Tetrapod tracks in Permo–Triassic eolian beds of southern Brazil (Paraná Basin)

Heitor Francischini¹, Paula Dentzien-Dias², Spencer G. Lucas³ and Cesar L. Schultz¹

¹ Laboratório de Paleontologia de Vertebrados, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil
² Laboratório de Geologia e Paleontologia, Instituto de Oceanografia, Universidade Federal do Rio Grande, Rio Grande, Rio Grande do Sul, Brazil
³ New Mexico Museum of Natural History and Science, Albuquerque, NM, USA

ABSTRACT

Tetrapod tracks in eolianites are widespread in the fossil record since the late Paleozoic. Among these ichnofaunas, the ichnogenus *Chelichnus* is the most representative of the Permian tetrapod ichnological record of eolian deposits of Europe, North America and South America, where the *Chelichnus* Ichnofacies often occurs. In this contribution, we describe five sets of tracks (one of which is preserved in cross-section), representing the first occurrence of *Dicynodontipus* and *Chelichnus* in the “Piramboia Formation” of southern Brazil. This unit represents a humid desert in southwestern Pangea and its lower and upper contacts lead us to consider its age as Lopingian–Induan. The five sets of tracks studied were compared with several ichnotaxa and body fossils with appendicular elements preserved, allowing us to attribute these tracks to dicynodonts and other indeterminate therapsids. Even though the “Piramboia Formation” track record is sparse and sub-optimally preserved, it is an important key to better understand the occupation of arid environments by tetrapods across the Permo–Triassic boundary.

Subjects Evolutionary Studies, Paleontology, Zoology, Climate Change Biology

Keywords Piramboia Formation, Ichnology, *Dicynodontipus*, *Chelichnus*, Paleoerg, Dicynodontia, Vertebrate tracks, South America, Permian–Triassic boundary

INTRODUCTION

Tetrapods experimented with their first incursions into desert environments during the Carboniferous Period and, since then, they have come to occupy almost all desert elements, such as dunes, interdunes and sand sheets (*Krapovickas et al., 2016*). Although the composition of the desert ichnofaunas has changed through the Phanerozoic (e.g., the replacement of the *Chelichnus* ichnocoenosis by the *Brasilichnium* ichnocoenosis after the Permo–Triassic boundary), the relative abundance of tetrapod-related ichnotaxa in such environments has always been low (*Hunt & Lucas, 2007; Hunt & Lucas, 2016; Krapovickas et al., 2016*). On the other hand, tetrapod tracks comprise the only fossil record of tetrapods in several eolian deposits across the world (*Gilmore, 1926; Faul & Roberts, 1951; Leonardi, 1980; Lockley et al., 1995; Morales & Haubold, 1995; Dentzien-Dias, Schultz & Bertoni-Machado, 2008; Francischini et al., 2015*), making the ichnotaxonomic and facies studies of such tetrapod tracks extremely important to...
understanding the evolution of biodiversity in and the occupation of arid ecosystems throughout geological time.

Among the late Paleozoic and early Mesozoic record, the main desert tetrapod ichnofaunas comes from the Permian eolianites of Scotland (Locharbriggs, Corncockle and Hopeman sandstones), Germany (Cornberg Sandstein), the western USA (Coconino, DeChelly, Lyons and Casper sandstones) and Argentina (Yacimiento Los Reyunos and Patquía formations) (Jardine, 1853; Lull, 1918; Gilmore, 1926; McKee, 1944; Schmidt, 1959; Cei & Gargiulo, 1977; Fichter, 1994; Lockley et al., 1995; Morales & Haubold, 1995; Krapovickas et al., 2010; Krapovickas et al., 2014). However, despite the terrestrial tetrapod faunal turnover and extinctions that marked the Guadalupian–Lopingian transition (Day et al., 2015a; Lucas, 2017) and the end-Permian biotic crisis (Benton & Twitchett, 2003; Retallack, Smith & Ward, 2003; Lucas, 2009), the Permian eolian tetrapod track record is dominated by *Chelichnus* tracks, which are morphologically constant during the entire Permian (McKeever & Haubold, 1996). This dominance is partially explained by the role of the preservation of tetrapod tracks in eolian sands, which add new non-morphological, substrate-controlled features to the original autopodium impression, referred to as extramorphological characters (Peabody, 1948; Haubold et al., 1995; Mancuso et al., 2016). Also, species that lived in arid ergs often present similar adaptations to walk on desert eolian substrates (such as short and broad digits, wider than long soles and palms, and the lack of a tail dragging on the ground). Therefore, the recurrence of the morphological and extramorphological features of the tetrapod tracks made on eolian sand substrates results in desert facies-controlled ichnofaunas, which are broadly known as the *Chelichnus* Ichnofacies (Lockley et al., 1995; Hunt & Lucas, 2007; Hunt & Lucas, 2016).

Several studies argued that the *Chelichnus* Ichnofacies is a depauperate association of tetrapod tracks in eolian deserts, being particularly less diverse than other contemporaneous ichnofaunas produced in different environments (Lockley et al., 1995; McKeever & Haubold, 1996; Hunt & Lucas, 2007; Hunt & Lucas, 2016). The *Chelichnus* Ichnofacies is dominated mainly by Chelichnopodidae tracks, being represented by *Chelichnus Jardine, 1850* in the Paleozoic deposits, and *Brasilichnium Leonardi, 1981* in the Mesozoic deposits, in addition to surface-made arthropod tracks—such as *Diplichnites, Hexapodichnus, Paleohelcura* and *Octopodichnus* (Brady, 1947; Leonardi, 1980; Braddy, 1995; Hunt & Lucas, 2007; Ekdale & Bromley, 2012; Hunt & Lucas, 2016).

Here, we describe the first tetrapod tracks from the Lopingian–Induan eolian strata of southern Brazil, which are identified as *Dicynodontipus* isp. and *Chelichnus bucklandi*, besides other indeterminate trackways. These materials are the first tetrapod ichnocoenosis from an eolian environment in the late Paleozoic–early Mesozoic strata of Brazil, allowing the recognition of the *Chelichnus* Ichnofacies in the eolian dunes of the “Pirambóia Formation” from southwestern Rio Grande do Sul (Fig. 1). In addition, the ichnogenus *Dicynodontipus* is not often found in eolian deposits, making this record important in the understanding of the role of the extramorphological variations among tetrapod tracks.
Stratigraphic setting

The Pirambóia Formation was proposed as a formal lithostratigraphic unit in the Pirambóia district, Anhembi municipality, central region of São Paulo State, southeastern Brazil (Soares, 1975). Its type section is located in the surroundings of the Marechal Rondon (SP-300) highway and the unit is stratigraphically positioned between the upper Permian Passa Dois Group and the Lower Cretaceous Botucatu Formation (Soares, 1975; Figs. 1 and 2). Its lithologic characteristics allow the informal division of the unit into two members: the lower, composed mainly of clayey sandstones, with plano-parallel and small cross-bedded stratifications; and the upper, composed of sandstones with medium scale planar cross-stratification, overlain by sandstones and mudstones with plano-parallel stratification (Soares, 1975). Later, some authors (see historical review in Lavina, Faccini & Ribeiro, 1993) described stratigraphic units with a similar lithology and stratigraphic position in Paraná, Santa Catarina and Rio Grande do Sul states, which led them to consider these units to be the same as the Pirambóia Formation of São Paulo State, despite the lack of continuous exposure along the eastern border of the Paraná Basin (Fig. 1; Lavina, Faccini & Ribeiro, 1993). Notwithstanding, the stratigraphic correlation of several units attributed to the Pirambóia Formation is controversial, because there is no consensus about its lateral extent (Fig. 2; Lavina, Faccini & Ribeiro, 1993; Soares, Soares & Holz, 2008). Hitherto, fossils were unknown at both the type-locality and across the studied region (except by those described herein). In this

Figure 1 The Pirambóia Formation in São Paulo and Rio Grande do Sul states, Brazil. (A) São Paulo State. Locality 1: The type-locality in the Pirambóia district, Anhembi municipality. (B) Rio Grande do Sul State. Locality 2: The Ibicuí d’Armada locality, Santana do Livramento municipality. JMFZ, Jaguari-Mata Fault Zone; DCFZ, Dorsal de Canguçu Fault Zone. Modified from Scherer & Lavina (2005). DOI: 10.7717/peerj.4764/fig-1

GEOLOGICAL SETTING

Stratigraphic setting
section, the stratigraphic relationships of the Pirambóia Formation will be discussed, focusing on the deposits assigned to it in the southwestern portion of Rio Grande do Sul State (Southern Brazil) where the tracks described in this work were discovered.

The occurrence of these clay, silt and clayey sandstone beds in São Paulo State was recognized for the first time in the reports of the Comissão Geográfica e Geológica do Estado de São Paulo (“Geographical and Geological Survey of the São Paulo State”), that named it the “Grès de Pirambóia,” located under the “Grès de Botucatu” (actually, the Botucatu Formation, composed mainly of eolian sandstones) layers (Pacheco, 1927; Washburne, 1930). According to Pacheco (1927), the “Grès de Pirambóia” was a sandy Triassic unit that crops out only in São Paulo State. Although the early reports did not characterize this unit stratigraphically, Sanford & Lange (1960) raised it to the formal category of formation.

Soares (1975) was the first to define the Pirambóia Formation based on a type section and to delimit its occurrence in São Paulo State (Fig. 1). Accordingly, the Pirambóia Formation differs from the sandstones of the (superposed) Botucatu Formation by being a predominantly fluvial facies association (Soares, 1975), although according to Caetano-Chang (1997) this is subordinate to the eolian facies. In São Paulo and Goiás states, the Pirambóia Formation overlies the Permian Passa Dois Group (i.e., Teresina, Rio do Rasto and Corumbataí formations), and its lower boundary is marked by a debrite level, informally named the “Porangaba Bed” (Matos, 1995; Matos & Coimbra, 1997).
This bed was related to a tsunami deposit generated after the Araguainha impact event and a coherent population of detrital zircons was dated in 253.2 ± 3.0 Ma (Changhsingian, late Permian), suggesting that the overlying Pirambóia Formation is younger than this age (Tohver et al., 2018). However, there is no consensus about the nature (transitional or discordant) of this boundary in other regions of the Paraná Basin (Filfaro, Gama & Soares, 1980; Almeida & Melo, 1981; Lavina, 1992; Lavina, Faccini & Ribeiro, 1993; Faccini, 2000; Dias & Scherer, 2008).

In Rio Grande do Sul State, Lavina, Faccini & Ribeiro (1993) proposed that the lower beds of the Sanga do Cabral Formation (sensu Andreis, Bossi & Montardo, 1980) may be correlated to the Pirambóia Formation, as defined in São Paulo (Figs. 1 and 2). These beds, composed of an association of fine- to medium-grained sandstones with trough cross-bedded stratification, predominantly eolian in origin (but with subordinate lacustrine and fluvial levels), differ from the overlying succession (named the Sanga do Cabral Formation strictu sensu), composed of fluvial, lacustrine, deltaic and eolian mudstones and sandstones (Lavina, 1992; Lavina, Faccini & Ribeiro, 1993), with a tetrapod body fossil record (e.g., Procolophon trigoniceps) that indicates an Early Triassic age (Induan; Dias-da-Silva et al., 2017). On the other hand, the basal strata of the Pirambóia Formation in Rio Grande do Sul State contacts the top of the Rio do Rasto Formation, whose tetrapod (e.g., pareiasaurs, dinocephalians, anomodonts, among others), plant (e.g., the Glossopteris flora) and conchostracan records suggest a Guadalupian–Lopingian age (Holz et al., 2010; Dias-da-Silva, 2012). The exposures of the Pirambóia Formation are interrupted in the central region of Rio Grande do Sul State by two fault systems (the Jaguari-Mata Fault Zone, NW–SE, and the Dorsal de Canguçu Fault Zone, NE–SW), that restrict the occurrence of this unit to the southwestern and eastern regions of the State (Figs. 1 and 2) (Soares, Soares & Holz, 2008).

More recently, Soares, Soares & Holz (2008) recognized a conflict between the interpretations of the sandstone packages described by Lavina (1992) as Pirambóia Formation (that crops out west of the Jaguari-Mata Fault Zone) and those from the eastern region of Rio Grande do Sul (Fig. 2). According to these authors (Soares, Soares & Holz, 2008), the western package would have been deposited during the Permo–Triassic interval, based on its stratigraphic relationships with the lower and upper formations, the Rio do Rasto and the Sanga do Cabral formations, respectively (Lavina, Faccini & Ribeiro, 1993; Soares, Soares & Holz, 2008). On the other hand, the package that crops out in eastern Rio Grande do Sul (east of the Dorsal de Canguçu Fault Zone) should be chrono-correlated to the Upper Jurassic Guará Formation (Soares, Soares & Holz, 2008; Scherer & Lavina, 2005). Additionally, the “Porangaba Bed” does not occur in the Rio Grande do Sul State (Tohver et al., 2018), precluding further correlations with the deposits of the north region of the Paraná Basin. Therefore, to avoid conflict, we will refer to the eolianites of western Rio Grande do Sul as “Pirambóia Formation” (between quotes) henceforward.

