and references therein). The Gondwanan dinosaurs are titanosaurs (saltasaurine and eutitanosaurs), abelisaurid and non-ornithure ornithothoracean birds. Among the immigrants, ankylosaurian ornithischian and hadrosaurine and lambeosaurine hadrosaurid ornithopods were found. The anatomical features of the tracks PC-1-A and B, from the tracksite PC-1-23.7, have been related with hadrosaurid dinosaurs that, according with the proposal by Leanza et al. (2004), are typical of the Allen Formation. Besides, sedimentologically, the limit between floodplain-point bars facies and wet interdune facies is located approximately in the meter 23 of the log, close to the previously related tracksite (see Fig. 2). Both sedimentological and paleontological observations reveal differences between the lower-middle parts of the stratigraphical log and the upper part. Thus, we propose that the PC-1-10.2 and PC-1-15.9 tracks likely belong to the Anacleto Formation, PC-1-20.5 is in the transition, and the rest (PC-1-23.2, PC-1-23-7 and PC-1-24.3) would belong to the Allen Formation.

6. Conclusions

New vertebrate tracks have been found in the Cañadón del Desvío within the Paso Córdoba fossiliferous site (General Roca, northern of Patagonia, Argentina). They are in rocks of the Anacleto and Allen formations (Campanian-Maastrichtian). The tracksites are distributed in two distinct environments: floodplain deposits of a meandering fluvial to shallow lacustrine system, and wet interdune deposits of an aeolian setting. Based on the track preservation, the timing and formation history of each tracksite is discussed. The tracks are preserved in cross-sections, on bedding-planes as true tracks and as natural casts. Moreover, the tracking surface, true tracks, undertracks and overtracks/natural casts were identified. It is remarked that the presence of wrinkle structures in the substrate enabled tracks preservation. The stratigraphical, facial and palaeoenvironmental information sustain the idea of a transitional passage between the Anacleto and Allen Formation in Paso Córdoba. The presence of hadrosaurid dinosaur tracks allows discussing where the Allen Formation begins in this area. This study shows that fossil vertebrates are relatively abundant in the area because there are at least six trampled surfaces in the Cañadón del Desvío. The sum of the skeletal and ichnological record allows having a more complete picture of the vertebrate diversity in the Anacleto and Allen formations in the Paso Córdoba fossiliferous site.

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Table caption

Table 1. Facies, facies assemblages and fossil/ichnofossil record from the Cañadón del Desvío (Paso Córdoba, Río Negro province, Argentina).

Figure captions

Fig. 1. Location map of the Paso Córdoba locality, Río Negro province, Argentina, showing the ichnofossiliferous location. At left, the location of the detailed study area; the black tape indicates the stratigraphical log from the Cañadón del Desvío. VLR: Valle de la Luna Rojo.

Fig. 2. Integrated logged section and track-bearing strata of the Cañadón del Desvío (Paso Córdoba, Río Negro province, Argentina), Anacleto and Allen formations, Neuquén Basin.

Fig. 3. Sedimentary structures in the Cañadón del Desvío. Photography A, and interpretative outline drawing of a convolute structure B in a heterolitic mud-sand facies; Photography C, and interpretative outline drawing D of a convolute structure in a laminated sandy facies; Photography E, and interpretative outline drawing F of a convolute structure in a thin laminated sandy facies; Photography G, I, and interpretative outline drawing H, J of sand diapirs.

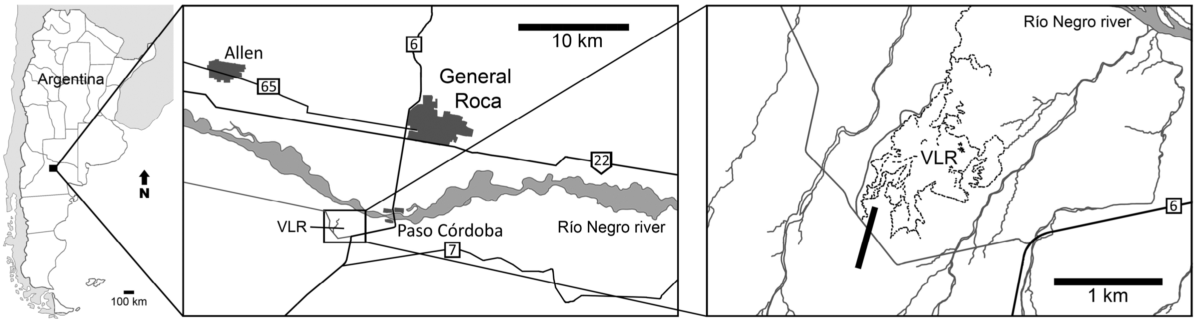
Fig 4. PC-1-10.2. A, general view of the tracksite (squares with dashed line are detailed areas); Photography B, and interpretative outline drawing C of a cross-section track; D, E, details of the tracksite bedding plane; F, Wrinkle structures; G, a detail of the tracksite bedding plane.

