A Triassic tetrapod footprint assemblage from southern South America: palaeobiogeographical and evolutionary implications

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Abstract

A new Triassic tetrapod track assemblage recorded from levels of the Cuyana Basin (west-central Argentina) is described. The tracks came from multiple track-bearing horizons of the Upper Triassic (Carnian) Portezuelo Formation that indicate recurrent playa to mudflat conditions in a marginal lacustrine succession. This footprint assemblage is the most important one described up to now for the lower Mesozoic of South America, and forms a significant estimate of the fauna represented during that time in the region. Therefore, in order to understand the faunal significance of the assemblage, the track-makers were identified within a phylogenetic context. Although at a coarse taxonomic level, this analysis indicates the presence of non-mammalian therapsids (small cynodonts and large dicynodonts) and a quite diverse archosaur fauna that includes members of both crurotarsal archosaurs and dinosaurs (sauropodomorphs and theropods). Comparisons between the studied assemblage and other Early Mesozoic tetrapod track records from Gondwana suggest close relationships with those described from the Upper Triassic of the Karoo Basin in South Africa. In addition, the presence of putative basal sauropodomorph dinosaur tracks in the Portezuelo levels suggests that the stratigraphic range of the group extends back into the Carnian, farther than that documented by the known body-fossil record of the group in western Gondwana.
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Keywords: Late Triassic; west-central Argentina; tetrapod footprints; phylogeny; palaeobiogeography

1. Introduction

Tetrapod footprints have been known in south-
ern South America since 1931, when von Huene (1931) described a large trackway of a quadruped animal (*Rigalites ischigualastianus*) from the Triassic Ischigualasto–Villa Unión Basin. Since then, a rather sparse Triassic track record has been reported from this part of Gondwana, mainly restricted to Middle–Upper Triassic sequences from west-central Argentina and northern Pata-

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gonia (Rusconi, 1952; Peabody, 1955; Casamiquela, 1964, 1975; Bonaparte, 1966; Stipanicic and Bonaparte, 1979; Leonardi and Oliveira, 1990; Leonardi, 1994; Arcucci et al., 1995, 2000, in press; Manera de Bianco and Calvo, 1999; Marsicano and Barredo, 2000; Marsicano et al., 2001; Melchor et al., 2002; Domnanovich, 2003). Among these, some trackways and isolated footprints referred to theropod dinosaurs were recorded from the Middle Triassic Los Rastros Formation (Stipanicic and Bonaparte, 1979; Arcucci et al., 1995), the same unit where von Huene's specimen was discovered. Additionally, many small and mostly isolated 'chirotheroid' footprints also occur in the same depositional center (Bonaparte, 1997; Arcucci et al., 2000, in press) but from levels attributed to the uppermost part of the Triassic sequence (Los Colorados Formation). In the nearby Cuyana Basin, footprint material was also mentioned but it appears to be even more scarce than in the Ischigualasto–Villa Unión Basin. Apparently, all tracks occur in levels assigned to the Middle Triassic Cerro de las Cabras Formation and consist of isolated 'chirotheroid' footprints and some small tracks referred to 'therapsid cynodonts' (Rusconi, 1952; Peabody, 1955; Bonaparte, 1966; Leonardi, 1994). Finally, a fairly diverse collection of trackways and footprints, nearly all representing small quadrupedal track-makers, has been described from the Upper Triassic Los Menucos Basin in northern Patagonia. These were mainly referred to several non-mammalian therapsid groups (Casamiquela, 1964, 1975; Leonardi, 1994; Manera de Bianco and Calvo, 1999; Domnanovich, 2003).

The new tetrapod track assemblage described herein was discovered in a thick continental Triassic succession in west-central Argentina that corresponds to part of the infilling of the Rincón Blanco depositional center, considered a northwestern extension of the main Cuyana Basin (Ramos and Kay, 1991; López Gamundí, 1994; Barredo and Ramos, 1997, 1998). The tracks are recorded from multiple track-bearing horizons of the Portezuelo Formation that indicate recurrent playa to mudflat conditions in a marginal lacustrine succession (Marsicano and Barredo, 2000). The Rincón Blanco sequence has been remarkably

devoid of skeletal remains and, therefore, the footprints and trackways from the Portezuelo levels are the only evidence of the presence of vertebrates in the basin.

In the present contribution, we describe the tracks and trackways of the Portezuelo Formation and evaluate the possible track-makers. A preliminary analysis of the ichnocoenosis indicates the presence of non-mammalian therapsids and a rather diverse archosaur fauna that includes both crurotarsal archosaurs and dinosaurs (Marsicano and Barredo, 2000). We compare the studied assemblage with other known Early Mesozoic tetrapod track records from Gondwana and discuss them within a palaeogeographical context. Finally, the temporal ranges of certain groups can be emended in light of their presence in the Portezuelo assemblage.

2. Geological setting

The Triassic sedimentary record of South America is mostly characterized by the development of rift basins along its western margin as a consequence of the breakup of the Pangean supercontinent (Uliana et al., 1989). They consist of northwest-trending narrow and elongated troughs set over a thick Precambrian–Palaeozoic continental crust.

The Rincón Blanco Group (Borrello and Cuerda, 1965) is located in San Juan Province (Argentina) and represents the continental infilling of the northern half-graben of the Cuyana Basin (Fig. 1). Its approximately 2300 m of non-marine clastic and epiclastic rocks record the evolutionary history of its active margin. The wedge-shaped succession of sediments (thicker to the east), distinctive depositional facies, and sediment transport directions along its margins all suggest an asymmetric basin shape (López Gamundí, 1994; Barredo and Ramos, 1997, 1998). The deposition begins with synrift sequences lying over marine rocks of Ordovician age; they correspond to coarse-grained deposits of the Ciénaga Redonda Formation (400 m) related with alluvial/fluvial environments (Fig. 2). These beds are interfingered with the conglomerates, sandstones and shales of
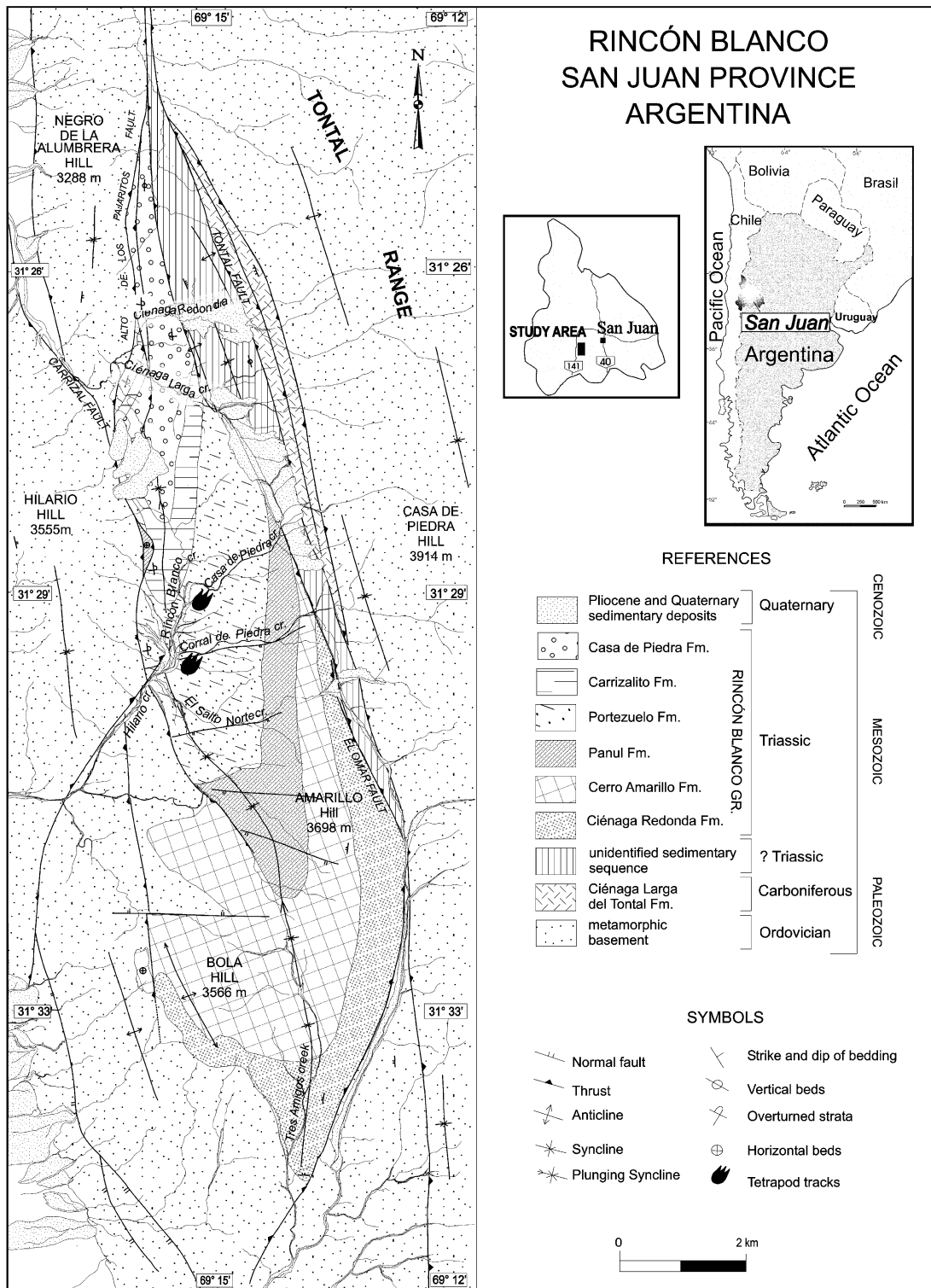
Fig. 1. Geological map of the Rincón Blanco Basin showing the locations of the track-bearing sites.
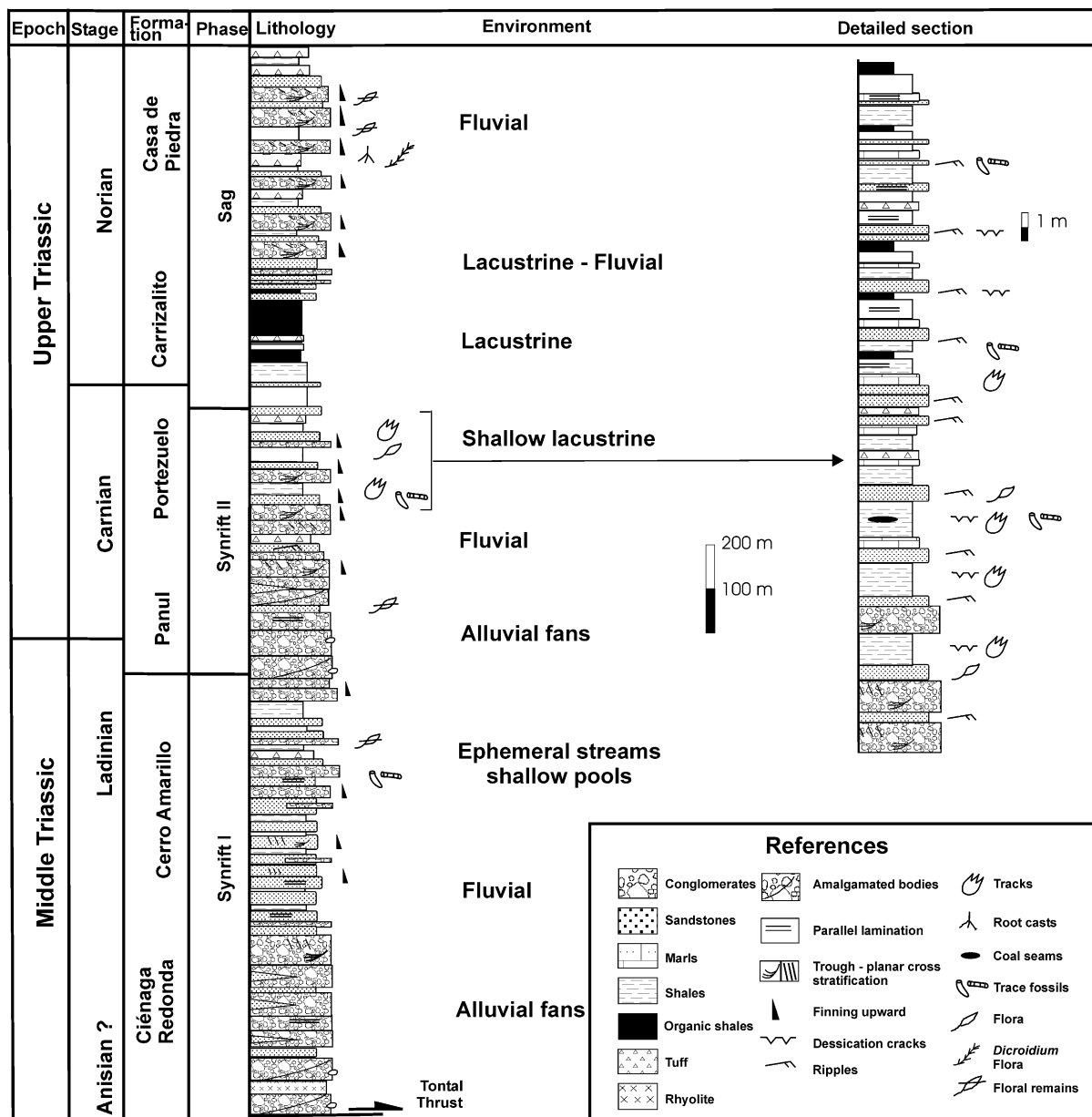
Fig. 2. Stratigraphic scheme of the Rincón Blanco Basin sequence showing the track-bearing horizons and depositional environments.

the Cerro Amarillo Formation (600 m), which correspond to ephemeral streams and shallow lake deposits developed along distal alluvial sandflats and mudflats/playa environments. The occurrence of a new coarse alluvial–fluvial environment was the result of reactivation along normal faults, thus suggesting two stages during the synrift phase (Barredo, 1998; Barredo, 1999) and represented by the Panul Formation (350 m). Following this, a strongly horizontal stratified succession of sandstones, shales, marls and tuffs, all deposited in fluvial and shallow lacustrine systems,

characterized the Portezuelo Formation (290 m). It is interpreted as the transition to the sag phase during which the fluvial systems prograded basinward into a perennial, deep, stratified alkaline lake composed of important organic-rich shales (Barredo, 1998). These characteristic lacustrine deposits correspond to the Carrizalito Formation (200 m), the productive oil shales widely known as the 'Rincón Blanco oil slates'.

The regionally extended thermal subsidence emplaced by Late Triassic times in the basin is clearly illustrated by the Casa de Piedra Formation (430 m). A gradual fall in the local base level allowed the evolution of deltas and braided fluvial systems over the previous lacustrine deposits, accompanied by intense pyroclastic activity in a no longer closed basin. During Tertiary time the basin underwent an intense compressional deformation that produced a complex structure. At present, it is a tight, asymmetric syncline almost completely bounded by faults. Moreover, the upper limit of the Triassic sequence is truncated by an axial thrust and, consequently, is unknown (Fig. 1).

2.1. Paleoenvironments of the Portezuelo Formation

The Portezuelo Formation outcrops are characterized by a dominantly tabular succession of sandstones and shales alternating with lenticular conglomerates, whitish tuffs, and marls, all very well exposed between El Salto Norte Creek and Ciénaga Larga Creek in the east-central portion of the basin (Fig. 1). The sequence conformably overlies the conglomerates of the Panul Formation and gradually passes upwards into the deep-lake deposits of the Carrizalito Formation (Stipanicic, 1979; Barredo, 1999).

The sequence begins with granular to fine-grained, moderately to well-sorted sandstones, siltstones, and mudstones with pebble to subordinate cobble, and poorly sorted conglomerate interbeds. The latter are frequently amalgamated and mostly composed of 1.5 m thick lenticular beds. Individual beds show sharp to erosional bases, and are normally graded, massive or trough/planar cross-stratified with common lag

veneers of pebbles. Sandstones are also lenticular, up to 3 m thick and laterally extended for more than 20 m. They correspond to medium-grained sandstones with small-scale trough-cross stratification and ripple-cross lamination, capped by thin beds of massive or rippled greenish-gray siltstones, tuffs, and mudstones with desiccation cracks. The sandstones merge laterally into massive tuffs and greenish-gray mudstones that become increasingly important upwards in the sequence. These beds contain badly preserved floral remains and scarce burrows. The trace fossils were mostly identified on bedding planes which show horizontal, simple burrows interpreted here as *Palaeophycus* and *Planolites*. This succession (Fig. 2) can be considered as the result of deposition in braided fluvial systems with sand-rich stream channels running over distal alluvial plains, mainly characterized by mudstone overbank deposits (Barredo, 1998).

The sequence passes upward into a series of fining-upward cycles characterized by lenticular, trough-cross conglomerates at the base (related to fluvial channels), grading into medium fine-grained, moderately to well-sorted tabular sandstones/tuffaceous sandstones and thick overbank mudstones at the top. Sandstones are massive or planar stratified with granules locally scattered through the beds; predominantly cross-stratified beds with lateral accretion surfaces are interpreted as point bars associated with sinuous channels. Floodplain sequences are dominant-upwards and are composed of thick, greenish-gray, massive clayey mudstones/tuffaceous siltstones, and tuffs. Carbonaceous shales, coal seams, and gray laminated levels are interbedded, representing the stratigraphically lowest tetrapod track-bearing horizons of the Portezuelo Formation. These beds also frequently contain trace fossils (assigned here to the *Scoyenia* ichnofacies), abundant floral remains, and well-developed paleosols. All these data, and the presence of overprinted raindrop impressions and desiccation cracks on the tracks, suggest periodic flooding of the plain with the progressive development of shallow lagoons or ponds and even swamps. Alternating shallowing and deepening lacustrine cycles dominate the uppermost part of the Portezuelo unit (Fig. 2).

The occurrence of these marginal lacustrine facies could be considered as an anticipation of the subsequent emplacement of a deep, steadier and more persistent lacustrine environment in the basin, the Carrizalito Formation (Borrello and Cuerda, 1965). Each cycle (0.6–1.0 m thickness) is characterized by massive and bioturbated (*Mermia* ichnofacies) fine sandstones, greenish-gray siltstones and mudstones which alternate with light-brown marls, tuffs, and interbeds of yellowish rippled (wave and current) sandstones, sometimes with hummocky cross stratification and flat-top ripples. They suggest shallow standing waters with important wave reworking. These sequences are laterally and vertically interfingered with thinly stratified silty sandstones and massive mudstones related to deeper facies. The shallowing cycles (nearly 20 in the eastern margin) are very well preserved in the studied area. They correspond to subaereal exposures of the lake margin and are represented by massive sandstones, tuffaceous sands, tuffs, and clayey mudstones. Dominant structures comprise desiccation cracks, synaeresis cracks, raindrops, trace fossils assigned to the ichnogenera *Palaeophycus*, *Planolites*, *Taenidium*, and *Scoyenia*, and tetrapod tracks. Toward the top of the sequence, fine to medium-grained sandstones heterolithically interbedded with mudstones were deposited in a more distant shore setting. Occasionally, they are associated with massive or horizontally laminated marls (30 cm in thickness) and pale-gray organic levels. Finally, this sequence passes upward into the deep-lake deposits of the Carrizalito Formation (Fig. 2).

2.2. Age of the Portezuelo Formation

The age of the Portezuelo Formation is constrained by dates assigned to the underlying and overlying units. The underlying Panul Formation is considered to be of late Middle–early Late Triassic age based upon its correlation with equivalent beds in the southern part of the main Cuyana Basin (Stipanicic, 1979; Barredo, 1999). Thus, the deposition of the Panul conglomerates, which conformably passes upwards into the fluvial–lacustrine deposits of the Portezuelo Formation, are related to a regional unconformity associated

with the reactivation of the main faults along the entire Cuyana Basin (Kokogian et al., 1993, 2001; Barredo, 1999). This unconformity is dated as Middle Triassic by stratigraphic relationships (Kokogian et al., 1993, 2001), palynological data (Zavattieri and Batten, 1996; Barredo et al., 1999) and the absolute age of syntectonically emplaced basalts (Ramos and Kay, 1991; Mendoza and Moreiras, 1997; Spalletti, 2001). The floral content of the overlying thick deposits of the Carrizalito and Casa de Piedra Formations includes 'Ipswich-type Microflora' (with the absence of *Classopollis*-type pollen) and specimens of the '*Dicroidium*-type Flora' (Borrello and Cuerda, 1965; Yrigoyen and Stover, 1970; Barredo et al., 1999). In Gondwana these floral types indicate a Middle to Late, not latest, Triassic age (e.g. Helby et al., 1987; Zavattieri and Batten, 1996; Zavattieri, 2002). The same micro- and macrofloral types were also described for the Portezuelo levels (Yrigoyen and Stover, 1970; Baldoni and Durango de Cabrera, 1977; Barredo et al., 1999). Therefore, all this evidence is in agreement with an early Late Triassic (probably Carnian) age for the Portezuelo track-bearing horizons.

3. Description of the footprints and trackways

3.1. Trackways of bipeds

Three different types of trackways representing both facultative bipedal and full bipedal progression are present in the assemblage. The footprints assigned to facultative bipeds (Type FB) are arranged in approximately eight trackways that derive from different stratigraphic levels within the upper third of the sequence (measurements summarized in Table 1). All footprints are preserved as natural molds on the surface of large fallen slabs and consist of consecutive sets of between three and six footprints, depending on the size of the slab. The manus impressions are smaller than those of the pes and have an erratic distribution in the trackways. Digits are not distinguishable in either manus or pes impressions, probably because many of the tracks are quite deeply impressed due to the high water content of the sedi-

Table 1
Measures of three different trackways of Type FB

Trackway number	Manus	Pes
Trackway 1		
Width (cm)	n.d.	10
	7	12
	6.8	12
	n.d.	13
	n.d.	11
	n.d.	11
average	*7.4*	*11.5*
Length (cm)	n.d.	n.d.
	5	24
	4.5	23
	n.d.	24
	n.d.	19
	n.d.	n.d.
average	*4.7*	*22.5*
Stride length (cm) *average*	65	65
Pace length (cm) *average*	n.d.	40
Pace angulation (degrees)	n.d.	120
Width of the pace (cm)	25	32
Distance m–p (cm) *average*	*27*	
Trackway 2		
Width (cm)	n.d.	16
	17	18
	n.d.	18
	n.d.	17
average	*17*	*17.3*
Length (cm)	n.d.	n.d.
	10	27
	n.d.	27
	n.d.	26
average	*10*	*26.6*
Stride length (cm) *average*	n.d.	*135*
Pace length (cm) *average*	n.d.	*84*
Pace angulation (degrees)	n.d.	135
Width of the pace (cm)	n.d.	24
Distance m–p (cm) *average*	*30*	
Trackway 3		
Width (cm)	15	20
	15	20
	17	21
	17	20
average	*16*	*20.3*
Length (cm)	10	27
	11	27
	12	26
	12	n.d.
average	*11.3*	*20*
Stride length (cm) *average*	105	105
Pace length (cm) *average*	50	50
Pace angulation (degrees)	120	140
Width of the pace (cm)	25	20
Distance m–p (cm) *average*	*27*	

n.d., not datum.

ment during their emplacement; in addition, some of them appear to be underprints. The digits are evident in only one specimen as a rather deep scratch impression showing three anteriorly directed toes with pointed claw marks.

As mentioned above, the presence of a manus impression in this type of trackway is rather erratic. In a large slab bearing three trackways on its surface with approximately the same orientation and preservation, one of the six-step trackways has only two consecutive pes prints (second and third) with the corresponding manus impressions. The remaining trackways on the slab, one of three steps and another of two, do not present any evidence of manus impressions. In a different stratigraphic level, a large slab has preserved two trackways (Figs. 3 and 4), each with three deeply impressed prints. In one of them all the corresponding manus impressions are present, whereas in the other the second pes impression preserved do not have the corresponding manus print.

The remaining trackways attributed to this type have the same kind of irregular manus imprint distribution, but they are mainly represented as underprints. Generally, pes impressions are anteroposteriorly elongated and their anterior border is slightly convex, as a result of which there is no indication of a prominent longer digit. The pedes are broader anteriorly and with a rounded apex posteriorly; the anterior half of the pes impressions are rotated towards the midline, thus suggesting that the digits were curved inwards (Figs. 3 and 4). The manus impressions are generally slightly less impressed than those of the pes. They are transversally oval and imprinted in front of or external to the pes impressions. This type of trackway (Type FB) shows a relatively high pace angulation (average 130 degrees) and a narrow-gauge. These measurements suggest a narrow, upright stance for the track-maker. Moreover, the somewhat unpredictable placement of the manus prints, probably not attributable to preservational effects, suggests that the forelimbs did not have a major supportive role (see Thulborn, 1989). Estimated hip height indicates an animal that stood approximately 1.65 m high at the hip (Thulborn, 1989).

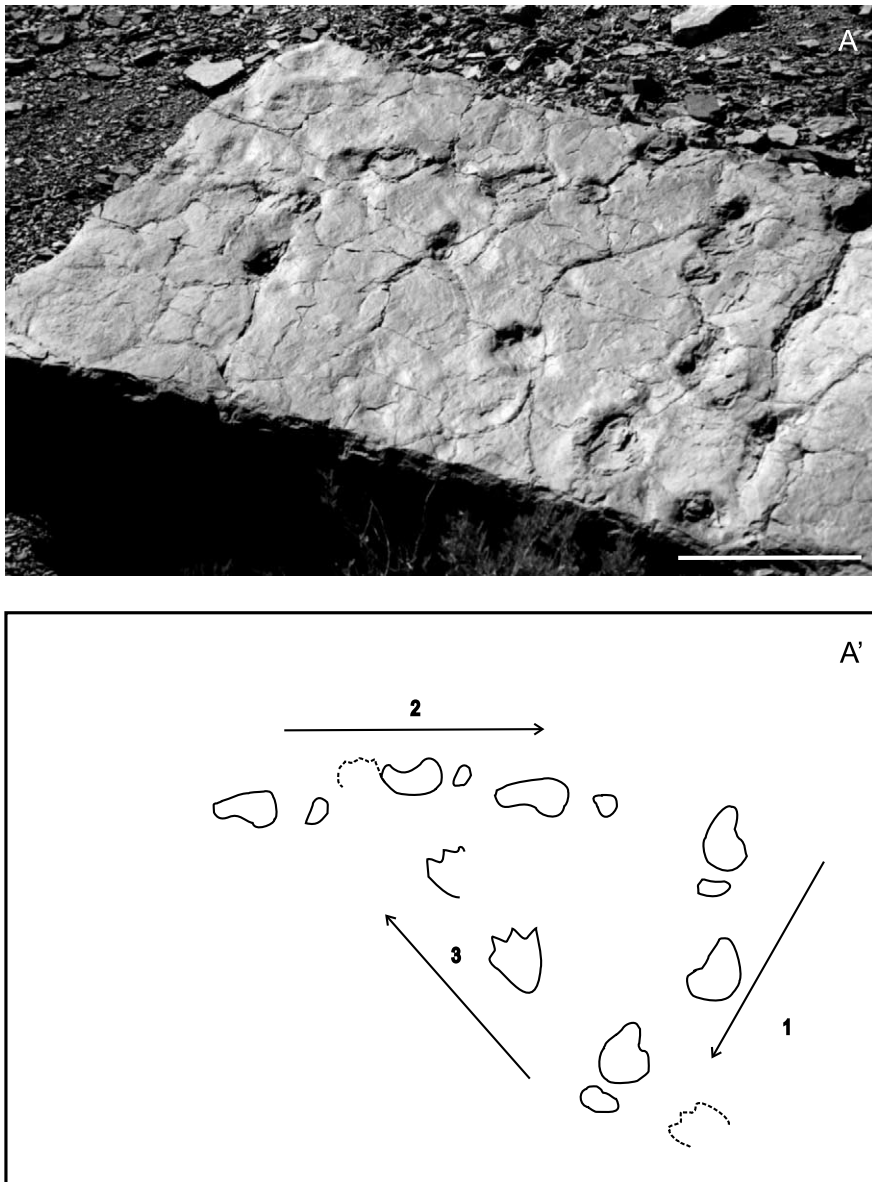Two different kinds of footprints representing

Fig. 3. Field photograph (A) of uncollecting slab and interpretative line sketch (A′) showing several trackways as natural molds on the slab surface: (1,2) Type FB; (3) Type B1. Scale bar = ca. 50 cm.

full bipedal progression are found in the Portezuelo levels (Types B1 and B2). Type B1 is preserved as natural molds arranged in two short trackways, one of four steps and the other one of two. The longer one (measurements summarized in Table 2) is present on the same surface as the two deeply impressed trackways of Type FB, described above

(Figs. 3 and 5). Apparently, it was made later as it crosses over the Type FB ones and is less impressed, thus suggesting less water content in the sediment during the emplacement. The trackway consists of four consecutive, large, tridactyl footprints that are rather elongated and unrotated. The digits are anteriorly directed, and pads are
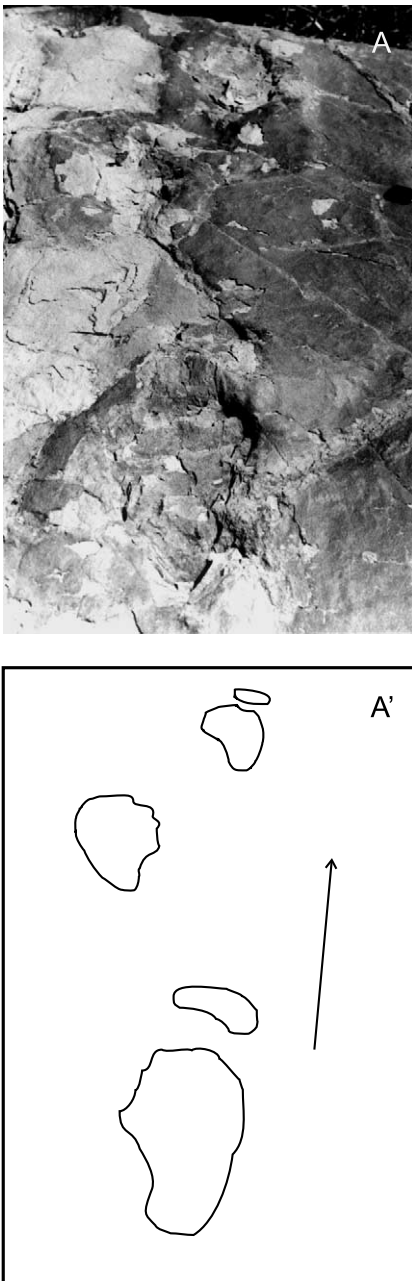
Fig. 4. Field photograph (A) and interpretative line sketch (A′) of a trackway of Type FB corresponding to the one numbered (1) in Fig. 3.

not discernible. Digits II and IV are of nearly equal size, with digit III slightly longer. The average divarication angle between digits III–II and III–IV is 25 degrees. The second track of the se-

ries, which corresponds to a right pes, preserves the outline of a smooth concave projection on its internal border that might correspond to a poorly preserved digit I impression. All the digits have claws marks, which are triangular, broad-based and acuminate. The trackway has a very high pace angulation (150 degrees), suggesting a narrow upright stance for its maker. According to Thulborn's ratios (Thulborn, 1989), the calculated track-maker's hip height is approximately 2 m.

The second type of footprints of a biped (Type B2; Fig. 6) was recorded as both a trackway (three steps) and one isolated footprint, all preserved as natural molds. The trackway is associated on the same surface with large footprints and trackways of quadruped animals. It consists of three consecutive steps of medium-sized tridactyl footprints with somewhat indistinct pads (measurements summarized in Table 2). Digit III is projected farther anteriorly than digits II and IV; the divarication angle between digits III–II and III–IV is 40 degrees. All digit impressions present well-developed, pointed claw marks. The trackway corresponds to a medium-sized, bipedal, functionally tridactyl animal with a very high pace angulation (aproximately 170 degrees), as a result of which the tracks of the left and right footfalls lie on a nearly straight line. Calculated measurements on the trackway suggest an animal of approximately 75 cm hip height (Thulborn, 1989).
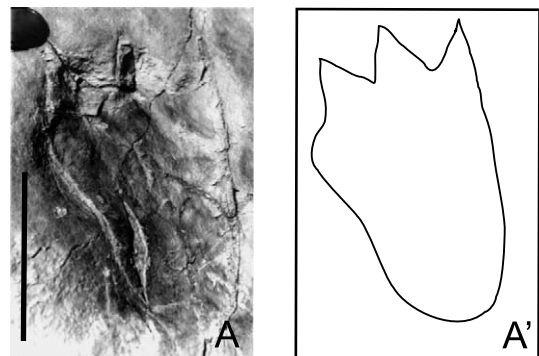

Fig. 5. Field photograph (A) and interpretative line sketch (A′) of a right pes impression of Type B1 corresponding to the trackway numbered (3) in Fig. 3. Scale bar = 20 cm.

Table 2
Measures of trackways of bipeds (Types B1 and B2)

Trackway type	Stride length (cm)	Pace length (cm) *average*	Pace angulation (degrees)	Pace width (cm)	Footprints	Width (cm)	Length (cm)
Trackway Type B1							
1	170	80	150	16	1	n.d.	n.d.
					2	20	35
					3	21	37
					4	n.d.	n.d.
2	n.d.	69	n.d.	12	1	25	34
					2	26	34
Trackway Type B2							
1	200	100	170	10	1	n.d.	n.d.
					2	13	16
					3	12	16

n.d., not datum.

3.2. Trackways of quadrupeds

Two different types of trackways representing quadrupedal progression are recorded in the Portezuelo Formation levels. Type Q1 is a small isolated trackway where footprints are preserved as natural casts on a slab surface, and are superimposed by very fine mudcracks (Fig. 7). The trackway includes a series of three sets of manus and pes impressions which are morphologically quite similar and nearly equal-sized (see Table 3). The manus impressions are slightly smaller and located anterolaterally to those of the pes, and are somewhat rotated inwards. The palm and sole of both manus and pes impressions are preserved as rounded, slightly tranversely oval pads; in some impressions an anteroposterior groove is visible crossing the pad medially, thus dividing it into two rounded pads of nearly equal size. Four short digits are present in the footprints, represented by oval impressions somewhat separated from the palm/sole. They are anteriorly directed and nearly parallel, and have blunt tips lacking claw marks. The digits are subequal, with digit III slightly longer.

The trackway pattern shows that the first set of footprints, corresponding to the right side of the animal, are more separated from the second set than the latter are from the third one. The size of the footprints, the stride length, and the narrowness of the trackway all suggest an upright posture for the track-maker's limbs. The speed of the track-maker was estimated using Alexander's formula (Alexander, 1976; see Table 3). Assuming that *h* (hip height) is about four times the pes length (mean estimated for erect reptiles sensu Thulborn, 1989, 1990), the resulting speed of the track-maker is rather high (1.81 m/s), and the stride length is three times the estimated track-maker's hip height (relative stride length), indicating a trotting/running gait for the track-maker (Alexander, 1976; Thulborn, 1989, 1990). If the calculation of hip hight is considered less than four times the pes length, as was used for Permian

Table 3
Measures of the trackway Type Q1

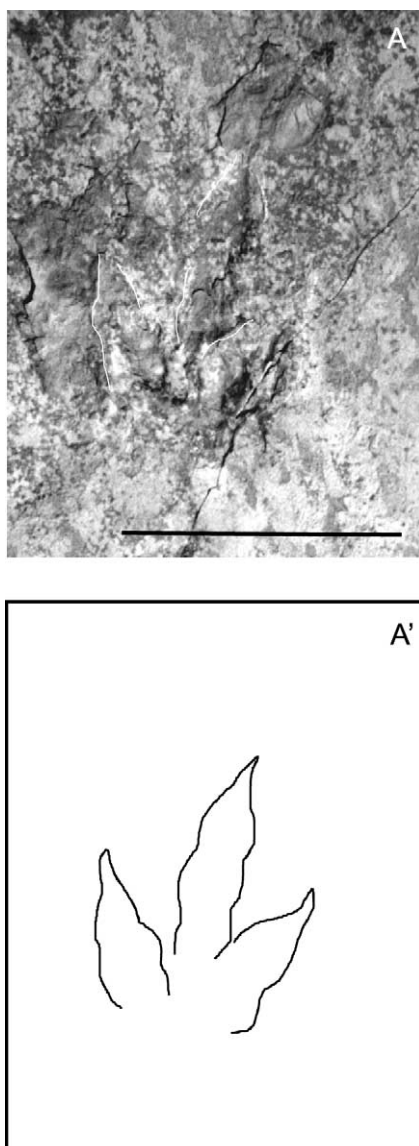| Trackway Q1	Manus	Pes
Width (cm)	3	3.3
	3.2	3.5
	3	3.5
average	*3*	*3.4*
Length (cm)	3.7	4
	3.5	3.7
	3.5	4
average	*3.6*	*3.9*
Stride length (cm)	43	45
Pace length (cm)	24	24
	16	19
average	*20*	*21.5*
Pace angulation (degrees)	130	150
Width of the pace (cm)	6.5	4
Distance m–p (cm) *average*	*4.5*	
Speed *u* (m.1/s)	1.81	
Relative stride length, λ/h	2.88	

Fig. 6. Field photograph of uncollecting material (A) and interpretative line sketch (A′) of a left pes impression of Type B2 preserved as a natural mold. Scale bar = 15 cm.

therapsids (McKeever, 1994), the speed values calculated become even higher.

The second kind of trackways of quadrupeds (Type Q2) corresponds to large pentadactyl tracks recorded as both trackways and isolated footprints, and as natural casts as well as molds (Fig. 8). They are present in at least four different levels in the sequence, one close to the first track-bearing horizon recorded, and the remaining tracks in the uppermost levels. As with the trackways described above, the number of steps present in each trackway is constrained by the size of the surface exposed in the fallen blocks. The measurements in Table 4 are based on the trackway with the largest number of steps, which also represents the largest footprints measured; there is isolated material consisting of slightly smaller footprints. Generally, the manus and pes prints have a similar shape and size and are anteriorly directed. They have a rather rounded, large palm/sole pad impression and five very short subequal toe prints directed outwards. These are clearly imprinted in the best preserved tracks (Fig. 8C). The outward rotation of the digits is more evident in the manus tracks than in the pes ones. The toes left an oval impression with blunt tips that are more deeply impressed than the palm/sole pad, especially those corresponding to digits II, III and IV; digits I and V appear to be the shortest of the series. Regarding the analyzed material of Type Q2, the trackway pattern shows a regular progression of the track-maker, with short steps where the manus and pes impressions are always close to the midline of the trackway (narrow-gauge). Moreover, the moderately high pace angulation (approximately 100 degrees extrapolating from the footprint impressions) indicates a semi-erect to fully erect quadrupedal animal.

3.2.1. Isolated footprints

Two isolated symmetrical, pentadactyl foot-

Table 4
Measures of the trackway Type Q2

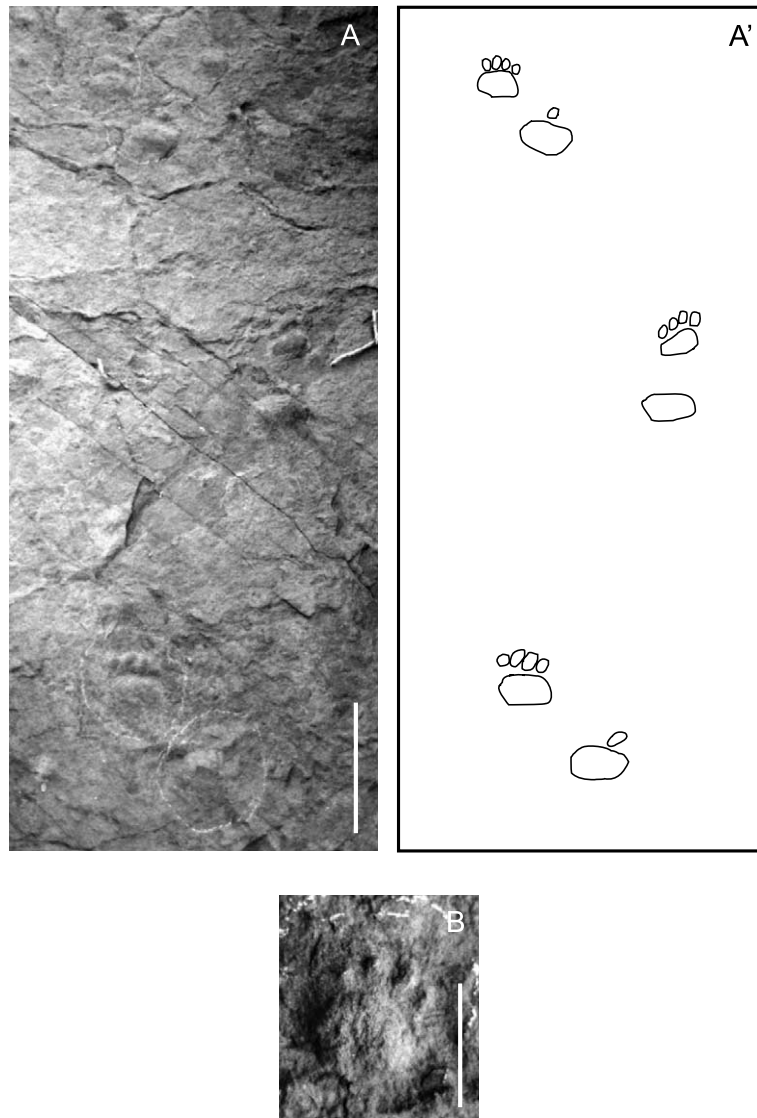| Trackway Q2	Manus	Pes
Width (cm)	35	34
	35	35
average	*35*	*34.5*
Length (cm)	34	35
	35	33
average	*34.5*	*34*
Stride length (cm)	140	n.d.
Pace length (cm)	n.d.	78
Pace angulation (degrees) aprox.	100	
Width of the trackway (cm) *average*	50	
Distance m-p (cm) *average*	65	

n.d., not datum.

Fig. 7. Field photograph of uncollecting slab (A) and interpretative line sketch (A′) of a trackway of Type Q1 preserved as a natural cast; scale bar = 10 cm. (B) Detailed photograph of one left pes impression; scale bar = 4 cm.

prints corresponding to 'chirotheroid' right pes impressions are also present in the assemblage (Fig. 9). The two footprints are preserved as natural casts and have a similar size, although their morphology is quite different. The first one is located near the first track-bearing horizon in the sequence, and due to the lack of detail in the footprint (e.g. digital pad impressions) it appears to be an underprint (Fig. 9A). Digits I to IV are

anteriorly directed with an average divarication angle of 20 degrees between digits I–II, II–III and III–IV; digit V is anterolaterally directed and is quite robust. Digits II, III and IV are of similar size, with III slightly longer and II slightly shorter; digit I is the shortest of the series. All digits bear pointed claw impressions.

The second recorded 'chirotheroid' footprint, located higher in the track-bearing beds, is par-
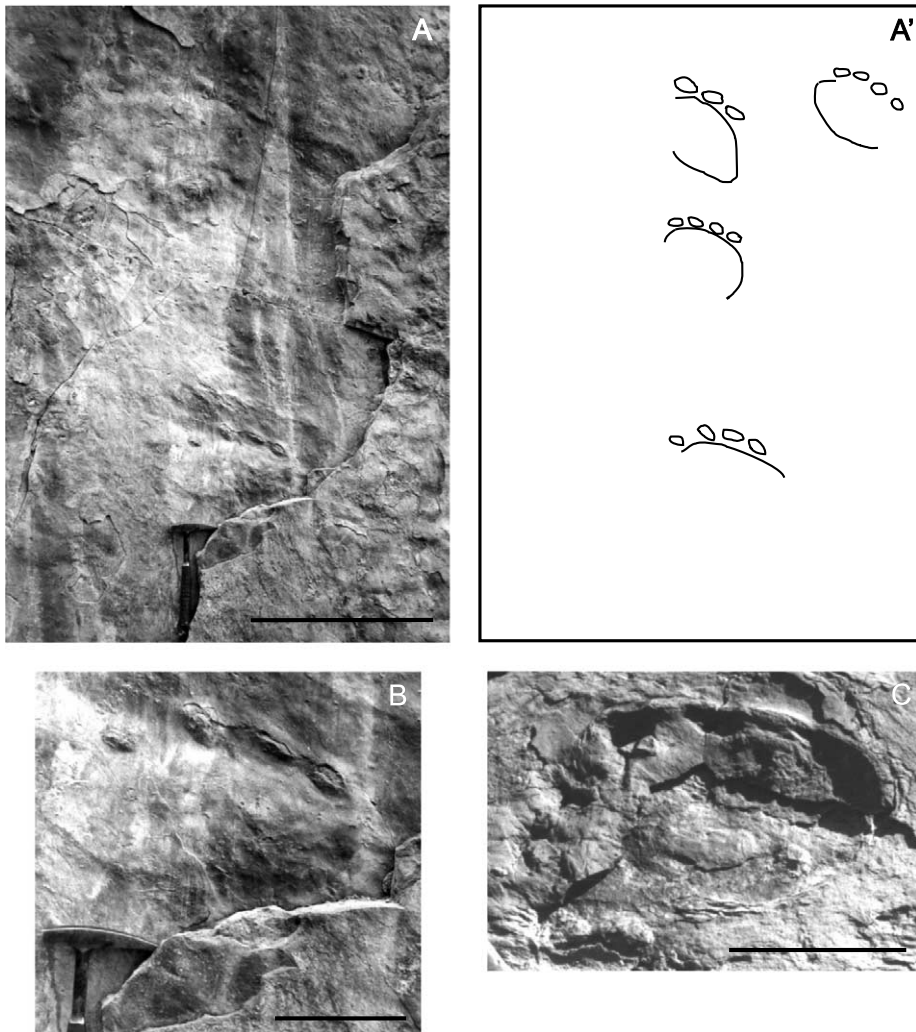
Fig. 8. Field photograph of uncollecting slab (A) and interpretative line sketch (A′) of a trackway of Type Q2 where the footprints are preserved as natural casts; scale bar = ca. 50 cm. (B) Detailed photograph of the first footprint preserved of the series in (A); scale bar = 20 cm. (C) Field photograph of a left isolated footprint of Type Q2 preserved as a natural mold; scale bar = 20 cm.

tially preserved, with part of the digit I impression missing (Fig. 9B). In spite of this, the footprint appears to be wider and a little smaller than the other 'chirotheroid' footprint. Digit III is the longest one of the series, and digits II and IV are of similar size and a bit longer than digit I. The average divarication angle between digits II–III and III–IV is 25 degrees. Digit V is the smallest and is strongly posterolaterally everted. All preserved tips of the digits are pointed, suggesting

the presence of well-developed claws in the track-maker.

4. Discussion

4.1. Track-makers and comparisons

Tracks and trackways are an important source of information that provides, among other things,
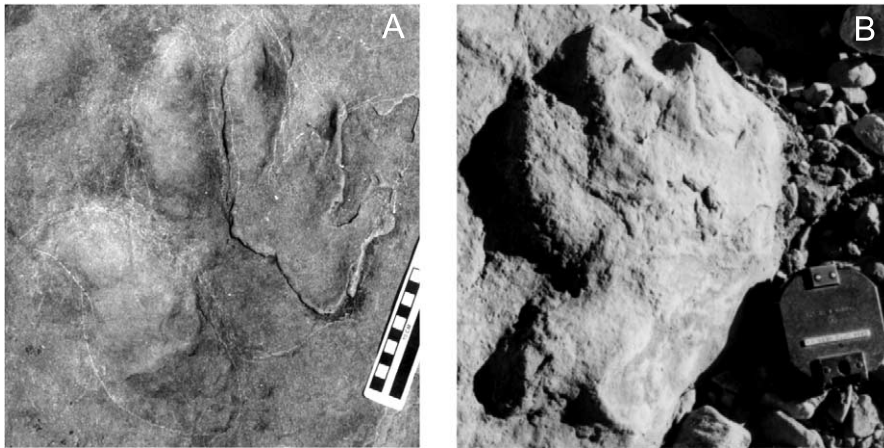
Fig. 9. (A,B) Field photographs of uncollecting material that correspond to right pes impressions of 'chirotheroid' type of footprints preserved as natural casts. Scale in (A) is ca. 8 cm width; scale in (B) is 10 cm.

an estimation of the spatial and temporal distribution of tetrapod taxa (e.g. Lockley, 1986; Lockley et al., 1994). Interpretations based on footprints require the identification of the track-maker through integration of skeletal and ichnological data, a relationship which often has been tenuous (Padian, 1986). Recently, a new approach to this practice has been proposed (Olsen et al., 1998; Carrano and Wilson, 2001) as an alternative to the traditional method based on general similarity between tracks and known foot skeletons ('phenetic correlation' sensu Carrano and Wilson, 2001). Synapomorphy-based track-maker identification is focused on the recognition of shared derived characters present in the pedal skeleton of some body-fossil clade and the inferred structure of the pedal impressions of the ichnite (Carrano and Wilson, 2001). Therefore, in order to understand the faunistic significance of the Rincón Blanco footprint assemblage, the track-makers were identified and discussed within a phylogenetic context. It is noteworthy that the ichnites from the Portezuelo Formation represent the most diverse Triassic tetrapod footprint assemblage described up to now from South America, and therefore are significant for estimating the composition of the Late Triassic fauna in the region.

As previously discussed, tracks and trackways of Type FB are considered to represent facultative bipeds because of the somewhat unpredictable

placement of the front footprints (apparently not attributable to preservational effects); this evidence suggests that the forelimbs did not have a major supportive role (Thulborn, 1989). It is interesting to note that the track-maker of Type FB might be a semiplantigrade form due to the presence of a narrow rounded posterior apex (?heel) in the prints, which could indicate a metatarsal impression (see Kuban, 1989). The trackways show a relatively high pace angulation and narrow pace width, therefore suggesting a narrow gait and parasagittal posture for their makers. All this evidence suggests that the track-maker is related to the Dinosauria clade.

According to the present understanding of dinosauriform phylogeny (e.g. Gauthier, 1986; Sereno, 1986, 1999; Parrish, 1992, 1993; Benton, 1999), only some taxa of ornithischian (e.g. heterodontosaurids, *Pisanosaurus*, *Lesothosaurus*, *Scutellosaurus*) and prosauropod dinosaurs are interpreted as possible facultative bipeds (Bonaparte, 1976, 1997; Olsen and Baird, 1986; Thulborn, 1989; Galton, 1990; Farlow and Chapman, 1997). The relatively large size of the Portezuelo track-maker (estimated height at the hip approximately 1.65 m) and the absence of a prominent longer medial digit in the tracks exclude heterodontosaurids and basal ornithischians as the possible makers of the trackways. Moreover, the only known postcranial skeletons referred to Heterodontosauridae (e.g. Santa Luca, 1980; Weisham-

pel and Witmer, 1990) and basal ornithischians (Bonaparte, 1976; Sereno, 1991) are small-sized animals with a tridactyl, symmetrical pes bearing a relatively long digit III, and thus would be expected to imprint tracks similar to those attributed to theropod dinosaurs (Olsen and Baird, 1986; Farlow and Chapman, 1997; Olsen et al., 1998). In addition, most ornithischians, except derived iguanodontids, retain a relatively large pedal digit I, which might be expected to leave a fourth digit print in addition to the three main toe prints. Thus constrained, the putative track producer of the Type FB footprints might be a medium-sized, facultatively bipedal prosauropod dinosaur. Nevertheless, facultative bipedal posture may have also occurred in basal sauropods, which are secondarily obligate quadrupeds (Wilson and Sereno, 1998). The earliest body fossils of Sauropoda (Buffetaut et al., 2000, 2002; Gillette, 2003) are known from the Upper Triassic of Laurasia (Thailand), and their sister-taxon relationship with Prosauropoda suggests that the sauropods had diverged by at least the early Late Triassic (Wilson and Sereno, 1998; Sereno, 1999; Carrano and Wilson, 2001). Thus, basal sauropod affinities for the Type FB track-maker cannot be rejected. The general shape of the pes prints (semi-plantigrade), size disparity between the manus and pes, and the relatively equal length of the digits support this hypothesis, as suggested by Lockley et al. (2001).

Comparable footprints to those mentioned above have been previously described in Gondwana only from the Late Triassic lower Elliot Formation of the Karoo Basin of South Africa (Ellenberger et al., 1970; Ellenberger, 1970, 1972, 1974). These large tetradactyl footprints ('*Tetrasauropus*' and '*Pseudotetrasauropus*') have been referred to different groups of prosauropod dinosaurs with, apparently, both bipedal and quadrupedal progression (Olsen and Galton, 1984; Lockley and Hunt, 1995; Lockley et al., 1996; Lockley and Meyer, 2000) and recently also to sauropods (Lockley et al., 2001). This South African material closely resembles that described herein, particularly with respect to the inward rotation of the digits (see Ellenberger, 1970, plates 2 and 3, 1974, plates 2 and 3). In contrast,

alleged '*Tetrasauropus*' tracks from the Upper Triassic of the western USA and England have the pes impressions strongly rotated outwards (Lockley and Hunt, 1995; Lockley et al., 1996, 2001; Lockley and Meyer, 2000).

Two different kinds of footprints representing full bipedal progression are found in the assemblage, Types B1 and B2. These footprints are markedly different, especially in the general morphology of the foot and overall size, nevertheless, both trackways are quite narrow and have very high pace angulation, thus suggesting a fully erect gait for their makers. Accordingly, both types are recognized as dinosaur trackways; bipedal progression was developed in several dinosaur groups, such as basal ornithischians, ornithopods, prosauropods and theropods (Farlow and Chapman, 1997; Sereno, 1999; Carrano, 2000; Farlow et al., 2000; Carrano and Wilson, 2001). The tracks of Type B1 are relatively large and broad, with digits II, III and IV nearly equal-sized and showing triangular broad-based claws marks. The morphology of the pes print, particularly the relative length of the digits, prevents any comparison with members of the theropod clade, because in that group digit III is further anteriorly projected than digits II and IV (e.g. Olsen and Baird, 1986; Parrish, 1989; Thulborn, 1989; Farlow and Lockley, 1993; Farlow and Chapman, 1997; Olsen et al., 1998; Farlow et al., 2000); this condition also occurs in basal ornithischians, heterodontosaurids and basal euornithopods (e.g. Bonaparte, 1976, 1978; Santa Luca, 1980; Weishampel and Witmer, 1990; Farlow and Chapman, 1997). Moreover, the large size of the track-maker (hip height approximately 2 m) would exclude basal ornithischians and basal ornithopods as possible makers of Type B1. Therefore, prosauropod affinities are also suggested for the Type B1 track-maker; the size and morphology of the footprints with the possible presence of a reduced digit I impression support that assignment. When compared with the putative sauropodomorph trackways mentioned above (facultative biped), this animal was larger, with a more upright stance and full bipedal progression. Besides, the pes prints of this animal were anteriorly directed, without rotation of the digits. Footprints compa-

rable to those described above have not been described from the Early Mesozoic deposits of Gondwana to date.

The remaining trackways of bipeds in the assemblage (Type B2) correspond to a small-to-medium-sized, functionally tridactyl animal (height at hip approximately 75 cm). The pes prints show an anteriorly directed digit III, much longer than digits II and IV, and all bearing well-developed pointed claws. The trackway has a very high pace angulation, and thus the footfall pattern in the trackway is on a nearly straight line. Therefore, according to this pattern, trackway size, and digit morphology, the track-maker could be allied with either theropods or ornithischians (basal ornithischians or heterodontosaurids). No synapomophies are preserved in the three-toed footprints that might discriminate between theropod and ornithischian groups as possible track-makers (Olsen et al., 1998). Despite this, some authors have suggested that proportional differences measured in very well preserved tridactyl footprints can be compared with the same ratios measured from skeletal material. This method was proposed to discriminate among different dinosaur groups, especially between Triassic theropods and ornithischians (Farlow and Lockley, 1993; Farlow and Chapman, 1997; Olsen et al., 1998). The quality and number of impressions in the material described herein are not good enough to be analyzed in this morphometric context and thus cannot be used to discern between the mentioned tridactyl dinosaur groups. Nevertheless, theropod tracks can be also identified by the asymmetrical arrangement of the digits, with a distinct divergence of digit IV from II and III (Carrano and Wilson, 2001). In the present case, digit IV is slightly more laterally projected from digit III, which is relatively closer to digit II, therefore suggesting that the track-maker could be allied to Theropoda.

Tridactyl footprints related to both theropods and basal ornithischians have been described from several Early Mesozoic sequences from Gondwana and Laurasia (e.g. Ellenberger, 1970, 1972, 1974; Olsen and Galton, 1984; Farlow and Lockley, 1993; Farlow and Chapman, 1997; Olsen et al., 1998; Lockley and Hunt, 1995; Haubolt and Klein, 2000; Lockley and Meyer, 2000). In particular, rather diverse assemblages of tridactyl tracks are known from the Late Triassic (lower Elliot Formation) and Early Jurassic (Clarens Formation) beds of the Karoo Basin (Ellenberger, 1970, 1972, 1974; Olsen and Galton, 1984), and they are comparable to those described above (Marsicano, pers. observation).

The Portezuelo levels also include two isolated tracks that correspond to pes impressions of 'chirotheroid'-type footprints, which have been often regarded in the literature as crurotarsal archosaur tracks (= crocodile-normal archosaurs sensu Parrish, 1989; Haubold, 1983, 1986; Demathieu and Wright, 1988; Courel and Demathieu, 1995; Haubold and Klein, 2000; Lockley and Meyer, 2000). They represent a quadruped animal with a symmetrical pes and manus with reduced digits I and V. The presence in the assemblage of two footprints with quite different digit V impressions (one anterolaterally directed and the other strongly everted) documents the presence of at least two groups of medium-sized crurotarsal archosaurs. 'Chirotheroid' tracks are an important component of the Triassic footprint assemblages of Pangea, and they have been widely used biostratigraphically and as Triassic 'markers' due to their absence after the Triassic–Jurassic boundary (e.g. Peabody, 1948; Haubold, 1983, 1986; Olsen and Galton, 1984; Courel and Demathieu, 1995; Parrish, 1989; Lockley and Hunt, 1995; Lockley and Meyer, 2000; Arcucci et al., in press).

Trackways and footprints of Types Q1 and Q2 also denote quadrupedal progression, but in this case the manus and pes impressions are quite similar (homopody) and show a relatively symmetrical, anteriorly-directed manus and pes. Early Mesozoic tracks and trackways with this morphology have long been attributed to non-mammalian therapsid track-makers (e.g. Haubold, 1971; Olsen and Galton, 1984; Hunt et al., 1993; Retallack, 1996; Lockley and Meyer, 2000). Recent phylogenetic analysis of the Synapsida (Hopson, 1994; Sidor and Hopson, 1998) and discussions related to limb posture and manus/pes evolution in non-mammalian therapsids (Hopson, 1995; Blob, 2001) provide a framework for interpreting the possible track-makers of these footprints.

The Type Q1 track-maker represents a small animal that could develop a running gait, with an upright limb posture for both the forelimbs and hindlimbs. Also, the prints indicate a quite symmetrical manus and pes with nearly equal-sized, anteriorly directed digits. This manus and pes morphology and trackway pattern, together with the Late Triassic age of the levels, suggest that the track-maker might be related to cynodont therapsids (?Eucynodontia). In Gondwana, ichnites attributed to cynodont therapsids have been described from Upper Triassic levels from both southern South America and South Africa. In southern South America many small footprints and trackways related to non-mammalian therapsids have been described from Upper Triassic levels (Los Menucos Basin) of northern Patagonia (Casamiquela, 1964, 1975; Leonardi, 1994; Manera de Bianco and Calvo, 1999; Domnanovich, 2003); some of the Patagonian specimens are fairly similar to those described herein (Marsicano, pers. observation). In the Cuyana Basin, the Middle Triassic Cerro de las Cabras Formation has yielded several mostly isolated footprints attributed to non-mammalian therapsids (Leonardi, 1994). They have a relatively long, curved, separated digits with pointed claw marks, characters that clearly differentiate them from the Rincón Blanco ichnites (Marsicano, pers. observation). In the Karoo Basin, track-bearing horizons from the lower part of the Early Jurassic Clarens Formation have yielded several different types of isolated tetradactyl and pentadactyl footprints related to therapsids (Ellenberger, 1970, 1972). These footprints show relatively separated, subequal digits, thus differing from the material from Rincón Blanco.

Tracks of Type Q2 were produced by a quite different therapsid track-maker than the one described above. It was a large quadruped animal with the limbs held beneath the body, based on the relative narrowness of the trackways. The toes were very short and are more deeply imprinted in the sustrate than the palm/sole pad. The morphology and size of the tracks, together with the Triassic age of the track-bearing levels, strongly suggests that the track-maker was a member of the dicynodont anomodont clade (sensu Hopson,

1994; Sidor and Hopson, 1998); furthermore, it might be referable to the large herbivorous kannemeyerids, which include the largest described dicynodonts (e.g. Walter, 1986; King, 1990; Cox, 1991). A nearly upright posture of the hindlimbs has already been indicated for members of this group (Walter, 1986), although the trackways described above suggest that an upright posture was also developed in the forelimbs of the Portezuelo track-maker, because both the manus and pes impressions are close to the midline of the trackway. Moreover, the moderately high pace angulation (approximately 100 degrees extrapolating from the footprint impressions) indicates a semi-erect to fully erect quadrupedal animal. In the Late Triassic assemblage of the Karoo Basin (lower Elliot Formation), large trackways of quadruped pentadactyl animals ('*Pentasauropus*' spp.; Ellenberger, 1970, 1972) are known which have been attributed to large dicynodont anomodonts (Olsen and Galton, 1984; Lockley and Meyer, 2000); these tracks are indistinguishable from those described herein (Marsicano, pers. observation).

As discussed above, close similarities between the footprints and trackways of the Portezuelo levels with those described from southern South Africa (lower Elliot Formation) are quite evident. This situation is particularly significant with the co-ocurrence in both areas of tracks here attributed to facultative bipedal basal sauropodomorphs (Type FB) and large dicynodonts (Type Q2).

4.2. Palaeobiogeographic and evolutionary significance

Relevant Gondwanan Early Mesozoic tetrapod faunal assemblages are known from Africa, India and South America. The rich faunal content of the upper Karoo succession, which includes both body fossils and tracks, was used to support the idea that the deposition of the sequence occurred during the Late Triassic (Molteno and lower Elliot Formations) and extended into the Early Jurassic (upper Elliot and Clarens Formations) (e.g. Kitching and Raath, 1984; Olsen and Galton, 1984; Lucas and Hancox, 2001). The Late Trias-

sic tetrapod assemblage is characterized by the presence of crurotarsal archosaurs (rauisuchians), non-mammalian therapsid cynodonts (traversodontids) and dicynodonts (only footprint material), and dominant prosauropod (*Euskelosaurus*) and theropod (only footprint material) dinosaurs (Kitching and Raath, 1984; Olsen and Galton, 1984; Anderson et al., 1998; Lucas, 1998; Lucas and Hancox, 2001). Conversely, the Early Jurassic fauna is mainly characterized by a variety of dinosaurs (prosauropods, theropods, ornithischians), sphenosuchian archosaurs, non-mammalian therapsid cynodonts, and mammals (Kitching and Raath, 1984; Olsen and Galton, 1984; Anderson et al., 1998; Lucas, 1998; Lucas and Hancox, 2001). The Rincón Blanco assemblage closely resembles that of the lower Elliot Formation, particularly because of the presence in both sequences of crurotarsal archosaurs, prosauropod and theropod dinosaurs, and large non-mammalian therapsid dicynodonts. Recently, a new Middle–Late Triassic tetrapod fauna was described from Madagascar, which also includes kannemeyeriid dicynodonts, eucynodonts and two prosauropod dinosaurs, among others (Flynn et al., 1999). In east India, an apparently equivalent faunal assemblage has been described from the Late Triassic Maleri and Dharmaram Formations of the Pranhita–Godavari Valley (Chatterjee and Roy-Chowdhury, 1974; Kutty and Sengupta, 1989; Loyal et al., 1998).

In southern South America, two different areas (southern Brazil and west-central Argentina) have produced very important Triassic tetrapod assemblages comparable to that of Rincón Blanco. The upper Santa María and Caturrita formations (Paraná Basin, Brazil) have yielded a rich Late Triassic tetrapod fauna. The upper Santa María levels include a variety of non-mammalian therapsids (cynodonts), crurotarsal archosaurs, and dinosaurs (theropods, prosauropods), among other groups (e.g. Bonaparte and Barberena, 2001; Barberena et al., 1985; Schultz et al., 2000); this fauna has been widely correlated with the one present in the Ischigualasto Formation levels (Bonaparte, 1970, 1982; Lucas, 1998; Schultz et al., 2000). The Carnian Ischigualasto unit (Rogers et al., 1993) corresponds to part of the Triassic in-

filling of the Ischigualasto–Villa Unión Basin (west-central Argentina), which records one of the most taxonomically diverse Middle–Late Triassic tetrapod assemblages of Gondwana (e.g. Bonaparte, 1970, 1982, 1997; Rogers et al., 1993; Martínez et al., 1996; Lucas, 1998; Arcucci et al., in press). Tetrapods from the Ischigualasto Formation include crurotarsal archosaurs (rauisuchids, aetosaurs, ornithosuchids), dinosaurs (theropods, ornithischians), non-mammalian therapsid cynodonts (e.g. traversodontids) and large kannemeyerid dicynodonts, among other groups. Nevertheless, prosauropod dinosaurs remain unknown from this unit. In southern South America, prosauropods characterize somewhat younger levels, particularly in west-central Argentina and Patagonia. They are quite abundant in the top of the overlying Los Colorados Formation (Late Triassic, Ischigualasto–Villa Unión Basin) and the Laguna Colorada Formation of northern Patagonia (Casamiquela, 1977, 1980; Bonaparte and Vince, 1979; Arcucci and Coria, 1996; Arcucci et al., in press). Recently, new prosauropod material has been recorded from even younger levels (Early Jurassic) of west-central Argentina (Martínez, 1999).

The presence in the Rincón Blanco tetrapod assemblage of putative basal members of Sauropodomorpha, perhaps both prosauropods and basal sauropods, of lower Late Triassic age (probably Carnian) implies an earlier distribution of these dinosaurian herbivores in western Gondwana than previously recorded by body fossils. To date, the oldest body-fossil record of sauropods in that area is of Early–Middle Jurassic age (e.g. Wilson and Sereno, 1998; Sereno, 1999; Carrano and Wilson, 2001; Gillette, 2003). This fact strongly supports previous assumptions that the initial radiation of sauropodomorph dinosaurs and close relatives might have occurred during the Middle Triassic (Sereno, 1999; Carrano and Wilson, 2001).

5. Conclusions

The Rincón Blanco footprint assemblage constitutes a significant estimate, although at a coarse

taxonomic level, of the fauna represented during the Late Triassic in the Cuyana Basin. This is the most extensive Triassic Basin of southern South America and Patagonia; nevertheless, tetrapods were poorly represented in the sequence and mainly restricted to temnospondyl amphibians and non-mammalian therapsid cynodonts (Báez et al., 1993; Marsicano, 1999; Marsicano et al., 2000; Desojo et al., 2002). Moreover, to date dinosaurs were completely unknown from the Cuyana sequence.

This Mesozoic ichnocoenosis, the most diverse of South America, provides a new perspective on the spatial and temporal distribution of tetrapod taxa during the Late Triassic in the area and new data for intercontinental correlations across the Triassic sections of Gondwana.

Acknowledgements

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