Regarding the Pirambóia Formation fossil record, deposits bearing two associations described as belonging to the Santana Facies (lacustrine and flood-plain deposits) of the Botucatu Formation (Almeida, 1950; Souza, Sinelli & Gonçalves, 1971) were included...
in the Pirambória Formation, in the definition proposed by Soares (1975). The fauna described by Almeida (1950) is composed of conchostracans (Bairdestheria barbosai, Euestheria mendesi and Palaeolimnadia petrii) and ostracods (Candonopsis sp., Candona pyriformis and Pachecoia rodriguesi) from the mudstones of the Rio Claro municipality (central São Paulo State). According to this author, this fauna indicates a Triassic age (Almeida, 1950).

The second fossil assemblage, described by Souza, Sinelli & Gonçalves (1971) from the clayey rhythmites of Serrana municipality (northeastern São Paulo State), is composed of an abundant fauna of ostracods (Cypridea oblonga) and conchostracans (Estheriella sp., E. ribeiropretensis, E. triangularis, Lithoestheria elliptica and Pseudestheria sp.), besides remains of the lycopsid plant Lycopodiopsis derbyi. Based on this, the age of this association is contradictory: while *L. derbyi* indicates a Permian age, *C. oblonga* suggests a Jurassic–Cretaceous age for those beds (Souza, Sinelli & Gonçalves, 1971). On the other hand, other than the trace fossils described here (see below), the “Pirambória Formation” of western Rio Grande do Sul has no fossil record. Therefore, there is no consensus on the spatial and temporal definitions of the Pirambória Formation, even in the original area in São Paulo State.

The material described in this work comes from the eolian sandstone package that crops out west of the Jaguari-Mata Fault Zone, being stratigraphically positioned between the Rio do Rasto and the Sanga do Cabral formations, corresponding to the Pirambória Formation sensu Lavina (1992). Accordingly, the tetrapod track-bearing eolian sandstones of the Santana do Livramento municipality were deposited during the interval late Lopingian–Induan (late Permian–Early Triassic). This inferred age is based on the stratigraphic position of this package between the Rio do Rasto and the Sanga do Cabral formations.

**Geology and meaning of the “Pirambória Formation” in southwestern Rio Grande do Sul**

Despite all the stratigraphic contradictions described above, it is clear that the fluvio-eolian deposits from southwestern Rio Grande do Sul State represent a humid eolian system deposited in the interval Guadalupian–Induan (Dias & Scherer, 2008). The depositional age of this unit is based on its lower and upper unconformable contacts with the Rio do Rasto Formation (Guadalupian–Lopingian) and the Sanga do Cabral Formation (Induan) (Dias & Scherer, 2008; Soares, Soares & Holz, 2008; Rodrigues, 2014; Soares, Soares & Bettú, 2014).

In southwestern Rio Grande do Sul State, the “Pirambória Formation” is composed of 10 lithofacies that indicate deposition under eolian settings with braided and ephemeral fluvial channels (Rodrigues, 2014). A drying-upward trend is proposed based mainly on the high frequency of sandy sheets and interdune deposits in the lower half and the predominance of eolian dunes in the upper half of the “Pirambória Formation” (Rodrigues, 2014) and the increase in thickness of the dune deposits upward through the entire unit (Dias & Scherer, 2008).
Biogenic structures were observed in at least three lithofacies: eolian sandy sheets, dry and wet eolian interdunes and eolian dunes (Rodrigues, 2014). Even though these trace fossils were not properly described, Rodrigues (2014) was able to recognize the Scoyenia Ichnofacies (i.e., an ichnofacies characterized mainly by the co-occurrence of vertebrate and invertebrate mobile deposit feeding traces and locomotion tracks and trails, besides dwelling burrows and rhizoliths; e.g., McEachern et al., 2012 and references therein) in the interdune deposits.

MATERIALS AND METHODS

The track-bearing outcrop studied in this contribution (Coordinates: UTM 21J 0687503/6600663; Fig. 3) is located in the Santana do Livramento municipality, in the southwestern region of Rio Grande do Sul State, southern Brazil (Fig. 3A). The outcrop is an exposure on the right side of an unnamed secondary road, west of the Ibicuí d’Armada River, which gave its name to the region. In the entire region it is possible to see eolian deposits cropping out, though the fossil tracks are found in situ only in one small area of 10 m$^2$ (Fig. 3B). Permit for field work in this area was provided by the Departamento Nacional de Produção Mineral (Process Number: 000.820/2015).

Apparently, a single eolian dune deposit is exposed in the Ibicuí d’Armada outcrop, reaching nearly 1.5 m of height. This deposit is composed of a set of inverse graded strata with dip angles of 20° and 32°. The eolian paleoflow azimuths vary between 150° and 230°, with a mean of 187°. All these data were collected in situ. Beside the tracks described below, a tetrapod burrow also occurs in the same strata (Fig. S1 in the Supplemental Information File).
A total of five trackways (four complete trackways in plan view and one in cross-section) was discovered in the Ibicuí d’Armada outcrop. All the trackways were represented by four letters (SLIA), the first two referring to the municipal district (SL, Santana do Livramento) and the last two to the locality (IA, Ibicuí d’Armada). Arabic numbers differentiate the trackways among themselves (SLIA-1 to SLIA-5). The Roman numbers following the trackway abbreviation represents each footprint in the order of the successive set in the trackway. The trackways SLIA-1 and SLIA-4 occur in the same eolian stratum with a 20° inclination, while SLIA-2, SLIA-3 and SLIA-5 occur in another, with a 32° inclination.

The trackways were photographed in situ and subsequently replicated as silicon rubber casts that are housed in the Laboratório de Paleontologia de Vertebrados of the Universidade Federal do Rio Grande do Sul (UFRGS), in Porto Alegre (Brazil), under the collection numbers UFRGS-PV-0391-P (mold of the SLIA-1 tracks) and UFRGS-PV-0392-P (mold of the surface that contains the SLIA-2 and SLIA-3 tracks). Additionally, trackway SLIA-2 was collected and deposited in UFRGS under the number UFRGS-PV-0601-P. The quantitative and qualitative parameters of each footprint and the whole trackways were obtained based on the methodology proposed by Leonardi (1987). The morphology (i.e., number and shape of digits, autopodium axis, position of the autopodium) and measurements (i.e., width and length of each footprint, the divarication of the digits, length of the pace, oblique pace and stride, pace angulation, distance between manus and pes and the divarication of the manus from the midline) were obtained in situ using a measure tape and a caliper and confirmed using the free software ImageJ®. The trackway SLIA-5 (collected and deposited in UFRGS under the number UFRGS-PV-0602-P) is preserved in cross-section and its study follows the criteria proposed by Loope (1986). The gleno-acetabular distance (i.e., the distance between the center of the glenoid cavity and the center of the acetabular cavity) was estimated based on the measurement of the distance between the intersections with the midline of the line of the hands and of the line of the feet with both these lines being more or less subparallel (Leonardi, 1987).

A total of three approaches were used to determine the identities of the probable trackmakers. Firstly, the morphology and measurements were compared with several mid- to large-sized ichnotaxa found in Permian–Triassic deposits (Fig. 4). The main comparisons were made with the quadrupedal ichnotaxa recorded in eolian facies, such as Chelichnus Jardine, 1850 (including the type material proposed by Lull, 1918 and Gilmore, 1926 as “Laoporus,” “Agostopus,” “Allopus,” “Baropezia,” “Barypodus,” “Dolichopodus,” “Nanopus” and “Palaeopus,” all of them considered junior synonyms of Chelichnus by McKeever & Haubold, 1996); Navahopus Baird, 1980; and Brasilichnium Leonardi, 1981. However, in order to better understand the role of extramorphological variation of the Ibicuí d’Armada tracks, they were also compared with Permian–Cretaceous ichnotaxa produced in fluvio-lacustrine and volcaniclastic facies, such as Ameghinichnus Casamiquela, 1961; Brontopus Heyler & Lessertisseur, 1963; Catoecapes Mateus et al., 2017; Dicynodontipus Rühle von Lilienstern, 1944 (including “Calibarichnus” and
“Gallegosichnus”; Casamiquela, 1964; Pachypes Leonardi et al., 1975 (including “Sukhonopus”; Gubin et al., 2003); and Therapsipus Hunt et al., 1993.

In addition, the anatomy of the manus and pedes of Permo–Triassic tetrapods was analyzed, mainly in those taxa whose complete phalangeal formula was preserved, based on the available published data (see the bibliography). Lastly, the faunal composition of deposits of the same age (Lopingian–Induan) as that inferred for the “Pirambóia Formation” was considered.

RESULTS
Systematic Paleoichnology

Dicynodontipus Rühle von Lilienstern, 1944

Type ichnospecies. Dicynodontipus hildburghausensis Rühle von Lilienstern, 1944.

Diagnosis. Relatively narrow trackways, pace angulation at normal gait at least 100°, at higher pace angulation manus impressions can be overstepped, only at lower pace angulation manus impressions are positioned at short distance anterior to the feet. Manus and pes showing the same shape, plantigrade, pentadactyl; short, anteriorly orientated...
digits, digit IV the longest, digit V slightly laterally and posteriorly shifted (modified from Melchor & de Valais, 2006).

**Age and occurrence.** Permian–Triassic strata of Germany (Solling Formation, Buntsandstein of Thuringia), Italy (Val Gardena Sandstone of the Dolomites region), England (Helsby Sandstone of Cheshire), South Africa (Oudeberg Member of the Balfour Formation, Beaufort Group, Karoo Basin), Australia (Coal Cliff Sandstone of the Sidney Basin), Argentina (Vera Formation of the Los Menudos Depocentre; Sierra de las Higueras Formation of the Las Higueras-Santa Clara Basin; and Cerro de las Cabras Formation of the Cuyo Basin) and Brazil (Rio do Rasto and “Pirambóia” formations of the Paraná Basin) (Fig. 4; Table 1).

**Remarks.** The material that has been assigned to *Dicynodontipus* is highly variable in morphology and has a puzzling ichnotaxonomic history (Table 1). *Rühle von Liliensstern* (1944) erected this ichnogenus based on tracks from the Buntsandstein of

| Original description | Age and locality | Other interpretations |
|----------------------|------------------|----------------------|
| *Dicynodontipus hildburghausensis* (*Rühle von Liliensstern, 1944)* | Lower Triassic of Thuringia, Germany | *Chelichnus geinitzi* (*Haubold, 1965*) *Dicynodontipus geinitzi* (*Haubold, 1971a, 1971b*) |
| *Chirotherium geinitzi* (*Hornstein, 1876*) | Lower Triassic of Thuringia, Germany | *Chelichnus geinitzi* (*Haubold, 1965*; *Kahn, 1963*) *Dicynodontipus geinitzi* (*Haubold, 1971a, 1971b*) |
| *Onkichnium beasleyi* (*Kahn, 1963*) | Lower Triassic of Thuringia, Germany | *Dicynodontipus geinitzi* (*Haubold, 1971a, 1971b*) |
| *Agostropus falcatus* (*Rühle von Liliensstern, 1939*) | Lower Triassic of Thuringia, Germany | *Dicynodontipus geinitzi* (*Haubold, 1971a, 1971b*) |
| *Dicynodontipus geinitzi* (*Conti et al., 1977*) | Lopingian of Trentino-Alto Adige, Italy | *Dicynodontipus* isp. (*Avanzini et al., 2001*; *Avanzini & Tomasoni, 2004*; *Marchetti, Voigt & Klein, 2017*) *Dicynodontipus geinitzi* (*Avanzini, Bernardi & Nicosia, 2011*; *Bernardi et al., 2017*) |
| *Dicynodontipus icelsi* (*De Klerk, 2002*) | Lopingian of the Eastern Cape, South Africa | cf. *Dolomitipes* isp. (*Marchetti, Voigt & Klein, 2017*) |
| *Dicynodontipus bellambiensis* (*Retallack, 1996*) | Lower Triassic of New South Wales, Australia | – |
| *Calibarichnus ayesterani* (*Casamiquela, 1964*) | Upper Triassic of Río Negro, Argentina | *Dicynodontipus* isp. (*Melchor & de Valais, 2006*) |
| *Gallegosichnus garridoi* (*Casamiquela, 1964*) | Upper Triassic of Río Negro, Argentina | *Dicynodontipus* isp. (*Melchor & de Valais, 2006*) |
| *Palaciosichnus zetti* (*Casamiquela, 1964*) | Upper Triassic of Río Negro, Argentina | *Dicynodontipus* isp. (*Melchor & de Valais, 2006*) |
| *Stipanicichnus bonnetti* (*Casamiquela, 1975*) | Upper Triassic of Río Negro, Argentina | *Dicynodontipus* isp. (*Melchor & de Valais, 2006*) |
| cf. *Dicynodontipus* (*Leonardi, 1994*) | Middle Triassic of Mendoza, Argentina | – |
| cf. *Dicynodontipus* (*Leonardi, Sedor & Costa, 2002*) | Guadalupian–Lopingian of Paraná, Brazil | *Dicynodontipus* isp. (*Silva, Sedor & Monteiro-Filho, 2012*) *Dicynodontipus penugu* (*Silva, Sedor & Fernandes, 2012*) Non-*Dicynodontipus* (*Marchetti, Voigt & Klein, 2017*) |
| *Dicynodontipus protherioides* (*Silva et al., 2008*) | Upper Triassic of Río Grande do Sul, Brazil | *Procolophonichnium* isp. (*Klein, Lucas & Voigt, 2015*) |