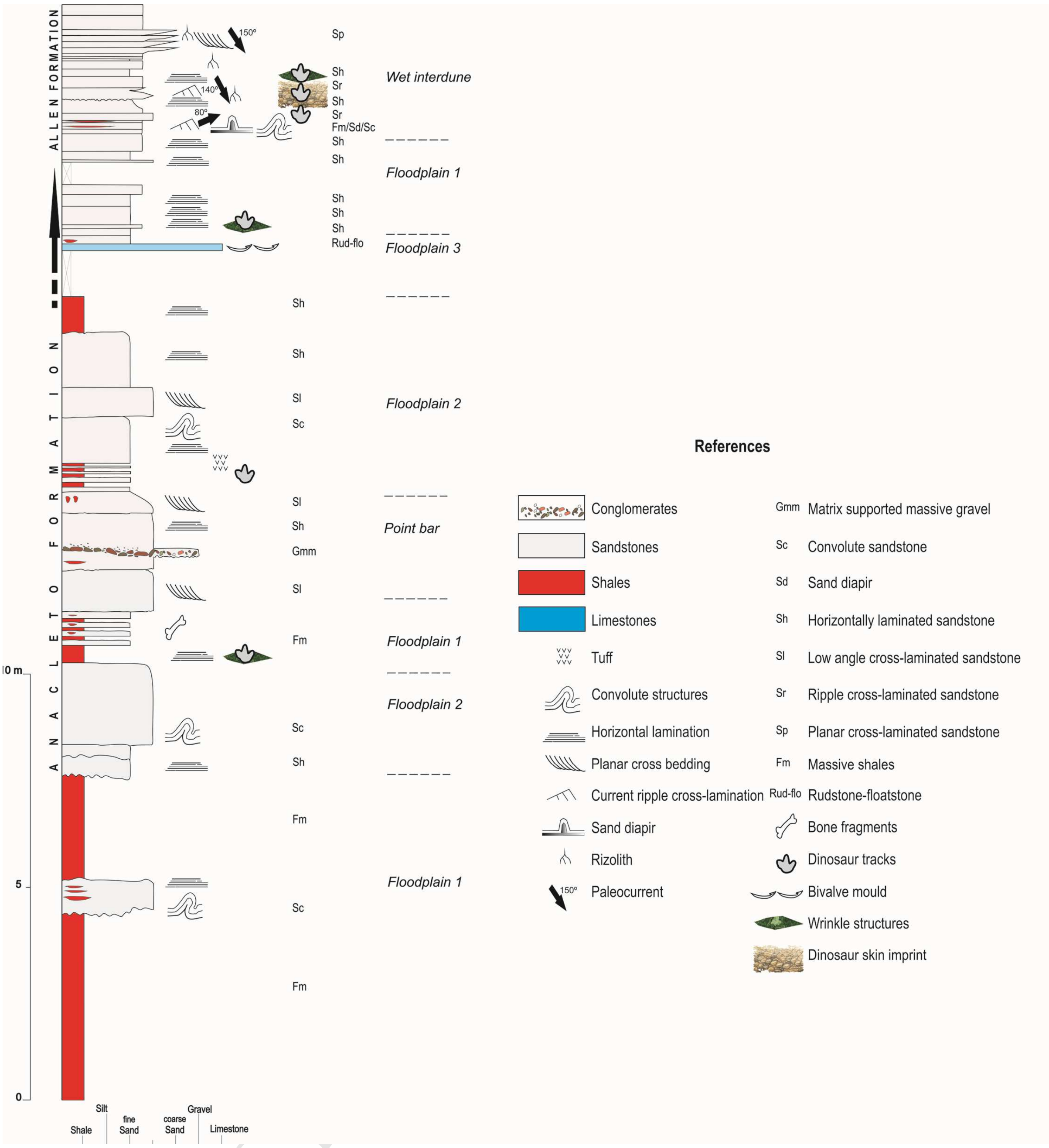
Fig 5. PC-1-15.9. Photography A, and interpretative outline drawings B, C, of a cross-section track.

