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Fluvial and eolian ichnofaunas from the Lower Permian of South America (Patquía Formation, Paganzo Basin)

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ABSTRACT

The Lower Permian Patquía Formation is the youngest unit of the Paganzo Basin, western Argentina. The lower section consists of red mudstones, and fine- and coarse-grained sandstones deposited in fluvial systems with extensive and thick floodplain deposits. These rocks contain a low-diversity and relatively abundant association of trace fossils suggesting the activity of a sub-superficial to superficial fauna. The association is characterized by *Rusophycus carbonarius* (Cubichnia), *Cruziana problematica* (Repichnia), and *Palaeophycus tubularis* (Domichnia) of the *Scoyenia* ichnofacies. Disarticulated fish remains are also present. The upper section is dominated by red, cross-bedded, medium- to fine-grained sandstones deposited in eolian systems that host a low-diversity and low-abundance association of trace fossils that indicates the activity of a mainly superficial fauna. Tetrapod footprints (*Chelichnus duncani*, oval digit imprints, short parallel grooves, and sinusoidal grooves), horizontal to vertical burrows (*Palaeophycus tubularis* and *Skolithos* isp. respectively), and arthropod trackways are the typical components of these deposits. The association shows elements of the three presently proposed eolian ichnofacies (*Chelichnus*, *Octopodichnus* and *Entradichnus* ichnofacies) suggesting the necessity of revision and the possible integration of these separate ichnofacies into a single model. The record of fossil vertebrate tracks is uncommon in Lower Permian strata of South America. Therefore, the ichnologic record of the Patquía Formation is a significant contribution to the understanding of Lower Permian South American ichnofaunas.

KEYWORDS | ***Scoyenia*** **ichnofacies. Eolian ichnofacies. Tetrapod footprints. Early Permian. Patquía. Formation.**

INTRODUCTION

Upper Paleozoic ichnofaunas have been extensively recorded in the Northern Hemisphere including both vertebrate and invertebrate trace fossils (*e.g.* Gilmore, 1926; Hunt et al., 1995; Haubold and Lucas, 2003; Minter, et al., 2007). The records of trace fossils mostly correspond to strata assigned by different authors to the Lower Permian (Artinskian-Kungurian) including the well-known occurrences from the Robledo Mountains in the USA. The tetrapod trackway associations have been divided in two groups, recently formalized as the *Chelichnus* and *Batrachichnus* ichnofacies, corresponding to eolian and redbed depositional settings respectively (Hunt et al. , 1995; Hunt and Lucas, 2007).

Continental body fossils and trace fossils are very rare in South America considering the widespread exposure of Permian rocks in various basins. The great majority of Permian tetrapods and fishes are recorded in Brazil, although a precise chronostratigraphic framework is still lacking (*e.g.* Richter and Langer, 1998). Recently, new outcrops of undetermined Permian age have been found in the Buena Vista Formation, Uruguay. A diverse but fragmentary record of tetrapod body fossils has been recently recovered and is currently under study (*e.g.* Piñeiro et al., 2007).

In Argentina, the Permian record of tetrapod body fossils is scarce, consisting only in sparse occurrences (Siano, 1990; Cisterna and Simanauskas, 2000). Tetrapod footprints are known in three geological units from three different late Paleozoic basins in Argentina. Eolian facies in the Yacimiento Los Reyunos Formation at Southern Mendoza province yields a tetrapod footprint association dominated by *Chelichnus* (Cei and Gargiulo, 1977; Melchor, 2001). ^{40}Ar/^{39}Ar analysis indicates a Wordian/Capitanian (Kazanian /Tatarian) age of 266.31 ±0.82 Ma. for the Yacimiento Los Reyunos Formation (Melchor, 2000). The Carapacha basin records diverse invertebrate and tetrapod trackway associations that were compared with what was later called the *Batrachichnus* ichnofacies, and corresponds to shallow-lake facies (Melchor and Sarjeant, 2004). Paleofloristic elements indicate a late Early Permian to early Late Permian age for the Carapacha Formation (Melchor and Césari, 1991). Finally, there are several isolated occurrences of tetrapod footprints in eolian facies of the Lower Permian Patquía Formation (Paganzo Basin), in La Rioja Province. These tetrapod footprints were compared provisionally with *Dromopus* and *Gilmoreichnus* by Caselli and Arcucci (1999), and are re-analyzed in this contribution.

Permian invertebrate trace fossils from Argentina have been documented mainly in fluvial and shallow-lacustrine deposits (Aceñolaza and Buatois, 1991; 1993), floodplains of high-sinuosity rivers (Buatois et al., 1996), low-energy ponds in floodplains of braided fluvial systems (Buatois et al., 1997), and playa-lake complexes (Zhang et al., 1998). Little is known of invertebrate traces in eolian environments. Globally, trace fossil assemblages reported from eolian facies are scarce in the geologic record and more examples are needed to improve our knowledge of such ichnofaunas. Several eolian ichnofacies models have been proposed: the *Octopodichnus* ichnofacies (Hunt and Lucas, 2007), *Entradichnus* ichnofacies (Morrissey, 2006; Ekdale et al., 2007) and the *Chelichnus* ichnofacies (Hunt and Lucas, 2007), although they seem to be superposed.

The ichnologic record of Argentina provides the only evidence of the distribution of tetrapods for the Early Permian. There has been little crossover between the studies of vertebrate and invertebrate ichnofossils in nonmarine ichnology (*cf.* Lockley, 2007). Herein we use a more integrated approach to study tetrapod footprints and invertebrate trace fossils from the Lower Permian Patquía Formation. These findings, although fragmentary, are the first record of tetrapods in the Paganzo basin and may be the oldest in the Permian of Argentina. The main purpose of this contribution is to document invertebrate and vertebrate trace fossils in the Lower Permian Patquía Formation. In addition, we attempt to discus this evidence in a paleobiologic context, and to compare the ichnofauna with other Lower Permian associations.

Specimens collected are preserved at (CRILAR) Centro Regional de Investigaciones Científicas y Transferencia Tecnológica (CRILAR Ic), Anillaco, La Rioja Province, Argentina.