**Note:** The type material is indicated by the asterisk.
Hildburghausen (Thuringia, Germany), coining the ichnospecies *D. hildburghausensis*. The material previously described by Hornstein (1876) as *Chirotherium geinitzi* was lately classified within the ichnogenus *Chelichnus* by Haubold (1965), proposing the new combination *C. geinitzi*. Some years later, Haubold (1971a, 1971b) reinterpreted both materials as *D. geinitzi*. Since then, several authors (e.g., Conti et al., 1977; Retallack, 1996; Melchor & de Valais, 2006; Silva et al., 2008; Silva, Sedor & Fernandes, 2012; Marchetti, Voigt & Klein, 2017, among others) have followed Haubold’s (1971a, 1971b) assignment, using *D. geinitzi* as the type-ichnospecies of *Dicynodontipus*. However, this is contrary to the Paragraph 61.1.3. of the Article 61 of the International Code of Zoological Nomenclature (*ICZN*, 1999), which claims that “the name-bearing type of any nominal taxon, once fixed in conformity with the provisions of the Code, is not subject to change.” Therefore, *D. hildburghausensis* must be considered the type-material of the ichnogenus *Dicynodontipus*, even if the name *D. geinitzi* is considered a senior synonym. Table 1 summarizes the main historical changes in the ichnotaxonomic interpretation of the materials attributed to *Dicynodontipus*.

Nevertheless, other materials from Argentina, Australia, Brazil, England, Italy and South Africa have been described since then (Fig. 4; Table 1). The specimens from the Lopingian Val Gardena Sandstone (northern Italy) were originally interpreted as *D. geinitzi* (Conti et al., 1977), but recently reinterpreted as *Dicynodontipus* isp. (Marchetti, Voigt & Klein, 2017). Melchor & de Valais (2006) also recognized the presence of four different ichnospecies of *Dicynodontipus* in the Upper Triassic Vera Formation of Rio Negro, Argentina, all of them originally described by Casamiquela (1964, 1975) as distinct, endemic ichnogenera. In addition, Leonardi (1994) reported the presence of cf. *Dicynodontipus* in the Sierra de las Higueras Formation of Mendoza, also in Argentina. Although the age of this unit is not well-known, Bonaparte (1966) proposed a Ladinian age for these tracks.

Leonardi, Sedor & Costa (2002) described the presence of *Dicynodontipus* isp. in the Guadalupian–Lopingian Morro Pelado Member of the Rio do Rasto Formation from the Paraná State, Brazil. This record was later revisited by Silva, Sedor & Fernandes (2012), who proposed a new ichnospecies: *D. penugnu*. Silva et al. (2008) described *D. protherioides* from the Upper Triassic deposits of the Alemao Member of the Santa Maria Formation (*Hyperodapedon* Assemblage Zone; Candelária Sequence) of the Rio Grande do Sul State, in southern Brazil. But these materials were reinterpreted by Klein, Lucas & Voigt (2015) as belonging to *Procolophonichnium*.

New ichnospecies were also described from the Lower Triassic of Australia (*D. bellambiensis*; Retallack, 1996) and the Lopingian of South Africa (*D. icelsi*; De Klerk, 2002). The later was reinterpreted by Marchetti, Voigt & Klein (2017) as belonging the ichnogenus *Dolomitipes*. Klein & Niedźwiedzki (2012) reported the presence of tracks similar to *Dicynodontipus* in the Olenekian Wióry Formation of the Holy Cross Mountain of southern Poland, but the incompleteness and suboptimal preservation do not allowed a definitive assignment.
Dicynodontipus isp.

**Referred material.** The trackway SLIA-1, a set of 14 consecutive footprints, and the respective mold (UFRGS-PV-0391-P).

**Horizon and locality.** Ibicuí d’Armada locality (21J 0687503/6600663), Santana do Livramento municipality, southwestern region of Rio Grande do Sul State, southern Brazil; “Piramboíia Formation,” Lopingian–Induan of the Paraná Basin.

**Description:** The SLIA-1 trackway consists of a set of 14 footprints (eight *pes* and six *manus* impressions) preserved as concave epireliefs and produced by a quadrupedal...
animal (Fig. 5). No tail- or body-drag traces were observed in association with the set of footprints. Claw-drag traces are not seen in both manus and pedes, except for the pedal track SLIA-1-V (Figs. 5F–5G). The mean internal and external trackway widths are 155 and 328.3 mm, respectively.

The manus imprints are pentadactyl, mesaxonic (i.e., the main digit is the central one; Leonardi, 1987) and semi-palmigrade to digitigrade (i.e., the tracks are formed only by the impressions of the anterior portion of the manus or only by the digits; Leonardi, 1987), with a straight proximal end of the palm. The mean sizes of the manus prints are 47.5 mm length and 72.33 mm width, with a width/length ratio of about 1.52 (Table S1 in the Supplemental Information File). The manus prints are deeper than the pedal ones, showing a mean depth of about 46 mm (Table S1 in the Supplemental Information File). The mean values of the manual oblique pace length, pace angulation and stride length are about 274.2 mm, 57.5° and 261.2 mm, respectively (Table S2 in the Supplemental Information File). The manus impressions show a negative (inward) divarication from the midline of about 30° (Table S1 in the Supplemental Information File) and are located about 165 mm from the associated pes print (Table S2 in the Supplemental Information File).

The pes prints are plantigrade (i.e., formed by the impression of the complete autopodium; Leonardi, 1987), nearly mesaxonic and also pentadactyl (Figs. 5C–5G). The heel is elongated, with a V-shaped sole in the proximal end, giving a subtriangular shape to the entire footprint. The pedes are directed forward, being sub-parallel to the midline. The mean sizes of the pes tracks are about 77.83 mm length and 86 mm width, with a width/length ratio about 1.10. (Table S1 in the Supplemental Information File). The mean of the pedal oblique pace length, pace angulation, stride length and depth are about 262.8 mm, 64.6°, 280.8 mm and 38.87 mm, respectively (Table S2 in the Supplemental Information File). The DPIA-1-I pes track has a well preserved sole pad, which covers almost the entire heel (Figs. 5D–5E). The proximo-lateral zone of the sole pad is very marked and represents the deepest part of the track. Also, at least one nearly round phalangeal pad can be recognized in each pedal digit of DPIA-1-I.

The gleno-acetabular distance of the trackmaker is estimated as 408.8 or 300.5 mm, respectively, considering alternate walk and amble gaits.

Remarks. As pointed out by McKeever & Haubold (1996), a digitigrade stance is not inferred from the Permian tetrapod body fossil record. According to these authors, the manual digitigrady present in some Chelichnus tracks (making reference to those from Scotland) is due to their preservation. Actually, it can be a variation related to the gait of a palmigrade producer, especially when made upslope or downslope in eolian sediments. Once the SLIA-1 travel direction is upslope, we use the same argument to explain the digitigrady of its manus tracks.

Chelichnopodidae Lockley, 2011
Chelichnus Jardine, 1850

Type ichnospieces. Chelichnus duncani (sensu Owen, 1842) Jardine, 1850.
Revised diagnosis. Tetrapod trackways with mammal-like reptile (theromorph) characteristics; complete manus and pes impressions rounded and of nearly equal size; manus impressions usually slightly smaller in size and, apparently, more digitigrade in style; pes impression size ranges from approximately 10 mm up to approximately 200 mm in length. Complete manus and pes impressions show round pads with up to five short digits, although usually only three to four digits are found impressed; first four digits directed anteriorly and display low degree of divarication with fifth digit situated markedly postero-laterally; digits usually somewhat separated from sole. Normal trackway pattern shows pes pace angulation of up to 90°, with manus and pes impressed close together, or with slight overlap of pes on manus (after McKeever & Haubold, 1996).

Age and occurrence. Permian strata of Scotland (Corncockle Sandstone Formation of the Lochmaben Basin; Locharbriggs Sandstone Formation of the Dumfries Basin; and Hopeman Sandstone Formation of the Elgin area), Germany (Cornberger Sandstein of Hessen), southwestern USA (Coconino Sandstone, Arizona; DeChelly Sandstone, Arizona; Lyons Sandstone, Colorado; Cedar Mesa Sandstone, Utah; and Casper Sandstone, Wyoming and Colorado), Argentina (Yacimiento Los Reynos Formation of the San Rafael Block and Patquía Formation of the Paganó Basin) and Brazil (“Pirambéia Formation” of the Paraná Basin) (Fig. 4; Table 2).

Remarks. Despite the proposition of McKeever & Haubold (1996) that the ichnogenus Chelichnus is restricted to the late Permian, and it should not be expanded to include trackways from older or younger strata, important material of Chelichnus has been described from the Coconino Sandstone (USA) and the Yacimiento Los Reynos Formation (Argentina), both Cisuralian in age (Lull, 1918; Gilmore, 1926; Cei & Gargiulo, 1977, Krapovickas et al., 2014).

As in Dicynodontipus, Chelichnus encompasses a wide range of morphological variation in tracks made in eolian deposits. The ichnogenus was erected by Jardine (1850) in order to reallocate the tracks described by Owen (1842) as Testudo duncani. Several other similar ichnotaxa found in eolian deposits of Scotland, Germany, and the USA were erected (Table 2; e.g., Harkness, 1850; Harkness, 1851; Jardine, 1853; Huxley, 1877; Dudgeon, 1878; Lull, 1918; Gilmore, 1926, 1927; Schmidt, 1959; Delair, 1966; McKeever, 1994), but they were reassigned to Chelichnus by McKeever & Haubold (1996). In addition, besides the four Chelichnus ichnospecies recognized by McKeever & Haubold (1996) (i.e., C. bucklandi, C. duncani, C. gigas and C. titan), three others were also erected: C. incurvus Gand, Demathieu & Ballestra (1995), C. lutevanus Ellenberger (1984) and C. tazelwürmi Ceoloni et al. (1988). The latter was recently re-evaluated (Citton et al., 2017) and now it belongs to the ichnogenus Contiichnus, but the taxonomic meaning of the two former ichnospecies is still problematic.

Andreis & Carvalho (2001) described about 82 isolated tracks from the Pau Preto Quarry at the Taquáí municipality (São Paulo State), where the Guadalupian–Lopingian Corumbatá Formation crops out. According to the authors, these tracks are tridactyl and, based on the age of this unit (considered Lopingian–Early Triassic at that time), they were attributed to archosaurs. These tracks were not collected and were subsequently
Table 2  Summary of the main ichnotaxonomic changes of the materials assigned to *Chelichnus*.

| Original description                                                                 | Other interpretations                                             |
|--------------------------------------------------------------------------------------|------------------------------------------------------------------|
| *Agostopus matheri* (Gilmore, 1926), *Amblyopus* (Schmidt, 1959), *Baropezia eakini* (Gilmore, 1926), *Barypodus gravis* (Schmidt, 1959), *Barypodus metzeri* (Gilmore, 1927), *Barypodus mildei* (Schmidt, 1959), *Barypodus tridactylus* (Gilmore, 1927), *Chelichnus ambiguus* (Jardine, 1853), *Chelichnus locharbriggsensis* (McKeever, 1994), *Chelichnus plagiopterus* (Jardine, 1853), *Chelichnus *tripodizon* (Schmidt, 1959), *Harpagichnus acutum* (Schmidt, 1959), *Herpetichnus laxodontus* (Dudgeon, 1878), *Herpetichnus sauroplesius* (Jardine, 1850), *Laoporus noblesi* (Lull, 1918), *Nanopus maximus* (Gilmore, 1927), *Palaepus regularis* (Gilmore, 1926), *Palmichnus resinum* (Schmidt, 1959), *Phalangichnus alternans* (Schmidt, 1959), *Phalangichnus similans* (Schmidt, 1959), *Testudo duncani* (Owen, 1842) | *Chelichnus duncani* (McKeever & Haubold, 1996) |
| *Amblyopus pachypodus* (Gilmore, 1927), *Barypodus palmatus* (Gilmore, 1926), *Chelichnus megalichrus* (Huxley, 1877), *Herpetichnus robustus* (Delair, 1966) | *Chelichnus gigas* (McKeever & Haubold, 1996) |
| *Allopus arizonae* (Gilmore, 1926)                                                   | *Chelichnus titan* (McKeever & Haubold, 1996)                    |
| *Chelichnus incurvus* (Gand, Demathieu & Ballestra, 1995)                          | –                                                               |
| *Chelichnus lutevanus* (Ellenberger, 1984)                                          | –                                                               |
| *Chelichnus tazelwurmi* (Ceoloni et al., 1988)                                      | *Contiichnus tazelwurmi* (Citton et al., 2017), *Contiichnus tazelwurmi* (Bernardi et al., 2017), *Procolophonichnium tirolensis* (Marchetti, Voigt & Klein, 2017) |
| Indeterminate tracks (Andreis & Carvalho, 2001)                                    | Tridactylichnium isp. (Silva & Fernandes, 2004; Silva & Fernandes, 2005), *Chelichnus* isp. (Silva, Sedor & Fernandes, 2012), Non-Chelichnus (This paper) |

Note: The type material is indicated by the asterisk.