Fig. 6. A, general view of the PC-1-20.5 tracksite (square with dashed line is for a detailed area); B, Wrinkle structures in the PC-1-20.5 tracksite; C, general view of the PC-1-23.2 trackiste (the arrow indicate the level where the tracks come from); D, E, photographs of the natural casts found in PC-1-23.2 tracksite (III indicate de third digit impression of each track); F, general view of the PC-1-23.7 tracksite; G, detail of a natural cast with skin grooves found in PC-1-23.7.

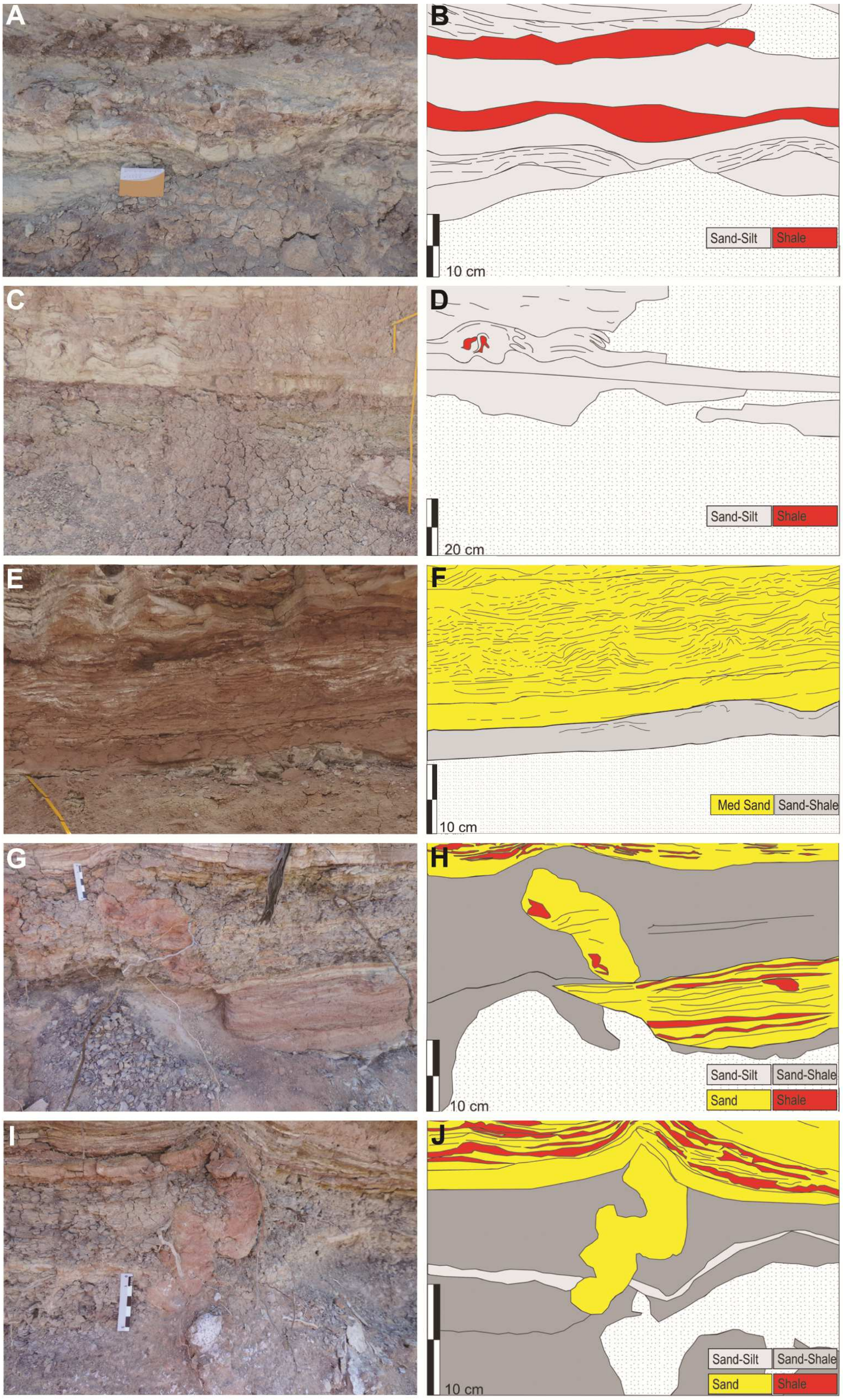
Fig. 7. A, general view of PC-1-24.3 tracksite (squares with dashed line are detailed areas). Photography B, and interpretative outline drawing C of a PC-1-24.3 cross-section track; D, E, detail of vertebrate tracks with wrinkle structures in bedding plane.

