Historical Biology, 2015
Vol. 27, No. 7, 827–842, http://dx.doi.org/10.1080/08912963.2014.904857

Tetrapod and invertebrate trace fossils from aeolian deposits of the lower Permian of central-western Argentina

Verónica Krapovickas[a]*, Claudia A. Marsicano[a], Adriana C. Mancuso[b], Marcelo S. de la Fuente[c] and Eduardo G. Ottone[a]

[a]*Departamento de Cs. Geologicas, FCEN, Universidad de Buenos Aires, IDEAN-CONICET, Ciudad Autónoma de Buenos Aires, Argentina;* [b]*IANIGLA-CONICET, Mendoza, Argentina;* [c]*Museo de Historia Natural de San Rafael, Mendoza, Argentina*

(*Received 25 September 2013; accepted 12 March 2014; first published online 29 April 2014*)

Abundant tetrapod footprints are described from the Early Permian Yacimiento Los Reyunos Formation including both collected and *in situ* specimens. The slabs come from several quarries at the Sierra Pintada and Sierra de las Peñas area, south-west of Mendoza, Argentina. The trace fossil assemblage, which constitutes one of the oldest known from Gondwana, comprises excellent-preserved tetrapod tracks (*Chelichnus duncani*, *Chelichnus gigas* and 'pear-like' footprints) and invertebrate simple sub-horizontal (*Palaeophycus tubularis*) and vertical (*Skolithos* isp.) burrows formed in a aeolian dune field. The analysis of the tetrapod track producers indicates the presence of at least three different taxa of sprawling to semi-erect therapsids, thus suggesting the presence of members of this clade, or closest relatives, in the Early Permian of southern Gondwana. Moreover, a series of measurements and simple indexes were developed to estimate body proportions and locomotion styles of the putative trackmakers. The new assemblage, analysed in the context of other known Permian assemblages from Pangea, is one the few known in Gondwana to be present in an aeolian environment. The evaluation of the assemblage, in the light of aeolian ichnofacies (*Chelichnus*, *Octopodichnus* and *Entradichnus*), shows that it has common elements with the *Chelichnus* and *Entradichnus* ichnofacies.

Keywords: *Chelichnus*; Therapsida; Yacimiento Los Reyunos Formation; locomotion; *Chelichnus* ichnofacies; *Entradichnus* ichnofacies

Introduction

In Laurasia, footprints and trackways preserved in aeolian facies are common during most of the Permian. The first mentioned records are those from the Upper Permian of Scotland, well known as they constitute the first scientific report of tetrapod tracks (e.g. Buckland 1828; Duncan 1831; Jardine 1850; McKeever 1991; McKeever and Haubold 1996; Pemberton and Gingras 2003; Lucas and Hunt 2006). In continental Europe, tetrapod footprints in aeolian facies were only described from the Middle–Upper Permian of Germany (e.g. Haubold 1971; Lucas and Hunt 2006). In North America, there is an extensive record of tracks associated with aeolian deposits described from several localities in the southwest of the USA. They were first described by Lull (1918) and Gilmore (1926, 1927, 1928) from the Lower Permian Coconino Sandstone that crops out in Arizona, but later they were also mentioned from equivalent levels in Utah, Colorado and New Mexico (e.g. Lockley and Madsen 1993; Lockley and Hunt 1995; Lockley et al. 1995, 1998; Lucas and Hunt 2006).

Conversely in Gondwana, Permian tetrapod footprints are, in general, fairly scarce and more striking when those preserved on aeolian facies are only considered. In general, Gondwanan Permian footprint records include those from Lower and Upper Permian of Morocco (Voigt et al. 2010, 2011), the Upper Permian of South Africa (Smith 1993), the Upper Permian of southeastern Brazil (Costa da Silva et al. 2012) and the Lower Permian of Argentina, where these are the only known Gondwanan Permian tracks associated with aeolian deposits. These records include relatively small footprints recently described from fluvial–aeolian deposits of the Early Permian Patquia Formation, La Rioja Province (Krapovickas et al. 2010), and the footprints and trackways described herein from the Early Permian Yacimiento Los Reyunos Formation. This unit includes several footprint-bearing levels related to dune deposits that were for the first time described by Cei and Gargiulo (1977) who studied a single slab from Dr Baulíes quarry in the San Rafael area (Mendoza province). Subsequently and from the same locality, Aramayo and Farinati (1983) studied another single slab. After that, several slabs were gathered from several small quarries located at the Dr Baulies area and several kilometres northwards, in the Sierra de las Peñas area (see Figure 1(a)). At present, all this material is housed in the collections of the Museo de Historia Natural of San Rafael and was collected by one of its former

*Corresponding author. Email: vkrapovickas@gl.fcen.uba.ar

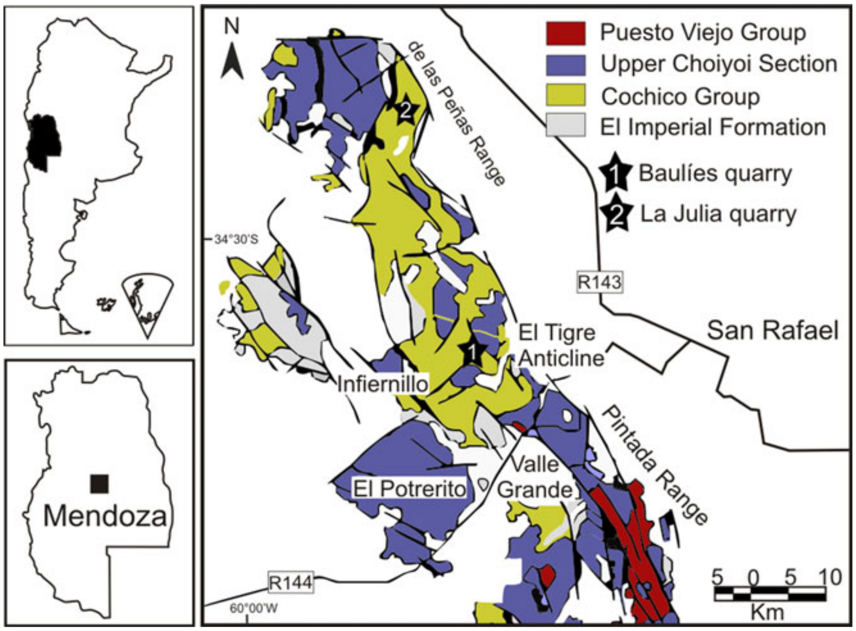

Figure 1. (Colour online) Geological map of the San Rafael Block, central-western Argentina showing the study area (stars). Source: Modified from Kleiman and Japas (2009).

directors, Dr H. Lagiglia. Recently, only part of these tracks were briefly described and figured by Melchor (1997, 2001), without mention of the invertebrate traces associated.

The main goal of the present contribution is for the first time to accurately describe all known materials from the Yacimiento Los Reyunos Formation, including that previously mentioned in the literature plus undescribed collected specimens and also *in situ* trackways. Moreover, the identity of the putative trackmakers and their body proportions and locomotion styles are discussed. As this assemblage is one of the oldest known from Gondwana, comparisons with other Permian track records from Pangea are presented. Finally, an evaluation of all known aeolian ichnofacies is also included in the light of the new ichnoassemblage described herein.

Geological setting

The late Paleozoic in the San Rafael Block (south of the Mendoza province) is mainly represented by a complex Permian volcano-sedimentary succession (the Choiyoi succession) related to the Gondwanic orogeny (Figure 1). It is divided into two sections; one deposited during the Early Permian (the Cochicó Group) and the second mainly during the Middle–Late Permian (The Upper Choiyoi Section) (Kleiman and Japas 2009; Rocha-Campos et al. 2011). This Permian volcano-sedimentary succession rests unconformably on the glaciomarine deposits of the El Imperial Formation, deposited during the Late Carboniferous–Early Permian (Azcuy et al. 1999; Rocha-Campos et al. 2011) and is covered by the Triassic Puesto Viejo Group, composed of continental sediments, rhyolites, ignimbrites and basalts (Stipanicic et al. 2007; Rocha-Campos et al. 2011). The Cochicó Group alternates sedimentary and volcanic rocks such as andesitic breccias, subvolcanic bodies, dacitic to rhyolitic ignimbrites, and continental deposits of alluvial–fluvial and aeolian deposits derived from the reworking of ignimbrites. The Late Permian rhyolites, dacites, and basalts of the Agua de los Burros Formation and the Cerro Carrizalito Group compose the Upper Choiyoi Section (Kleiman and Japas 2009; Rocha-Campos et al. 2011).

The material described herein was exhumed from Early Permian aeolian beds included in the Yacimiento Los Reyunos Formation (Cochicó Group), which consists of alluvial and fluvial deposits with aeolian facies-associated and pyroclastic deposits (Figure 1). The succession is overlying by conglomerates, volcanic breccias, dacites and ignimbrites of the Arroyo Punta del Agua Formation (López-Gamundi 2006).