Francischini et al. (2018), *PeerJ*, DOI 10.7717/peerj.4764

destroyed. *Silva & Fernandes* (2004, 2005) attributed preliminarily these tracks to *Tridactylichnium* isp. (a *nomen dubium* according to Marchetti, Belvedere & Mietto, 2017) and, more recently, *Silva, Sedor & Fernandes* (2012) redescribed these tracks, based on digitally enhanced versions of the original images of *Andreis & Carvalho* (2001), and attributed them to *Chelichnus* isp. However, there are some discrepancies between the poorly preserved morphology of the tracks and the interpretive drawing of *Silva, Sedor & Fernandes* (2012), such as the estimation of the digit count and the outline of each imprint. Therefore, we do not consider valid the ichnotaxonomy proposed for the Corumbataí tracks (*Silva, Sedor & Fernandes, 2012*). Thus, at present, the “Pirambóia Formation” contains the only valid record of *Chelichnus* in Brazil.

*Chelichnus bucklandi* Jardine, 1850

**Referred material.** SLIA-2 (UFRGS-PV-0601-P), a set of 14 consecutive footprints; SLIA-5 (UFRGS-PV-0602-P), a small slab of tracks in cross-section. The silicon mold UFRGS-PV-0392-P includes the trackway SLIA-2.
Horizon and locality. Ibicuí d’Armada locality (21J 0687503/6600663), Santana do Livramento municipality, southwestern region of the Rio Grande do Sul State, southern Brazil; “Pirambóia Formation,” Lopingian–Induan of the Parana Basin.

Revised diagnosis. Chelichnus in which pes length ranges from 10 to 25 mm; pes digit base II–IV separation does not exceed 15 mm; mostly digitigrade but also occasionally plantigrade; trackway pattern most strongly influenced by substrate and slope conditions and may become very irregular in preservation; trackway often found preserved as undertracks (after McKeever & Haubold, 1996).

Description. The specimen SLIA-2 (UFRGS-PV-0601-P) is a set of 14 shallow tracks, preserved in concave epirelief (Figs. 6A–6B). Trackway with a wide gauge and marked homopody (i.e., the manus and pes are dimensionally and morphologically the same; Leonardi, 1987). The mean values of the oblique pace length, pace angulation and stride length are about 66.3 mm, 83.5° and 84.5 mm, respectively (Table S3 in the Supplemental Information File). The mean internal and external trackway widths are about 12.9 and 74.8 mm.

The autopodia are wider than long (width/length ratio about 1.64) and have an elliptical shape (Table S4 in the Supplemental Information File). The digit imprints are not preserved, but paraxonic or mesaxonic conditions are inferred by the oval shape of the tracks. Some autopodia are oriented inwards (about 21°). The digits cannot be recognized in any track, and tail- or body-drag traces are not present. Displacement rims of sediment and “sand crescents” are not present.

The gleno-acetabular distance inferred for the SLIA-2 trackmaker is about 121.4 or 78.9 mm, considering alternative walk or amble gaits, respectively.

SLIA-5 (UFRGS-PV-0602-P) preserves some indeterminate autopodia imprints in cross-section, easily recognized by the folded laminae of the substrate (Figs. 6C–6D). They are concave up, about 15 mm long, and the deformed layers are 6 mm deep. On one of the sides of the slab, it is possible to see two potential consecutive tracks that are 108.9 mm apart. Despite the lack of morphological details, the measurements of these tracks are in accordance with those expected for C. bucklandi. Therefore, we attribute the tracks preserved in cross-section on the slab UFRGS-PV-0602-P to this ichnospecies. The level in which these tracks were produced is 8.2 mm below the SLIA-1 and SLIA-2 level, so we consider them contemporaneous.

Remarks. SLIA-2 has several features that often occur in chelichnopodid trackways with an uphill travel direction, such as: alternate gait, notable homopody, wider than long autopodia with inward rotation and absence of distinct digits and sole/palm pads. These characters are present in several C. bucklandi tracks from the Coconino Sandstone (such as MNA-V3331, MNA-V3338 and MNA-V3349), DeChelly Sandstone (such as MNA-V3456) and Brasilichnium elusivum tracks from the Lower Cretaceous Botucatu Formation of Brazil (such as the type-materials MN-3902-V and MN-3903-V) (Fig. 7). However, B. elusivum has marked heteropody (i.e., manus and pes are dimensionally and/or morphologically different; Leonardi, 1987) and manus imprints are not that often preserved or shallowly imprinted (Fig. 7), so the SLIA-2 tracks are closely more similar to C. bucklandi.
As discussed by Loope (1986), tetrapod tracks in cross-section are easily misinterpreted as non-biogenic deformation structures such as lateral compression or convolute bedding. However, convolute bedding is an indication of rapid deposition, so it is not congruent with the eolian strata in which the tracks were found (Loope, 1986; Collinson & Thompson, 1982). Lateral compression structures in sand tend to have a large size and are...
not common in strata deposited by grain saltation (Loope, 1986; McKee, Douglass & Rittenhouse, 1971). According to Mancuso et al. (2016), the biogenic origin of the structures in cross section from the Areniscas Altigradas Member of the Yacimiento Los Reyunos Formation in Argentina were justified by their frequency in size and regular shape, features also observed in the Brazilian materials. Additionally, the size of the cross-section structures described here (SLIA-5; UFRGS-PV-0602-P) is in accordance with the C. bucklandi tracks from the same strata (i.e., SLIA-2). Also, given that the tracks recorded in the bedding plane do not show any sort of compression or deformation, this is strongly indicative that the eolian strata of the Ibicuí d’Armada locality were only disturbed by biogenic activity.

**Indeterminate tracks**

**Referred material.** SLIA-3, a set of six consecutive footprints; SLIA-4, a set of 22 tracks. Both are recorded in the silicon mold UFRGS-PV-0392-P.

**Horizon and locality.** Ibicuí d’Armada locality (21J 0687503/6600663), Santana do Livramento municipality, southwest region of Rio Grande do Sul State, southern Brazil; “Pirambóia Formation,” Lopingian–Induan of the Paraná Basin.

**Description.** The trackway SLIA-3 is a set of six tracks that occurs in the same bedding plane as SLIA-2 (C. bucklandi; Figs. 3B and 6A). All the tracks are poorly preserved so they could not be assigned to an ichnotaxon. The mean length and width of the tracks are 165 and 157.5 mm, respectively, representing the largest tracks recorded in the Ibicuí d’Armada outcrop. The width/length ratio is 0.95, and the distance of the tracks from the trackway midline is 100.6 mm (Table S5 in the Supplemental Information File). Oblique pace length and stride length reach 416 and 315 mm, respectively (Table S6 in the Supplemental Information File).

The trackway SLIA-4 is a set of 22 tracks (Figs. 3B and 8) whose limits and dimensions are difficult to identify. The manus and pedes are not well enough preserved for us to be able to characterize them. Although SLIA-4 shares with SLIA-1 the same bedding plane, size and travel direction, it is poorly preserved, preventing an accurate ichnotaxonomic assignment. Additionally, there is a fracture that exposes the sandstone layer below that in which the original tracks were produced, so that almost two-thirds of the SLIA-4 tracks are preserved as undertracks (Fig. 8). In spite of being at the same level as SLIA-1, the original SLIA-4 (the remaining one-third) tracks present displacement rims positioned in the posterior margin of the autopodium impressions.

**DISCUSSION**

**Ichnotaxonomic comparison**

The specimens described here as Dicynodontipus isp. and C. bucklandi share several morphological features with other ichnotaxa, mainly C. duncani Jardine, 1850, Brasilichnium Leonardi, 1981, Navahopus Baird, 1980 and some material attributed to Dicynodontipus Rühle von Lilienstern, 1944.

Triangular-shaped tracks (similar to SLIA-1) occur in materials attributed to C. duncani. For example, the material proposed by Gilmore (1926) to be the holotype of
“Baropezia eakini” (USNM-11137; now considered to be a junior synonym of C. duncani; Fig. 9A; McKeever & Haubold, 1996) has deep tracks, with subtriangular pedes and a suboval manus, which are evident in both part and counterpart. The specimen USNM-11138 (formerly, the paratype of “B. eakini”) also presents the same morphology, but due
to its suboptimal preservation, the complete shapes of the tracks are not so evident. However, the SLIA-1 tracks are different from “B. eakini” mainly in the forward orientation of the pes tracks and the manual digitigrady. In addition, the specimen USNM-11137 has rounded digits (Fig. 9A), which is very different from the typical Chelichnus tracks, but more like the drumstick-shaped digits of Ichniotherium (Voigt, Berman & Henrici, 2007). In USNM-11138, the right digit traces are longer and seems to form drag marks (Fig. 9B). Notwithstanding, the similarity between the triangular shape of “B. eakini” and SLIA-1 tracks, the digit configuration of the former prevents an assignment of the Brazilian tracks to C. duncani.

The SLIA-1 tracks are also close in morphology to C. duncani (=“Agostopus matheri”) from the DeChelly Sandstone of Arizona, mainly with those where the travel orientation

Figure 8 Indeterminate tracks (SLIA-4) from the “Pirambóia Formation,” Brazil. The dashed line indicates a fracture in the substrate, causing differences in the preservation of the tracks. Black arrows indicate the displacement rims on the posterior margins of the true tracks and the white arrow indicates the direction of the trackmaker’s travel. Scale: 15 cm.
is straight uphill (such as MNA-V1556; Fig. 9B), which have anteriorly or slightly inward oriented autopodia and short strides. However, some specimens (such as MNA-V3442) have particular features that result from the change in the gait adopted during downhill locomotion on dunes, such as strong inward rotation of both manus and pedes, incomplete palm and sole imprints, long strides and digit drag traces (Morales & Haubold, 1995). Even though the SLIA-1 trackway is clearly oriented uphill, its manual tracks are also rotated inwards, whereas the feet point anteriorly.

Brasilichnium also comprises quadrupedal, heteropod, synapsid-related tracks with a rounded to transversely oval shape, being grouped with Chelichnus under the ichnofamily Chelichnopodidae (Fig. 7; Leonardi, 1981; Fernandes & Carvalho, 2008; Lockley, 2011). However, they differ mainly by the digit count (Chelichnus is pentadactyl, though Brasilichnium is tetradactyl) and by the marked heteropody presented by Brasilichnium (Leonardi, 1981; Fernandes & Carvalho, 2008; Lockley, 2011). The ichnogenus Brasilichnium was initially erected to describe only one of the mammaloid track morphotypes from the Lower Cretaceous Botucatu Formation of Brazil (Fig. 7; Leonardi, 1981), but it was also recognized in several eolian and non-eolian units throughout the Mesozoic of Brazil, Namibia and the United States (Hunt & Lucas, 2006; Fernandes & Carvalho, 2008; Lucas et al., 2010; Lockley, 2011; Porchetti & Wagensommer, 2015). Brasilichnium is also known by its wider temporal range (Late Triassic–Late Cretaceous), contrasting with Chelichnus, which is confined to the Permian (McKeever & Haubold, 1996). However, both ichnogenera do not occur in the same strata, and there is a gap without chelichnopodid tracks between the latest Permian and the Late Triassic. Therefore, both morphology and temporal range are in favor of an interpretation of the SLIA-2 tracks as belonging to Chelichnus.