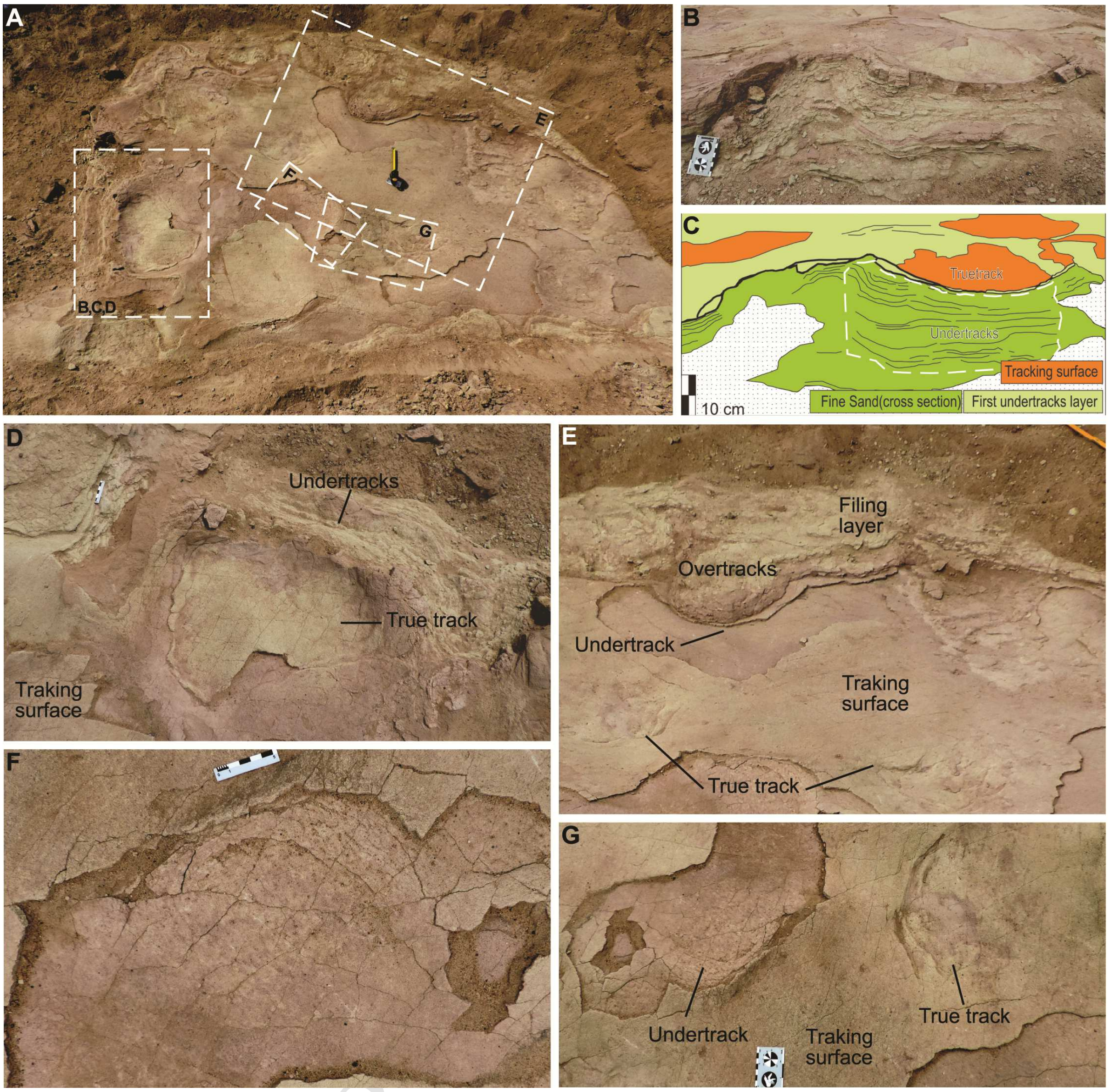
Facies associations	**Sedimentary facies**	**Body fossils**	**Biogenic structures**
A- Floodplain AI. Floodplain 1 AII. Floodplain 2 AIII. Floodplain 3	Fm, Sc, Sh Sh, Sl, Sc Rudstone–floatstone	Indet. Bones ?*Corbicula* moulds	Vertebrate tracks, wrinkle structures Vertebrate tracks
B- Point bar	Gmm, Sh, Sl, St		
c- Wet interdune	Fm/Sa/Sc, Sh, Sp and Sr		Vertebrate tracks, Rizoliths

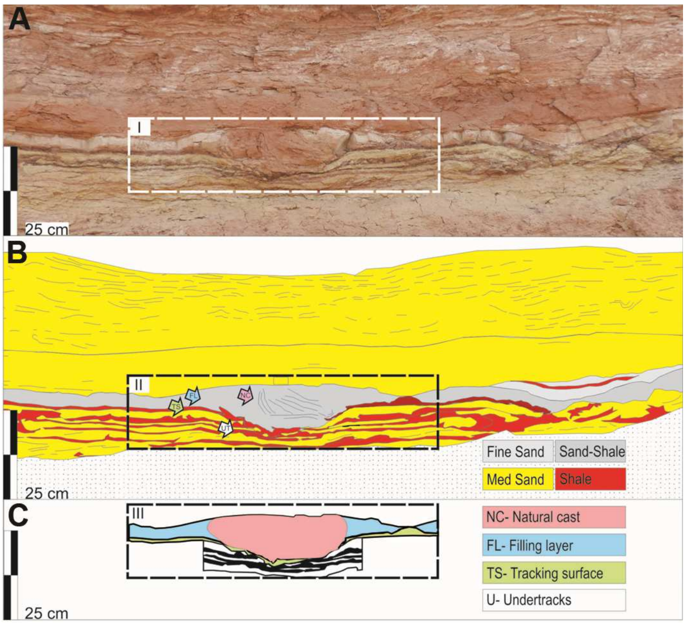

Argentina
100 km
N
Allen
65
6
General Roca
22
10 km
VLR
Paso Córdoba
Río Negro river
7
Río Negro river
VLR
6
1 km



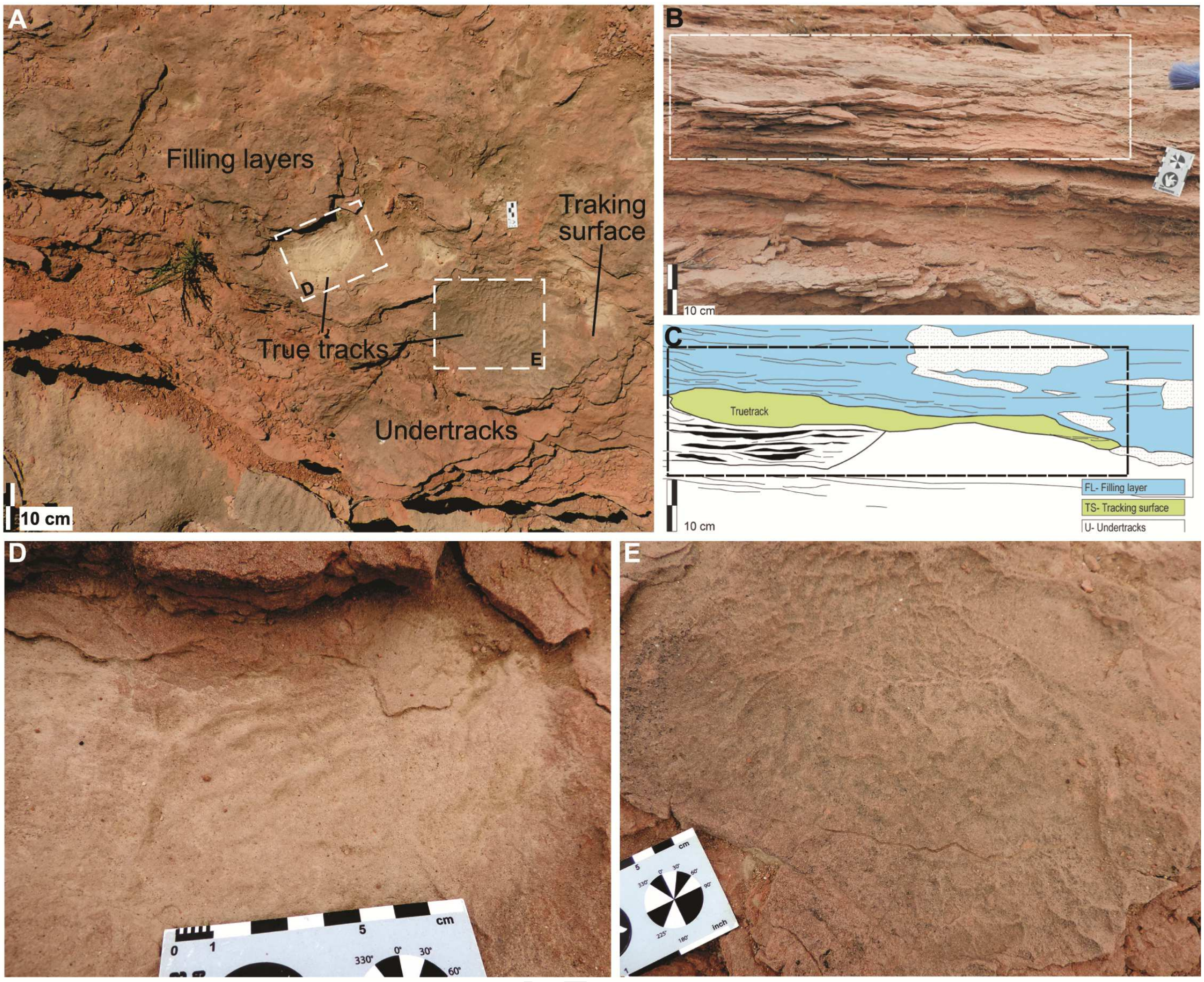
ALLEN FORMATION
ANACLETO FORMATION
150°
140°
80°
Sp
Sh
Sr
Sh
Sr
Fm/Sd/Sc
Sh
Sh
Wet interdune
Floodplain 1
Sh
Sh
Sh
Rud-flo
Floodplain 3
Sh
Sh
Sl
Sc
Floodplain 2
Sl
Sh
Gmm
Point bar
Sl
Fm
Floodplain 1
Floodplain 2
Sc
Sh
Fm
Floodplain 1
Sc
Fm
10 m
5
0
Shale
Silt
fine Sand
coarse Sand
Gravel
Limestone
References
Conglomerates
Sandstones
Shales
Limestones
Tuff
Convolute structures
Horizontal lamination
Planar cross bedding
Current ripple cross-lamination
Sand diapir
Rizolith
Paleocurrent
Gmm Matrix supported massive gravel
Sc Convolute sandstone
Sd Sand diapir
Sh Horizontally laminated sandstone
Sl Low angle cross-laminated sandstone
Sr Ripple cross-laminated sandstone
Sp Planar cross-laminated sandstone
Fm Massive shales
Rud-flo Rudstone-floatstone
Bone fragments
Dinosaur tracks
Bivalve mould
Wrinkle structures
Dinosaur skin imprint


A
B
Sand-Silt
Shale
10 cm
C
D
Sand-Silt
Shale
20 cm
E
F
Med Sand
Sand-Shale
10 cm
G
H
Sand-Silt
Sand-Shale
Sand
Shale
10 cm
I
J
Sand-Silt
Sand-Shale
Sand
Shale
10 cm


A
E
F
G
B,C,D
B
C
Truetrack
Undertracks
Tracking surface
10 cm
Fine Sand(cross section)
First undertracks layer
D
Undertracks
True track
Traking
surface
E
Filing
layer
Overtracks
Undertrack
Traking
surface
True track
F
G
Undertrack
Traking
surface
True track


A
I
25 cm
B
II
TS
FL
NC
UT
Fine Sand
Sand-Shale
Med Sand
Shale
25 cm
C
III
NC- Natural cast
FL- Filling layer
TS- Tracking surface
U- Undertracks
25 cm


A
B
B
C
D
III
III
E
F
G
6
7
8
9
10
5 mm


A
Filling layers
Traking
surface
D
True tracks
E
Undertracks
10 cm
B
10 cm
C
Truetrack
10 cm
FL- Filling layer
TS- Tracking surface
U- Undertracks
D
E

Highlights.

- The track record from Paso Córdoba area, Río Negro province, Argentina.
- The track preservation indicates different conditions of depositional paleoenvironments.
- About the transition between the Anacleto and Allen formations in Paso Córdoba.
- These tracks are a complement to the paleofauna from the Anacleto and Allen fms.