GEOLOGIC SETTING

The Paganzo Basin was developed as a foreland basin in western Argentina, bounded to the east by the Sierras Pampeanas cratonic area (Limarino et al., 2002). The basin includes one of the most important Late Paleozoic successions of South America. The Carboniferous successions record the Gondwana glaciation (Limarino et al., 2002; Geuna et al., 2010). The thick and geographically extensive Permian redbed successions record the arid and semiarid continental events observed globally (Spalletti et al., 2010; Tedesco et al. 2010). Outcrops of this basin are documented in Sierras Pampeanas, Precordillera, and the Famatina System (La Rioja, San Juan, and San Luis provinces).

The succession outcropping nearby the town of Paganzo is the type section of the Carboniferous-Permian “Estratos de Paganzo” (Bodenbender, 1911, 1912), subsequently referred to as the “Paganzo Group” (Azcuy and Morelli, 1970). This succession is located in the eastern domain of the basin (Limarino et al., 2002) in the central-south area of La Rioja province (Fig.1). The upper Paleozoic strata unconformably overlie the crystalline basement (Azcuy et al., 1979). They include grey sandstones and mudstones of the Carboniferous Lagares Formation, and Permian red beds of the Patquía Formation. This upper Paleozoic succession is overlain by the Triassic Talampaya Formation (Fig. 1).

The sedimentary facies of the Patquía Formation were studied in detail by Caselli (1998). This author included several Permian redbed successions that occur in the basin at the Patquía Formation (see also Caselli and Limarino, 2002). Two intervals within the Patquía Formation were recognized in the Paganzo area (Fig. 2). The lower interval is 240m-thick, and is characterized by red mudstones and fine-grained sandstones interbedded with light red pebbly and coarse-grained sandstones. The tabular mudstones and fine-grained sandstone beds are either massive or show parallel- or ripple cross-lamination. Individual beds are 0.20-1.5m thick. These deposits contain invertebrate trace fossils (*Rusophycus carbonarius*, *Cruziana problematica*, and *Palaeophycus tubularis*) and disarticulated fish remains (Fig.2). The lenticular pebbly and coarse-grained sandstone beds are 0.20- 0.80m thick and display parallel, planar, and trough cross-stratification. The lower interval was interpreted as deposited in fluvial environments, in which floodplain areas dominated over channel subenvironments (Caselli, 1998).

The upper interval is 160 m-thick and is dominated by red, high-angle planar cross-bedded, well-sorted, mature, medium- to fine-grained sandstones. The basal succession is dominated by 0.10-0.20m thick, parallel-laminated, ripple cross-laminated, and planar cross-stratified sandstones interpreted as low-angle sand-sheet deposits (Caselli, 1998). This facies records invertebrate trace fossils (*Palaeophycus tubularis*, *Skolithos* isp., and arthropod trackway), and a variety of tetrapod fossil footprints (*Chelichnus duncani*, oval digit imprints, short parallel grooves, and sinusoidal grooves) (Fig.2). The succession passes upwards into thick-bedded, high-angle cross-stratified sandstone beds. This interval has been interpreted as dune and interdune deposits of an extensive eolian system developed under arid conditions (Caselli, 1998).

The age of the Patquía Formation is poorly constrained. The fossil content suggests an Early Permian age (*e.g.* Frenguelli, 1949; Limarino and Césari, 1985). Paleomagnetic information and absolute ages (K-Ar) of basalt interbedded near the base of the Patquía Formation in the Paganzo area indicate a Late Carboniferous to Early Permian age (263 ± 4 a 302 ± 6 M.a.) (Thompson and Mitchell, 1972; Valencio, 1972; Valencio and Mitchell, 1972; Valencio et al., 1977; Sinito et al., 1979).

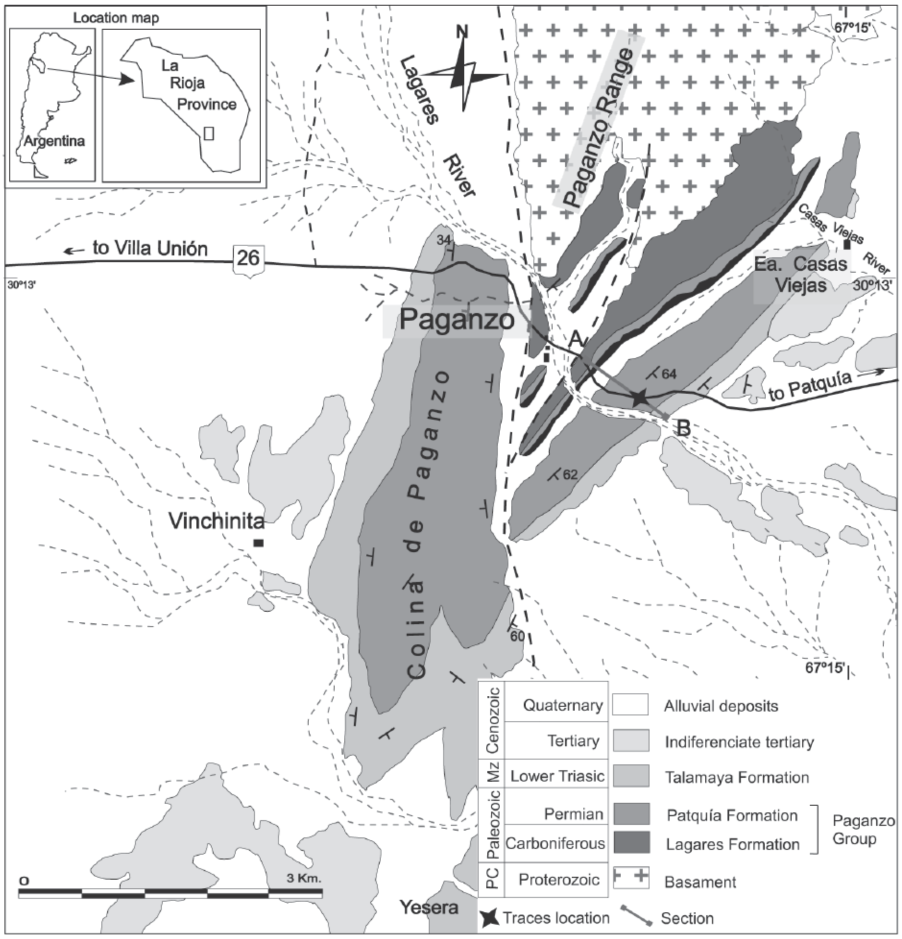

FIGURE 1 | **Geologic map of the Paganzo Group in the Paganzo area.**

INVERTEBRATE TRACE FOSSILS

Ichnogenera are placed in alphabetic order, and are followed by those described in open nomenclature. The preservational nomenclature of Seilacher (1964) is followed.