Another ichnotaxon that is similar to the tracks described here is the poorly known Navahopus falcipollex, from the Lower Jurassic Navajo Sandstone of the western USA (Figs. 10A–10C; Baird, 1980; Hunt & Lucas, 2006). Although the validity of this ichnotaxon was disputed because it is known only by its suboptimally preserved type material (MNAV3430; Lockley & Hunt, 1995; Lockley et al., 1995; Lockley & Tedrow, 2009), it is currently considered valid (Hunt & Lucas, 2006; Lockley, 2011). N. falcipollex was
described by Baird (1980) as tracks of a quadrupedal, heteropodous and tetradactyl animal with falciform pollexes that are directed inwards. But, according to Hunt & Lucas (2006), this latter character is more likely an extramorphological feature, an opinion that is closely followed here. The reinterpretation of the claw traces of Navahopus approximates this ichnogenus morphologically to the Chelichnopodidae. Actually, several authors noted the similarity between Navahopus and Brasilichnium (Lockley & Hunt, 1995; Hunt & Lucas, 2006; Reynolds, 2006; Lockley & Tedrow, 2009; Lockley, 2011), including Milán, Loope & Bromley (2008), who reinterpreted a trackway previously attributed to Brasilichnium by Loope & Rowe (2003) as a different ichnospecies of Navahopus (N. coyoteensis). However, N. falcipollex has pes imprints that are longer than wide, different from the usually wider than long pes tracks of Chelichnus and Brasilichnium (Hunt & Lucas, 2006). Notwithstanding, this feature is also present on the SLIA-1 trackway, which differs from N. falcipollex mainly in the pedal digit count and the divarication of the manus (inward directed in the Brazilian tracks). Also, the “Pirambóia” tracks have more defined triangular-shaped feet, contrasting with the triangular to

Figure 10 Navahopus falcipollex (A–C) and Dicynodontipus isp. (D–E) tracks. (A) Specimen MNA-V3430 (Holotype) from the Navajo Sandstone (Lower Jurassic of the Unites States). (B–C) Details of the same specimen. Note the marked heteropody and the tetradactyly in Navahopus, but absent in the “Pirambóia” tracks. (D) Specimen MLP-66-XI-15-3 (“Gallegosichnus garridoi”). (E) Specimen MLP-60-XI-31-4 (“Calibarichnus ayesterani”). (D–E) from the Vera Formation (Upper Triassic of Argentina). Scales: 15 cm (A) and 5 cm (D–E).
rounded pedes of *N. falcipollex*, which have been more influenced by extramorphological variation.

In addition to the *Brasilichnium* classic gait, represented by its type ichnospecies *B. elusivum* Leonardi (1981), two other ichnospecies were recently erected: *B. saltatorium* Buck et al. (2017a), which is represented by the hopping variation in the gait of the same producer of *B. elusivum*; and *B. anaiti* Porchetti, Bertini & Langer (2017), a supposed large form of *Brasilichnium*. Porchetti, Bertini & Langer (2017) noted that *B. anaiti* is extremely similar to *Navahopus* but they were not able to stress the differences between both ichnotaxa.

Simultaneously, Buck et al. (2017b) described the same material as belonging to a new monospecific ichnogenus, *Aracoaraichnium leonardii*, but they also ignored *Navahopus*. Although it is not within the scope of this contribution to revise these newly proposed ichnotaxa (Buck et al., 2017b; Porchetti, Bertini & Langer, 2017), we are confident that *B. anaiti* and *A. leonardii* are junior subjective synonyms of *Navahopus*, especially because the morphology of both is very much influenced by the extramorphological features related to walking on eolian sands (e.g., the manual digit count and variation of the manus shape) and it is not possible to differentiate the anatomical differences between their trackmakers. As explained above, the morphology of the SLIA-1 tracks indicates that it is closely related to *Navahopus, B. anaiti* and *A. leonardii*. However, the pentadactyly and the inward rotation of the manus imprints (not seen in *N. falcipollex*, *B. anaiti* and *A. leonardii*) are sufficient to differentiate them and place SLIA-1 within the ichnogenus *Dicynodontipus*.

Besides the typical ichnotaxa of the *Chelichnus* Ichnofacies (i.e., *Chelichnus, Brasilichnium* and *Navahopus*), the most similar tracks are some of those described by Casamiquela (1964, 1975) from the Upper Triassic volcanioclastic Vera Formation of the Los Menucos Depocentre (Río Negro Province) of Argentina (Figs. 10D–10E). Originally, Casamiquela (1964, 1975) recognized four theromorphoid ichnotaxa (“*Calibarichnus ayesterani,*” “Gallegosichnus garridoi,” “Palaciosichnus zetti” and “Stipanicichnus bonnetti”) that are currently interpreted as belonging to four different ichnospecies of *Dicynodontipus* (Melchor & de Valais, 2006). Two of these ichnotaxa (“*C. ayesterani*” and “*G. garridoi*”) are represented by triangular, pentadactyl footprints with short and broad digits, which are clearly similar to the SLIA-1 tracks of Brazil (Figs. 10D–10E).

The type materials of “*Calibarichnus*” and “*Gallegosichnus*” were interpreted originally as being produced by the right autopodia of the trackmaker (Casamiquela, 1964; Melchor & de Valais, 2006), which implies an outward rotation of the manus. However, Leonardi & Oliveira (1990) and Domnanovich et al. (2008) described new, more complete material from the Cerro de las Lajas locality, with a clear inward position of the manus with respect to the track midline. According to these authors, the foot imprints are oriented forward (Domnanovich et al., 2008). These features are also seen in the tracks attributed to “*Gallegosichnus*” (Casamiquela, 1964; Leonardi & Oliveira, 1996; Domnanovich & Marsicano, 2006; Domnanovich et al., 2008), although the opposite pattern was proposed by Melchor & de Valais (2006). In a general overview, both “*Calibarichnus*” and “*Gallegosichnus*” share several characters with the SLIA-1 tracks: these quadrupedal
trackways are composed of an inward oriented manus placed anterior to the pentadactyl, nearly mesaxonic, plantigrade, forward oriented and triangular-shaped pes imprint (Figs. 10D–10E). Because the Los Menudos tracks preserve several fine details (such as digits and sole/palm pads), we understand that they reliably represent the anatomy of the trackmakers, and their similarity to the SLIA-1 tracks should correspond to the anatomical similarity of the producers.

*Dicynodontipus hildburghausensis* and *D. geinitzi*, from the Early Triassic of Germany, also shares several features with SLIA-1 (*Hornstein*, 1876; *Rühle von Lilienstern*, 1944). *D. geinitzi* is an ichnotaxon of a quadrupedal, homopod animal, with the phalangeal formula 2-3-3-3-3 (*Rühle von Lilienstern*, 1944; *Haubold*, 1965). The manus is rotated inwards (30°–40°) and the pedes are positioned parallel to the trackway midline (*Rühle von Lilienstern*, 1944), as occur in the Ibicuí d’Armada tracks. Nevertheless, in contrast to the German material, the “Pirambóia” tracks have only one metacarpal pad preserved in each pes, a condition equivalent to the *Dicynodontipus* isp. (i.e., “*Calibarichnus*” and “*Gallegosichnus*”) from Argentina.

*Citton et al.* (2017) have noted the similarity between *D. geinitzi* and *Contiichnus tazelwurmi* (Lopingian of Italy), this latter originally described as “*Chelichnus* tazelwürmi.” As stated by these authors, *C. tazelwurmi* differs from *Chelichnus* mainly because of its strong heteropody, manual entaxyony, the triangular shape of the pes and the continuity between the sole/palm print and the digit prints (*Citton et al.*, 2017; *Bernardi et al.*, 2017). On the other hand, *Marchetti, Voigt & Klein* (2017) consider that this material belongs to the ichnogenus *Procolophonichnium* (Table 2).

Among other *Dicynodontipus* ichnospecies, *D. icelsi* from the late Permian Asante Sana paleosurface in the *Cistecephalus* Assemblage Zone of the Karoo Basin (South Africa) is the ichnotaxon that shares more features with SLIA-1 (*De Klerk*, 2002). *De Klerk* (2002) described *D. icelsi* based on seven trackways (H, J, K, N, P, Q and Z) produced by a quadrupedal and heteropodous, medium-sized animal. The manus and pedes of *D. icelsi* are pentadactyl, plantigrade and wider than long (*De Klerk*, 2002), similar to SLIA-1 from Brazil. However, *D. icelsi* has long digit imprints (*De Klerk*, 2002), which do not occur in the Brazilian tracks. The trackway also has an alternate gait, and both autopodia vary in divarication, being inward oriented (as in the trackway Z) or with the main axis parallel to the trackway midline (as in the trackway Q). Additionally, *D. icelsi* has well marked and rounded pedal pads, different from the SLIA-1 pads, which give a triangular shape to the feet. Although SLIA-1 has the same alternating gait, its manus imprints are always oriented inward, at about 30°, whereas its pedes imprints point forward. However, as seen in several *Chelichnus* materials (e.g., the specimens RAM 123 and RAM 131) from the Coconino Sandstone, autopodium divarication can change in response to the variation of dune slopes and the direction of travel relative to the dune crest. As discussed below, the ichnotaxonomy of these tracks formerly assigned to *Dicynodontipus* is not universally accepted and *Marchetti, Voigt & Klein* (2017) assigned them to *Dolomitipes* isp. (Table 2).

Another large *Dicynodontipus* track is *D. bellambiensis* from the Lower Triassic Coal Cliff Sandstone of Australia (*Retallack*, 1996). However, despite its size and Early Triassic...
age, it is very different from SLIA-1, mainly in having long (19–54 mm) and much
divaricated digits (about 65º–133º) and a forward oriented manus (Retallack, 1996).

The trackway SLIA-1 also shares several features with Pachypes, a pareiasaur-related
ichnogenus from the Lopingian Val Gardena Sandstone and Bellerophon Formation of
Italy and the Ikakern Formation of Morocco (Leonardi et al., 1975; Valentini, Conti &
Nicosia, 2008; Valentini, Nicosia & Conti, 2009; Voigt et al., 2010). Both have a strongly
inward turned manus and forward directed pedes, with well-developed sole impressions
(Leonardi et al., 1975; Valentini, Nicosia & Conti, 2009). However, the pedes of Pachypes
are markedly ectaxonic (i.e., the most important digit is the digit IV; Leonardi, 1987),
with a small digit V that is consistent with pareiasaurian foot morphology (Valentini,
Conti & Nicosia, 2008), whereas the mesaxonic pedes of SLIA-1 fit better with therapsid
morphology (see below). Additionally, it is important to mention the similarity between
the alternate gait of SLIA-1 and TW-1, a trackway first described as “Sukhonopus” by
Gubin & Bulanov (in Gubin et al., 2003) and later synonymized with Pachypes (Valentini,
Conti & Nicosia, 2008). According to Gubin & Bulanov (in Gubin et al., 2003), manus
and pedes of “Sukhonopus” are arranged in the alternately opposite pattern of Haubold
(1971b), a pattern also observed in SLIA-1. However, this gait pattern is not
ichnotaxonomically diagnostic, because several quadrupedal animal taxa can produce
alternating trackways when they walk with normal paces (sensu Leonardi, 1987), including
the Chelichnus trackmakers (see examples in Gilmore, 1926).

Another medium- to large-sized Permian ichnogenus is Brontopus from the upper
Permian of the Lodève Basin of France (Heyler & Lessertisseur, 1963; Gand et al., 2000).
Although Gand et al. (2000) have compared this French ichnotaxon with Chelichnus
from the Elgin area of Scotland and considered them very similar in size and morphology,
they maintained both ichnogenera as valid taxa. Brontopus digits decrease in size from II
to V, and the digit I is the smallest (Gand et al., 2000). This pattern led Gand et al. (2000)
to attribute this ichnogenus to dinocephalians, even though late Permian dicynodonts,
therocephalians and eucynodonts also have nearly symmetrical, mesaxonic autopodia
with digit I smaller than the more external digits (Hopson, 1995). The SLIA-1 pes also has
this pattern, but the manus differs from Brontopus in proportions (the manus of Brontopus
has a nearly equal length and width).

Some Mesozoic synapsid ichnegenera compose the ichnofamily Ameghinichnidae
Casamiquela, 1964, represented by Ameghinichnus from the Middle Jurassic La Matilde
Formation of Argentina and Catocapes from the Lower Cretaceous Continental
Intercalaire Group of Angola (Casamiquela, 1964; De Valais, 2009; Mateus et al., 2017).
Although these ichnogenera also are represented by nearly homopodous, plantigrade,
mesaxonic and wider than long and pentadactyl tracks, there are several differences
between them and the material described here. Because these ameghinichnid tracks were
produced on fine sediments, they have preserved fine details that clearly are related to the
producer’s anatomy. For example, the manual and pedal digits of Ameghinichnus and
Catocapes are widely divaricated, reaching 151º in A. patagonicus (Casamiquela, 1964;
De Valais, 2009; Mateus et al., 2017), whereas the digits in Dicynodontipus and Chelichnus
(including SLIA-1 and SLIA-2, respectively) are mostly forward directed and less
divaricated. Other important differences are the sinuous and continuous tail traces associated with *Ameghinichnus* autopodia and its outward rotated feet, which can be observed in the alternating and opposite arrangements of the manus-pes sets (Casamiquela, 1964; De Valais, 2009).