The Yacimiento Los Reyunos Formation is divided into three members, the Psefítico (Maloberti 1983 *fide* Lardone et al. 1993), Areniscas Atigradas (Holmberg 1948; Lardone et al. 1993) and Toba Vieja Gorda (Rodriguez and Valdiviezo 1970; Ortega Furlotti et al. 1974; Lardone et al. 1993). The lowermost member is characterised by polymictic fanglomerate and conglomerate with dominance of blocks and angular pebbles. The matrix is reddish silty sandstone, which gives the general reddish colour to the Psefítico Member (Llambías et al.

1993). To the top, some yellow cross-stratified sandstone intercalations occur. Greyish yellow, fine- to coarse-grained arkosic sandstones and subordinate siltstones with horizontal and cross-bedded stratification dominate the overlying Areniscas Atigradas Member (Spalletti and Mazzoni 1972), which is covered by the greyish purple porphyritic tuffs of the Toba Vieja Gorda Member (Lardone et al. 1993; Llambías et al. 1993). Laterally, the members are interfingered to each other with a dominance of ignimbrite deposits to the west and the siliciclastic deposits towards the east. Some authors recognise a fourth member named Andesitico (Meza 1988 *fide* Lardone et al. 1993; Llambías et al. 1993). The Andesitico Member is composed of porphyry, lava and breccias intermediate in composition, mainly darker grey epiclastic breccias with dimly stratification (Lardone et al. 1993). However, this member is not recognised in the study area. The Yacimiento Los Reyunos Formation was interpreted as alluvial fan deposits that pass to aeolian sandstones deposited in an erg environment with a dominance of the ignimbrites to the western depocentres (Polanski 1964; Spalletti and Mazzoni 1972; Llambías et al. 1993). Recently, an ignimbrite close to the base of the Yacimiento Los Reyunos Formation was dated (281.4 ± 2.5 Ma, Rocha-Campos et al. 2011), as Kungurian (Early Permian), according to the latest International Chronostratigraphic Chart (2013).

The tetrapod footprints, both collected and *in situ*, come from two series of outcrops located in the sierra Pintada-de las Peñas, west of San Rafael. The first locality corresponds to Yacimiento Dr Baulíes-Los Reyunos (34°40′43.5″S, 68°35′37.3″W): an area with several sandstone quarries exploited because of its uranium content (La Caverna, Cuesta de los Terneros, Dr Baulíes, Los Reyunos) by the Comision Nacional de Energía Atomica (Figure 1). The second locality is situated farther north (approximately 50 km) in the sierra de las Peñas (La Tosca stream), at La Julia quarry (34°18′54.5″S 68°45′00.5″W) (Figure 1).

The tetrapod and invertebrate trace fossils described herein were found in sandstone levels from the Psefítico and Areniscas Atigradas members. At Dr Baulíes quarry, the section starts with the Psefitico Member (Figure 2). It consists of poorly sorted, clast-supported, angular and subangular pebble- to cobble-conglomerate and pebbly medium red sandstones. The conglomerate bodies are of lenticular geometry (up to 1 m thick) with erosive contacts. Internally, they show trough cross-stratification (Gt), planar cross-stratification (Gp) and clast imbrication. These bodies grade upwards and laterally to massive tabular pebbly red sandstone and lenticular pebbly red sandstone (30 cm thick) with planar cross-stratification (Sp) and clasts imbrication. The massive red sandstone records locally abundant trace fossils corresponding to sub-horizontal dwelling structures assigned to *Palaeophycus tubularis* (Figure 2). These deposits of conglomerate and associated red sandstones are interpreted as distributary channel and overbank deposits. Interbedded with the overbank sandstone are preserved lenses of greyish yellow well-sorted fine sandstone. Internally, they show trough cross-bedded stratification (St), inverse grading and are interpreted as aeolian in origin. These aeolian deposits record isolated *Chelichnus gigas* footprints and correspond to the lowest track-bearing levels in the column (Figure 2). Altogether these deposits represent an environment with fluvio-aeolian interaction within a distal alluvial fan context (Rey 2011). The Areniscas Atigradas Member consists of greyish yellow to greyish pink cross-bedded well-sorted fine, medium and coarse-grained sandstone forming strata of 4.5 m thick in average. The sandstone beds are composed almost exclusively of subangular to subrounded clasts of quartz and feldspar. The sandstone levels present trough cross-stratification (St), planar cross-stratification (Sp) and wind-ripple lamination (Sr), often with inverse-graded lamina, and local mottling. The trace fossils recorded in these deposits correspond to tetrapod footprints assigned to *Chelichnus duncani* and *C. gigas* and invertebrate traces to *P. tubularis*, and *Skolitos* isp. In polished slabs, the mottles reveal to be calcitic in composition and thus the mottled levels are interpreted as incipient paleosol formation (Freytet and Plaziat 1982). The sandstone sedimentary structures indicate wind ripples, grainfall and grainflow deposits caused by wind traction and gravity-driven processes associated with aeolian dune migration in a dune field environment (Mountney 2006).

At the La Julia quarry area crops out only the Areniscas Atigradas Member. It consists of greyish yellow cross-bedded well-sorted medium and coarse sandstones. As occurring in Dr Baulíes area, the sandstone beds are composed of subangular to subrounded clasts of quartz and feldspar. Planar cross-stratification (Sp) dominates the succession with ripple lamination (Sr), and inverse grading. Most of the slabs with footprints housed at the San Rafael museum come from this locality and they correspond to *C. duncani*, *C. gigas* and the Pear-like footprints. The sedimentological features of the bearing levels also suggest, as occurring in the Baulíes area, that they were deposited during dune migration in a dune field environment (Mountney 2006).

Materials and methods

The studied material comprises single tracks, isolated *manus–pes* sets and trackways with up to 12 consecutive *manus–pes* sets, preserved in both concave epirelief and convex hyporelief, associated with scarce invertebrate traces.

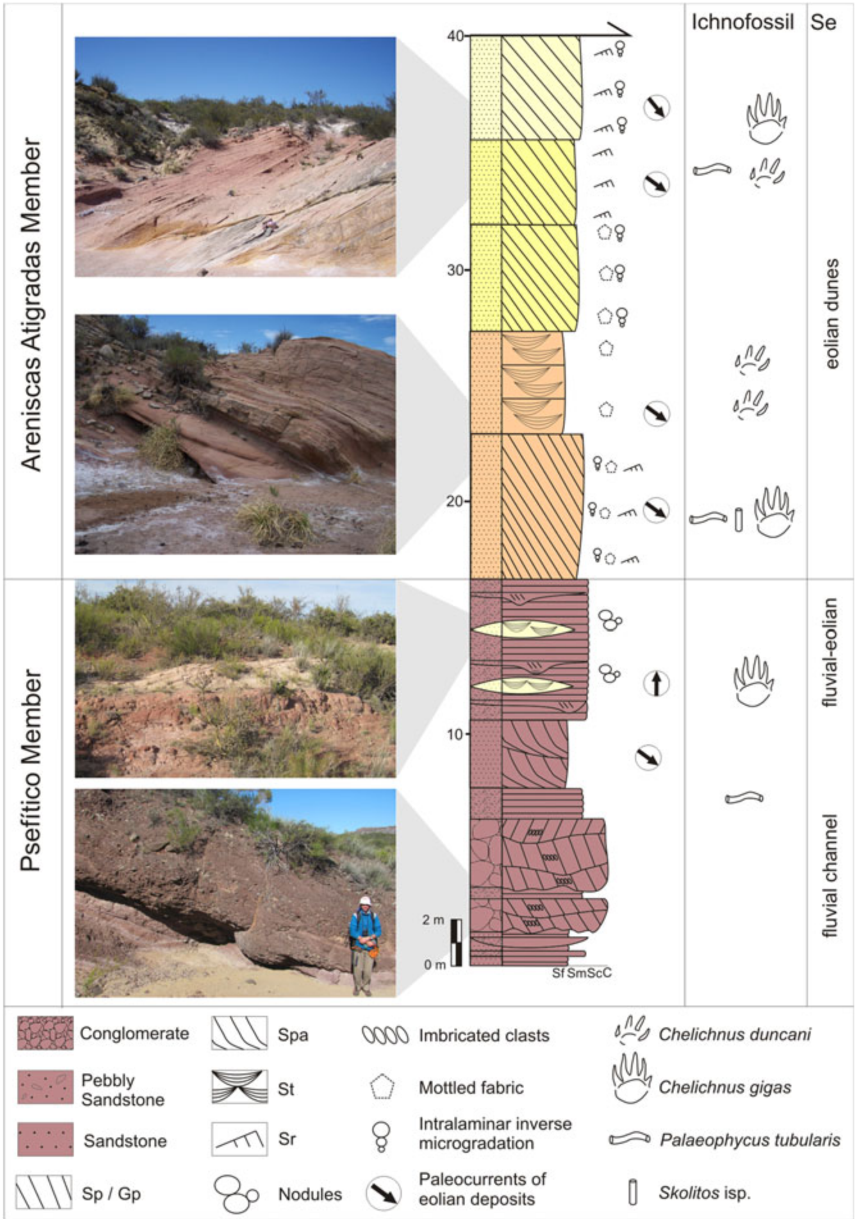

Figure 2. (Colour online) Stratigraphic section of Yaciemiento Los Rayunos Formation in Yacimiento Dr Baulíes-Los Reyunos area. Se: sedimentary environment.

In order to infer body proportions and locomotion styles of their trackmakers, we elaborate a series of measurements and simple indexes from the trackways. The *pes*-width/inner trackway-width ratio (PW/ITW) embodies the distance between limbs of each side of the body in a given posture and indirectly represents the relative stance width in relation to the trackmaker size. The *pes*-length/stride-length ratio (PL/SL) is a good indicator of the limb length of the trackmaker in relation to the length of the body (gleno-acetabular distance) for quadrupeds; this is evidenced by variations in the distance between *manus*–*pes* sets. In all cases and where available, the average value was used for each measurement. The (PL/SL) ratio has a similar meaning to that of the 'coupling value' proposed by Peabody (1959). The latter was determined analysing living animals, but in the case of fossil trackways the resultant values are of questionable utility (Leonardi 1987).

Institutional abbreviations

MMHNSR/PV, Museo de Historia Natural de San Rafael; MSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan; PV UNS, Vertebrate Paleontology collection Universidad Nacional del Sur, Bahía Blanca.

Systematic ichnology

Ichnogenera are placed in the alphabetical order and the preservational nomenclature of Seilacher (1964) is followed.

Invertebrate trace fossils

Ichnogenus ***Palaeophycus*** Hall, 1847

Figure 3. (Colour online) Invertebrate trace fossils. (a) *P. tubularis* preserved in aeolian deposits; (b) *Skolitos* isp. preserved in aeolian deposits; (c) *P. tubularis* preserved in overbank deposits.

Palaeophycus tubularis Hall, 1847

(Figure 3a)

Material. Material preserved in the field.

Horizon and locality. The material is preserved at the Dr Baulies quarry in greyish yellow, fine- to coarse-grained sandstones and massive red sandstones.

Description. Horizontal to sub-horizontal, straight to slightly curved, unbranched tubular trace fossils. The sections are circular to elliptical and of 5–10 mm in diameter. The infill is similar to the host rock and the lining is smooth. Preserved as full relief.

Remarks. *Palaeophycus* differs from *Planolites* by the presence of a wall lining and infill similar to that of the host rock (Pemberton and Frey 1982). The ichnospecies *P. tubularis* is distinguished from the other ichnospecies of *Palaeophycus* by its thin burrow lining and lack of conspicuous wall ornamentation, according to Pemberton and Frey (1982).

Ichnogenus ***Skolithos*** Haldeman, 1840

Skolithos isp

(Figure 2b)

Material. Material preserved in the field.

Horizon and locality. The material is preserved at the Dr Baulies quarry in greyish yellow, fine- to coarse-grained sandstones.

Description. Simple, elongate and cylindrical vertical trace fossils. The wall is smooth and the infill is similar to the host rock. The diameter is 5–10 mm. The examples are short tubes with unknown lower end. Preserved as full relief.

Remarks. Specimens are typically preserved in bedding plane view. No ichnospecific assignment can be made for the studied material due to its incomplete preservation.

Vertebrate trace fossils

Ichnogenus ***Chelichnus*** Jardine, 1850

Chelichnus duncani (Owen, 1842)

(Figure 4)

Material. Two trackways were measured and photographed in the field (Table 1). One trackway (Tw1) includes 12 *manus–pes* sets and the second trackway (Tw2) includes 10 *manus–pes* sets. All materials are preserved as concave epirelief.

Horizon and locality. Both trackways are preserved at the top of greyish yellow, fine- to coarse-grained sandstones; Tw1 is recorded at Dr Baulíes quarry and Tw2 at the La Julia quarry.

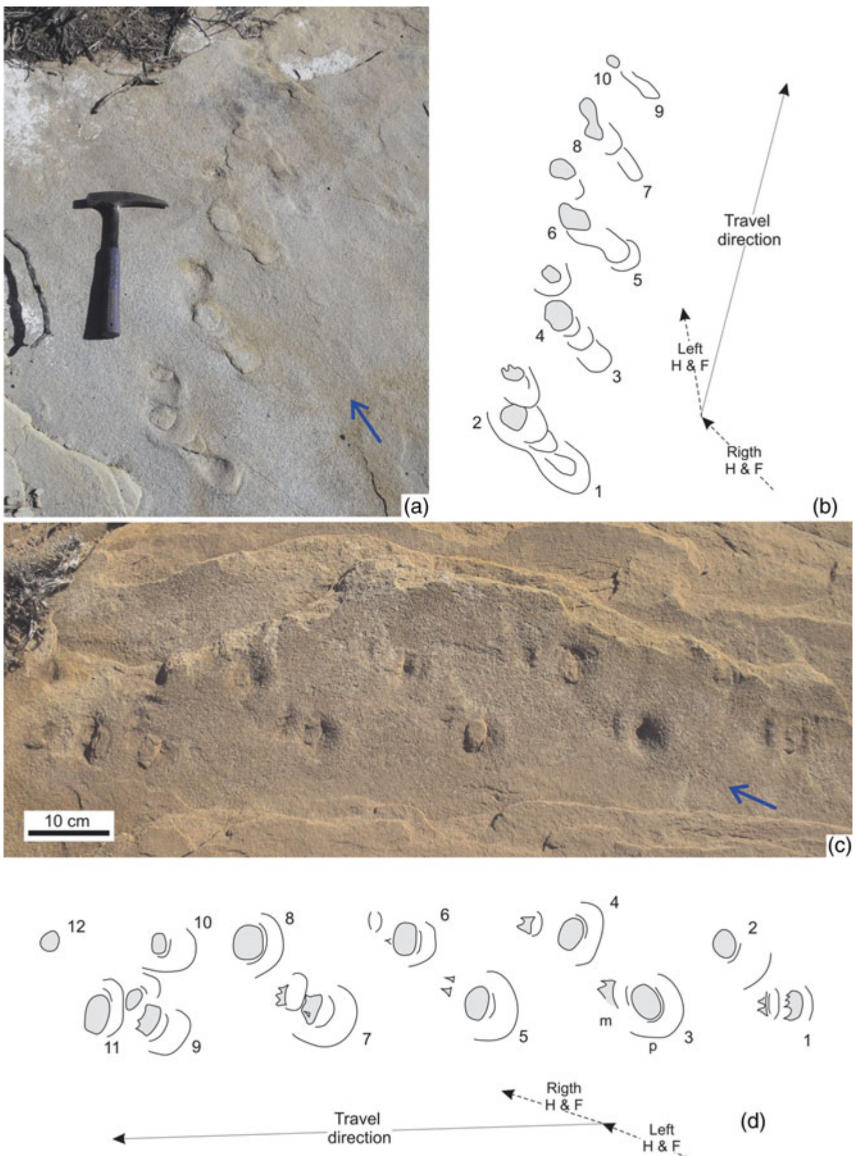

Figure 4. (Colour online) Trackways of *C. duncani*. (a) Tw2 preserved at La Julia quarry, the arrow indicates the upslope direction. (b) Diagram of Tw2 with the travel direction and feet orientation indicated. (c) Tw1 preserved at the Dr. Baulíes quarry, the arrow indicates the upslope direction. (d) Diagram of Tw1 with the travel direction and feet orientation indicated. m, *manus*; p, *pes*; H&F, hind foot and forefoot, numbers correspond to *manus–pes* set number.

Description. The trackways represent the quadrupedal progression of a plantigrade homopod animal. The *manus* prints are relatively smaller than the *pes* prints (Table 1). In the best-preserved trackway, the average length and width of the *manus* is 15.3 and 27.9 mm, respectively, while in the *pes* they are 27.3 and 38.6 mm, respectively (Figure 4). In both, *manus* and *pes*, the palm and sole pads are wider than long. The digit impressions are mostly evidenced by a maximum of usually three short parallel groves with pointed ends, which consist mostly on digit scratch marks of the three inner digits (II–IV) (Figure 4). Commonly, the imprints preserve an infill that partially obscures the footprint morphology.

In the trackways, the *manus–pes* sets show a regular pattern with the *manus* impressions located just in front of the *pes*. In both trackways, the *manus–pes* sets of one side (left side on Tw1 and right side on Tw2) are facing inwards, meanwhile the sets of the other side (right side on Tw1 and left side on Tw2) are directed slightly outwards in relation to the trackway midline (Figure 3(b),(d)).

Another common feature observed in all the imprints is the presence of rims of displaced sediment (sand crescents). In Tw1 (Dr Baulíes quarry), the rounded sand crescent is present backward and slightly outward on the left-side sets, where they are more evident than on the right side of the trackway (Figure 4(c),(d)). In contrast, in Tw2

Table 1. Track and trackway measurements of *C. duncani*.

Tw #	TL m	TL p	TW m	TW p	Pace	Stride	Pace α
Tw1-1	12	30	23	44	–	–	–
Tw 1-2	n.d.	30	n.d.	32	107	–	–
Tw 1-3	15	20	26	33	128	184	90
Tw 1-4	n.d.	30	n.d.	34	113	183	90
Tw 1-5	13	33	26	43	134	175	90
Tw 1-6	n.d.	23	n.d.	34	121	182	90
Tw 1-7	17	25	29	39	116	175	90
Tw 1-8	n.d.	30	n.d.	41	102	162	90
Tw 1-9	18	28	32	45	127	166	90
Tw 1-10	n.d.	n.d.	n.d.	36	82	99	90
Tw 1-11	17	30	31	44	83	55	45
Tw 1-12	15	21	28	38	n.d	n.d.	45
Average	15.3	27.3	27.9	38.6	111.3	153.4	81
Tw 2-1	n.d.	47	n.d.	51	–	–	–
Tw 2-2	35	51	n.d.	52	130	–	–
Tw 2-3	n.d.	62	n.d.	58	195	220	80
Tw 2-4	n.d.	64	n.d.	n.d.	125	225	80
Tw 2-5	n.d.	n.d.	n.d.	n.d.	195	225	80
Tw 2-6	n.d.	n.d.	n.d.	n.d.	130	230	80
Tw 2-7	n.d.	n.d.	n.d.	n.d.	175	n.d.	n.d.
Average	35	56.0	47	53.7	158.3	225.0	80
Total average	17.8	34.9	30.3	41.6	128.9	175.5	81

Notes: Tw, trackway; TL, track length; TW, track width; p, *pes*; m, *manus*. Measurements in mm and degrees.

(La Julia quarry) the sand crescents are well defined on both sides of the trackway. On the left-side sets, the sand-crescents are developed on the inner border of each imprint, while on the right-side sets are positioned behind the footprints (Figure 4(a),(b)).

Remarks. The taxonomic assignment of the footprints described follows McKeever and Haubold's review on the Permian Laurasian tetrapod footprints (McKeever and Haubold 1996). According to the size of the footprints and the general structure of the trackways combined with the high manoeuvrability of the trackmaker expressed, as evidence of uphill movement, they are here ally to *C. duncani*. Characteristically, the *manus–pes* sets of each side of the trackway are always separated from each other in the material from Mendoza.

Chelichnus gigas Jardine, 1850

(Figures 5 and 6)

Material. Twelve slabs (MMHNSR/PV 245, MMHNSR/PV 247, MMHNSR/PV 248, MMHNSR/PV 345, MMHNSR/PV 346, MMHNSR/PV 347, MMHNSR/PV 348, MMHNSR/PV 349, MMHNSR/PV 359, MMHNSR/PV 490, MSJ 175 and PV UNS 10501) were measured and numerous individual footprints and scarce trackways were studied and photographed in the field. The material is preserved as both concave epirelief and convex hyporelief.

Horizon and locality. The material is preserved at the top of greyish yellow, fine- to coarse-grained sandstones and recorded at both the Dr Baulies and La Julia quarries.

Description. The trackways represent the quadrupedal progression of a plantigrade homopod animal. The *manus* and *pes* imprints are nearly of the same size and equally orientated; the digit impressions are sub-parallel and anteriorly directed. The *manus* and *pes* imprints are longer than wide (Table 2). The average size of the *manus* is 91.4 mm in length and 85.4 mm in width; the average size of the *pes* is 97.7 mm in length and 91.3 mm in width. In some cases, the *manus–pes* sets are difficult to identify as all the imprints in the series are rather equally close to each other (Figures 5 and 6). Nevertheless, occasionally, the *pes* imprints slightly overlap the *manus* at its posterior margin. All trackways show that the *manus* prints are somewhat imprinted closer to the midline than the *pes*. Both *manus* and *pes* tracks have a rather transversely orientated oval palm and sole pads, separated from the digit impressions. In well-preserved imprints, the sole impression is slightly inclined to the trackway midline. The *manus* have the three inner digits (II–IV) anteriorly directed and approximately of the same size; the outer digits (I and V) are shorter and of similar size. All digit imprints are preceded by claw drag marks that are frequently preserved as long, sharply incised grooves. All of the *pes* have the digits II–V anteriorly directed and sub-equal in size, digit I is shorter and imprinted slightly

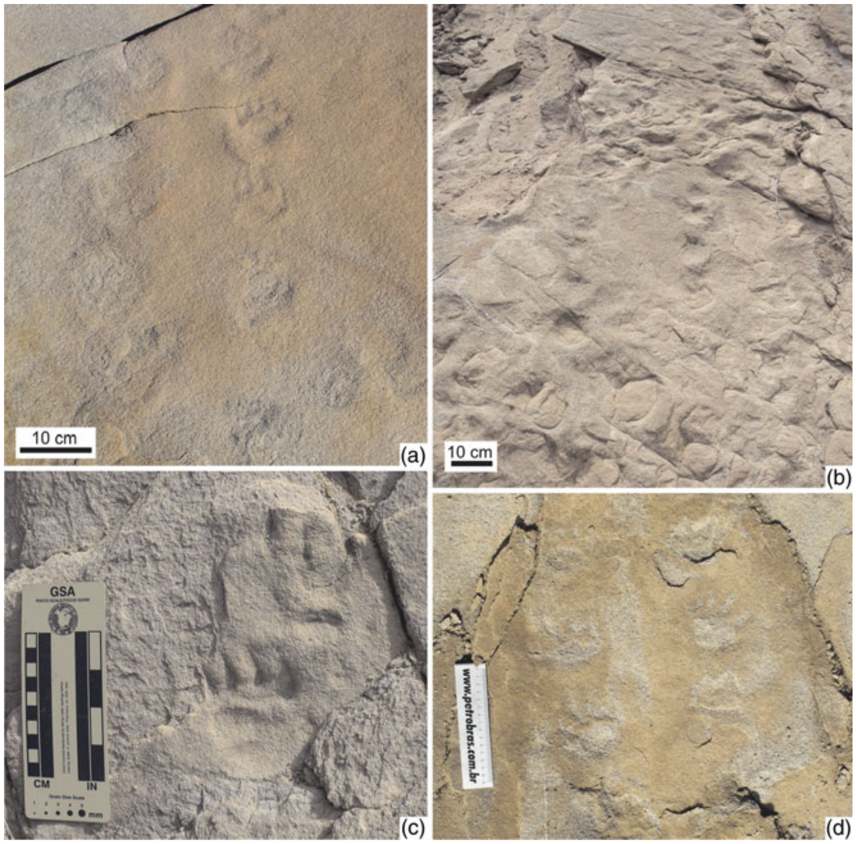

Figure 5. (Colour online) Tracks and trackways of *C. gigas* preserved in the field. (a) Trackway preserved at La Julia quarry. (b-d) Trackways preserved at Dr. Baulíes quarry.

behind digit II; all digits show deep claw drag marks, similar to those of the *manus* prints.

The trackway pattern indicates a regular progression of the trackmaker with short steps (average pace 225.4 mm and average stride 245.8 mm) moving with a sprawling gait. The *manus* and *pes* imprints are rather separated from the midline of the trackway (pace angulation average 66°) and, the internal trackway width is at least as wide as the *pes* imprints (Figure 5(a)–(c)). In none of the observed specimens is evidence of tail and/or belly drag marks, although most tracks are deeply impressed in the sediment.

Remarks. According to the size and general structure of the tracks and trackways, the described material is assigned to *C. gigas* (*sensu* McKeever and Haubold 1996). In the material from Mendoza, the size of the *manus* is equal to the *pes*, thus differing from the diagnosis of *Chelichnus* ichgen. where it was stated that the *manus* impressions are usually slightly smaller in size and, apparently, more digitigrade than the *pes* impressions (McKeever and Haubold 1996, p. 1012).

Part of the *C. gigas* specimens (Figure 6(c)) was originally considered the type of *Paredichnus rodreguenzi* (Aramayo and Farinati 1983) that was later synonymised with *Chelichnus*, as was most of the collected material from San Rafael, by Melchor (2001).

Pear-like footprints

(Figure 7)

Material. Only one trackway measured and photographed in the field (Table 3). It includes eight *manus–pes* sets and the material is preserved as a concave epirelief.

Horizon and locality. The trackway is preserved at the La Julia quarry, at the top of greyish yellow, fine- to coarse-grained sandstones.

Description. The trackway consists of a series of *manus–pes* sets of a plantigrade quadruped animal with heteropody. The *manus* are smaller than the *pes*, with the average size of the *manus* is 62.9 mm in length and 67 mm in width; the average size of the *pes* is 84.4 mm in length and 64.6 mm in width (Figure 7). In each set, the *pes* is imprinted in front of the *manus*. All *manus* are preserved as a single rounded impression where the digits are not discernible from the palm. The *pes* imprints are more triangular with the posterior margin elongated, which probably relates to the presence of a ‘heel’ impression. Individual digit impressions are not visible, although in some prints the anterior border is indented showing three lobules that might correspond to the three inner digits. These digital impressions indicate that the *pedes* were directed forward (Figure 7).

Figure 6. (Colour online) Tracks and trackways of specimens of *C. gigas* housed on museum collections. (a) MMHNSR/PV 348; (b) MMHNSR/PV 490; (c) MSJ 175, courtesy of S. Aramayo; (d) MMHNSR/PV 347.

Table 2. Track and trackway measurements of *C. gigas*.

	TL		TW				
Tw #	m	p	m	p	Pace	Stride	Pace α
MMHNSR/PV 348-1	86	77	88	93	–	–	–
MMHNSR/PV 348-2	81	94	78	93	170	–	–
MMHNSR/PV 348-3	n.d.	84	n.d.	90	210	240	74
MMHNSR/PV 346-1	81	n.d.	72	n.d.	–	–	–
MMHNSR/PV 346-2	89	76	94	93	n.d.	–	–
MMHNSR/PV 346-3	n.d.	94	n.d.	104	n.d.	225	60
MMHNSR/PV 490-1	n.d.	n.d.	95	n.d.	–	–	–
MMHNSR/PV 490-2	87	107	103	91	n.d.	–	–
MMHNSR/PV 490-3	n.d.	95	n.d.	92	n.d.	250	n.d.
MMHNSR/PV 349-1	97	n.d	80	n.d.	–	–	–
MMHNSR/PV 349-2	n.d.	n.d.	n.d.	n.d.	n.d.	–	–
MMHNSR/PV 349-3	106	120	95	80	n.d.	250	n.d.
Field specimen-1	99	108	80	78	–	–	–
Field specimen-2	89	111	80	93	271	–	–
Field specimen-3	99	97	84	90	244	276	66
Field specimen-4	n.d.	109	n.d.	99	232	234	57
Average	91.4	97.7	86.3	91.3	225.4	245.8	64.3

Notes: Tw, trackway; TL, track length; TW, track width; p, *pes*; m, *manus*. Measurements in mm and degrees.

Figure 7. (Colour online) (a) Trackway of Pear-like footprints at La Julia quarry. (b) Diagram of Pear-like footprints, arrow indicates travel direction. m, *manus*; p, *pes*, numbers correspond to *manus*–*pes* set number.

The trackway pattern shows that the animal was moving with relatively short steps and *manus* and *pes* imprints were separated from the midline of the trackway (average pace angulation 68°), suggesting an animal with a sprawling gait (Table 3). On the left side of the trackway, the *manus* are directed inwards in relation to the *pes* prints. Conversely, on the right side, the *manus* are facing outwards in relation to the *pes* direction. Moreover, the pace length change alternatively in between short and long paces (average short pace length = 181.5 mm; average long pace length = 218 mm) (Figure 7(b)). This pattern is more evident on the second half of the trackway where the animal seems to be turning to the left. This change in progression seems to be affected by the position of the pectoral girdle that was apparently not aligned with the pelvic one, therefore the *manus* imprints appears to be displaced to the opposite side of the turn direction. Sand crescents are preserved around the posterior margin of each print.

Remarks. These footprints are characterised by the presence of a 'heel' impression and the regular location of the *pes* in front of the *manus*, both uncommon characters among other Early Permian taxa. In *Baropezia* Gilmore, the 'heel' is more laterally impressed just behind digits I–II. Another difference is that in *Baropezia*, the *manus* impression is in front of the *pes* in each set. The footprints assigned to *Dimetropus* Romer and Price (1940) are also relatively large but with a remarkable elongated heel impression, not comparable with the material described herein.

Table 3. Track and trackway measurements of Pear-like footprints.

	TL		TW				
Tw #	m	p	m	p	Pace	Stride	Pace α
Tw1-1	59	93	70	68	–	–	–
Tw1-2	57	84	85	71	198	–	–
Tw1-3	62	87	66	64	214	248	65
Tw1-4	51	80	73	52	185	269	75
Tw1-5	79	79	63	65	221	250	70
Tw1-6	61	80	55	71	175	256	75
Tw1-7	71	88	57	61	219	233	60
Tw1-8	n.d.	n.d.	n.d.	n.d.	168	220	65
Average	62.9	84.4	67.0	64.6	197.1	246.0	68.3

Notes: Tw, trackway; TL, track length; TW, track width; p, *pes*; m, *manus*. Measurements in mm and degrees.

Table 4. Body proportion and locomotion ratios measured on trackways.

	C. duncani Tw1	*C. duncani* Tw2	*C. gigas*	Pear-like footprints
PL/SL	0.18	0.25	0.38	0.34
PW/ITW	1	–	0.75	0.98

Note: PW/ITW, *pes*-width/inner trackway-width ratio; PL/SL, *pes*-length/stride-length ratio.

Discussion

Body proportions and locomotion styles of the trackmakers

All the San Rafael trackways indicate the presence of quadrupedal pentadactyl animals progressing with a wide-gauged stance, evidenced by the PW/ITW. The calculated ratio is 1 in *C. duncani*, representing the smaller limb span, while *C. gigas* occasionally located the limbs reaching wider positions (Table 4). In addition, all *manus* and *pes* prints are anteriorly directed and in most cases the claw trailing marks are straight, thus suggesting that at the beginning of the 'swing phase' of the stride, the limbs moved forward without marked outward excursions, as seen in other sprawling tetrapods, such as salamanders and lizards (Figure 8) (e.g. Peabody 1959; Farlow and Pianka 2000; Ashley-Ross and Bechtel 2004).

Figure 8. Reconstruction of a trackway surface showing the putative therapsid producer of *C. gigas* during progression.

The main differences among the ichnotaxa described herein consist of the relationship between the length of the stride relatively to the *pes* length, evidenced by variations in the distance between *manus*–*pes* sets of the same side in the trackways (Table 4). In *C. duncani*, the *manus*–*pes* sets are well separated from each other and have an alternate position in relation to the midline. The forefeet in each set are slightly smaller than the hind feet. The PL/SL is 0.18 and the pace angulation is ca. 90°. This ichnotaxon represents the smallest trackmaker with an approximate gleno-acetabular length of 140 mm (Figure 9). In contrast, *C. gigas* and the Pear-like footprints have a similar PL/SL ratio, 0.38 and 0.34, respectively, and average pace angulation, 64° and 68°, respectively. Nevertheless, the trackmakers were of different size. The calculated gleno-acetabular distance for the *C. gigas* trackmaker is approximately 450 mm and for the Pear-like footprints approximately 300 mm. In both ichnotaxa, the succession of prints in the trackways is regular and almost continuous. This makes it very difficult to identify *manus*–*pes* sets, particularly in *C. gigas*. In the case of Pear-like footprints, this is facilitated by the heteropody expressed by the presence/absence of heel impression in the prints. The mentioned trackway structure suggests that the track-makers of *C. gigas* and the Pear-like footprints possessed relatively shorter limbs in relation to the trunk length than the *C. duncani* trackmaker (Figures 8 and 9).

A common feature observed in most of the study specimens from San Rafael is the presence of rims of displaced sand around the prints. These rims correspond to gravitational or downslope avalanche structures produced when the animal cross the foreset of the sand dune. Accordingly, the dip of the foreset at the moment of imprinting can be inferred by observation of the position of the sand crescents preserved around the imprints. This type of preservation and the oblique up-dune progression has been well documented in many examples of footprints emplaced in aeolian facies (e.g. Leonardi 1987; Fornós et al. 2002; Hunt and Lucas 2005; Loope 2006).

When the two trackways of *C. duncani* (see description of trackways and Figure 3(b),(d)) are compared with respect to the position of the rims, they are different. The rims are located in the Dr Baulies material nearly behind each print in contrast to the La Julia material, where they are laterally located. It is most likely that this is the result of an increase in the slope angle between the two surfaces. The major slope angle corresponds to the La Julia tracking

Figure 9. Reconstruction of a trackway surface showing the putative therapsid producer of *C. duncani* during progression.

surface (Tw2) while the Dr Baulíes tracking surface (Tw1) had a lower slope angle. Consequently, the trackways of these animals indicate that when they were moving across the incline surface, the forefoot and the hindfoot of the downslope side of the body were aligned with the dip of the foreset; conversely, the upslope sets were almost parallel to the direction of movement (Figure 3(b),(d)).

In the case of the Pear-like footprints, sand crescents are preserved around the posterior margin of each print indicating that the animal was moving uphill across the foreset of the dune.

Identification of the trackmakers

Original speculations about *Chelichnus* trackmaker affinities regarded it as a chelonian (see Jardine 1850; McKeever 1994). Subsequent discussions (Lull 1918; Gilmore 1928) including new material from North America considered the putative trackmakers difficult to determine, so that both reptilian and/or amphibian origin were alternatively suggested. In subsequent years, several revisions including both the European and North American specimens explored the possible affinities of the *Chelichnus* (= *Laoporus*) trackmaker and thus several different groups of tetrapods were proposed. In his extensive revisions on tetrapod ichnology, Haubold (1971, 1984) recognised caseid synapsids ('pelycosaurs') as the possible trackmakers of *Chelichnus*, although more recently he considered them more conservatively just as synapsids (Haubold 2000). McKeever (1994) proposed three different groups of tetrapods as responsible for the Scottish *Chelichnus* footprints, mainly based on comparisons with the known Late Permian skeletal record of southern Africa and Europe. Thus, this author related the trackmakers to pareiasaurs, non-therapsid synapsids ('pelycosaurs') and anomodont therapsids (McKeever 1994, p. 485).

It is important to remark that in the Northern Hemisphere, the *Chelichnus* track-bearing levels span most of the Permian (Lucas and Hunt 2006), thus probably making trackmaker interpretations so vague.

In the context of the present study, all *Chelichnus* trackways denote the presence of quadruped animals moving with a sprawling gait. There is no evidence of body/tail dragging thus indicating their relatively more upright posture during progression when compared with other sprawling animals, such as salamanders and lizards (e.g. Peabody 1959; Farlow and Pianka 2000). In general, the *manus* and *pes* impressions in the trackways do not present a markedly heteropody, apart for the 'heel' impression in the Pear-like *pes* prints. Therefore, *manus* and *pes* were quite similar, symmetrical and anteriorly directed. The digits were relatively short and sub-equal in size that bored sharp narrow claws.

Recent phylogenetic analysis of the Synapsida (Hopson 1991; Sidor and Hopson 1998; Rubidge and Sidor 2001; Amson and Laurin 2011) and discussions related to limb posture and *manus*/*pes* evolution in non-mammalian therapsids (Hopson 1995; Blob 2001) provides a framework for interpreting the possible trackmakers of these footprints. The similar anteriorly directed autopodia, combined with the sub-equal clawed digits, relate the trackmaker to Therapsida. Moreover, in the evolution of therapsids, the increasing symmetry in the autopodia, associated with a more forward position of the *manus* and *pes*, characterised the increasingly less-sprawling posture in the group (Hopson 1995; Rubidge and Sidor 2001). These improved locomotor abilities in therapsids, correlated with several synapomophies in the postcranial skeleton of the group, differentiate them from the most basal synapsids, the 'pelycosaurs' (see Rubidge and Sidor 2001). A recent phylogeny on basal therapsids suggest the origin of the group as early as the beginning of the Permian (Amson and Laurin 2011) thus in accordance with the Early Permian age of the Yacimiento Los Reyunos footprints described herein.

Comparison with other Early Permian tetrapod footprints from South America and the Northern Hemisphere

Early Permian tetrapod footprints in South America are known from three different late Paleozoic basins of Argentina. Apart from the material described herein, levels of the Patquía Formation in the Paganzo Basin (La Rioja Province) record tetrapod trace fossils preserved in aeolian sand-sheet facies (Krapovickas et al. 2010). The aeolian facies host a low-diversity and low-abundance association composed of *C. duncani* Jardine, 1850, undistinguishable oval digit imprints, short parallel grooves and sinusoidal grooves. The footprints are preserved in a trampling surface that record scarce autopodium impressions and is mostly composed of digital and tail impressions and scratch marks. The material was tentatively assigned to the ichnogenus *Chelichnus* but it differs from the one described herein by its relatively longer digits (Krapovickas et al. 2010).

The third record corresponds to the Carapacha Basin of central Argentina (Melchor and Sarjeant 2004). The footprints are recorded in levels of the Carapacha Formation, considered to span from the upper Early Permian to the lower Late Permian, based on its paleofloristic content (*Glossopteris* flora, Melchor and Césari 1991). The tetrapod ichnotaxa recognised are *Batrachichnus salamandroides* (Geinitz, 1861), *Hyloidichnus bifurcates* Gilmore, 1927, cf. *Amphisauropus* isp., cf. *Varanopus* isp., two forms of vertebrate swimming traces and a putative fish trail (Melchor and Sarjeant 2004). This association greatly differs from the tetrapod association presented herein. On the first place, the Carapacha tracks were interpreted to represent the activity of a more diverse community of small tetrapods that imprinted in substrates subject to frequent water-table changes in ephemeral shallow-lake and playa-lake mudflats settings. This ichnoassociation would correspond to the *Batrachichnus* ichnofacies *sensu* Hunt and Lucas (2007).

Finally, there is a single slab housed in the collection of the Museo de Historia Natural de San Rafael (Mendoza Province, Argentina) labelled as collected from Permian rocks of the Sauce Grande Basin (south of the Buenos Aires province) in eastern Argentina. Melchor (1997) tentatively assigned these footprints to the ichnogenus *Batrachichnus*, although later he considered that the lithology do not correspond to that of the referred locality and, on the other hand, the lithology and track morphology are similar to the slabs that bears the well-known ichnogenus *Ameghinichnus* Casamiquela, 1964 from the Middle Jurassic of Patagonia (Melchor and Sarjeant 2004). There are no other Early Permian records of tetrapod tracks and trackways known in Gondwana.

Permian footprints assigned to *Chelichnus* have been recognised principally from North America and Europe. Classical ichnoassemblages are that of the Coconino Sandstone of Arizona (Gilmore 1926, 1927, 1928) and from the Corncockle, Lochabriggs and Hopeman Sandstone of Scotland (Duncan 1831; McKeever 1991; McKeever and Haubold 1996). *Chelichnus* footprints are also recorded in the Permian DeChelly Sandstone of Arizona, the Lyons Sandstone of Colorado, the Cedar Mesa Sandtone of Utah and the Cornberg Sandstein of Germany (Loope 1984; Lockley and Madsen 1993; Lockley and Hunt 1995; McKeever and Haubold 1996; Lockley et al. 1998). The American and European footprints are highly comparable with those of Yacimiento los Reyunos in both autopodia morphology and locomotion patterns expressed on trackways. Furthermore, *Chelichnus* footprints are mostly, if not exclusively, preserved in aeolian facies and all shows recurrent behaviours of their trackmakers as, for example, the record of oblique up-dune progressions with downslope sand crescents.

Ichnofacies

Overbank deposits of Yacimiento los Reyunos consist of locally intensely bioturbated (BI 3) massive red sandstones. These deposits are characterised by an infaunal invertebrate assemblage of low diversity, composed exclusively by domichnion structures, most likely produced by insects and/or oligochaete worms. The assemblage is composed of horizontal to inclined simple trace fossils (*P. tubularis*) and constitutes an impoverish example of the *Scoyenia* ichnofacies. The assemblage corresponds to a soft ground suite of the *Scoyenia* ichnofacies with traces showing no ornamentation. This ichnofacies characterises low energy deposits periodically exposed to air or periodically inundated, situating it as intermediate between aquatic and non-aquatic environments (Frey et al. 1984). The Yacimiento los Reyunos ichnoassemblage represents an example of the *Scoyenia* ichnofacies in overbank deposits of a fluvio–aeolian succession.

Aeolian dune strata of the Yacimiento los Reyunos consist of cross-bedded sandstones with mostly low, but occasionally medium, (BI 1–3) bioturbation intensity. The ichnocoenosis is mainly composed of superficial imprints (*C. duncani*, *C. gigas* and Pear-like footprints), produced by tetrapods (therapsid synapsids), and very few domichnion structures (*P. tubularis* and *Skolithos* isp.) most likely produced by arthropods. The correspondence between *Chelichnus* footprints and aeolian environments is such that Lockley et al. (1994) and McKeever and Haubold (1996) proposed a widespread Early Permian aeolian ichnoassemblage, named originally the *Laoporus* ichnofacies. Later, the ichnoassemblage was renamed as the *Chelichnus* ichnofacies because of the synonymy of the two ichnogenera (*Chelichnus* = *Laoporus*) (Lockley et al. 1995; Morales and Haubold 1995; McKeever and Haubold 1996; Hunt and Lucas 2005, 2006). Recently, Hunt and Lucas (2007) proposed the *Chelichnus* ichnofacies for tetrapod associations recurrent in dune facies of aeolian environments from the Permian to the Jurassic, including *Brasilichnus*, an ichnogenus originally described from the Cretaceous of Brazil (Leonardi 1981; Fernandes and Carvalho 2008), which resemble *Chelichnus* and also *Ameghinichnus*. In the same contribution, Hunt and Lucas (2007) erected the *Octopodichnus* ichnofacies for aeolian invertebrate trace–fossil associations dominated by arthropod locomotion traces, mainly spiders and scorpions (e.g. *Octopodichnus* and *Paleohelcura*); they also emphasised the close correspondence between their aeolian ichnofacies *Chelichnus* and *Octopodichnus* (Hunt and Lucas 2007, p. 67). Coincidently, Ekdale et al. (2007) defined the *Entradichnus* ichnofacies also for aeolian invertebrate trace–fossil associations but represented by simple shallow burrows of vertical (e.g. *Skolithos* and *Arenicolites*) and horizontal (e.g. *Palaeophycus*) disposition, in addition to meniscated traces (e.g. *Entradichnus*) produced by arthropod inhabitants of deserts.

Buatois and Mángano (2011) attempted to integrate the available aeolian ichnofacies models, and combined other two invertebrate ichnofacies in the *Octopodichnus*–*Entradichnus* ichnofacies. Accordingly, Krapovickas et al. (2010) expressed that the trace–fossil association preserved in the Patquia Formation from the Lower Permian of Argentina shows elements of the three presently proposed aeolian ichnofacies (*Chelichnus*, *Octopodichnus* and *Entradichnus* ichnofacies) and suggested the possible integration of these separate ichnofacies into a single model. Finally, Ekdale and Bromley (2012) in a recent review on aeolian ichnology also discussed the validity of the three mentioned ichnofacies. The Yacimiento los Reyunos trace–fossil assemblage described herein constitutes an example of aeolian ichnofacies, with components of the *Chelichnus* and *Entradichnus* ichnofacies, although there is no evidence of surficial arthropod locomotion traces (*Octopodichnus* ichnofacies) until now. This absence can be the result of a taphonomical bias due to the predominance of medium- to coarse-grained sandstone in the studied succession that could have precluded the preservation of delicate arthropod tracks.

Acknowledgements

We are indebt with Serguio Dieguez (Assistant Manager) of the Complejo Minero Fabril de Sierra Pintada CNEA (Comisión Nacional de Energía Atómica) for his support during this project. We are also profoundly grateful to Sr. Santiago Ferron, the owner of the La Julia quarry field, who generously opened the doors of his house and lands, and to L. Darío Benedito and Cecilia Benavente for their assistance during field work. V.K. and C.A. M. thank Matthew Carrano, Charyl Ito and Amanda Millhouse (Smithsonian Institution Natural History Museum), and Mark Goodwin and Patricia Holroyd (University of California Museum of Paleontology), for allowing them to study the Coconino Sandstone footprint collections under their care. This is the contribution R-99 of the Instituto de Estudios Andinos Don Pablo Groeber.

Funding

Funding for this research was provided by projects UBACyT 20020100100728 (C.A.M.), PICT 07-373 (M.S.D.L.), PICT-2011-2334 (V.K.), PIP CONICET 0709 (E.G.O.) and PIP CONICET 11420090100209 (A.C.M.).

References

Amson E, Laurin M. 2011. On the affinities of *Tetraceratops insignis*, an Early Permian synapsid. Acta Palaeontol Pol. 56(2):301–312.

Aramayo S, Farinati E. 1983. “Paredichnus rodriguezi” n. sp. Nuevas icnitas de tetrápodos de la Formación Los Reyunos (Grupo Cochicó), Pérmico inferior, Mendoza. Mundo Ameghiniana. 4:47–58.

Ashley-Ross M, Bechtel BF. 2004. Kinematics of the transition between aquatic and terrestrial locomotion in the newt *Tarichatorosa*. J Exp Biol. 207:461–474.

Azcuy CL, Carrizo HA, Caminos R. 1999. Carbonífero y Pérmico de las Sierras Pampeanas, Famatina, Precodillera, Cordilera Frontal, Bloque de San Rafael. Geol Arg An Inst Geol Rec Min. 29:26–318.

Blob RW. 2001. Evolution of hindlimb posture in nonmammalian therapsids: biomechanical tests of paleontological hypotheses. Paleobiology. 27(1):14–38.

Buatois LA, Mángano MG. 2011. Ichnology: the role of organism–substrate interactions in space and time. New York: Cambridge University Press.

Buckland W. 1828. Note sur les Traces de Tortues observeés dans les grés rouge. Ann Sci Nat. 13:85–86.

Casamiquela RM. 1964. Estudios icnológicos. Problemas y métodos de la icnología con aplicación al estudio de pisadas mesozoicas (Reptilia,

Mammalia) de la Patagonia. Buenos Aires: Colegio Industrial Pío IX.
Cei R, Gargiulo J. 1977. Icnitas de tetrápodos Pérmicos del sur de Mendoza. Ameghiniana. 14:127–132.
Costa da Silva R, Sidor FA, Sequeira Fernandes C. 2012. Fossil footprints from the Late Permian of Brazil: an example of hidden biodiversity. J South Amer Earth Sci. 38:31–43.
Duncan H. 1831. An account of the tracks and footmarks of animals found impressed on sandstone in the quarry of Corncockle Muir, in Dumfriesshire. Trans Roy Soc Edin. 11:194–209.
Ekdale AA, Bromley RG. 2012. Eolian environments. In: Knaust D, Bromley RG, editors. Trace fossils as indicators of sedimentary environments: developments in sedimentology. Vol. 64. Amsterdam: Elsevier; p. 419–437.
Ekdale AA, Bromley RG, Loope DB. 2007. Ichnofacies of an ancient erg: a climatically influenced trace fossil association in the Jurassic Navajo Sandstone, southern Utah, USA. In: Miller W, editor. Trace fossils: concepts, problems, prospects. Amsterdam: Elsevier; p. 562–574.
Farlow JO, Pianka ER. 2000. Body form and trackway pattern in Australian desert monitors (Squamata: Varanidae): comparing zoological and ichnological diversity. Palaios. 15:235–247.
Fernandes MA, Souza Carvalho I. 2008. Revisão diagnostica para a icnoespécie de tetrápode Mesozóico *Brasilichnium elusivum* (Leonardi, 1981) (Mammalia) de Formação Botucato, Bacia do Paraná, Brasil. Ameghiniana. 45(1):167–173.
Fornós JJ, Bromley RG, Clemmensen LB, Rodriguez-Perea A. 2002. Tracks and trackways of Myotragusbalearicus Bate (Artiodactyla, Caprinae) in Pleistocene aeolianites from Mallorca (Balearic Islands, Western Mediterranean). Palaeogeogr Palaeoclim Palaeoec. 180:277–313.
Frey RW, Pemberton SG, Fagerstrom JA. 1984. Morphological, ethological and environmental significance of the ichnogenera *Scoyenia* and *Ancorichnus*. J. Paleontol. 58:511–528.
Freytet P, Plaziat JC. 1982. Continental carbonate sedimentation and pedogenesis. Late Cretaceous and Early Tertiary of Southern France. In: Purser BH, editor. Contributions to sedimentology. Vol. 12. Stuttgart: Schweizerbart'sche Verl.; p. 1–213.
Geinitz HB. 1861. Dyas oder die Zechsteinformation und das Rhotliegende, Heft I. Leipzig: Wilhelm Engelmann.
Gilmore CH. 1926. Fossil footprints from the Grand Canyon. Smith Misc Coll. 77:1–41.
Gilmore CH. 1928. Fossil footprints from the Grand Canyon: third contribution. Smith Misc Coll. 80:1–16.
Gilmore CW. 1927. Fossil footprints from the Grand Canyon: second contribution. Smith Misc Coll. 80(3):1–78.
Haldeman SS. 1840. Supplement to number one of "A monograph of the Limniades, or fresh-water univalve shell of North America", containing descriptions of apparently new animals in different classes, and the name and characters of the subgenera in Paludina and Anculosa. Philadelphia (PA): J. Dobson.
Hall J. 1847. Palaeontology of New York. Vol. I: Containing descriptions of the organic remains of the Lower Division of the New York System (equivalent to the Lower Silurian rocks of Europe). Albany (NY): C. van Benthuysen.
Haubold H. 1971. Ichnia amphibiorum et Reptiliorum fossilium. In: Kuhn O, editor. Handbuch der Paliioherpetologie No. 18. Stuttgart: Fisher-Verlag; p. 1–122.
Haubold H. 1984. Saurierfiihrten. Wittenberg Lutherstadt: A. Ziemsen Verlag.
Haubold H. 2000. Tetrapodenfährten aus dem Perm-Kenntnisstand und Progress 2000. Hallesches Jahrb Geowiss B. 22:1–16.
Holmberg E. 1948. Geología del Cerro Bola. Contribución al conocimiento de la tectónica de la Sierra Pintada. Bol Dir Nac Geol Min. 68:313–361.
Hopson JA. 1991. Systematics of the non-mammalian Synapsida and implications of evolution in synapsids. In: Schltze HP, Trueb L, editors. The origin of higher groups of tetrapods: controversy and consensus. Ithaca (NY): Cornell University Press; p. 635–693.
Hopson JA. 1995. Patterns of evolution in the *Manus* and *Pes* of non-mammalian therapsids. J Vertebr Paleontol. 15(3):615–639.
Hunt AP, Lucas SG. 2005. Tetrapod Ichnofacies and their utility in the Paleozoic. In: Buta RJ, Rindsberg AK, Kopaska-Merkel D, editors. Pennsylvanian footprints in the black warrior basin of Alabama. Alabama: Alabama Paleontological Society; Monograph 1. p. 113–119.
Hunt AP, Lucas SG. 2006. Permian tetrapod ichnofacies. In: Lucas SG, Cassinis, Schneider JW, editors. Non-marine permian biostratigraphy and biochronology. Vol. 265. London: Geol Soc Spec Publ; p. 137–156.
Hunt AP, Lucas SG. 2007. Tetrapod ichnofacies: a new paradigm. Ichnos. 14:59–68.
Jardine W. 1850. Note to Mr. Harness's paper "On the position of the impressions of footsteps in the Bunter sandstones of Dumfriesshire". Ann Mag Nat Hist. 6:208–209.
Kleiman LE, Japas MS. 2009. The Choiyoi volcanic province at 34°–36°S (San Rafael, Mendoza, Argentina): implications for the late Paleozoic evolution of the southwestern margin of Gondwana. Tectonophysics. 473:283–299.
Krapovickas V, Mancuso AC, Arcucci A, Caselli A. 2010. Fluvial and eolian ichnofaunas from the Lower Permian of South America. Geol Acta. 8:449–462.
Lardone L, Meza JC, Salaverri JA. 1993. Yacimiento Uraníferos. In: Ramos V, editor. Relatorio. Vol. 4(5). Mendoza: Geología y Recursos Naturales de Mendoza; p. 537–542.
Leonardi G. 1981. Novo icnogênero de tetrápode Mesózoico da Formação Botucatu, Araraquara, SP. An Acad Bras Cienc. 53:793–805.
Leonardi G. 1987. Glossary and manual of tetrapod footprint palaeoichnology. Brasília: República Federativa do Brasil, Ministério das Minas e nergia, Departamento Nacional da Producão Mineral.
Llambías EJ, Kleiman LE, Salvarredi JA. 1993. El Magmatismo Gondwánico. In: Ramos V, editor. Relatorio. Vol. 1(6). Mendoza: Geología y Recursos Naturales de Mendoza; p. 53–64.
Lockley MG, Hunt AP. 1995. Dinosaur tracks and other fossil footprints of the Western United States. New York: Columbia University Press.
Lockley MG, Hunt AP, Haubold H, Lucas SG. 1995. Fossil footprints in the DeChelly Sandstone of Arizona: with paleoecological observations on the ichnology of dune facies. Bull New Mexico Mus Nat Hist Sci. 6:225–233.
Lockley MG, Hunt AP, Meyer C. 1994. Vertebrate tracks and the ichnofacies concept: implications for paleoecology and palichnostratigraphy. In: Donovan S, editor. The palaeobiology of trace fossils. London: John Wiley; p. 241–268.
Lockley MG, Hunt AP, Meyer CA, Rainforthd EC, Schultz RJ. 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. 5:177–211.
Lockley MG, Madsen JH, Jr. 1993. Early Permian vertebrate trackways from the Cedar Mesa Sandstone of eastern Utah. Ichnos. 2:147–153.
Loope DB. 1984. Eolian origin of upper Paleozoic sandstones, southeastern Utah. J Sed Petrol. 54:563–580.
Loope DB. 2006. Dry-season tracks in dinosaur-triggered grainflows. Palaios. 21:132–142.
López-Gamundi OR. 2006. Permian plate margin volcanism and tuffs in adjacent basins of west Gondwana: age constrains and common characteristics. J South Amer Earth Sci. 22:227–238.
Lucas SG, Hunt AP. 2006. Permian tetrapod footprints: biostratigraphy and biochronology. In: Lucas SG, Cassinis G, Schneider JW, editors. Non-marine permian biostratigraphy and biochronology. Vol. 265. London: Geol Soc Spec Publ; p. 179–200.
Lull RS. 1918. Fossil footprints from the Grand Canyon of the Colorado. Am J Sci. 45:337–346.
McKeever PJ. 1991. Trackway preservation in eolian sandstones from the Permian of Scotland. Geology. 19:726–729.
McKeever PJ. 1994. A new vertebrate trackway from the Permian of Dumfries and Galloway. Scot J Geol. 30:11–14.
McKeever PJ, Haubold H. 1996. Reclassification of vertebrate trackways from the Permian of Scotland and related forms from Arizona and Germany. J Paleontol. 70:1011–1022.
Melchor RN. 1997. Permian tetrapod ichnofaunas from Argentina: further evidence for redbed shallow lacustrine and aeolian vertebrate ichnofacies. In: Workshop ichnofacies and ichnotaxonomy of the terrestrial Permian, Abstracts and Papers, Halle: Martin Luther

University, Halle-Wittenberg Institute of Geoscience and Geiselthal-museum; p. 59–60.

Melchor RN. 2001. Permian tetrapod footprints from Argentina. Hallesches Jahrb Geowiss. 23(B):35–43.

Melchor RN, Césari S. 1991. Algunos elementos paleoflorísticos de la Formación Carapacha (Pérmico Inferior), Prov. de La Pampa, Rep. Argentina. Ameghiniana. 28(3–4):347–352.

Melchor RN, Sarjeant WAS. 2004. Small amphibian and reptile footprints from the Permian Carapacha Basin, Argentina. Ichnos. 11:57–78.

Morales M, Haubold H. 1995. Tetrapod tracks from the Lower Permian DeChelly sandstone of Arizona: systematic description. Bull New Mexico Mus Nat Hist Sci. 6:251–261.

Mountney NP. 2006. Eolian facies models. In: Posamentier HW, Walker RG, editors. Facies models revisited. Vol. 84. Tulsa: SEPM Special Publication; p. 19–83.

Ortega Furlotti A, Rodriguez Pujada EJ, Prieto AG, Prieto A. 1974. El nuevo Distrito Uranifero de Sierra Pintada, provincia de Mendoza (República Argentina). Actas Quinto Congr Geol Arg Buenos Aires. 2:267–284.

Owen R. 1842. Report on British fossil reptiles: part 2. Report of the British Association for the Advancement of Science (for 1841). Plymouth: British Association for the Advancement of Science; p. 60–204.

Peabody FE. 1959. Trackways of living and fossil salamanders. Univ California Publ Zool. 63:1–72.

Pemberton SG, Gingras M. 2003. The Reverend Henry Duncan (1774–1846) and the discovery of the first fossil footprints. Ichnos. 10:69–75.

Pemberton SG, Frey RW. 1982. Trace fossil nomenclature and the *Planolites Palaeophycus* dilemma. J Paleontol. 56:843–881.

Polanski J. 1964. Descripción geológica de la hoja 26c La Tosca, provincia de Mendoza. Bol Dir Nac Geol Min. 98:1–94.

Rey FM. 2011. Variaciones paleoclimáticas y Paleoambientales en la Formación Yacimiento Los Reyunos (Cisuraliano), Cuenca de San Rafael, Mendoza Argentina [master's thesis]. Buenos Aires: Universidad de Buenos Aires.

Rocha-Campos AC, Basei MA, Nutman AP, Kleiman LE, Varela R, Llambías E, Canile FM, da Rosa OR. 2011. 30 million years of Permian volcanism recorded in the Choiyoi igneous province (W Argentina) and their source for younger ash falldeposits in the Paraná Basin: SHRIMP U-Pb zircon geochronology evidence. Gondwana Res. 19:509–523.

Rodriguez EJ, Valdivieso A. 1970. Informe sobre resultados de la investigación geológica semiregional (perfiles y planos geológicos) en el área de las manifestaciones nucleares de Sierra Pintada, Mendoza. Comisión Nacional de Energía Atómica, Informe interno, RM-O-M-135.

Romer AS, Price LI. 1940. Review of the Pelycosauria. Geol Soc Am Spec. 28:1–538.

Rubidge BS, Sidor CA. 2001. Evolutionary Patterns among Permo-Triassic Therapsids. Annu Rev Ecol Syst. 32:449–480.

Seilacher A. 1964. Biogenic sedimentary structures. In: Imbrie J, Newell N, editors. Approaches to paleoecology. New York: John Wiley and Sons, Inc.; p. 296–316.

Sidor CA, Hopson J. 1998. Ghost linages and "mammalness": assessing the temporal pattern of character acquisition in the Synapsida. Paleobiology. 24:254–273.

Smith R. 1993. Sedimentology and ichnology of floodplain paleosurfaces in the Beaufort Group (Late Permian), Karoo Sequence, South Africa. Palaios. 8:339–357.

Spalletti L, Mazzoni M. 1972. Paleocorrientes del Miembro medio de la Formación Yacimiento Los Reyunos, Siera Pintada, ptovincia de Mendoza. Rev Asoc Arg Miner Petrogr Sedimentol. 3:77–90.

Stipanicic PN, González Díaz EF, Zavattieri AM. 2007. Grupo Puesto Viejo nom. transl. por Formación Puesto Viejo González Díaz, 1964, 1967: nuevas interpretaciones paleontológicas, estratigráficas y cronológicas. Ameghiniana. 44:759–761.

Voigt S, Hminna A, Saber H, Schneider JW, Klein H. 2010. Tetrapod footprints from the uppermost level of the Permian Ikakern Formation (Argana Basin, Western High Atlas, Morocco). J Afr Earth Sci. 57:470–478.

Voigt S, Saber H, Schneider JW, Hmich D, Hminna A. 2011. Late Carboniferous–Early Permian Tetrapod Ichnofauna from the Khenifra Basin, Central Morocco. Geobios. 44:399–407.