Ichnogenus *Cruziana* d'Orbigny, 1842
Cruziana problematica (Schindewolf, 1928)
Figure 3A, 3C, 3D, 3E

Material. CRILAR Ic-2, CRILAR Ic-3, CRILAR Ic-4 and material preserved in the field.

Description. Two parallel rounded ridges separated by a central groove. The ridges are generally featureless, although some traces display fine, nearly transverse, striae. External width is from 1.5-8.0mm. Preserved as convex hypichnia.

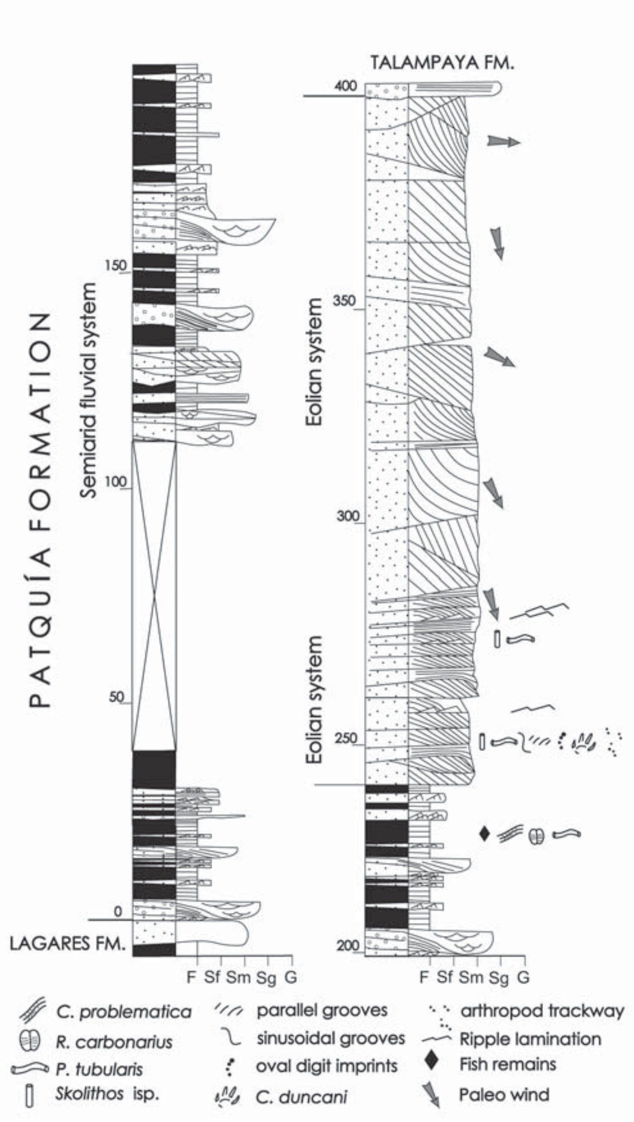

FIGURE 2 | **Sedimentologic section of the Patquía Formation in the Paganzo area. F: mudstone; Sf: fine-grained sandstone; Sm: medium-grained sandstone; Sg: coarse-grained sandstone; G: pebble conglomerate.**

Remarks. This ichnospecies displays two main size ranges in the Patquía Formation: 1.5-3mm (highly abundant) and 5-8mm (Fig. 3C-D).

The distinction between *Isopodichnus*, *Rusophycus,* and *Cruziana* has been largely discussed (*e.g*. Bromley and Asgaard, 1972, 1979; Trewin, 1976; Pollard, 1985; Keighley and Pickerill, 1996). A few authors (*e.g*. Häntzschel, 1975; Seilacher, 1955) have regarded *Rusophycus* as a junior synonym of *Cruziana*, although others have argued that *Rusophycus* must be retained for short bilobate resting traces (*e.g*. Osgood, 1970). The ichnogenus *Isopodichnus* has also been traditionally applied to small bilobate trace fossils in continental environments, particularly redbeds (Trewin, 1976; Seilacher, 1985; Pollard, 1981, 1985), covering both crawling and resting traces. Bromley and Asgaard (1979) placed these bilobate traces in the ichnogenera *Cruziana* and *Rusophycus*, a decision endorsed here. It is highly accepted between ichnologists that paleoenvironment is not a valid ichnotaxobase (Bertling et al., 2006). The presence of *Cruziana problematica* has been documented for the Patquía or equivalent formations (*e.g*. Aceñolaza and Buatois, 1991, 1993; Zhang et al., 1998). *Cruziana* is known from the Cambrian to the Recent.

Ichnogenus *Palaeophycus* Hall, 1847
Palaeophycus tubularis Hall, 1847
Figure 4A, 4C

Material. CRILAR Ic-5 and material preserved in the field.

Description. Horizontal to sub-horizontal, straight to slightly curved, unbranched and branched tubular trace fossils. Circular to elliptical sections are 5-10mm in diameter. Infill similar to the host rock and smooth lining. 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 systematics of *Palaeophycus* has been reviewed by Pemberton and Frey (1982). *Palaeophycus tubularis* is distinguished from the other ichnospecies of *Palaeophycus* by its thin burrow lining and lack of conspicuous wall ornamentation. The presence of *Palaeophycus tubularis* was documented for the Patquía or equivalent formations (*e.g*. Aceñolaza and Buatois, 1991, 1993; Zhang et al., 1998). The ichnogenus is present from the Ediacaran to the recent (Pemberton and Frey, 1982).

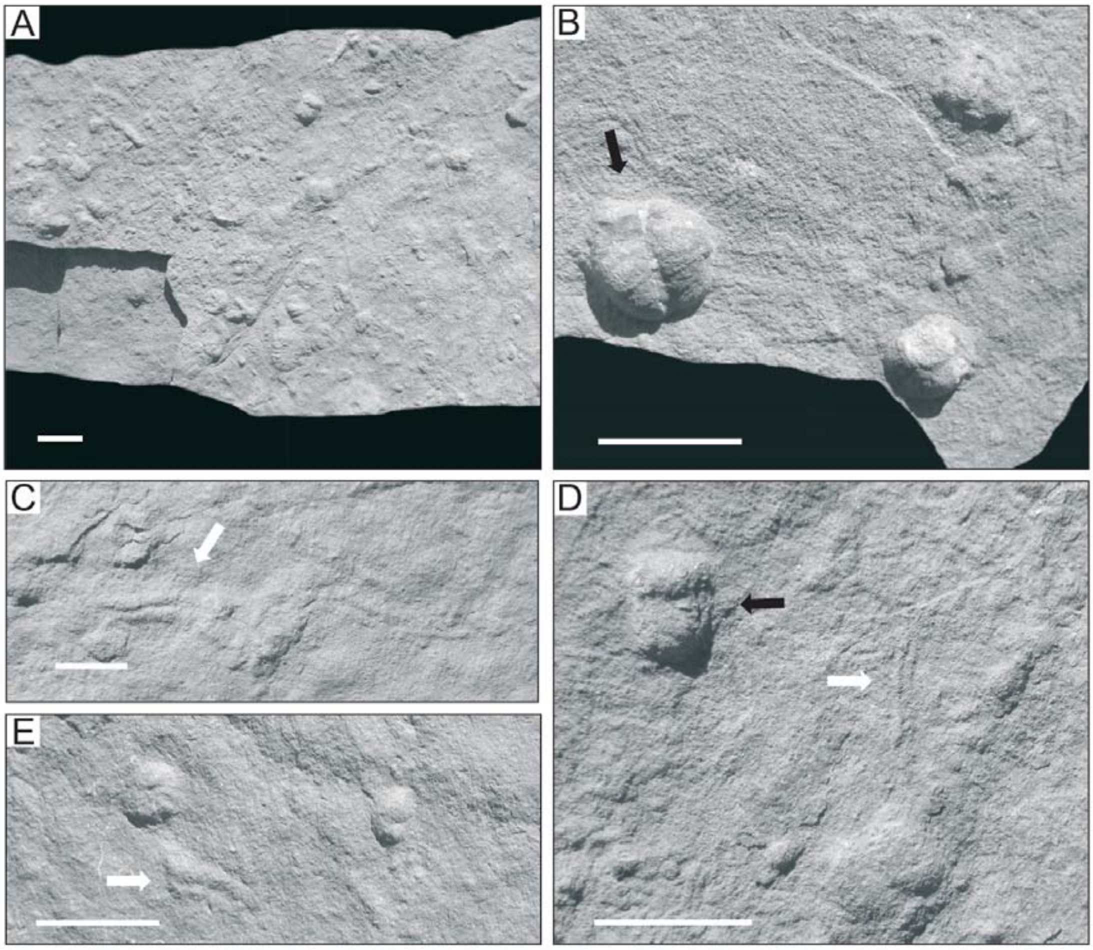

FIGURE 3 | ***Rusophycus carbonarius*** **(black arrow), note transverse scratch marks, and** ***Cruziana problematica*** **(withe arrow). A) CRILAR Ic-2, general view. B) CRILAR Ic-3, note abundant small** ***Cruziana problematica*****. C) CRILAR IC-4,** ***Cruziana problematica*** **of medium size. D) CRILAR Ic-2, note small** ***Cruziana problematica*****. E) CRILAR Ic-4. Scales bars are 1cm.**

Ichnogenus *Rusophycus* Hall 1852
Rusophycus carbonarius Dawson, 1864
Figure 3A, 3B, 3D, 3E

Material. CRILAR Ic-2, CRILAR Ic-3, CRILAR Ic-4 and material preserved in the field.

Description. Subcircular trace fossil consisting of two parallel lobes separated by a central groove and resembling a coffee bean. Some specimens display an anterior subtriangular gap (see Fig. 3D). Lobes are covered by fine transverse striae that extend almost to the margin. Lengths are 5-9mm and widths are 5-10mm. Preserved as convex hypichnia.

Remarks. Schlirf et al. (2001) noted that, in contrast to the widely held view, *Rusophycus* (*Isopodichnus*) *eutendorfensis* does not in fact possess transverse to oblique striations because the original description by Linck (1942) identifies the presence of mostly smooth lobes, separated by a longitudinal furrow. Thus, *R. carbonarius* is distinguished from *R. eutendorfensis* by the presence of transverse striae (Schlirf et al., 2001), from *R. stromnessi* by the absence of expanded, smooth and lily-like ends (Trewin, 1976; Keighley and Pickerill, 1996), from *R. furcosus* in the arrow shape of the latter (Gand, 1994), and from *R. minutus* in its triangular shape (Debriette and Gand, 1990). This ichnogenus is present from the Cambrian to the recent.

Ichnogenus *Skolithos* Haldeman, 1840
Skolithos isp.
Figure 4A, 4B

Material. Material preserved in the field.

Description. Simple, elongate, cylindrical vertical trace fossils. Wall is smooth and infill similar to the host rock. Diameter is 8-11mm. Short tubes with unknown lower end. Preserved as full relief.

Remarks. Specimens are typically preserved in bedding-plane view with maximum observed depths up to 30mm. No ichnospecific assignment can be made for the material from the Patquía Formation due to its partial preservation. *Skolithos* ranges from the Cambrian to the recent (Alpert, 1974; Seilacher et al., 2005).

Arthropod trackway
Figure 5A, 5D, 5H

Material. One trackway with nine tracks preserved in the field.

Description. Partially preserved trackway consisting of one row of tracks grouped in a series of two to four tracks with a medial impression. Individual imprints are oval or bifurcating tracks of approximately 13-20mm long. The trackway presents series of tracks partially preserved. It varies from two tracks arranged in a straight line, three tracks arranged in a triangular pattern, and four tracks arranged in a rhomboidal parallelogram. The distance between the medial impression and the outer track range from 50-64mm.