*Hunt et al. (1993)* described some trackways from the Middle Triassic Holbrook Member of the Moenkopi Formation (Arizona, USA), naming them *Therapsipus*. This ichnogenus is represented by large quadrupedal animal tracks in an alternating pattern, but the outward direction of both the manus and the pes imprints is very different from the morphology observed in SLIA-1 (*Hunt et al., 1993*).

Based on the information provided above, the SLIA-1 and SLIA-2 tracks from the “Pirambóia Formation” have a high morphological affinity with the ichnogenera *Dicynodontipus* (mainly the materials from Germany and Argentina) and *Chelichnus* (materials from Scotland, Germany, the USA and Argentina). However, several ichnotaxa have been synonymized with *Dicynodontipus* and *Chelichnus* (Tables 1 and 2; e.g., McKeever & Haubold, 1996) and now they are known by many morphological and extramorphological variations that make difficult the understanding of the real ichnotaxonomic meaning of their diagnoses. A comprehensive ichnotaxonomic revision of the ichnogenera *Dicynodontipus* and *Chelichnus* is imperative to allow the recognition of these ichnotaxa in other deposits and avoid mistakes in ichnostratigraphic studies and correlations between the track and their trackmakers. However, even knowing this problem, we opted to attribute the “Pirambóia Formation” tracks to *Dicynodontipus* isp. (SLIA-1) and *C. bucklandi* (SLIA-2 and SLIA-5), since they are very close in morphology. Future advances in the understanding of extramorphological variation among the tracks produced in eolian deposits and in the ichnotaxonomy of these ichnogenera should shed additional light on this issue.

**The trackmackers’ identities**

The morphology of SLIA-1 indicates that its producer was a quadrupedal, pentadactyl and middle-sized animal, with nearly symmetrical feet and short, subequal digits. This morphology is very different from temnospondyl amphibian tracks (e.g., *Batrachichnus*, *Palaeosauropus* and *Limnopus*), because they have ectaxonic pedes and a tetractyl manus (*Marsh, 1894; Baird, 1952; Turek, 1989; Haubold et al., 1995; Melchor & Sarjeant, 2004; Marsicano, Wilson & Smith, 2014*).

Another middle- to large-sized group of animals that lived in Guadalupian–Lopingian environments is Pareiasaura (e.g., *Cisneros, Abdala & Malabarba, 2005* and references therein). Short, broad digits with the pedal phalangeal formula 2-3-3-4-3 and the fusion between astragalus and calcaneum are apomorphies that define the taxon Pareiasauroid (Pareiasaura + Sclerosaurus) (*Romer, 1976; Jalil & Janvier, 2005; Valentini, Conti & Nicosia, 2008; Valentini, Nicosia & Conti, 2009*). Additionally, pareiasaurs have small pedal fifth digits, which are shorter than or as large as the hallux (*Jalil & Janvier, 2005*). *Leonardi et al. (1975)* were the first to relate the pareiasaur autopodium anatomy to footprints from the Lopingian Val Gardena Sandstone (Italy), naming them *Pachypes dolomiticus*. Later, other *Pachypes* materials were described from Italy, Russia and Morocco, and the affinity between this ichnotaxon and pareiasaurs
was strengthened (Gubin et al., 2003; Valentini, Conti & Nicosia, 2008; Valentini, Nicosia & Conti, 2009; Voigt et al., 2010).

As mentioned above, we noted some similarities between SLIA-1 and the trackway TW-1 from the late Permian (Proelginia permiana Zone, Severodvinian Horizon) of Russia. This trackway was first described as “Sukhonopus” (Gubin et al., 2003), but Valentini, Conti & Nicosia (2008) considered it to belong to Pachypes. The Russian trackway TW-1 is composed of triangular-shaped pedes with short digits and an elliptical manus, grouped in a “reciprocal opposed” condition (sensu Haubold, 1971b), similar to SLIA-1 (Gubin et al., 2003). However, Voigt et al. (2010) argued that the Russian material is not sufficiently well-preserved to confirm its attribution to Pachypes and, as a consequence, to pareiasaurs. Therefore, based on the morphological differences between Pachypes and the trackways described here (i.e., the typical ectaxonic configuration of Pachypes with diminutive pedal digit V) and the lack of confidence in the pareiasaurian affinity of the Russian tracks, we conclude that the Ibicuí d’Armada trackways were not produced by Pareiasauria.

Late Permian–Early Triassic archosaumorph tracks (e.g., Protochirotherium) show a unique morphology, with a pedal digit V strongly reduced and posterolaterally positioned and a digit IV shorter than or as long as digit III (e.g., Conti et al., 1977; Mietto & Muscio, 1987; Klein et al., 2013; Bernardi et al., 2015). These characters are considered archosaumorph apomorphies and can be traced in several Permo–Triassic species, such as the archosauriform Euparkeria and erythrosuchians (Klein et al., 2013; Bernardi et al., 2015). The SLIA-1 pedes are mesaxonic and show forward directed digits that are very similar in size, which is contrary to archosaumorph foot morphology.

On the other hand, late Permian–Early Triassic therapsid synapsids have more symmetrical, mesaxonic autopodia (Hopson, 1995; Kümmell & Frey, 2012), which corresponds to the morphology of SLIA-1 and SLIA-2. The reduction in the number of phalanges in the third and fourth manual and pedal digits from the “pelycosaur” condition (manual and pedal phalangeal formulae 2-3-4-5-3 and 2-3-4-5-4, respectively) to the mammalian condition (both manual and pedal phalangeal formulae 2-3-3-3-3) was a transition that occurs convergently among the major groups of therapsids (Hopson, 1995), giving a more symmetrical shape to their autopodia. The therapsid feet are plantigrade, and some advanced taxa (mostly therocephalians and cynodonts) have a posterior border of the calcaneum forming a projection (the tuber calcis) for the insertion of the distal tendons of the musculus gastrocnemius and other calf muscles (e.g., Jenkins, 1971; Kemp, 1982; Szalay, 1993; Oliveira, Soares & Schultz, 2010 and references therein). However, some taxa seem to not have an ossified tuber calcis, such as the basal cynodont Thrinaxodon (Jenkins, 1971). On the other hand, the therapsid manus is more conservative, in spite the tendency to lose the phalanges (Kemp, 1982). The mammalian condition of pollex divergence, however, is not widespread among non-mammalian therapsids (Romer, 1976).

According to Kümmell & Frey (2012), the morphology of the metapodial articular heads in non-mammalian archosaumorph therapsids indicates that their main body mass was transferred to the substrate through the distal part of the metapodials and the proximal...
part of the proximal phalanges. Therefore, the deepest region of the therapsid footprints should be the metapodial-phalangeal articulation, as can be observed in the pes prints of the SLIA-1 trackway (Figs. 5D–5G).

The primitive phalangeal formula (2-3-4-5-3) was retained by biarmosuchians and several gorgonopsians, although few complete autopodial skeletons of these therapsids are known (Hopson, 1995; Rowe & van den Heever, 1986). Consequently, we do not consider these groups as possible trackmakers of the Ibicui d’Armada tracks.

Besides some contradictions, all dinocephalians seems to have had the mammalian phalangeal formula (Rowe & van den Heever, 1986). According to Hopson (1995) and Kemp (1982), the carnivore clade Brithopia (represented by the anteosaurid Titanophoneus from the Guadalupian of Russia) had four phalanges in the manual digit IV. However, several authors agree that the phalangeal formula 2-3-3-3-3 is widespread within dinocephalians (Orlov, 1958; Chudinov, 1983; Rowe & van den Heever, 1986). This phalangeal formula is the same as expected for the SLIA-1 trackmaker, making dinocephalians potential trackmakers. However, dinocephalians were completely extinct during the middle Lopingian (e.g., Boonstra, 1971; Rubidge & Sidor, 2001; Pearson et al., 2013; Day et al., 2015b and references therein), and, according to Carrano & Wilson (2001), the temporal distribution of biological taxa can be used to refine the trackmaker identification. Therefore, we prefer to attribute the Ibicui d’Armada tracks to another group of therapsids (see below) whose temporal range best fits with the Lopingian–Induan “Piramboía Formation” record.

Among the late Permian–Early Triassic therapsids, dicynodonts, theroccephalians and cynodonts were the most abundant. However, Lopingian–Induan taxa of Cynodontia, such as Procynosuchus (manus 2-3-4-4-3), Galesaurus (manus 2-3-4?-4-3; pes 2-3-4?-4-3) and Thrinaxodon (manus 2-3-4-4-3; pes 2-3-4-4-3), have asymmetrical manus and pedes (Hopson, 1995) that are not compatible with the mesaxony observed in the “Piramboía” tracks. More symmetrical autopodia (i.e., phalangeal formulae of 2-3-3-3-3 in both anterior and posterior autopodia) appeared in the clade Eucynodontia, but manus and pes records are unknown or incomplete in eucynodont taxa older than Early Triassic (Jenkins, 1970, 1971; Hopson, 1995). Theroccephalians have the 2-3-3-3-3 phalangeal formula, but their autopodia show asymmetrical metacarpal proportions, in which metacarpal II is smaller than metacarpal IV (Hopson, 1995), indicating a slightly ectaxonic condition.

Regarding the dicynodonts, all the species that have preserved autopodia show both manus and pedes phalangeal formulae of 2-3-3-3-3 and metacarpals II and IV of very similar length (Watson, 1913, 1960; Cluver, 1978; King, 1985, 1990; Rubidge, King & Hancox, 1994; Hopson, 1995), giving a symmetrical, near mesaxonic condition to their hands and feet, similar to the SLIA-1 and SLIA-2 tracks. Although this morphology is also common among non-dicynodont anomodonts (Hopson, 1995; Cisneros et al., 2015), some of them have an elongated metacarpal IV (e.g., Galechirus) or discoidal extra-phalanges in the third and fourth digits (e.g., Suminia), making their autopodia more asymmetrical (Fröbisch & Reisz, 2009).
Dicynodonts are known by their dual gait, which resulted from adducted (upright) hind limbs and more abducted (sprawling) fore limbs (Kemp, 1982; King, 1985, 1990; Blob, 2001; Vega-Dias & Schultz, 2004; Fröbisch, 2006; Ray, 2006; Morato et al., 2008). According to Fröbisch (2006), the astragalus and calcaneum morphology of the Triassic kannemeyeriid Tetragonias limits the flexibility of the ankle joint, making it unable to rotate. This feature was also observed in the Lopingian Dicynodontoides (=Kingoria) by King (1985), indicating that movements of its feet were limited to flexion and extension. Similarly, the SLIA-1 trackway was produced by an animal that had forward-directed feet and fore limbs able to rotate inward, which fits with the functional anatomy of some Permian and Triassic dicynodonts (King, 1985; Fröbisch, 2006). The opposite condition was described in Cistecephalus, which has a fused astragalus and calcaneum (Cluver, 1978).

The triangular shape of SLIA-1 foot impressions seems to be an anatomical feature of the trackmaker, produced by a posterior expansion of the pes. Anatomically, this projection should be related to the tuber calcis, which is a mammalian-grade evolutionary acquisition (Szalay, 1993). Nevertheless, several species of dicynodonts (such as Eodicynodon, Lystrosaurus, Tetragonias, Dinodontosaurus and Jachaleria) have a rounded calcaneum and lack evidence of an ossified tuber calcis (Watson, 1913; King, 1991; Rubidge, King & Hancox, 1994; Vega-Dias & Schultz, 2004; Fröbisch, 2006; Morato et al., 2008). In such cases, the insertion of the musculus gastrocnemius and the other calf muscles is inferred to have been at the plantar face of the calcaneum, following the sauropsid condition (Haughton, 1864–1866; Fröbisch, 2003; Morato, 2006). The only known exception to this morphology is the calcaneum of Dicynodontoides (=Kingoria). In this case, the posterior process of the Dicynodontoides calcaneum was considered homologous to the mammalian tuber calcis (King, 1985). However, in spite of the data provided by King (1985), we follow Fröbisch (2003) and Morato (2006), considering that the insertion site of the musculus gastrocnemius was in the plantar face of the foot. In this way, even though the presence of an ossified tuber calcis is not an anatomical feature that occurs within the clade Dicynodontia, the postero-plantar region of their feet is considered the main area for the insertion of the musculus gastrocnemius via the calcaneum tendon (Fröbisch, 2003, 2006; Morato, 2006). The triangular shape of the SLIA-1 pedal tracks could be derived from the presence of soft tissues in the posterior margin of the pes, because it is to be expected that the calcaneum tendon was inserted in the postero-plantar face of the feet.

Given that SLIA-1 is composed of relatively deep plantigrade footprints (Table S1 in the Supplemental Information File), the gross morphology of its pes prints should represent the anatomy of the trackmaker’s feet. This statement is reinforced by the presence of fine details in some pedal tracks, such as the presence of pads. A triangular pedal outline is also observed in some of the D. icelsi tracks from the Permian of South Africa and in “Calibarichnus” and “Gallegosichnus” from the Late Triassic of Argentina. De Klerk (2002) and Kümmel & Frey (2012) related D. icelsi to dicynodonts, based on the impressions of the terminal pads of this ichnotaxon, the morphology of the dicynodont autopodia and its coincident occurrence with Aulacephalodon and Dicynodon in the Cistecephalus.
Assemblage Zone of the Karoo Basin (South Africa). The former ichnogenera “Calibarichnus” and “Gallegosichnus” from the Vera Formation of Argentina are actually considered synonyms of *Dicynodontipus* by Melchor & de Valais (2006), who attributed these tracks to therapsids. Given the similarity between the Argentinean tracks (Late Triassic) and SLIA-1 (Lopingian–Induan) and their age, here we considered both records as dicynodont related (Fig. 11), also given that this group of therapsids was the only tetrapod lineage with conservative autopodium morphology in this temporal range. The trackway SLIA-4 was produced by a trackmaker of a similar size and, both SLIA-1 and SLIA-4 are parallel tracks produced by animals crossing the dune in the same direction, leading us to hypothesize that they may have been produced by individuals of the same species. However, SLIA-4 lacks morphological details that can corroborate this assumption, and other hypotheses can be raised to explain the co-occurrence of SLIA-1 and SLIA-4 in the same level and the attribution of the latter to a trackmaker.

Regarding SLIA-2 and SLIA-5, both are included in the ichnospecies *C. bucklandi*, which is synapsid related (Lockley *et al.*, 1995 and references therein). Even though these tracks do not preserve the full anatomy of the trackmaker’s autopodia, it is possible to see that their manus and pes are similar in size and overall shape, different than that expected for “pelycosaur” tracks. These basal synapsids were heteropod and had a sprawling gait, features seen in the “pelycosaur”-related ichnogenus *Dimetropus* (Romer & Price, 1940). Among the synapsids, therapsids are known by their more homopod, symmetrical autopodia and, besides that, there is no record of “pelycosaurs” in the Lopingian (Modesto *et al.*, 2011), favoring the hypothesis of the attribution of SLIA-2
and SLIA-5 to indeterminate therapsids. Other *C. bucklandi* records were attributed to therapsids (Krapovickas et al., 2014), strengthening the coherency of our hypothesis.

**Taphonomy and preservation of the Ibicuí d’Armada trackways**

The trackways of the “Pirambóia Formation” occur in two different strata of the same dune with different inclination and preservation. The SLIA-1 and SLIA-4 trackways are associated in the same 20° dipping dune foreset, whereas SLIA-2, SLIA-3 and SLIA-5 occur in another stratum with a 32° dip (Fig. 3). The most well preserved tracks (i.e., those that have more anatomically-related features, such as the presence of digits and pads, in addition to a regular track outline) are those from SLIA-1 that are attributed to *Dicynodontipus* isp. The trackways SLIA-2 and SLIA-5 preserve few morphological characters of the autopodium anatomy of its trackmaker. However, based on their size and the proportion of the autopodia, they can be attributed to *C. bucklandi*. In the case of SLIA-5, the trackway is preserved in cross-section. On the other hand, trackways SLIA-3 and SLIA-4 do not provide sufficient morphological evidence to be attributed to an ichnotaxon nor have their trackmakers been inferred (despite of the discussion above).

Because SLIA-1 and SLIA-4 occur on the same bedding plane that represents a 20° dip dune, we discard the degree of dip of the strata as the main cause of the preservational variation among these trackways. A fracture occurs perpendicular to SLIA-4, exposing part of the undertracks produced during the trackmaker’s progression. On the other hand, some of the true tracks could be recognized by the presence of displacement rims on the posterior margin of some tracks. Based on this and on the absence of these rims in SLIA-1, we assume that the exposed level does not represent the original eolian surface in which the tracks were produced. However, because SLIA-1 is composed of deep tracks, the erosion of the original upper level of the surface did not affect its preservation as in SLIA-4.

In addition, SLIA-1 has an asymmetrical preservation, in which the left set of *manus* and *pedes* preserves more clearly the anatomical details (e.g., digit counts and pedal pads). Intratrackway variations are common in the fossil track record and can be explained by diverse factors, such as variations of substrate consistency and water content (Milán, 2006; Milán & Bromley, 2006; Razzolini et al., 2014), abnormal gaits due pathologies and injuries (McCrea et al., 2015; Razzolini et al., 2016), or when the animal is crossing slopes (Razzolini & Klein, 2017). Asymmetrical preservation of trackways (i.e., with one side better preserved than the other) can be observed in several *Chelichnus* tracks from the Coconino Sandstone (e.g., the specimens RAM 247, RAM 382 and RAM 394). We could not relate this variation in preservation to any factor, once the analyzed slabs were *ex situ* (no information about the dune dip was available) and the trackmakers were traveling in different directions (perpendicular, parallel and oblique relative to the dune crest). Nevertheless, these examples from the Coconino Sandstone illustrate that intratrackway variation in preservation is common in the track record of the *Chelichnus* Ichnofacies, including the “Pirambóia Formation” tracks.

Intratrackway variations are also recorded in actual trackways made in eolian environments. For example, tracks produced on the eolian dunes of the Great Sand Dunes
National Park (Colorado State, USA) during summer vary enormously in depth and the presence of displacement rims (Fig. S2 in the Supplemental Information File). Even being produced by the same trackmaker (in this case, a human) in strata with the same dip and with no time-averaging, these tracks present different morphologies. This example just shows that the role of the variation of eolian substrate humidity and consistency in trackway preservation is not yet completely understood.

Even though several authors provided important data for vertebrate and invertebrate tracks from controlled experiments (McKee, 1947; Brand, 1979; Davis, Minter & Braddy, 2007; Scott, Renaut & Owen, 2010), the preservational modes of Permian eolian tracks are not yet well understood (Mancuso et al., 2016). Mancuso et al. (2016) recognized five taphonomic modes of preservation (“Modes 1–4” and “Trampling”) for the Yacimiento Los Reyunos Formation (Cisuralian of Argentina) Chelichnus tracks. Morphological and extramorphological features (such as shape of the palm outline, connection between the palm and the digits, and presence or absence of digit impressions, claw-drag traces and sedimentary marginal rims) vary among these taphonomic modes, being related to variations in the texture and color of the sediment, lamination type and dip angle of the surface (Mancuso et al., 2016). These authors consider that these variations in the preservation of the tracks are related to substrate consistency and trackmaker speeds. Although the preservation of the Brazilian tracks does not allowed us to replicate the methodology proposed by Mancuso et al. (2016), some information can be discussed.

Substrate consistency depends on its rheology and mechanics and varies with the texture (i.e., size, sorting, sphericity, roundness, etc.) of the sand grains, the mineralogical composition of the clasts and the moisture, but other conditions also affect track preservation in an eolian setting, such as the rapid burial of the perturbed sediment, the dip angle of the substrate, and the moisture content at the exact moment of the production of the tracks (McKee, 1944, 1947; Allen, 1997; Manning, 2004; Milàn, 2006; Milàn & Bromley, 2006; Jackson, Whyte & Romano, 2009; Jackson, Whyte & Romano, 2010; Scott, Renaut & Owen, 2010; Razzolini et al., 2014; Mancuso et al., 2016; Milàn & Falkingham, 2016). Biological (such as the animal’s mass, limb dynamics and the geometry of the autopodia) and ecological (such as the trackmaker’s speed and direction of the travel) variations are also known to affect the preservation of tetrapod tracks (Thulborn, 1990; Falkingham, Margetts & Manning, 2010; Falkingham et al., 2011; Falkingham, Hage & Bäker, 2014).

However, because the trackways described here occur in two strata that belonged to the same eolian dune, it is here understood that their differences in preservation cannot be explained by variations in the substrate texture, mineralogical composition or dip slope. Neoichnological observations and laboratory-controlled simulations indicate that tracks made on moist substrates preserve more accurately the morphology of the trackmaker’s autopodia rather than completely dry or saturated substrates (Manning, 2004; Milàn, 2006; Jackson, Whyte & Romano, 2009, 2010). Moisture variations could have occurred between the time of deposition of the cross-bedded strata in which the tracks were produced, but given that the Ibicuí d’Armada outcrop is a small exposure and the...
“Pirambóia” tracks occur only locally, it is difficult to known how moisture variation could have biased the local ichnological record.

According to Mancuso et al. (2016), tracks produced in dry sand surficial layers with moist subsurfaces often preserve more detailed anatomical information. As mentioned above, the facies association of the “Pirambóia Formation” indicates a humid eolian system with the influence of ephemeral braided fluvial channels (Dias & Scherer, 2008; Rodrigues, 2014). Adhesion structures on the interdune and sand sheet deposits also indicate some influence of the high phreatic level on the deposition of the eolian strata (Rodrigues, 2014). These sedimentary structures indicate that the phreatic level was high enough to provide some quantity of moisture to the dunes, influencing its consistency. Moreover, we found raindrop marks on the sandstones from the Ibicuí d’Armada area (Fig. S3 in the Supplemental Information File), which indicates that meteoric water also contributed as a moisture source. Consequently, the Ibicuí d’Armada trackways probably were produced in dunes with definite moisture content, preserving some morphological details of the trackmakers, as can be observed on the SLIA-1 trackway.

Additionally, the trackmakers’ differences in size, body mass, and speed could have been the source of variation between the preserved tracks. There is a wide range of size among the Ibicuí d’Armada trackmakers, indicated by their inferred gleno-acetabular distances. The producer of SLIA-2 tracks was from 78.9 to 121.4 mm in length, while the SLIA-1 trackmaker could have been 408.8 mm long. Although we could not infer the gleno-acetabular length of the SLIA-3 trackmaker, its tracks indicate an even larger animal (Tables S1–S6 in the Supplemental Information File). Accordingly, besides the substrate consistency, these biological variations were the main cause of the taphonomic variability among the Ibicuí d’Armada trackways.

CONCLUSION

Here, we describe from the first time five tetrapod trackways (SLIA-1 to SLIA-5) from the Lopingian–Induan “Pirambóia Formation.” The stratigraphy of this unit is unresolved for deposits that occur along the northeastern border of the Paraná Basin (in the São Paulo State), but the age of the deposits from the southwestern region of Rio Grande do Sul can be determined by their lower and upper contacts with the Rio do Rasto Formation (Guadalupian–Lopingian) and the Sanga do Cabral Formation (Induan–Olenekian), respectively.

The “Pirambóia” tracks occur in two strata (20° and 32° dip) that were part of the same dune. The lack of variation in substrate texture, mineralogical composition and bedding dip among the track-bearing strata indicates that the preservational variation among the trackways should be related to biological (e.g., size and weight of the trackmakers) or behavioral (e.g., speed) traits.

Among the described trackways, three of them are assigned to the ichnogenera Dicynodontipus and Chelichnus. While this latter ichnogenus is widespread among dune deposits of the Permian, the presence of Dicynodontipus in the Chelichnus Ichnofacies of the “Pirambóia Formation” is remarkable, because it is not often found in desert deposits. The trackway SLIA-1 (Dicynodontipus isp.) preserves some features that could
be related to its trackmaker (e.g., size and proportion of the tracks, triangular-shaped, forward oriented pedes with sole pads and blunt, short digits). Comparisons with other Permo–Triassic ichnogenera and the anatomy of the autopodia of tetrapods of this age allow us to attribute SLIA-1 to dicynodonts. SLIA-2 and SLIA-5 (C. bucklandi) are composed of oval-shaped tracks that are here interpreted as therapsid–related. Regarding SLIA-3 and SLIA-4, we have hypothesized that they were produced by therapsids (based on their homopody and symmetry, the co-occurrence with SLIA-1 and SLIA-2, and in the age of the “Pirambóia” deposits) but no morphological details were preserved, making it difficult to make a more assertive attribution. The presence of therapsid tracks in the Lopingian–Induan of Brazil is noteworthy and fundamental to the understanding of the occupation of desert environments by tetrapods during such a crucial interval in Earth history.

INSTITUTIONAL ABBREVIATIONS
MLP Museo de La Plata, La Plata, Buenos Aires Province, Argentina
MN Museu Nacional, Rio de Janeiro, Rio de Janeiro State, Brazil
MNA Museum of Northern Arizona, Flagstaff, Arizona, United States of America
RAM “Raymond M. Alf” Museum of Paleontology, Claremont, California, United States of America
SLIA non-collected track, Ibicuí d’Armada locality, Santana do Livramento, Rio Grande do Sul, Brazil
UFRGS Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil
UFRJ Universidade Federal do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro State, Brazil
USNM United States National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, United States of America.

ACKNOWLEDGEMENTS
We would like to thank Milena Carniel, Morgan Guignard, Dr. Marcel Lacerda (UFRGS), Dr. Flávio Pretto (CAPP-AUFSM, Brazil), Dr. Alexandre Lipparini (UFSP, Brazil), Ana Emília Figueiredo, Dr. Juan Cisneros (UFPI, Brazil), Dr. Daniel Perea, Dr. Cesar Goso and Dr. Valeria Mesa (UdelaR, Uruguay) for the field assistance. We are indebted to Dr. Deise Henriques (MN, Brazil), Dr. Alejandro Kramarz, Dr. Laura Chornogubski (MACN, Argentina), Dr. Marcelo Reguero, Dr. Alejo Scarano (MLP, Argentina), Dr. Umberto Nicosia, Dr. Paolo Citton (Sapienza Università di Roma, Italy), Dr. Robert Emry, Dr. Amanda Millhouse (USNM, USA), Mrs. Janet Gillette, Dr. David Gillette (MNA, USA), Dr. Andrew Farke, Mr. Gabriel Santos (RAM, USA), Dr. Vincent Santucci and Mrs. Coleen Hyde (GRCA, USA) for allowing the analysis of specimens under their care. Dr. Lorenzo Marchetti (Urweltmuseum Geoskop, Germany) and Dr. Téo Oliveira (UEFS, Brazil) provided useful comments on an earlier draft of this paper. We also thank Sheron Medeiros (FURG) and Voltaire Paes Neto (UFRGS) for the artistic reconstructions presented in Figs. 5 and 11, respectively. This paper was greatly improved by the
comments of the Editor Dr. Kenneth De Baets and the reviewers Dr. Verónica Krapovickas and Dr. Sebastian Voigt.

**ADDITIONAL INFORMATION AND DECLARATIONS**

**Funding**
This work was supported by CNPq and CAPES with grants to Heitor Francischini (CNPq: 140581/2014-6; CAPES: 88881.133764/2016-01) and to Cesar L. Schultz (CNPq: 458187/2014-3). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Grant Disclosures**
The following grant information was disclosed by the authors:
CNPq: 140581/2014-6 and 458187/2014-3.
CAPES: 88881.133764/2016-01.

**Competing Interests**
The authors declare that they have no competing interests.

**Author Contributions**
- Heitor Francischini conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft, collected the materials.
- Paula Dentzien-Dias conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the paper, approved the final draft.
- Spencer G. Lucas analyzed the data, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.
- Cesar L. Schultz conceived and designed the experiments, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.

**Field Study Permissions**
The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):
- The permit for field work was provided by the Departamento Nacional de Produção Mineral (DNPM, Process Number: 000.820/2015).

**Data Availability**
The following information was supplied regarding data availability:
- The raw data are provided in a Supplemental File.

**Supplemental Information**
Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.4764#supplemental-information.
REFERENCES

Allen JRL. 1997. Subfossil mammalian tracks (Flandrian) in the Severn Estuary, S.W. Britain: Mechanics of formation, preservation and distribution. Philosophical Transactions of the Royal Society B: Biological Sciences 352(1352):481–518 DOI 10.1098/rstb.1997.0035.

Almeida FFM. 1950. Uma fauna de crustáceos bivalvos do Arenito Botucatu no Estado de São Paulo. Boletim do Departamento Nacional de Produção Mineral 134:1–36.

Almeida FFM, Melo C. 1981. A Bacia do Paraná e o vulcanismo Mesozóico. In: Bistrichi CA, Carneiro CDR, Dantas ASL, Ponçano WL, eds. Mapa geológico do Estado de São Paulo. São Paulo: Instituto de Pesquisas Tecnológicas, 6–77.

Andreis RR, Bossi GE, Montardo DK. 1980. O Grupo Rosário do Sul (Triásico) no Rio Grande do Sul. In: Anais do XXXI Congresso Brasileiro de Geologia, Balneário de Camboriú, 659–673.

Andreis RR, Carvalho IS. 2001. A Formação Corumbataí (Permiano Superior–Triássico Inferior, Bacia do Paraná) na Pedreira Pau Preto, Município de Taguaí, São Paulo, Brasil: análise paleoambiental e das pegadas fósseis. Revista Brasileira de Paleontologia 2:33–46.

Avanzini M, Bernardi M, Nicosia U. 2011. The Permian–Triassic tetrapod faunal diversity in the Italian Southern Alps. In: Dar IA, ed. Earth and Environmental Sciences. Rijeka: InTech, 591–608.

Avanzini M, Ceoloni P, Conti MA, Leonardi G, Manni R, Mariotti N, Mietto P, Muraro C, Nicosia U, Sacchi E, Santi G, Spezzamonte M. 2001. Permian and Triassic tetrapod ichnofaunal units of Northern Italy: their potential contribution to continental biochronology. Natura Bresciana 25:89–107.

Avanzini M, Tomasoni R. 2004. Giornate di Paleontologia 2004–Bolzano 21–23 maggio 2004, Guida all’escursione: La gola del Bletterbach. Studi Trentini di Scienze Naturali, Acta Geologica 79:1–34.

Baird D. 1952. Revision of the Pennsylvanian and Permian footprints Limnopus, Allopus and Baropus. Journal of Paleontology 26(5):832–840.

Baird D. 1980. A prosauropod dinosaur trackway from the Navajo Sandstone (Lower Jurassic) of Arizona. In: Jacobs LL, ed. Aspects of Vertebrate History: Essays in Honor of Edwin Harris Colbert. Flagstaff: Museum of Northern Arizona, 219–230.

Benton MJ, Twitchett RJ. 2003. How to kill (almost) all life: the end-Permian extinction event. Trends in Ecology & Evolution 18(7):358–365 DOI 10.1016/s0169-5347(03)00093-4.

Bernardi M, Klein H, Petti FM, Ezcurra MD. 2015. The origin and early radiation of archosauriforms: integrating the skeletal and footprint record. PLOS ONE 10(6):e0128449 DOI 10.1371/journal.pone.0128449.

Bernardi M, Petti FM, Citton P, Romano M. 2017. L’ichnoassociazione a tetrapodi del Bletterbach (Trentino Alto-Adige) e le sue relazioni con gli ecosistemi terrestri di fine Permiano. Geo.Alp 14:63–83.

Blob RW. 2001. Evolution of hindlimb posture in nonmammalian therapsids: biomechanical tests of paleontological hypotheses. Paleobiology 27(1):14–38 DOI 10.1666/0094-8373(2001)027%3C0014:EOHPIN%3E2.0.CO;2.

Bonaparte JF. 1966. Chronological survey of the tetrapod-bearing Triassic of Argentina. Breviora 251:1–13.

Boonstra LD. 1971. The early therapsids. Annals of the South African Museum 59:17–46.

Braddy SJ. 1995. The ichnotaxonomy of the invertebrate trackways of the Coconino Sandstone (Lower Permian), Northern Arizona. New Mexico Museum of Natural History and Science Bulletin 6:219–224.
Brady LF. 1947. Invertebrate tracks from the Coconino Sandstone of Northern Arizona. *Journal of Paleontology* 21(5):466–472.

Brand L. 1979. Field and laboratory studies on the Coconino Sandstone (Permian) vertebrate footprints and their paleoecological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 28:25–38 DOI 10.1016/0031-0182(79)90111-1.

Buck PV, Ghilardi AM, Fernandes LBR, Fernandes MA. 2017b. A new ichnotaxon classification of large mammaliform trackways from the Lower Cretaceous Botucatu Formation, Paraná Basin, Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology* 485:377–388 DOI 10.1016/j.palaeo.2017.06.027.

Buck PV, Ghilardi AM, Peixoto BCPM, Fernandes LBR, Fernandes MA. 2017a. A new tetrapod ichnotaxon from Botucatu Formation, Lower Cretaceous (Neocomian), Brazil, with comments on fossil track preservation on inclined planes and local paleoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 466:21–37.

Caetano-Chang MR. 1997. A Formação Pirambóia no centro-leste do Estado de S Paulo. Livre-Docência thesis, Universidade Estadual Paulista “Júlio de Mesquita Filho”.

Carrano MT, Wilson JA. 2001. Taxon distribution and the tetrapod track record. *Paleobiology* 27(3):564–582.

Casamiquela RM. 1961. Sobre la presencia de un mamífero en el primer elenco (icnológico) de vertebrados del Jurásico de la Patagonia. *Physis* 22:225–233.

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.

Casamiquela RM. 1975. Nuevo material y reinterpretación de las icnitas mesozoicas (Neotriasásicas) de Los Menucos, provincia de Río Negro (Patagonia). In: 1er Congreso Argentino de Paleontología y Bioestratigrafía, Tucumán, 555–580.

Cei RL, Gargiulo J. 1977. Icnites de tetrapodos permicos del sur de Mendoza. *Ameghiniana* 14:127–132.

Ceoloni P, Conti MA, Mariotti N, Nicosia U. 1988. New Late Permian tetrapod footprints from southern Alps. *Memoria della Societa Geologica Italiana* 34:45–65.

Chudinov PK. 1983. The early therapsids. *Trudy Paleontologicheskogo Instuta, Akademiya Nauk SSSR* 202:1–229.

Cisneros JC, Abdala F, Jashashvili T, Bueno AO, Dentzien-Dias P. 2015. *Tiarajudens eccentricus* and *Anomocephalus africanus*, two bizarre anomodonts (Synapsida, Therapsida) with dental occlusion from the Permian of Gondwana. *Royal Society Open Science* 2(7):150090 DOI 10.1098/rsos.150090.

Cisneros JC, Abdala F, Malabarba MC. 2005. Pareiasaurids from the Rio do Rasto Formation, Southern Brazil: biostatigraphic implications for Permian faunas of the Paraná Basin. *Revista Brasileira de Paleontologia* 8(1):13–24 DOI 10.4072/rbp.2005.1.02.

Citton P, Carluccio R, Nicolosi I, Nicosia U. 2017. Re-evaluation of *Cheiichnus tazelwurmii*, a non mammalian therapsid-grade track from the Upper Permian Arenaria di Val Gardena. Epub ahead of print 1 September 2017. *Historical Biology* 1–19 DOI 10.1080/08912963.2017.1370586.

Cluver MA. 1978. The skeleton of the mammal-like reptile *Cistecephalus* with evidence for a fossorial mode of life. *Annals of the South African Museum* 76(5):213–246.

Collinson JD, Thompson DB. 1982. *Sedimentary Structures*. Winchester: Allen and Unwin.
Conti MA, Leonardi G, Mariotti N, Nicosia U. 1977. Tetrapod footprints of the “Val Gardena Sandstone” (North Italy). Their paleontological, stratigraphic and paleoenvironmental meaning. *Palaeontographia Italica* 40:1–91.

Davis RB, Minter NJ, Braddy SJ. 2007. The neoichnology of terrestrial arthropods. *Palaeogeography, Palaeoclimatology, Palaeoecology* 255(3–4):284–307 DOI 10.1016/j.palaeo.2007.07.013.

Day MO, Güven S, Abdala F, Jirah S, Rubidge B, Almond J. 2015b. Youngest dinocephalian fossils extend the *Tapinocephalus* Zone, Karoo Basin, South Africa. *South African Journal of Science* 111(3/4):78–82.

Day MO, Ramezani J, Bowring SA, Sadler PM, Erwin DH, Abdala F, Rubidge BS. 2015a. When and how did the terrestrial mid-Permian mass extinction occur? Evidence from the tetrapod record of the Karoo Basin, South Africa. *Proceedings of the Royal Society B: Biological Sciences* 282(1811):20150834 DOI 10.1098/rspb.2015.0834.

De Klerk WJ. 2002. A dicynodonts trackway from the *Cistecephalus* Assemblage Zone in the Karoo, east of Graaff-Reinet, South Africa. *Palaeontologia Africana* 38:73–91.

De Valais S. 2009. Ichnotaxonomic revision of *Ameghinichnus*, a mammalian ichnogenus from the Middle Jurassic La Matilde Formation, Santa Cruz province, Argentina. *Zootaxa* 2203:1–21.

Delair JB. 1966. Fossil footprints from Dumfriesshire, with descriptions of new forms from Annandale. *Transactions of the Dumfries and Galloway Natural History and Antiquities Society* 43:14–30.

Dentzién-Dias PC, Schultz CL, Bertoni-Machado C. 2008. Taphonomy and paleoecology inferences of vertebrate ichnofossils from Guará Formation (Upper Jurassic), southern Brazil. *Journal of South American Earth Sciences* 25(2):196–202 DOI 10.1016/j.jsames.2007.08.008.

Dias KDN, Scherer CMS. 2008. Cross-bedding set thickness and stratigraphic architecture of aeolian systems: an example from the Upper Permian Pirambóia Formation (Paraná Basin), southern Brazil. *Journal of South American Earth Sciences* 25(3):405–415 DOI 10.1016/j.jsames.2007.07.008.

Dias-da-Silva S. 2012. Middle–Late Permian tetrapods from the Rio do Rasto Formation, Southern Brazil: a biostratigraphic reassessment. *Lethaia* 45(1):109–120 DOI 10.1111/j.1502-3931.2011.00263.x.

Dias-da-Silva S, