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TETRAPOD TRACKS TAPHONOMY IN EOLIAN FACIES FROM THE PERMIAN OF ARGENTINA

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ABSTRACT: **Ancient desert deposits preserve a copious ichnofossil record, particularly Permian-age deposits where the record of tetrapod footprints is present and abundant in almost all desert settings. We propose to analyze, from a taphonomic perspective, Permian footprints preserved in eolian deposits from Argentina with a detailed sedimentological study of the trackway-bearing levels, in order to find evidence of processes that may have enhanced their preservation. We defined four taphonomic modes based on preservation quality, and the morphological and extra-morphological features of the footprints. Mode 1 includes footprints with detailed impressions of the palm, digits and claws. Mode 2 includes tracks with palm and digit impressions associated with small bulbous-shape marginal rims. Mode 3 includes tracks characterized by large, bulbous, marginal rims and randomly preserved palm impressions. Mode 4 includes footprints with shallow digit and palm impressions associated with sand-crescent marginal rims. The Los Reyunos footprints suggest preservation in: (1) dry sand, evidenced by sediment slipping down-slope structures and (2) subsurface damp sand, evidenced by digit impressions and claw drag traces. Also, we found vertical water content variations along the dune foresets, evidenced by a varying amount of sediment slipping down-slope in the same trackway. Moreover, differences in the time of entombment are suggested by the morphology of rims (bulbous-shape or sand-crescent). The stratigraphic genetic framework resulting from the Los Reyunos taphonomic analysis supports changes in the interstitial subsurface water and rapid entombment of the tracking surface due to a high rate of sediment supply as the main factor for footprint preservation.**

INTRODUCTION

Ancient eolian environments exhibit abundant trace fossils despite the misconceptions that deserts are nearly barren of life and that preservation in loose sandy substrates of mobile dunes requires exceptional conditions. In fact, desert trace fossils are abundant and widespread in Permian strata on a nearly global scale (Krapovickas et al. 2016). Ichnoassemblages are known from outcrops in North America, in the Pennsylvanian–Permian Weber Sandstone, the Permian Coconino, DeChelly, Lyons, Cedar Mesa, and Casper sandstones (Gilmore 1926, 1927, 1928; Brady 1947, 1961; Hanley et al. 1971; Lockley and Madsen 1993; Sadler 1993; Braddy 1995; Lockley and Hunt 1995; Lockley et al. 1998; Chure et al. 2014). They also occur in the Permian of Europe, in the Corncockle, Lochabriggs, and Hopeman sandstone of Scotland, and the Cornberg Sandstone of Germany (Duncan 1831; McKeever 1991, 1994; Haubold et al. 1995; McKeever and Haubold 1996), and in South America, in the Patquía and Yacimiento los Reyunos formations of Argentina (Aramayo 1993; Melchor 2001; Krapovickas et al. 2010, 2015). All these Permian eolian deposits contain essentially the ichnogenus *Chelichnus* occurring with other rare tetrapod footprints. Superficial arthropod locomotion structures are the dominant invertebrate trace fossils, particularly those produced by spiders and scorpions, and subsurface invertebrate activity is evident although to a lesser degree (Ekdale and Bromley 2012; Krapovickas et al. 2016).

This important record of eolian trace fossils with outstanding preservation is difficult to explain. During the last century the discussion about the preservation of tracks in cross-bedded sandstones mostly focused on the origin (eolian vs. subaqueous) of the bearing levels (McKee 1947; Brand 1979). Accordingly, unusual locomotion patterns observed in the Coconino Sandstone trackways influenced Brand and Tang (1991) to propose an underwater origin for the succession. The current consensus among researchers is a subaerial origin for the Coconino Sandstone trackways and that some of the unusual locomotion patterns represent sideways, oblique upslope, and downslope progression in dunes (Lockley 1992; Loope 1992; Milán et al. 2008). Ichnologists have proposed that just enough humidity (i.e., not too dry, not too moist) can produce sufficient cohesion within sand grains that favors the preservation of tracks and traces (Faul and Roberts 1951; McKeever 1991; Lea 1996; Bordy and Catuneanu 2002; Fornós et al. 2002). The presence of infiltrated clays, sun-cracked surfaces, and raindrop imprints points to moist sands with the necessary cohesiveness to allow track preservation in some examples (Loope 1986; McKeever 1991). However, this is not the case for numerous track-bearing beds where the presence of moisture has not been demonstrated. Thus, significant information about trackway morphology, formation, and survivorship under variable substrate conditions has been produced through experimental trackways made in controlled laboratory conditions (McKee 1947; Davis et al. 2007; Scott et al. 2010). However, some questions remain unanswered. What provides cohesion to the eolian loose sand grains to allow preservation of delicate features usually observed in the tracks, trails and burrows? Why are delicate tracks made in dunes not obliterated by the deposition of the next sand lamina? Is there an agent acting as a glue?

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The aim of the present contribution is to analyze, from a taphonomic perspective, a case study from the Permian of Argentina where footprints are preserved in eolian deposits. A detailed sedimentological study of the trackway-bearing levels was performed to find biological and/or mineral evidence (e.g., biofilms, bioglues, clay/smectite coating of sand grains) that might have enhanced preservation. Finally, the preservational conditions are evaluated in a stratigraphic genetic framework.

GEOLOGICAL SETTING

The studied trace fossils were recovered from the early Cisuralian Yacimiento Los Reyunos Formation, southern Mendoza Province, Argentina (Fig. 1). The unit is part of the extensive Choiyoi silicic volcanic province, included in the Gondwanic dystrophic cycle (late Paleozoic–early Mesozoic).

The Yacimiento Los Reyunos Formation consists of alluvial, fluvial, and eolian facies associated with pyroclastic layers interpreted as alluvial fan deposits that pass to eolian sandstone and it is attributed to a sand sea setting (Polanski 1964; Spalletti and Mazzoni 1972; Llambias et al. 1993). The unit is divided into four laterally interfingering members: the Psefitico (Maloberti 1983 *fide* Lardone et al. 1993), the Andesitic (Lardone et al. 1993; Llambias et al. 1993), the Areniscas Atigradas (Holmberg 1948; Lardone et al. 1993), and the Toba Vieja Gorda members (Rodriguez and Valdivieso 1970; Ortega Furlotti et al. 1974; Lardone et al. 1993). Of these, the Andesitic Member is not recognized in the study area. The Psefitico Member is characterized by polymictic fanglomerate and conglomerate dominated by blocks and angular pebbles with interbedding of yellow cross-stratified sandstone (Llambias et al. 1993). Grayish yellow, fine- to coarse-grained arkosic sandstone and subordinate siltstone with horizontal and cross-bedded stratification dominate the overlying Areniscas Atigradas Member (Spalletti and Mazzoni 1972). Finally, the Toba Vieja Gorda Member is mainly formed by grayish purple porphyritic tuff (Lardone et al. 1993; Llambias et al. 1993). The continental alluvial, fluvial, and eolian sedimentary rocks, known as the Psefitico and Areniscas Atigradas members, derived from reworking of ignimbrite known as the Toba Vieja Gorda Member (Rocha-Campos et al. 2011).

A recent SHRIMP U–Pb dating (281.4$\pm$2.5 Ma) from an ignimbrite close to the base of the Yacimiento Los Reyunos Formation constrain its deposition to the Kungurian (Cisuralian) (Rocha-Campos et al. 2011).

TRACK TAPHONOMY

Sedimentology of Track Bearing Levels

Footprints from the Yacimiento Los Reyunos Formation were found in outcrops situated in the Sierra Pintada and Sierra de las Peñas, West of San Rafael city (Fig. 1). Footprint-bearing levels are located in sandstone quarries exploited for their uranium content (Dr. Baulíes quarry; 34°40′43.5″S, 68°35′37.3″W) or for construction (La Julia quarry, 34°18′54.5″S, 68°45′00.5″W), each in different stratigraphic levels of the Psefitico and Areniscas Atigradas members (Fig. 1).

In the Dr. Baulíes quarry (Fig. 2), the Psefitico Member consists of poorly sorted, clast-supported, angular and subangular pebble- to cobble-conglomerate and pebbly medium-grained red sandstone. The conglomerate forms lenticular bodies (up to 1 m thick) with erosive basal contacts and grades upward and laterally to pebbly sandstone. The conglomerate lenses present planar cross-stratification (Gp), trough cross-stratification (Gt) (Fig. 3A), and clast imbrication (Fig. 3B). The sandstone units form massive tabular strata that laterally pass to lenses with planar cross-stratification (Sp) with 30-cm-thick cosets and clast imbrication. The massive red sandstone presents locally trace fossils assigned to *Palaeophycus tubularis* (Krapovickas et al. 2015, fig. 3C). The conglomerate and sandstone beds are interpreted as distributary channel and overbank deposits. Lenses of grayish yellow well-sorted fine-grained sandstone are interbedded in the red sandstone of the overbank (Figs. 2, 3C). The grayish yellow sandstone shows trough cross-bedded stratification (St), inverse grading, and corresponds to the lowest of the footprint-bearing levels (Figs. 2, 3C). The grayish yellow sandstone is interpreted as eolian in origin, and together with distributary channel and overbank deposits it represents a fluvio-eolian interaction within a distal alluvial fan setting (Rey 2011).

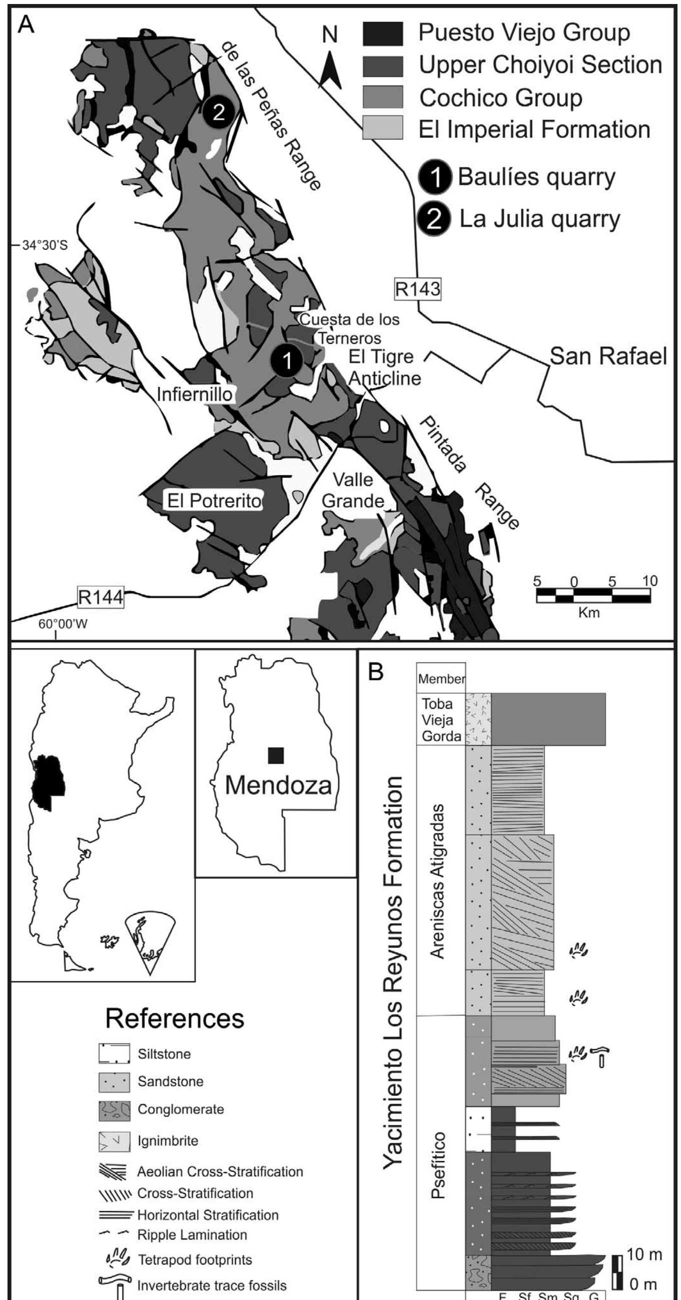

FIG. 1.—**A**) Geological map of the San Rafael Block, central-western Argentina showing the study area (cycles). **B**) Generalized stratigraphic section of Yacimiento Los Reyunos Formation showing track-bearing levels.

The Areniscas Atigradas Member, in the same area, consists of grayish yellow to grayish pink, well-sorted, fine- to coarse-grained arkosic sandstone (Figs. 2, 3D–3F). These texturally mature sandstone are composed almost exclusively of subangular to subrounded clasts of quartz and feldspar, with minor clastic calcite and biotite content and scarce lithic

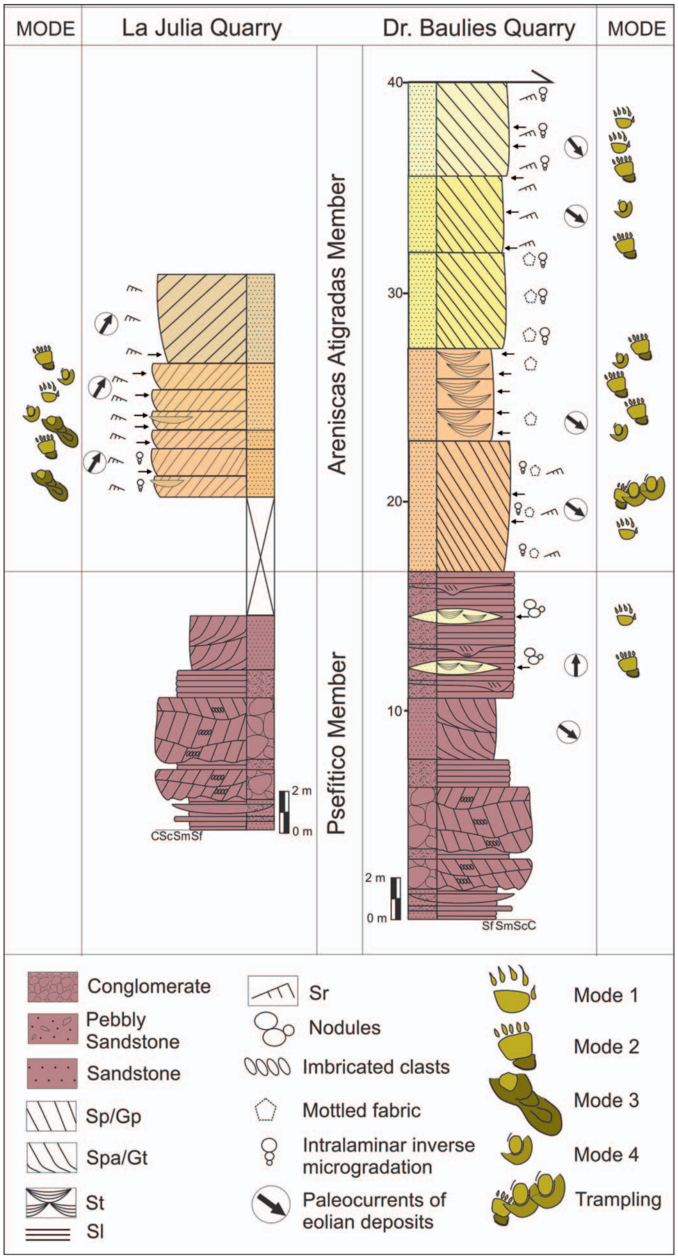

FIG. 2.—Schematic section of the Yacimiento Los Reyunos Formation at Dr. Baulíes and La Julia quarries including the track-bearing levels and footprint taphonomic modes.

fragments (Fig. 3G, 3H). The strata are tabular with 4.5 m average thickness. Fine-grained sandstone may contain trough cross stratification (St), planar cross stratification (Sp), ripple lamination (Sr) and mottling (Fig. 3I). The medium- to coarse-grained sandstone presents planar cross stratification (Sp) and wind-ripple lamination (Sr) with inverse-graded laminae (Fig. 3J). The sandstone fabric is texturally mature and grain-supported, however, thin-section analysis reveals an upward increase of clays cementing the siliceous grains (Fig. 3K). Also towards the top of the succession, the grain size of the siliceous clasts increases from 10–30 μm to 10–70 μm. In polished slabs, mottles are revealed to be calcitic in composition, rounded, and about 1 cm in diameter (Fig. 3L). Differential accumulation of minerals can be recognized in some of the samples. No textural features indicating microbial-mediated precipitation of carbonate have been observed. *Palaeophycus tubularis* and *Skolitos* isp. occur in these deposits (Krapovickas et al. 2015, fig. 3A, 3B).

Interpretation.—Sedimentary structures of the sandstone indicate wind ripples, grainfall, and grainflow deposits caused by saltation and gravity-driven processes. All these features indicate eolian dune migration in a dune field environment (Mountney and Jagger 2004; Mountney 2006). Mottled levels suggest incipient paleosol formation (Freytet and Plaziat 1982) or vegetated dune deposits (Alonso-Zarza et al. 2008). The mineralogical zonation in some of the samples might indicate a perched groundwater table favored by low permeability subsurface of the El Imperial Formation basement. The lack of microbial textures in the samples rules out an enhanced preservation of tracks by rapid biomineralization as has been observed in other cases, as around the margin of recent saline lakes (Scott et al. 2007, 2010) and other environments (Seilacher 2008).

At the La Julia quarry, the Yacimiento Los Reyunos Formation is only represented by the Areniscas Atigradas Member. Grayish yellow, cross-bedded, well-sorted medium- and coarse-grained sandstone characterize the unit. The sandstone, as occurs in the Dr. Baulíes section, are composed of subangular to subrounded grains of quartz and feldspar with minor calcite and biotite content and scarce lithic fragments. Planar cross stratification (Sp) and very low angle lamination (Sl) dominates the succession, with common ripple lamination (Sr) with inverse grading (Fig. 3J). A minor, reddish-brown clay component occurs in sandstone from the La Julia log (Fig. 3K). Some of the clasts show signs of corrosion in their margins by calcite and other clasts show fragmentation. In addition, a 10% biotite crystalline intergrowth is identified as a cement along the entire section. Sedimentologic features, such as lithology, sedimentary structures, and stratal geometry, suggest that this succession represents dune migration in a dune field environment (Mountney 2006) as in the Dr. Baulíes section.

The Yacimiento Los Reyunos Formation represents the initial sedimentary fill in the San Rafael Basin associated with arc magmatism developed eastward to Andes West front (López-Gamundí 2006; Kleiman and Japas 2009). The Los Reyunos alluvial and eolian environments occurred downwind of the Andes West front, in a region with relatively low rainfall where a rain shadow might have existed.

Taphonomic Modes

In the present study, four taphonomic modes of track preservation are defined based on the preservation quality of the footprints, and the presence or absence of different morphological and extra-morphological features, such as palm/sole-pads, digit impressions, digit scratch traces, and marginal rims, among others (see Table 1, Fig. 4, and Krapovickas et al. 2015 for detailed descriptions). Only the most complete trackway for each taphonomic mode was selected to calculate the speed of the track-maker, therefore there are no calculations for most of the tracks included in the taphonomic modes. Speeds were estimated using Alexander's formula (Alexander 1976) as a relationship between speed u, body size (expressed by h, the height at the hip) and the stride length λ such that:

$$\lambda/h = 2.3(u^2/gh)^{0.3}$$

In addition, we followed McKeever (1994) to estimate the hip height (h) of Permian therapsids as 1.5 times the length of the pes whereas the hip height for erect reptiles was estimated at four times the length of the pes.

Special cases are discussed separately due to their importance in the general context of the Los Reyunos footprint record.

All the tracks described occur at the base of the foresets of the sand-dune.

FIG. 3.—Outcrop and binocular low magnification photographs, and thin section microphotograph from the Yacimiento Los Reyunos Formation. **A**) Photograph of the conglomerate lenses showing Gp and Gt and an erosive base. **B**) Detail of the clasts imbrication present in the conglomerate lenses. **C**) Yellowish fine sandstone with St interbedded with reddish sandstone. **D**) Arkosic sandstone of the Areniscas Atigradas Member showing the grayish yellow to grayish pink coloration. **E**) Detail of the sandstone showing St. **F**) Detail of the sandstone in D with Sp. **G**) Areniscas Atigradas sandstone under binocular microscope where quartz and feldspar clasts can be seen. **H**) Microphotograph of the Areniscas Atigradas sandstone where minor clastic calcite can be identified showing high birefringence along with scarce lithic fragments. **I**) Lateral variation of the sandstone showing white mottling interpreted as a rhizohaloe. **J**) Detail of an inverse-graded laminae in the medium to coarse sandstone. **K**) Microphotograph in which a change in patterns can be recognized (blue arrow), from minor cement content below the arrow to higher cement content towards the top of the thin section. **L**) Polished slab showing the calcitic rhizohaloe disrupting the reddish fabric of the sandstone.

Mode 1.—The footprints included in this category are present in cross-stratified, sub-angular to sub-rounded well-sorted fine- to coarse-grained sandstone (Table 1, Figs. 2, 5). Some levels show an alternation of pink medium-grained and gray coarse-grained sandstone. The measured dip angles are 20° for the surfaces of the eolian dunes and 15° for the fluvial system dunes (Psefitico Member).

This taphonomic mode includes several footprints previously figured by Krapovickas et al. (2015) because they have the best preservation and show

TABLE 1.—*Morphological and extra-morphological features that characterize the taphonomic modes and the special cases of the footprints from Cisuralian Yacimiento Los Reyunos Formation.*

	Mode 1	Mode 2	Mode 3	Mode 4	Trampling	Museum
			Footprint features			
Palm outline	Oval	Circular or irregular	Irregular	Oval or irregular	Circular or irregular	Oval
Palm-digit connection	Separated	Connect	No info	Connect	Connect	Separated
Digit impressions	Yes	Yes	No	No	Few	Yes
Claw drag trace	Yes	No	No	No	Very few	Yes
Presence of rim	No	Yes	Yes	Yes	Yes	Few
Rim size	–	Small	Large	Large	Large	Small
Rim shape	–	Bulbous-shape	Bulbous-shape	sand crescent-shape	Bulbous-shape	Semicircle
Rim location	–	Down-slope	Down-slope	Down-slope	Down-slope	Posterior
			Bearing level			
Texture and color	Grayish yellow fine-grained, pink medium-grained and gray coarse-grained sandstone	Grayish yellow fine-grained, pink medium-grained and gray coarse-grained sandstone	Grayish yellow coarse-grained sandstone	Gray fine- to coarse-grained sandstone	Red medium- to coarse-grained sandstone	Grayish yellow coarse-grained sandstone
Type lamination	Grainfall Wind-rippled Inverse graded	Grainfall Wind-rippled Inverse graded	Wind-rippled Inverse graded	Grainfall Wind-rippled Inverse graded	Inverse graded	–
Dip angle surface	15°–20°	15°–20°	20°	20°	20°	–
Infill sediment	Following level	Following level	Bearing level	Following level	Following level	No info

detailed morphological features. The material remains *in situ* at both Dr. Baulíes and La Julia quarries (Fig. 1) and includes well-preserved tracks and trackways attributed to *Chelichnus gigas* (Krapovickas et al. 2015, fig. 5A, 5C). They are represented by isolated *manus-pes* sets and series of *manus-pes* sets forming trackways. The speed of the track-maker inferred by one trackway included in this mode is 2.5 km/h. Good preservation is evident in details of the digit and palm/sole impressions (Fig. 5). The palm/sole impressions have oval outline and are separated from the digit impressions. In most cases, footprints have five digit impressions associated with claw drag traces (Fig. 5). They are preserved as long, sharply incised grooves with a very well-defined border that delimits deep grooves of the claw trace. The marginal ridge is produced by sediment displacement due to compression by the animal foot during the step cycle. In this mode, the marginal ridge is mostly absent, but when present, it occurs as a small bulbous-shape recorded in a lateral-posterior position of the track, and generally is documented only in tracks located in up-slope positions within the trackway.

Interpretation.—The preservation of both digit impressions and claw drag traces suggests at least some plasticity in the sediment. The size and deepening of the tracks are related to the size and weight of the track-maker. The size of the track is directly related to the producer bodyweight but the footprint depth is related to both the bodyweight of the animal and the substrate consistency (e.g., Marsicano et al. 2010). The marginal rim is caused by the compression of the plastic soft ground by the foot during the step cycle (Allen 1997; Manning 2004; Milán et al. 2004). The inferred speed suggests that the animal was walking slowly accordingly to McKeever (1994), therefore facilitating the observed morphological details.

Mode 2.—Footprints included in this mode occur in grayish yellow, gray or pink, cross-stratified, sub-angular to sub-rounded well-sorted medium- to coarse-grained sandstone (Figs. 2, 6). The measured dip angles are 20° for the eolian dunes and 15° for the surface of the Psefitico Member (dunes in the fluvial system). This category includes some footprints attributed to *Chelichnus gigas* by Krapovickas et al. (2015, fig. 5D). Tracks and trackways of this type are also *in situ* in both studied localities (Fig. 1). The tracks show a well-defined circular to slightly irregular palm, the digit impressions are short and shallow grooves with well-defined but smooth borders (Fig. 6). Occasionally, some digit imprints are missing. The tracks present a well-developed asymmetric marginal rim formed by the displaced sediment (Fig. 6). The marginal rims present a bulbous-shape and are located latero-posteriorly to each print. They are more developed in the prints produced uphill, with lengths from 2 to 5 cm (Fig. 6).

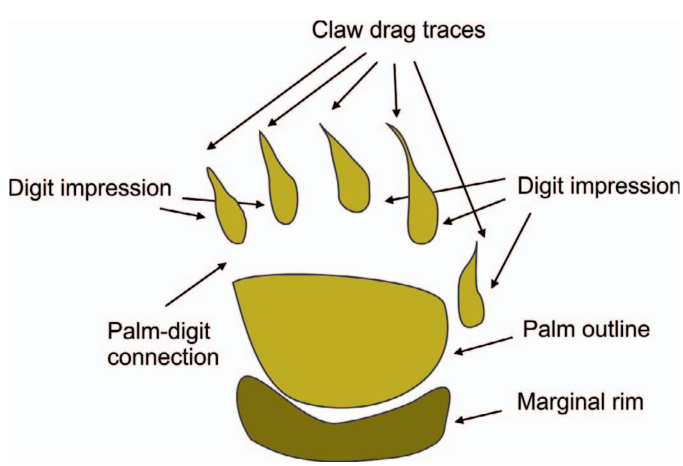

FIG. 4.—Morphological features recognized in the tracks that together with the extra-morphological features defined the taphonomic modes.

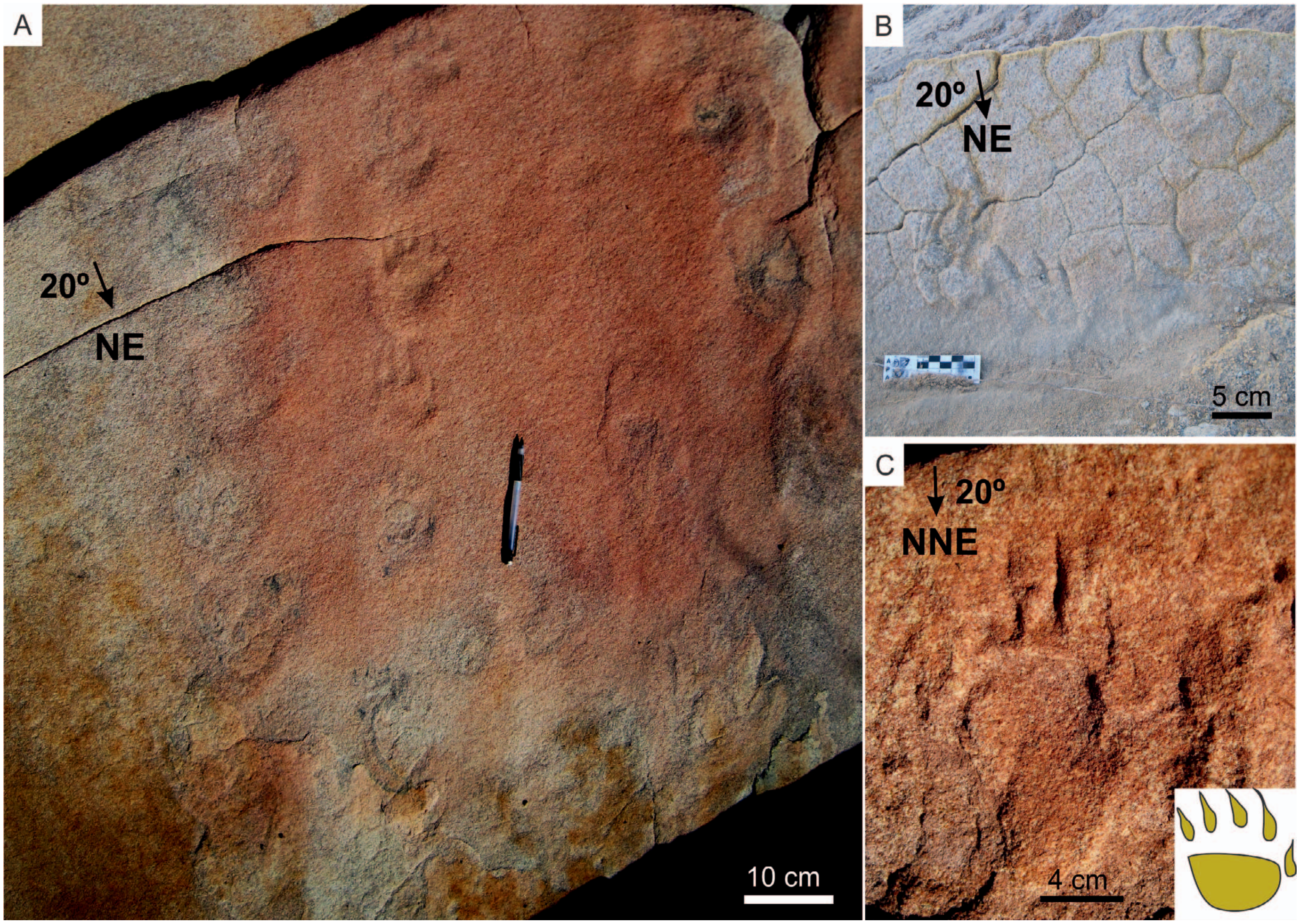

FIG. 5.—Field photos of the surfaces with footprints recognized as taphonomic mode 1. **A**) Trackway in surface from La Julia quarry. **B**) Three tracks in surface from Dr. Baulies quarry. **C**) Isolate *manus-pes* in surface from Dr. Baulies quarry.

Interpretation.—The displaced sediment of the rims corresponds to structures produced when the animal crossed the foreset of the sand-dune. The rim position is always according to the dip of the foreset and not according the direction of the animal progression.

Mode 3.—The track-bearing levels for this mode consist of grayish yellow, sub-angular to sub-rounded well-sorted coarse-grained sandstone. The measured dip angle of the surfaces is 20°. This category includes several trackways, one of them already described and attributed to *Chelichnus duncani* by Krapovickas et al. (2015, Tw2, fig. 4A). Most of the material included in this taphonomic mode (Figs. 2, 7) remains *in situ* in both studied localities (Dr. Baulíes and La Julia quarries). Some trackways are recognized mostly as a pattern of two parallel lines (Fig. 7). In a few cases, the tracks preserve an irregular palm impression with slight digit evidence. The speed inferred of the track-maker in the best preserved trackway (*Chelichnus duncani* Tw2, Krapovickas et al. 2015) is 4.23 km/h. The main feature observed in the footprints included in this category is the presence of a large bulbous asymmetric marginal rim developed latero-posteriorly (Fig. 7). Marginal rim sizes observed in these tracks are variable, showing significant differences among and throughout the trackways, but in all cases the displaced sediment covers either partially or totally the previous footprint (Fig. 7). Consequently, the imprints preserve an infill that partially obscures the footprint morphology.

Interpretation.—Each rim was produced when the soft sand was pushed behind each footprint and covered or completely obliterated the previous footprint in the trackway. The amount of obliteration by the avalanche structures would depend on the angle of slope and the direction of the animal progression. The inferred speed suggests that the animal was trotting during implantation (see McKeever 1994) while crossing the dune.

Mode 4.—Footprints included in this category are present in gray, cross-stratified sub-angular, well-sorted fine- to coarse-grained sandstone. The measured dip angle of the surfaces is 20°. Some of the footprints were attributed to *Chelichnus duncani* (Tw1) and another to pear-like footprints (Krapovickas et al. 2015, fig. 4C). Both Dr. Baulíes and La Julia quarries contain *in situ* tracks and trackways of this category (Figs. 2, 8). The tracks are preserved as well-defined oval or irregular impressions with a deep shaft and a marginal rim, however, there is no clear evidence of digits or the complete palm/sole dimensions (Fig. 8). The speed inferred of the track-maker in the more complete trackway (*Chelichnus duncani* Tw1 of Krapovickas et al. 2015) is 5 km/h. The track impressions are variable in size with lengths from 1.5 to 8.4 cm and the marginal rim range from 1 cm wide and 2 cm height to 6 cm wide and 4 cm height. The main feature of the footprints is the presence of marginal rims of displaced sediment with sand crescent shape (Fig. 8). They are located around the postero-lateral margin of each imprint. Several footprints show a shaft infill that

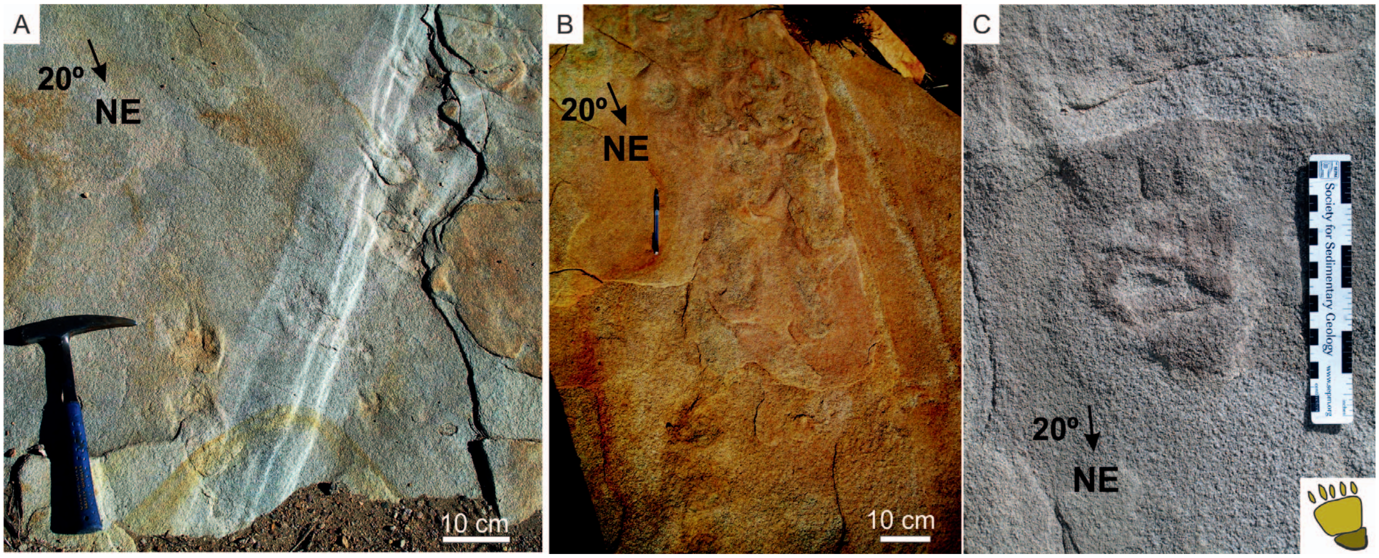

FIG. 6.—Field photos of the surfaces with footprints recognized as the taphonomic mode 2. **A**, **B**) Trackways in surface from La Julia quarry. **C**) Isolate footprints in surface from Dr. Baulies quarry.

corresponds to the sediment of the overlain sandstone level in the succession.

Interpretation.—The location of the rims is linked mainly to the slope angle (they point down the slope of the foreset) and to a lesser degree to the direction of progression. Different studies in eolian deposits suggest that the avalanche structure that a footprint displaces in soft sand invariably is directed down-slope on the depositional surface (e.g., Fornós et al. 2002; Krapovickas et al. 2015). The inferred speed suggests that the animal was running (see McKeever 1994) while crossing the dune foreset.

Special Cases

Trampling Surface.—This surface occurs on a red, cross- stratified, sub-angular to sub-rounded, well-sorted medium- to coarse-grained sandstone showing white mottling and scarce horizontal (*Palaeophycus tubularis*) and vertical (*Skolitos* isp.) invertebrate trace fossils (Krapovickas et al. 2015). The trampling surface was only identified at the Yacimiento Dr. Baulíes quarry and the measured dip angle of the surfaces is 20°. The bearing surface includes abundant tracks and only few of them are well defined (Fig. 9). In general, the tracks show a

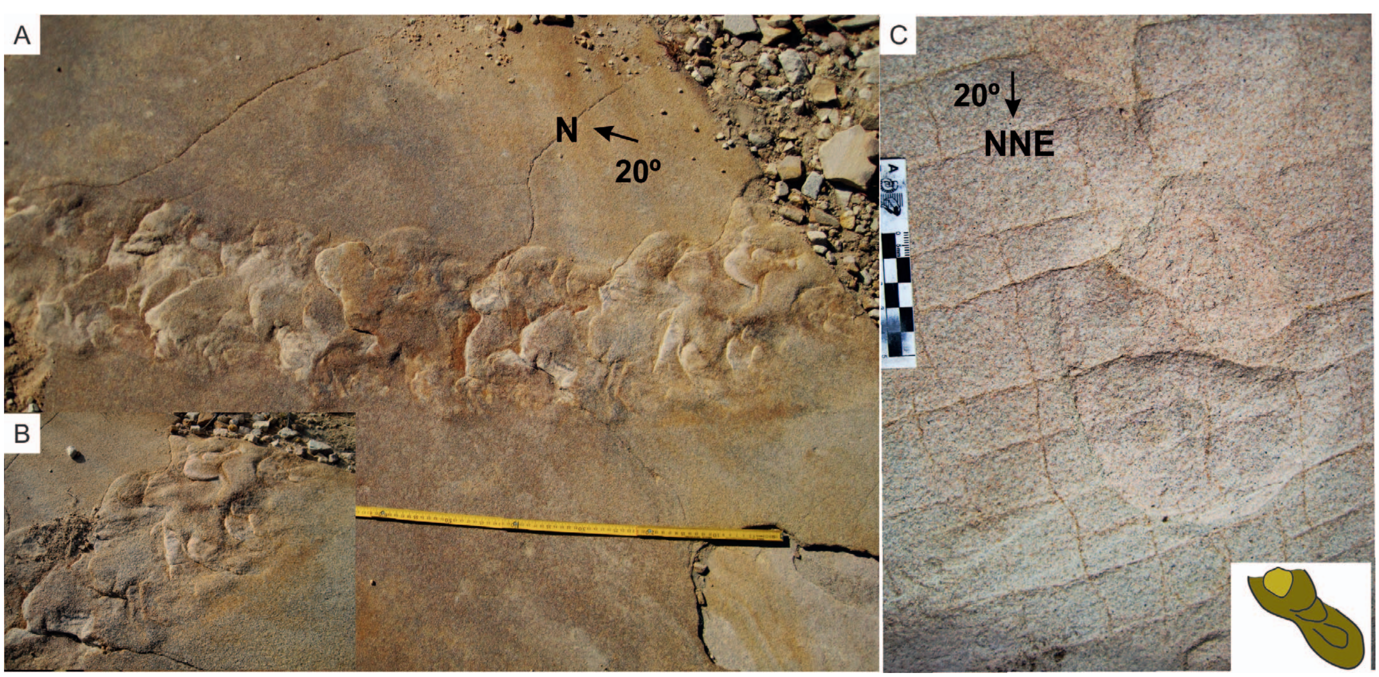

FIG. 7.—Field photos of the surfaces with footprints recognized as the taphonomic mode 3. **A**) Trackway in surface from La Julia quarry. **B**) Detail of trackway presented in A. **C**) Isolate footprints in surface from La Julia quarry.

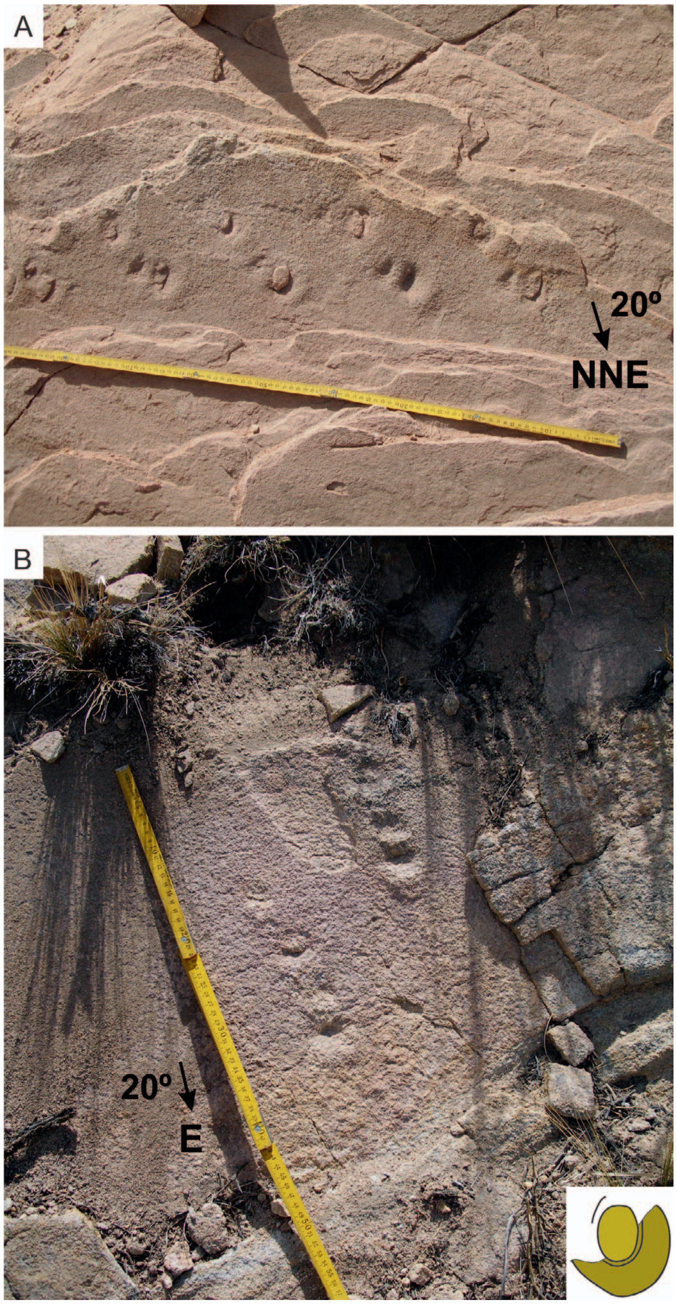

FIG. 8.—Field photos of the surfaces with footprints recognized as taphonomic mode 4. **A**, **B**) Trackways in surface from Dr. Baulies quarry.

pronounced circular to irregular shaft with well-developed asymmetric marginal rims that are systematically positioned NNE according to the present location of the tracks (Fig. 9). Only a few tracks preserve faint digit impressions that are less impressed than other footprints in this surface (Fig. 9). The impressions are variable in size with lengths from 1.5 to 8.4 cm and the rims are from 4.5 cm wide and 1.5 cm height to 9.5 cm wide and 5 cm height. As previously mentioned, the marginal rim of all footprints is in NNE direction, independent of the direction of the animal progression (Fig. 9). Two different track preservational patterns are recognized. In the area where the highest concentration of tracks occurs (in the center of the surface) (Fig. 9A, 9C), each one shows a deep shaft with greater depth in the heel area close to the marginal rim. In contrast, the other pattern presents best-defined tracks with shallower depth in the impressions, but with deeper digit impressions, not near the rims (Fig. 9B). The tracks display a shaft infill characterized by pink muddy medium-grained sandstone (Fig. 9D) from the overlying bed.

Interpretation.—The two different patterns recognized in this surface could be related to a change in the surface conditions between their imprinting, with some time occurring between them. These differences between patterns were also recognized in alluvial and freshwater successions (e.g., Bromley and Asgaard 1979, 1991; Gierlowski-Kodesch 1991; Buatois et al. 1996, 1997; Krapovickas et al. 2008). In the four modes described in this contribution, the marginal rims are in NNE position and oriented downslope.

Museum Slabs.—Several slabs with footprints are hosted in the collections of the Museo de Historia Natural de San Rafael, which consist of grayish yellow subangular well-sorted coarse-grained sandstone. Most of this material was previously described by different authors due to their good preservation and detailed features (Aramayo and Farinati 1983; Aramayo 1993; Melchor 2001; Krapovickas et al. 2015, fig. 6) and comes from several quarries at La Julia, Cuesta de los Terneros, and Dr. Baulíes areas (Fig. 1). In general, they consist of isolated *manus-pes* sets and series of *manus-pes* sets. The tracks are characterized by a good preservation with oval palm/sole pads generally separated from the digit impressions (Fig. 10). The digit impressions are all associated with deep claw drag traces, without collapse of the sediment (Fig. 10). The marginal rim around the prints is uncommon, and when it is present is located at the posterior area of the print (Fig. 10).

Interpretation.—The absence of collapse of the sediment among digit impressions and the claw drag traces suggests a plastic condition of the sediment. Nevertheless, Manning (2004) proposed that the amount of moisture in the sand was less than 25% because more liquid in the sediment would have caused the track features to collapse. The museum slabs could be considered part of the taphonomic mode 1, or could be considered the only report of footprints in horizontal deposits in the area (interdune). Unfortunately, the original bearing levels of the slabs are unknown, so it cannot be attributed to one mode or another.

Tracks in Cross Section.—Tracks in cross sections were also recorded on different levels of the Areniscas Atigradas Member at Dr. Baulíes quarry. They are imprinted in different beds, including red medium- to coarse-grained sandstone, gray coarse-grained sandstone, and pink medium- to coarse-grained sandstone (Fig. 11A–11D). The tracks are visible in transverse and longitudinal cross sections in some of the studied outcrops. They can be observed across the digits (Fig. 11A, 11B), but also across the palm/sole impression (Fig. 11C, 11D). In these vertical sections, several deformed layers are also observed that can be correlated with tracks in cross section.

Interpretation.—The identification as footprints in cross section is evidenced by the size-frequency distribution of the deformation structures, regular deformation, and compression of the lower layers in the deformation, as was reported by Loope (1986) for Cenozoic eolian deposits from Nebraska.

DISCUSSION

True Track, Undertrack, and Eroded Track

The exceptional therapsid footprint record from the Yacimiento Los Reyunos Formation involves isolate tracks and trackways of one

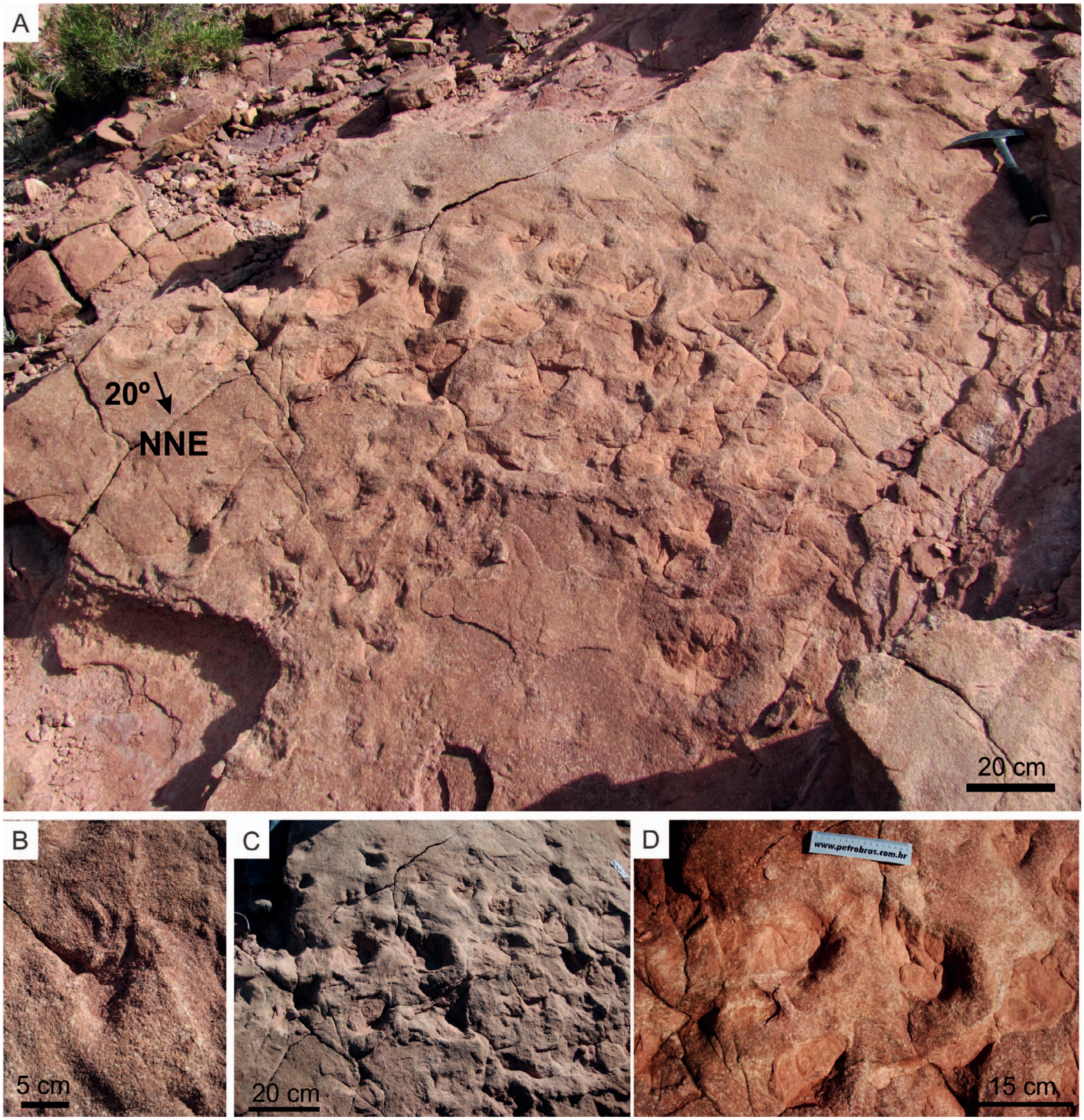

FIG. 9.—Field photos of the Trampling surface from Dr. Baulies quarry. **A**) Overview of trampling surface. **B**) Detail of footprint showing digit impressions and marginal rim. **C**) Crossing of two different track preservational patterns. **D**) Detail of footprint showing deep irregular shaft with well-developed asymmetric marginal rims.

ichnogenus with a variety of preservations. In addition to the four different taphonomic modes recognized above, the features shown by the tracks allow further distinctions. Our samples include true tracks as well as undertracks and eroded tracks, all of them recorded *in situ*.

The tracking surface is the actual level where the footprint was produced (i.e., the surface on which the animal walked) and these tracks are recognized as "true tracks" (Fornós et al. 2002). In contrast, the undertracks are those formed by the transmission of the deformation produced by the foot in the underlying sediment (Thulborn 1990).

The features that characterize true tracks are: (1) the presence of distinctive sediment infilling the track (whereas infilling of undertracks would cover not only the depression of the footprint but also the surface surrounding it as an unique layer); (2) the presence of marginal rims (see Allen 1997 and Fornós et al. 2002) and a well-preserved drag trace; and (3)

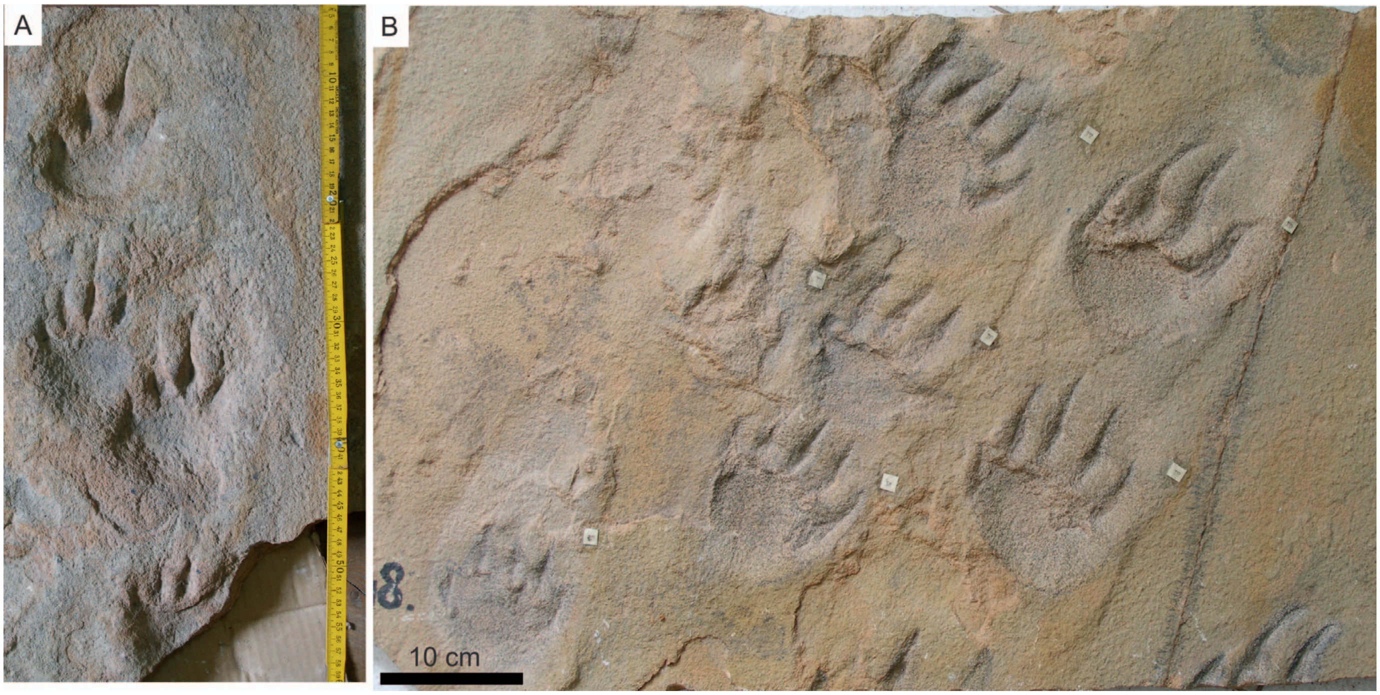

FIG. 10.—Photos of museum slabs. **A**) MHNSR-PV 490. **B**) MHNSR-PV 348. Both views show tracks with oval palm/sole pads separated from the digit impressions and claw drag traces.

the presence of avalanche structures produced by the sediment displaced by the animal (Fig. 6).

Most of the tracks analyzed in the present study are considered true tracks even though they exhibit varying degrees of morphological detail expressed by the taphonomic modes in which they are included: detail impression of the palm, digits and claws reported in modes 1 and 2 (Figs. 5, 6, respectively); small or large bulbous-shape marginal rims of displaced sediment documented in modes 2 and 3 (Fig. 7), and sand-crescent marginal rims in mode 4 (Fig. 8). The variation of the morphological detail in the footprints and the shape/size of the marginal rims are mostly explained by the substrate consistency and by the track-maker speeds.

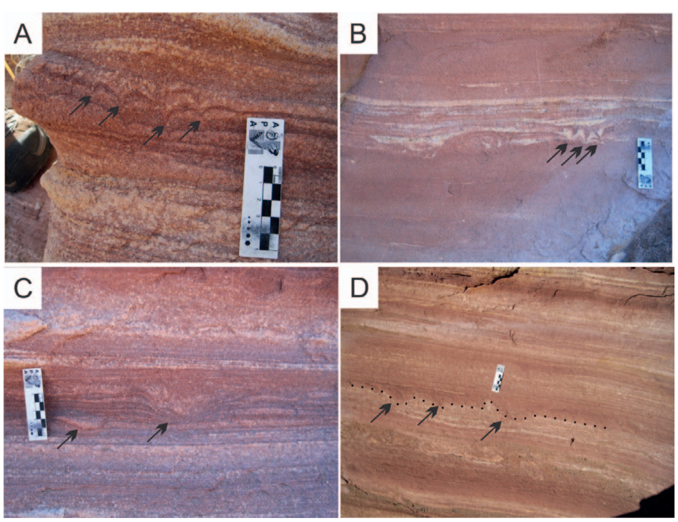

FIG. 11.—Tracks in cross-section from Dr. Baulies quarry. **A**, **B**) Digital impressions. **C**, **D**) Palm/sole and rim deformed layers. Arrows mark the deformation in layers.

Direct evidence of undertracks was recognized in an individual trackway included in taphonomic mode 2 (Fig. 11A). This trackway consists of nine tracks preserved in two levels; six of them are preserved as true tracks in the tracking surface and three as undertracks in the underlying level (Fig. 12A). The lack of marginal rims (of displaced sediment) and gently sloping walls on these undertracks was observed in laboratory experiments by Milán and Bromley (2006). Surprisingly, these transmitted imprints show more morphological detail (digit impression) and also are smaller and less deep than the true tracks (Fig. 12A). This is in contrast with what was observed by Milán and Bromley (2006) on firm substrates, where successive undertracks show a gradual increase in horizontal dimension and a steady degradation of the morphology of the true track. However, as the tracking surface includes the true tracks with infilling that covered them; it is not possible to know the degree of morphological detail that the true tracks present (Fig. 12A).

At present, the track-bearing surfaces are in an inclined position and it is likely that this condition caused all studied surfaces to be somewhat eroded. There are some footprints where a degree of erosion is marked ("eroded tracks", Fig. 12B, 12C). These are characterized by separate impressions of the deepest printed trace as sharp digits separated from the palm (see Milán and Bromley 2006). The footprints interpreted as eroded tracks are included in the taphonomic mode 1 due to the detailed preservation of the palm, digit, and claw impressions. Moreover, they are characterized by preservation on a coarse fraction of sand. This condition has been attributed to the microtopographic depression produced by the tracks that can become a deflation lag caused by the removal of the fine-grained sediment and light mineral fraction and preserves a thin layer of the coarse sediment and heavy minerals (Buynevich et al. 2011).

Substrate Consistency and Preservation

Several contributions discuss the preservation of tracking surfaces, including both field and laboratory information (e.g., McKee 1947; Thulborn 1990; Manning 2004). A range of conditions is established for

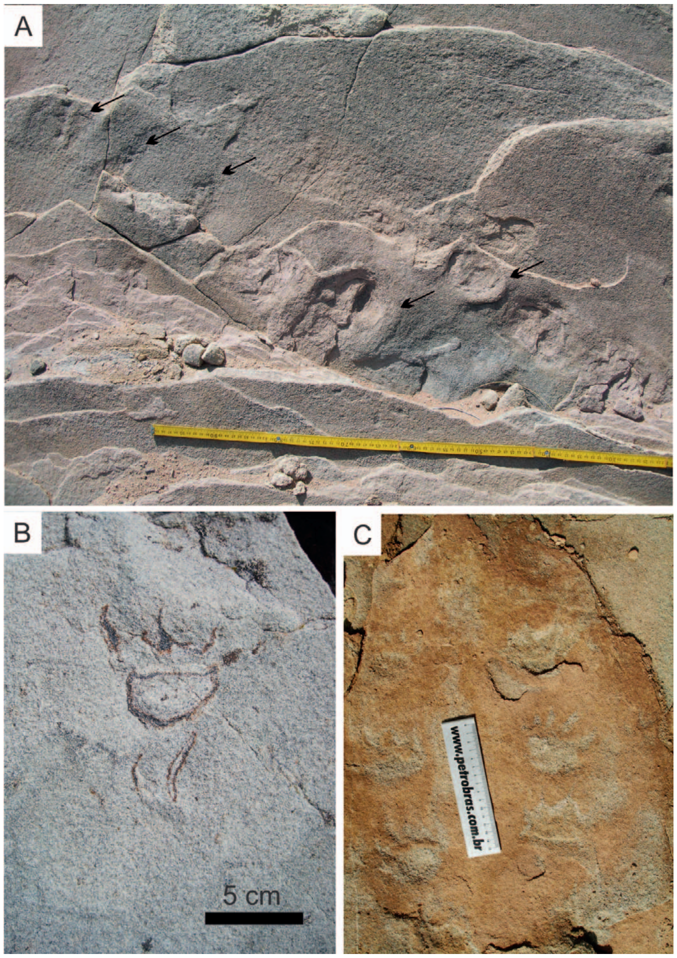

FIG. 12.—**A**) True tracks and undertracks in a surface from Dr. Baulies quarry showing in the true track marginal rims and sediment displaced is infilled the impressions, in the undertracks smaller size and lower depth of the track and digit impression can be seen. **B**) Eroded track in surface from La Julia quarry showing concentration of heavy particles. **C**) Eroded track in surface from Dr. Baulies quarry showing concentration of the coarse-grained fraction.

the best preservation potential for a foot print and a significant role in this matter is played by rheological stratigraphy as grain size, mineralogy, and moisture content at the moment of implantation (e.g., McKee 1947; Allen 1997; Manning 2004). Nevertheless, quick burial of the tracks is also a very important factor for their preservation. Also, the time-scales on which accretion-erosion occur modify preservation, producing partial or total infilling or erosion before final entombment, and/or modification by trampling (Allen 1997).

Particularly in eolian deposits, the main discussion about the genesis and preservation of prints concerns fluid content of the sand (dry, damp, wet, or underwater) and the dip of the sandy surface. In laboratory experiments McKee (1947) concluded that the best conditions for track preservation was when animals walked over dry sand that was subsequently moistened and then later covered by more dry sand, and also after the sand was dampened (e.g., during a heavy downpour) (McKeever 1991). Others discussed that sand under water, or totally saturated, cannot offer good footprint preservation (e.g., Scrivner and Bottjer 1986; McKeever 1991). Related to other preservation factors, some authors have also included in this discussion the presence of clay partings within the sand (Harkness 1850), or smectite coating (Loope 1986). Nevertheless, all cases indicate that the amount of water in sand needed for the best preservation of tracks is restricted to a narrow preservation window, much narrower, for example, than in mud (e.g., Laporte and Behrensmeyer 1980; Scrivner and Bottjer 1986).

In the present analysis, we document several sloped surfaces showing similar dip ($\sim 20°$) with abundant tetrapod tracks from sandstone that show a texturally mature and grain-supported fabric. Sandstone is included in a succession that comprises the consistent development of large-scale cross-stratification, wind-ripple lamination with inverse-graded laminae, and a geometry of beds that, as a whole, characterize it as a dune field with sets of dune migration (Mountney 2006). The Los Reyunos succession in the studied areas presents common mottled levels, which suggest incipient paleosol formation (Freytet and Plaziat 1982; Alonso-Zarza et al. 2008) in the dune deposits. Their development indicates a pause during sedimentation and a slightly wetter condition (Alonso-Zarza et al. 2008) linked probably to a high water table; which is supported also by the presence of invertebrate traces (Krapovickas et al. 2015).

Typical interdune facies having horizontal, sabkha-type laminations, desiccation cracks, rhizoliths, high degree of bioturbation (Kocurek 1981; Mountney 2006; Seiler and Chan 2008) are not present in the studied sections (Dr. Baulíes and La Julia quarries). However, the interdune facies (horizontal laminated dark mudrock) was identified (Spalletti and Mazzoni 1972; Rey 2011) in another section (Cerro Bola quarry; Fig. 13) but footprints have not been reported from this facies.

FIG. 13.—**A**) Location of the interdune facies Cerro Bola quarry (1) and the studied area without interdune facies Dr. Baulies quarry (2). **B**, **C**) Detail of interdune facies showing horizontal laminated dark mudstone interbedded with horizontal laminated yellow sandstone.

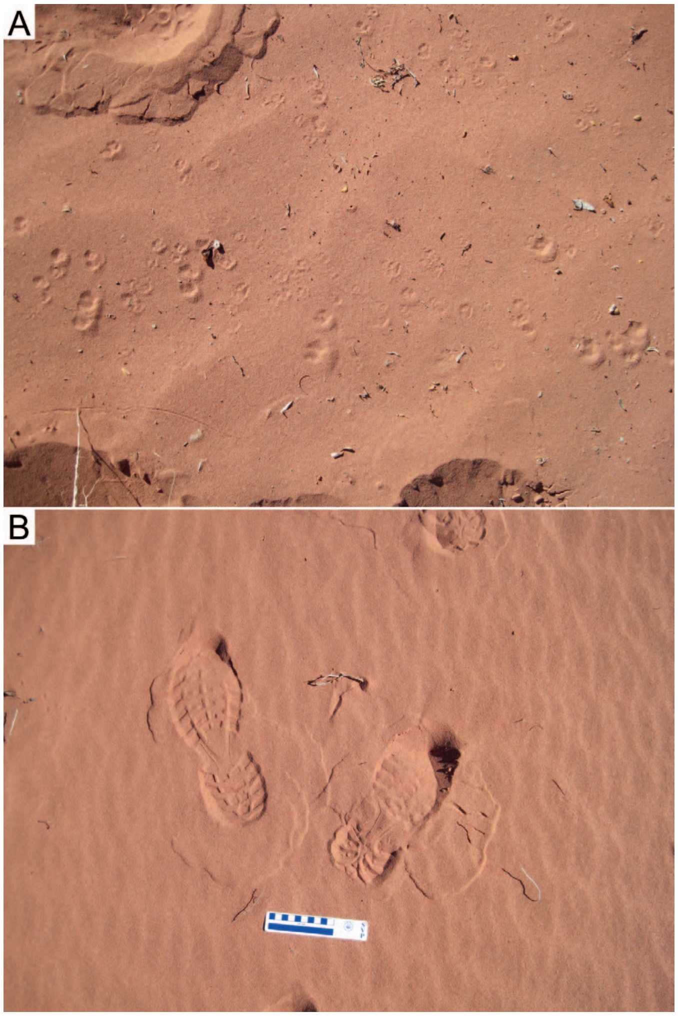

FIG. 14.—Field photos of recent dune sand in Talampaya National Park. **A**) Human footprint with bulbous-shape rim and small animal footprints with sand crescent-shape rims. **B**) Human footprints with bulbous-shape rims.

The Los Reyunos tracks present a wide preservation range, from very good with clear digit impressions and claw drag traces (taphonomic modes 1 and 2), up to poor preservation, where only the general trackway pattern can be recognized (taphonomic modes 3 and 4). Sedimentologic analysis of the bearing-levels (e.g., texture, type lamination, dip angle surface) has shown that there are not significant differences among them. Polished slabs and thin sections show that all levels lack fundamental elements that can improve preservation of footprints in eolian environments (e.g., Harkness 1850; Loope 1986; McKeever and Haubold 1996; Seilacher 2008), such as bacterial or algal mats or clay (Fig. 3). The very low content of clay in Los Reyunos succession can be associated with the close proximity of the basin to the source area.

Observations made by Loope (2006) for Jurassic dinosaur tracks in dune deposits indicated that the tracks produced in moist sand generate breccia blocks in unlithified sand (Loope 2006, fig. 9). These structures, produced at the air-water interface on subaerial sand deposits (Doe and Dott 1980); the sand below is dry and cohesionless as is evidenced by the free movement of the sand grains. The Los Reyunos tracks present no association with breccia. The absence of breccia suggests the tracks occurred without a superficial film of water, such as morning dew.

The trampling surface displays variations in the track preservation on the same single level, thus recording different times of impression with different local moisture in the subsurface and/or track-maker speed. The relationship between the different preservation tracks and trackways, suggests that the sequence of events started with the impression of the well-defined tracks (shallow digit impressions and small marginal ridge) followed by the print of the deeper tracks with a strong developed marginal rim, since these crosscut the well-preserved trackways (see Fig. 9). This observation suggests a progressive loss of firmness in the tracking surface. It is in contrast with the general condition where the progressive firmness relates to dewatering of the sediment (e.g., Bromley and Asgaard 1979, 1991; Gierlowski-Kodesch 1991; Buatois et al. 1996, 1997; Krapovickas et al. 2008). The progressive loss of firmness in the tracking surface is related to a rise in interstitial water, which could be caused by local storms or subsurface flow. Particularly in the trampling case, the loss of firmness is more likely related to interstitial water rise associated with a storm in the source/catchment area, since a local storm would obliterate the printed tracks.

Los Reyunos tracks were imprinted on inclined surfaces evidenced not only by the sedimentary structures that show similar dip angle surface (~ 20° angle) in all of them, but also by the down-slope structures (rims of displaced sediment) associated with the prints. The latter are interpreted as gravity-induced during the animal movement; their latero-posterior position suggests the animals were walking uphill (e.g., McKee 1947; McKeever 1994; Fornós et al. 2002; Krapovickas et al. 2015).

We document two different types of rims, the bulbous-shaped (modes 1–3, Figs. 5–7) and the sand crescent-shaped (mode 4, Fig. 8). All of them are developed down-slope of the track but the main difference between them is their general morphology. Whereas the bulbous-shape rims present sharp boundaries, which distinguish them from the bearing sediment (Figs. 6, 7), the sand crescent-shaped rims are continuous with the bed sediment (Fig. 8). The bulbous-shaped rims show different degrees of sediment slipping down-slope (see modes 1–3). This variation suggests that the Los Reyunos dunes had different substrate consistency, or different slope, or different track-maker speed, or a combination of them, at the time of imprinting. The same dip angle (~ 20°) of the different track-bearing surfaces of the taphonomic modes, suggest that this parameter is not particularly important in the preservation of the Los Reyunos tracks. The major development of rims reported on upslope tracks of trackways directed uphill of taphonomic modes 1 and 2 (Figs. 5, 6), indicate that the increase of sediment slipping down-slope could be associated to loss of moisture in the sediment upwards. About the track-maker speed, unfortunately few complete trackways allowed us inferring the speed, so the speeds inferred were not enough to discuss this factor in the preservation of the footprints.

Direct observation in modern dunes shows the development of bulbous-shaped rims (Fig. 14A, 14B) on the top of the surface without any evidence of moistness. However, we observed on the same single surface the presence of the two kinds of rims: the bulbous-shaped rims in the human footprints and sand crescent-shaped rims in the small animal footprints that were printed previously (see Fig. 14A). This observation suggests that substrate consistency and slope angle do not play a primary role in producing these two types of rims as they occur under the same conditions (same single surface). Thus, the differences between the observed shapes could be related instead to the pressure exerted by bodyweight of the track-maker and/or to the time between their impressions that allowed the wind to smooth the surface. However, the range of sizes recorded in Los Reyunos footprints is not sufficient to suggest it played a central role. Moreover, footprints of equivalent sizes present the two types of rims. Therefore, we propose that the differences in the rim shape (reported between mode 4 and modes 1 to 3) are related to differences in time of exposure before entombment where wind action occurred. Accordingly, the sand crescent-shaped rims suggest more time involved before entombment than the bulbous-shaped ones.

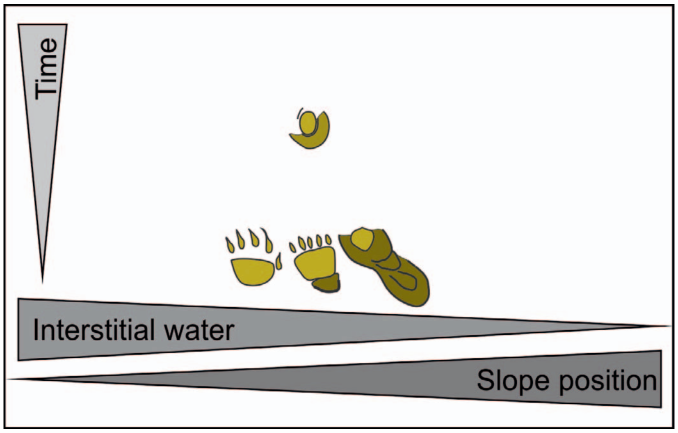

FIG. 15.—Summary of relationship between preservational conditions and taphonomic mode recognized and defined in this contribution showing the narrow preservational window.

Therefore, the Los Reyunos footprints indicate preservation (Fig. 15) in dry sand (down-slope structure; lack of breccia and tension cracks, in modes 2–4), damp sand (digit impressions and claw drag traces, pedogenic features, invertebrate trace fossils, in mode 1 and museum slabs). Additionally, they show change of substrate consistency throughout the slope and among different surfaces (varying in the degree of the sediment slipping down-slope, in modes 2–4; increase in moisture content, evidenced on the trampling surface), and time of entombment (morphology of rims, in modes 1–3 vs. mode 4).

Speed calculations performed on trackways of taphonomic modes 1, 3, and 4 exhibit an inverse relationship between morphological detail and rim development with the speed. Mode 1 presents high morphological detail on footprint while walking (low speed), and modes 3 and 4 show low morphological detail while trotting or running (high speed). Unfortunately, only one trackway for taphonomic mode 1, 3, and 4 allowed us to infer the track-maker speed. Therefore, we only suggest that this factor affected preservation of the Los Reyunos footprints though we believe it is an important factor that should be considered.

Stratigraphic Genetic Framework

In general, preservation of footprints in eolian environments depends on a combination of three variables: water content of the sediment, slope, and time of exposition. Erg construction is a function of sediment supply, sediment availability, and transport capacity of the wind. Preservation is a function of accommodation space (subsidence and water table) and sediment supply (Mountney 2006). An eolian system is dry if sediment supply exceeded the preservation space (subsidence + water table or only subsidence). An eolian system is wet if the sediment supply does not exceed the preservation space and also when the sediment supply does exceed the preservation space but this is compensated by a very high water table (Mountney 2006).

The evidence of damp sand by pedogenic features (mottling) in dune deposits and the presence of invertebrate trace fossils, suggests a relatively high water table in Los Reyunos system, despite the scarcity of interdune deposits in the outcrops and particularly in the sections containing footprints. Moreover, the well-preserved footprints reported in taphonomic modes 1 and 2 suggest damp sand below the surface, and without a superficial film of water (breccia structure is not observed). The high content of interstitial water could be related to local storms or subsurface flow water from source/catchment area. The porosity of the coarse-grained sand of the Los Reyunos probably promoted water drainage parallel to bedding, with water accumulating in the lowermost sand; therefore, more water would have collected in the lower sand than in sand higher on the slope. The evidence of loss of interstitial humidity uphill explains the increased development of rims in a single trackway (Fig. 6) and can explain part of the variability of rims among the preservation modes from 1 to 3. Therefore, the trampling case is an example of change in the subsurface interstitial water and not in the slope angle, so we report different possibilities with the change of the substrate consistency (throughout the slope and subsurface interstitial water drains).

In the stratigraphic genetic framework, we propose that a rise in interstitial water promoted preservation of the Los Reyunos footprints (without superficial film of water) at the lower part of the dune slope, and the rapid entombment on the tracking surface due to a high rate sediment supply. The scarce record of interdune facies suggests that the sequence was located in the erg center with subsurface interstitial water drain and high rate of coarse-grained sediment supply, which promoted the rapid entombment. The effect of a subsurface interstitial water drain accumulating within the lowermost parts of the dunes and not only restricted to the interdunes (Mountney 2006). Therefore, we interpret the Los Reyunos eolian system as a mixture eolian system with features characteristic of dry, wet, and stabilized systems as described by Mountney (2006) with slight water supply fluctuations evidenced by the presence of mottling throughout the succession.

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REFERENCES

ALEXANDER, R.M., 1976, Estimates of the speeds of dinosaurs: Nature, v. 261, p. 129–130.

ALLEN, J.R.L., 1997, Subfossil mammalian tracks (Flandrian) in the Severn Estuary, S. W. Britain: mechanics of formation, preservation and distribution: Philosophical Transactions of the Royal Society B, Biological Sciences, v. 352, p. 481–518, doi: 10.1098/rstb.1997.0035.

ALONSO-ZARZA, A.M., GENISE, J.F., CABRERA, M.C., MANGAS, J., MARTÍN-PÉREZ, A., VALDEOLMILLOS, A., AND DORADO-VALIÑO, M., 2008, Megarhizoliths in Pleistocene aeolian deposits from Gran Canaria (Spain): ichnological and palaeoenvironmental significance: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 265, p. 39–51, doi: 10.1016/j.palaeo.2008.04.020.

ARAMAYO, S.A., 1993, Vertebrados Paleozoicos, *in* Ramos, V.A. (ed.), XII Congreso Geológico Argentino Y II Congreso de Exploración de Hidrocarburos, v. 8, p. 303–307.

ARAMAYO, S.A. AND FARINATI, E., 1983, "Paredichnus rodriguezi" n. sp. Nuevas icnitas de tetrápodos de la Formación Los Reyunos (Grupo Cochicó), Pérmico inferior, Mendoza: Mundo Ameghiniana, v. 4, p. 47–58.

BORDY, E.M. AND CATUNEANU, O., 2002, Sedimentology of the Beaufort-Molteno Karoo fluvial strata in the Tuli Basin, South Africa: South African Journal of Geology, v. 105, p. 51–66, doi: 10.2113/1050051.

BRADDY, S.J., 1995, The ichnotaxonomy of the invertebrate trackways of the Coconino Sandstone (Lower Permian), Northern Arizona: New Mexico Museum of Natural History and Science Bulletin, v. 6, p. 219–224.

BRADY, L.F., 1947, Invertebrate tracks from the Coconino Sandstone of northern Arizona: Journal of Paleontology, v. 21, p. 466–472.

BRADY, L.F., 1961, A new species of *Palaeohelcura gilmore* from the Permian of Northern Arizona: Journal of Paleontology, v. 35, p. 201–202.

BRAND, L., 1979, Field and laboratory studies on the Coconino sandstone (Permian) vertebrate footprints and their paleoecological implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 28, p. 25–38, doi: 10.1016/0031-0182(79)90111-1.

Brand, L.R. and Tang, T., 1991, Fossil vertebrate footprints in the Coconino Sandstone (Permian) of northern Arizona: evidence for underwater origin: Geology, v. 19, p. 1201, doi: 10.1130/0091-7613(1991)019<1201:FVFITC>2.3.CO;2. http://geology.gsapubs.org/cgi/doi/10.1130/0091-7613(1991)019<1201:FVFITC>2.3.CO;2.

Bromley, R.G. and Asgaard, U., 1979, Triassic freshwater ichnocoenoses from Carlsberg Fjord, East Greenland: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 28, p. 39–90.

Bromley, R.G. and Asgaard, U., 1991, Ichnofacies: a mixture of taphofacies and biofacies: Lethaia, v. 24, p. 153–163.

Buatois, L.A., Jalfin, G., and Aceñolaza, F.G., 1997, Permian nonmarine invertebrate trace fossils from southern Patagonia, Argentina: Ichnologic signatures of substrate consolidation and colonization sequences: Journal of Paleontology, v. 71, p. 324–336.

Buatois, L.A., Mángano, M.G., and Aceñolaza, F.G, 1996, Icnofaunas paleozoicas en sustratos firmes no marinos: Evidencias del Pérmico de la cuenca Paganzo: Ameghiniana, v. 33, p. 265–270.

Buynevich, I.V, Darrow, J.S., Grimes, Z.T., Seminack, C.T., and Griffis, N., 2011, Ungulate tracks in coastal sands: recognition and sedimentological significance: Journal of Coastal Research, SI 64, Proceedings of the 11th International Coastal Symposium, p. 334–338.

Chure, D.J., Engelmann, F., Good, T.R., Haymes, G., and Hansen, R., 2014, The first record of vertebrate tracks from the eolian Weber Sandstone (Pennsylvanian–Permian), Northeastern Utah: a preliminary report: New Mexico Museum of Natural History and Sciesces Bulletin, v. 62, p. 95–102.

Davis, R.B., Minter, N.J., and Braddy, S.J., 2007, The neoichnology of terrestrial arthropods: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 255, p. 284–307, doi: 10.1016/j.palaeo.2007.07.013. http://linkinghub.elsevier.com/retrieve/pii/S0031018207004002. Checked September 2013.

Doe, T.W. and Dott, R.H., 1980, Genetic significance of deformed cross bedding—with examples from the Navajo and Weber Sandstones of Utah: Journal of Sedimentary Petrology, v. 50, p. 793–812.

Duncan, H., 1831, An account of the tracks and footmarks of animals found impressed on sandstone in the quarry of Corncockle Muir, in Dumfriesshir: Transactions of the Royal Society of Edinburgh, v. 11, p. 194–209.

Ekdale, A.A. and Bromley, R.G., 2012, Eolian Environments, *in* Knaust, D. and Bromley, R.G. (eds.), Trace Fossils as Indicators of Sedimentary Environments: Developments in Sedimentology, v. 64, p. 419–437.

Faul, H. and Roberts, W.A., 1951, New fossil footprints from the Navajo (?) Sandstone of Colorado: Journal of Paleontology, v. 25, p. 266–274.

Fornós, J.J., Bromley, R.G., Clemmensen, L.B., and Rodríguez-Perea, A., 2002, Tracks and trackways of *Myotragus balearicus bate* (Artiodactyla, Caprinae) in Pleistocene aeolianites from Mallorca (Balearic Islands, Western Mediterranean): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 180, p. 277–313, doi: 10.1016/S0031-0182(01)00431-X.

Freytet, P. and Plaziat, J.-C., 1982, Continental carbonate sedimentation and pedogenesis—Late Cretaceous and early Tertiary of southern France, in B.H. Purser (ed.), Contributions to Sedimentology, Stuttgart, Schweizerbart'sche Verlag, v. 12, 217 p.

Gierlowski-Kordesch, E., 1991, Ichnology of an ephemeral lacustrine alluvial plane system. Jurassic East Berlin Formation, Hartford Basin, U.S.A: Ichnos, v. 6, p. 221–232.

Gilmore, C.W., 1926, Fossil footprints from the Grand Canyon: Smithsonian Miscellaneous Collections 77, 41 p.

Gilmore, C.W., 1927, Fossil footprints from the Grand Canyon: second contribution: Smithsonian Miscellaneous Collections 80, 78 p.

Gilmore, C.W., 1928, Fossil footprints from the Grand Canyon: third contribution: Smithsonian Miscellaneous Collections 80, 16 p.

Hanley, J.H., Steidtmann, J.R., and Toots, H., 1971, Trace fossils from the Casper Sandstone (Permian) southern Laramie Basin, Wyoming and Colorado: Journal of Sedimentary Petrology, v. 41, p. 1065–1068.

Harkness, R., 1850, On the position of the impressions of footsteps in the Bunter Sandstone of Dumfriesshire: Annals and Magazine of Natural History, v. 6, p. 203–208.

Haubold, H., Lockley, M.G., Hunt, A.P., and Lucas, S.G., 1995, Lacertoid footprints from Permian dune sandstones, Cornberg and DeChelly sandstones: New Mexico Museum of Natural History and Science Bulletin, v. 6, p. 235–244.

Holmberg, E., 1948, Geología del Cerro Bola. Contribución al conocimiento de la tectónica de la Sierra Pintada: Boletín de la Direción Nacional de Geología y Minería, v. 68, p. 313–361.

Kleiman, L.K. and Japas, M.S., 2009, The Choiyoi volcanic province at 34°5–36°5 (San Rafael, Mendoza, Argentina): implications for the late Palaeozoic evolution of the southwestern margin of Gondwana: Tectonophysics, v. 473, p. 283–299.

Kocurek, G., 1981, Significance of interdune deposits and bounding surfaces in aeolian dune sands: Sedimentology, v. 28, p. 753–780.

Krapovickas, V., Mancuso, A.C., Arcucci, A., and Caselli, A., 2010, Fluvial and eolian ichnofaunas from the Lower Permian of South America (Patquía Formation , Paganzo Basin) : Geological Acta, v. 8, p. 449–462, doi: 10.1344/105.000001582.

Krapovickas, V., Mángano, M.G., Buatois, L.A., and Marsicano, C.A., 2016, Integrated ichnofacies models for deserts: recurrent patterns and megatrends: Earth-Science Reviews, v. 157, p. 61–85.

Krapovickas, V., Mángano, M.G., Mancuso, A.C., Marsicano, C.A., and Volkheimer, W., 2008, Icnofaunas triásicas en abanicos aluviales distales: evidencias de la Formación Cerro Puntudo, Cuenca Cuyana, Argentina: Ameghiniana, v. 45, p, 429–438.

Krapovickas, V., Marsicano, C.A., Mancuso, A.C., de la Fuente, M.S., and Ottone, E.G., 2015, Tetrapod and invertebrate trace fossils from aeolian deposits of the Lower Permian of central-western Argentina: Historical Biology, v. 27, p. 827–842, doi: 10.1080/08912963.2014.904857.

Laporte, L.F. and Behrensmeyer, A.K., 1980, Tracks and substrate reworking by terrestrial vertebrates in Quaternary sediments of Kenya: Journal of Sedimentary Petrology, v. 50, p. 1337–1346.

Lardone, L., Meza, J.C., and Salaverri, J.A., 1993, Yacimiento Uraníferos, *in* Ramos, V. (ed.), Geología y Recursos Naturales de Mendoza: Relatorio, v. 4, p. 537–542.

Lea, P., 1996, Vertebrate Tracks in Pleistocene eolian sand-sheet deposits of Alaska: Quaternary Research, v. 45, p. 226–240, doi: 10.1006/qres.1996.0023.

Llambias, E.J., Kleiman, L.E., and Salvarredi, J.A., 1993, El Magmatismo Gondwánico, *in* Ramos, V. (ed.), Geología y Recursos Naturales de Mendoza: Relatorio, v. 1, p. 53–64.

Lockley, M.G., 1992, Comment and reply on "Fossil vertebrate footprints in the Coconino Sandstone (Permian) of northern Arizona evidence for underwater origin": Geology, v. 20, p. 666–667.

Lockley, M.G. and Hunt, A.P., 1995, Dinosaur Tracks and Other Fossil Footprints of the Western United States: Columbia University Press, New York, 338 p.

Lockley, M.G., Hunt, A.P., Meyer, C., Rainforth, E.C., and Schultz, R.J., 1998, A survey of fossil footprint sites at glen canyon national recreation area (western USA): a case study in documentation of trace fossil resources at a national preserve: Ichnos, v. 5, p. 177–211, doi: 10.1080/10420949809386417.

Lockley, M.G. and Madsen, J., 1993, Early Permian vertebrate trackways from the Cedar Mesa Sandstone of Eastern Utah: evidence of predator prey interaction: Ichnos, v. 2, p. 147–153.

Loope, D.B., 1986, Recognizing and utilizing vertebrate tracks in cross section: Cenozoic hoofprints from Nebraska: PALAIOS, v. 1, p. 141–151, doi: 10.2307/3514507.

Loope, D.B., 1992, Comment and reply on "Fossil vertebrate footprints in the Coconino Sandstone (Permian) of northern Arizona evidence for underwater origin": Geology, v. 20, p. 667–668.

Loope, D.B., 2006, Dry-season tracks in dinosaur-triggered grainflows: PALAIOS, v. 21, p. 132–142, doi: 10.2110/palo.2005.p05-55.

López-Gamundí, O., 2006, Permian plate margin volcanism and tuffs in adjacent basins of west Gondwana: age constraints and common characteristics: Journal of South American Earth Sciences, v. 22, p. 227–238.

Manning, P.L., 2004, A new approach to the analysis and interpretation of tracks: examples from the dinosauria: Geological Society, London, Special Publications, v. 228, p. 93–123, doi: 10.1144/GSL.SP.2004.228.01.06.

Maloberti, A.L., 1983, Análisis estadístico de imbricaciones en el Miembro Psefítico Inferior de la Formación Cochicó. Flanco oriental de la Sierra Pintada. Departamento de San Rafael, Mendoza. Comision Nacional de Energía Atómica, informe interno D.E.E. p.22–83.

Marsicano, C.A., Mancuso, A.C., Palma, R.M., and Krapovickas, V., 2010, Tetrapod tracks in amarginal lacustrine setting (Middle Triassic, Argentina): taphonomy and significance: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 291, p. 388–399, doi: 10.1016/j.palaeo.2010.03.009.

McKee, E.D., 1947, Experiments on the development of tracks in fine cross-bedded sand: Journal of Sedimentary Research, v. 17, p. 23–28. doi: 10.1306/D4269292-2B26-11D7-8648000102C1865D.

McKeever, P.J., 1991, Trackway preservation in eolian sandstones from the Permian of Scotland: Geology, v. 19, p. 726–729. doi: 10.1130/0091-7613(1991)019<0726:TPIESF>2.3.CO;2.

McKeever, P.J., 1994, The behavioral from and the biostratigraphical origin of Permian vertebrate of Scotland significance and trackways: PALAIOS, v. 9, p. 477–487.

McKeever, P.J. and Haubold, H., 1996, Reclassification of vertebrate trackways from the Arizona and Germany: Journal of Paleontology, v. 70, p. 1011–1022.

Melchor, R.N., 2001, Permian tetrapod footprints from Argentina: Hallesches Jahrbuch für Geowissenschaften, Series B, v. 23, p. 35–43.

Milán, J. and Bromley, R.G., 2006, True tracks, undertracks and eroded tracks, experimental work with tetrapod tracks in laboratory and field: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 231, p. 253–264, doi: 10.1016/j.palaeo.2004.12.022.

Milán, J., Clemmensen, L.B., and Bonde, N., 2004, Vertical sections through dinosaur tracks (Late Triassic lake deposits, East Greenland)—undertracks and other subsurface deformation structures revealed: Lethaia, v. 37, p. 285–296.

Milán, J., Loope, D.B., and Bromley, R.G., 2008, Crouching theropod and Navahopus sauropodomorph tracks from the Early Jurassic Navajo Sandstone of USA: Acta Palaentologica Polonica, v. 53, p. 197–205.

Mountney, N.P., 2006, Eolian facies models, *in* Posamentier, H.W. and Walker, R.G. (eds.), Facies Model Revised, SEPM Special Publication 84: Society for Sedimentary Geology, Tulsa, Oklahoma, USA, p. 19–83.

Mountney, N.P. and Jagger, A., 2004, Stratigraphic evolution of an aeolian erg margin system: the Permian Cedar Mesa Sandstone, SE Utah, USA: Sedimentology, v. 51, p. 713–743, doi: 10.1111/j.1365-3091.2004.00646.x.

Ortega Furlotti, A., Rodriguez Pujada, E.J., and Prieto, A.G., 1974, El nuevo Distrito Uranifero de Sierra Pintada, provincia de Mendoza (República Argentina): Actas del Quinto Congreso Geológico Argentino, v. 2, p. 267–284.

Polanski, J., 1964, Descripción geológica de la hoja 26c La Tosca, provincia de Mendoza, carta geológico económica de la República Argentina. Escala, 1: 200.000: Direción Nacional de Geología y Minería, Buenos Aires, Boletín 101, 94 p.

Rey, F.M., 2011, Variaciones paleoclimáticas y Paleoambientales en la Formación Yacimiento Los Reyunos (Cisuraliano), Cuenca de San Rafael, Mendoza Argentina: M.Sc. thesis, Universidad de Buenos Aires, 130 p.

Rocha-Campos, A.C., Basei, M.A., Nutman, A.P., Kleiman, L.E., Varela, R., Llambias, E., Canile, F.M., and da Rosa, O.D.C.R., 2011, 30 million years of Permian volcanism recorded in the Choiyoi igneous province (W. Argentina) and their source for younger ash fall deposits in the Paraná Basin: SHRIMP U–Pb zircon geochronology evidence: Gondwana Research, v. 19, p. 509–523, doi: 10.1016/j.gr.2010.07.003.

Rodriguez, E.J. and Valdivieso, A., 1970, Informe sobre resultados de la investigación geológica semi regional (perfiles y planos geológicos) en el área de las manifestaciones nucleares de Sierra Pintada, Mendoza: Comisión Nacional de Energía Atómica (Informe interno), Buenos Aires, 44 p.

Sadler, C.J., 1993, Arthropod trace fossils from the Permian De Chelly Sandstone, Northeastern Arizona: Journal of Paleontology, v. 67, p. 240–249.

Scott, J.J., Renaut, R.W., and Owen, R.B., 2010, Taphonomic controls on animal tracks at saline, alkaline Lake Bogoria, Kenya Rift Valley: impact of salt efflorescence and clay mineralogy: Journal of Sedimentary Research, v. 80, p. 639–665, doi: 10.2110/jsr.2010.057.

Scott, J.J., Renaut, R.W., Owen, R.B., and Sarjeant, W.A.S., 2007, Biogenic activity, trace formation, and trace taphonomy in the marginal sediments of saline, alkaline Lake Bogoria, Kenya rift valley, in Bromley, R., Buatois, L.A., Mángano, M.G., Genise, J.F., Melchor, R.N. (eds.), Sediment-Organism Interactions: A Multifaceted Ichnology: SEPM Special Publication 88, p. 311–332.

Scrivner, P.J. and Bottjer, D.J., 1986, Neogene avian and mammalian tracks from Death Valley National Monument, California: their context, classification and preservation: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 57, p. 285–331.

Seilacher, A., 2008, Biomats, biofilms, and bioglue as preservational agents for arthropod trackways: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 270, p. 252–257.

Seiler, W.M. and Chan, M.A., 2008, A wet interdune dinosaur trampled surface in the Jurassic Navajo Sandstone, Coyote Buttes, Arizona: rare preservation of multiple track types and tail traces: PALAIOS, v. 23, p. 700–710, doi: 10.2110/palo.2007.p07-082r.

Spalletti, L. and Mazzoni, M., 1972, Paleocorrientes del Miembro medio de la Formación Yacimiento Los Reyunos, Siera Pintada, ptovincia de Mendoza: Revista de la Asociación Argentina de Mineria Petrografía y Sedimentología, v. 3, p. 77–90.

Thulborn, T., 1990, Dinosaur Tracks: Chapman and Hall, London, 410 p.

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