Remarks. This trackway resemble *Octopodichnus didactylus* in the large size of the trackway, the presence of bifurcated tracks, and tracks grouped in a series of four. On the other hand, it shows a medial impression, characteristic of specimens assigned to *Paleohelcura*. The ichnogenera *Paleohelcura* and *Octopodichnus* are similar enough in their morphology that difficulty in distinguishing between the two may arise (Sadler, 1993). At present, the two clearly distinguishing features of these two ichnogenera are the presence of absence of both a bifurcated track impression and a medial impression (Sadler, 1993). Unfortunately, this trackway can not be assigned with certainty to either ichnogenera (*Paleohelcura* or *Octopodichnus*) due to the fact that it presents characteristics mutually exclusive between them (bifurcated tracks and medial impression).

TETRAPOD TRACE FOSSILS

Tetrapod tracks and trackways are preserved on three closely spaced surfaces. All three levels comprise a single trampling surface where numerous imprints of appendages and tails are preserved (Fig. 5). Ichnogenera are placed in alphabetic order and are followed by those described in open nomenclature. The preservational nomenclature of Seilacher (1964) is followed. Material was studied directly in the field, and is preserved as concave epichnia.

Ichnogenus *Chelichnus* Jardine 1850
Chelichnus duncani Jardine 1850
Figure 5A, 5B, 5E

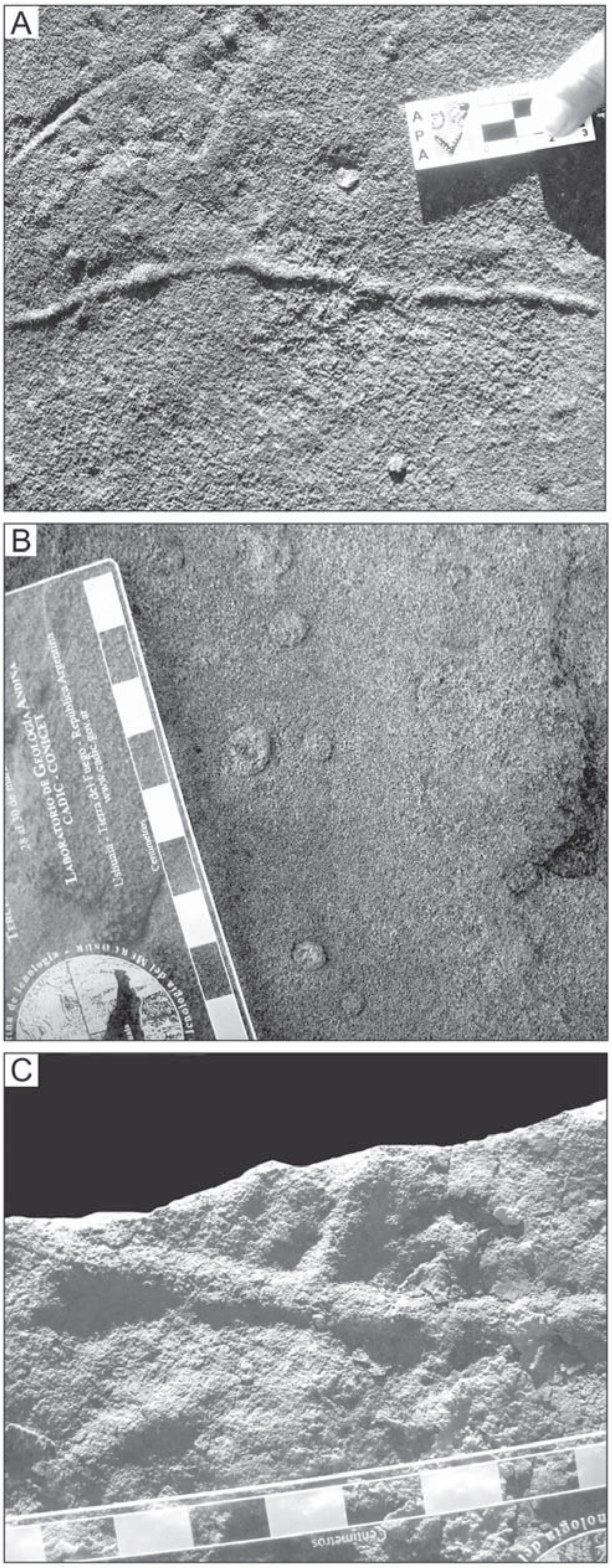

FIGURE 4 | ***Palaeophycus tubularis*** **and** ***Skolithos*** **isp. A)** ***Palaeophycus tubularis*** **and** ***Skolitos*** **isp. preserved in eolian deposits. B)** ***Skolithos*** **isp. preserved in eolian deposits. C) CRILAR Ic-5,** ***Palaeophycus tubularis*** **preserved in fluvial deposits. White areas on scales are 1cm.**

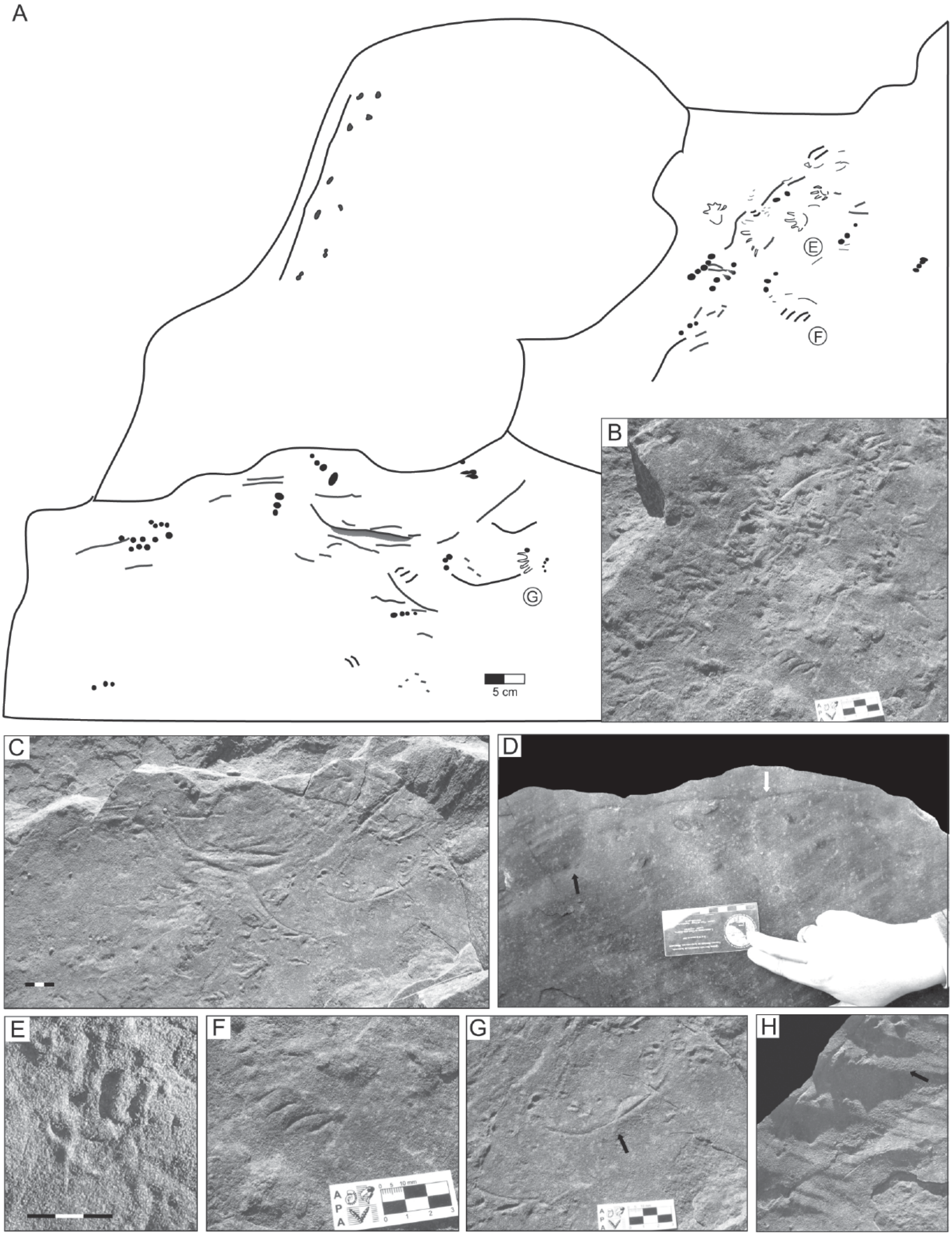

FIGURE 5 | **Tetrapod trampling surfaces. A) Diagram of the trampling surfaces showing all the specimens. Scale bar is 5cm. B) Detail of the upper right area of the diagram showing *Chelichnus duncani*, oval digit imprints, short parallel grooves, and sinusoidal grooves. Scale bar is 3cm. C) Detail of the lower left area of the diagram showing oval digit imprints, short parallel grooves, and sinusoidal grooves. Scale bar is 3cm. D) Detail of the upper left area of the diagram showing an arthropod trackway. Note bifurcated track (black arrow) and medial impression (white arrow). Scale bar 10cm. E) *Chelichnus duncani*. Scale bar 3cm. F) Short parallel grooves. Scale bar 3cm. G) Oval digit imprints. Two consecutive steps, note digit drag mark (arrow). Scale bar 3cm. H) Upper left area of the diagram, note ripple marks (arrow).**

Material. Three isolated tracks.

Description. Plantigrade tracks that show a rounded sole imprint and four subparallel, relatively short, anteriorly directed digit imprints. Footprint length is 32-37mm and footprint width is 28-35mm. Digit imprints are of approximately the same length as the sole imprint and lateral digit imprints (7-12mm) are shorter than central digit imprints (12-15mm). There is no clear trackway pattern of these footprints expressed on the trampling surface.

Remarks. According to McKeever and Haubold (1996) *Chelichnus* consists of rounded manus and pes tracks of nearly equal size. Complete manus and pes tracks are pentadactyl with a round sole imprint and five short digit imprints, although commonly only three or four digit imprints are visible. There are four recognized ichnospecies of *Chelichnus* differing principally in size. *Chelichnus bucklandi* has a pes track length of 10-25mm, *C. duncani* has a pes track length of 25-75mm, *C. gigas* has a pes track length of 75-125 mm, and *C. titan* displays a pes track length exceeding 125mm (McKeever and Haubold, 1996). The Patquía specimens are assigned to *Chelichnus duncani* on the basis of the plantigrade tracks with short and subparallel digit imprints that are oriented anteriorly.

Oval digit imprints
Figure 5A, 5B, 5C, 5G

Material. Eighteen individual tracks.

Description. Circular to oval digit imprints (4-7mm in width) parallel to each other and forming an arc. Distances between digit imprints are 2-3mm. In well-preserved specimens there are five digit imprints, although the number of digit imprints is commonly lower. It is not possible to observe their relation to forefoot or hind foot. Trackway pattern unclear.

Remarks. These imprints are most likely a differential preservation of *Chelichnus duncani* because the digit imprints of that ichnospecies are in the same size range.

Short parallel grooves
Figure 5A, 5B, 5C, 5F
Material. Six individual tracks.

Description. Parallel slightly curved grooves with pointed tips. Well-preserved specimens consist of four parallel grooves, although more partially preserved specimens display only two parallel grooves. Individual groove length is 10-20mm. They are sharply incised and are more similar to digit scratch marks than to digit imprints. No distinct trackways can be observed.

Remarks. Parallel furrows probably consist of scratch marks of a plantigrade quadruped with clawed tips. The Patquía parallel furrows strongly suggest a similar morphological pattern to that expressed by tracks where plantigrady and number of digits is typically reduced. Under somewhat dry conditions or in undertrack preservation, the number of digit imprints could gradually disappear.

Sinusoidal grooves
Figure 5A, 5B, 5C, 5G

Material. Six sinusoidal grooves.

Description. Sinusoidal grooves are present all over the tracking surface. They consist of sharp, curved impressions that locally show two parallel grooves but commonly consist of only one simple groove. The length of the grooves is 40-140mm. Small lobes commonly occur on the sides of the grooves, and represent sand deformation features.

Remarks. These sinusoidal grooves probably represent digit and tail drag marks.

DISCUSSION

Trace-fossil producers

Freshwater examples of *Cruziana* and *Rusophycus* have been interpreted as cubichnia and repichnia, respectively, of branchiopod crustaceans (notostracans) by Bromley and Asgaard (1972). These are mostly benthic organisms that crawl and burrow along the bottom of ephemeral ponds in continental environments. According to Bromley and Asgaard (1979), the morphology of very short freshwater *Rusophycus* with transverse striations could be compared with head-down burrowing behavior of trilobites of Seilacher (1970). As noted by Minter et al. (2007), anostracan and lipostracan branchiopods cannot be ruled out as possible producers of these striated trails. Some anostracans have been observed to feed by scraping the surface, and lipostracans, although extinct, are inferred to have had the same behavior on the basis of comparative functional morphology. Both scrape the substrate rather than ploughing through it, and so they are more likely to have produced superficial scratch traces rather than furrowed traces (Minter et al., 2007). Lipostracans are very small and so they can only be considered as potential tracemakers of the smallest (1.5-3mm) trace fossils.

Pemberton and Frey (1982) proposed several potential producers for *Palaeophycus*, in the marine realm. These structures were interpreted as passively infilled dwelling burrows of worm-like organisms. As suggested by Krapovickas et al. (2008 and references therein), some

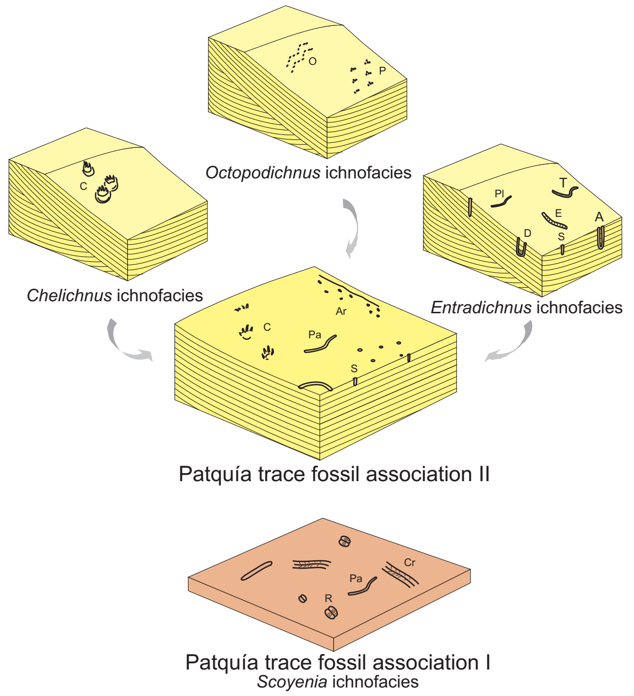

FIGURE 6 | **Idealized reconstruction of trace fossil associations of the Patquía Formation. Above, trace fossil association 2 developed in eolian sand-sheet deposits. Note its similarities with the three presently known eolian ichnofacies. Below, trace fossil association 1developed in floodplain deposits. A: *Arenicolites* isp.; Ar: Arthropod trackway; C: *Chelichnus duncani*; Cr: *Cruziana problematica*; D: *Diplocraterion parallelum*; E: *Entradichnus meniscus*; O: *Octopodichnus* isp.; P: *Paleohelcura* isp.; Pa: *Palaeophycus tubularis*; Pl: *Planolites beverleyensis*, R: *Rusophycus carbonarius*; S: *Skolithos* isp.; T: *Taenidium serpentinum*.**

modern producers of *Palaeophycus*-like structures in continental floodplains are semiaquatic organisms such as orthopterans (Tridactylidae), hemipterans (Salidae), beetles (Heteroceridae) and, non-aquatic cicindelinae beetles.

In non-marine environments, *Skolithos* is commonly recorded in subaerial and permanently subaqueous sediments (Gierlowski-Kordesch, 1991). Among recent organisms that construct vertical excavations are numerous groups of insects and arachnids (Smith and Hein, 1971, Ratcliffe and Fagerstrom, 1980, Bown, 1982).

The presence of two to four tracks in each series of imprints in the arthropod trackway indicates at least four appendages on each side of the body of the trackmaker, suggesting a member of the class Arachnida. In addition, the presence of a medial impression suggests a tail drag left by a scorpionid.

The poor preservation of the tetrapod tracks obscures diagnostic morphologic details of tracks and trackways, making it difficult to determine potential tracemakers. Specimens assigned to *Chelichnus* are interpreted to be produced by a non-mammalian synapsid (McKeever and Haubold, 1996).

Paleoecology and taphonomy of trace fossils

Fluvial deposits in the Patquía Formation comprise scarce fluvial channels and thick floodplain deposits with shallow-water bodies that contain an abundant invertebrate ichnofauna. The assemblage (trace-fossil association 1) includes crawling, resting and dwelling trace fossils (Fig. 6, 7) corresponding to *Rusophycus carbonarius* (Cubichnia), *Cruziana problematica* (Repichnia), and *Palaeophycus tubularis* (Domichnia). Disarticulated fish scales are also present. This low-diversity ichnofauna suggests the activity of a sub-superficial to superficial benthic invertebrate fauna. The taphonomic features of both invertebrate trace fossils and fish remains (*i.e.* disarticulate and dispersed scales and fish bones, of which some show a patterned arrangement and are densely packed and well sorted) suggest that they were preserved in a floodplain environment characterized by an alternation of overflow and fall-out deposits (Mancuso, 2008).

Eolian sand-sheet deposits of the Patquía Formation include tetrapod trace fossils (*Chelichnus duncani*, oval digit imprints, short parallel grooves, and sinusoidal grooves) and invertebrate locomotion and dwelling trace fossils (arthropod trackway, *Palaeophycus tubularis,* and *Skolithos* isp.) (Fig.6, 7). This low-diversity and low-abundance association (trace-fossil association 2) represents the activity of a terrestrial superficial ichnofauna produced by cursorial tetrapods and shallow burrowing desert-dwelling arthropods. The absence of morphologic details and the preservation of only the deepest features suggest that the tetrapod footprints in association 2 are preserved as "undertracks" and/or that the surface was partially eroded before final burial. The sediment grain-size (medium- to fine-grained sand) compared to the size of the footprints prevents the preservation of fine morphologic details. In addition, the production of tracks is linked to sediment grain size and substrate water content. Thus, in eolian environments moist sand is needed to preserve tracks (Fornós et al., 2002; Loope, 2006). The Patquía tetrapod trackway assemblage must have therefore been emplaced in a moist substrate. Therefore, the taphonomic characteristics allow us to interpret the track-bearing levels as humid sand-sheet deposits buried by small dune migration, after an exposure time long enough to record a succession of different overprinted trackways.

Early Permian tetrapod-track assemblages

The Permian vertebrate body-fossil and footprint record of Europe and North America is abundant and well studied (e.g. Olson, 1989; Milner, 1993; Hunt et al., 1995; Tverdokhlebov et al., 2005; Minter, et al., 2007). In the last

FIGURE 7 | **Reconstruction of the Permian Paganzo fluvio-eolian environment with the putative vertebrate and invertebrate trackmakers. Illustration by Boris Budiša.**

decades several authors have proposed different schemes to group trace-fossil associations from the Early Permian (Haubold, 1996; Lucas, 1998). These associations were mainly grouped in two principal clusters, originally named as ichnofacies. First, the association of eolian facies dominated by *Chelichnus* and, less abundantly, *Dromopus* (Lockley et al., 1994; McKeever and Haubold, 1996), and second, the association of red-beds in fluvio-lacustrine facies, characterized mainly by *Batrachichnus*, *Limnopus*, *Gilmoreichnus*, and *Dimetropus* (Hunt et al., 1995). In Argentina, tracks from the Yacimiento Los Reyunos Formation were assigned to the typical *Chelichnus* association (Melchor, 2001), and those from the Carapacha Formation were compared to the "redbeds" association, with a late (early Late Permian) representation in South America (Melchor and Sarjeant, 2004). The material of the Patquía Formation reveals some resemblance to those that were referred to the *Chelichnus* ichnofacies by Lockley et al. (1994).

Ichnofacies

Nonmarine ichnofacies are now receiving more attention by ichnologists (*e.g.* Buatois and Mángano, 2004, 2007; Hunt and Lucas, 2007; Ekdale et al., 2007; Minter et al., 2007; Melchor et al. 2006). Three archetypal nonmarine ichnofacies are widely accepted: *Scoyenia* (Seilacher, 1964, 1967), *Mermia* (Buatois and Mángano, 1995), and *Coprinisphaera* (Genise et al., 2000). Additionally, the typically marine *Skolithos* ichnofacies is recognized in nonmarine settings (Buatois and Mángano, 2004). Various eolian ichnofacies have been proposed: *Octopodichnus*, *Chelichnus,* and *Entradichnus* ichnofacies (Hunt and Lucas, 2007; Ekdale et al., 2007). And, a new model of tetrapod ichnofacies was recently presented (Hunt and Lucas, 2007), suggesting five ichnofacies (*Grallator*, *Brontopodus*, *Batrachichnus*, *Characichnos,* and *Chelichnus* ichnofacies) which correspond with aspects of invertebrate ichnofacies.

There is a strong need for integration of vertebrate and invertebrate trace fossils in continental ichnofacies models. There are several ichnofacies models proposed for eolian environments, but these are either based on invertebrate or vertebrate trace fossils. Hunt and Lucas (2007) proposed the *Chelichnus* ichnofacies for tetrapod associations recurrent in dune facies of eolian environments (Fig. 6). These authors also erected the *Octopodichnus* ichnofacies for eolian trace-fossil associations of the Coconino Sandstone (Fig. 6), whilst Ekdale et al. (2007) defined the *Entradichnus* ichnofacies for eolian trace-fossil associations based on the Navajo Sandstone (Fig. 6). The close correspondence between the *Chelichnus* and *Octopodichnus* ichnofacies in dune environments was suggested by Hunt and Lucas (2007). In the same vein, Buatois and Mángano (2008) attempted to integrate eolian ichnofacies models, and combined both ichnofacies in the *Octopodichnus*-*Entradichnus* ichnofacies. The Patquía trace-fossil association 2 has aspects in common with the *Octopodichnus*, *Chelichnus*, and *Entradichnus* ichnofacies (Fig. 6). It particularly resembles the *Entradichnus* ichnofacies in containing trace fossils that have been produced by shallow burrowing, desert-dwelling arthropods, such as beetles and others insects, that kept pace with dune migration (Ekdale et al., 2007). Also, it shares the presence of arthropod trackways with the *Octopodichnus* ichnofacies, which consists exclusively of locomotion trace fossils (Hunt and Lucas, 2007). Finally, it also reveals some resemblance to the *Chelichnus* ichnofacies. The material described here demonstrates the need to integrate both invertebrate and vertebrate trace fossils in ichnofacies models.

Trace-fossil association 1 from the Patquía Formation developed in floodplain deposits and is ascribed to the *Scoyenia* ichnofacies (Fig. 6). It displays many of the archetypal characteristics of the *Scoyenia* ichnofacies, including the presence of small horizontal bilobate trace fossils, such as *Cruziana* and *Rusophycus*. The *Scoyenia* ichnofacies occurs in low-energy settings periodically exposed to air or periodically inundated (Frey et al., 1984; Buatois and Mángano, 1995). In this case there is no clear evidence of subaerial exposure, although a progressive desiccation and stiffening of the substrate is probably indicated by the presence of striae in some *Rusophycus* specimens.

CONCLUSIONS

The vertebrate ichnofauna documented here represents the oldest record of tetrapods in Argentina. Floodplain deposits of the Patquía Formation record invertebrate trace fossils (trace-fossil association 1) that are an example of the *Scoyenia* ichnofacies displaying mostly arthropod trace fossil. Eolian sand-sheet deposits of the Patquía Formation record a second trace-fossil association that has aspects in common with the three proposed eolian ichnofacies, suggesting the need for revision and their potential integration. The *Octopodichnus*-*Entradichnus* ichnofacies (*sensu* Buatois and Mángano, 2008) seems to be characterized by horizontal (*e.g*., *Palaeophycus*, *Planolites*) and vertical burrows (*e.g*., *Skolithos*, *Digitichnus*), arthropod trackways (*e.g*., *Octopodichnus*, *Paleohelcura*), and vertebrate tracks chiefly produced by a non-mammalian synapsids and mammals (*e.g*. *Chelichnus*, *Brasilichnus*).

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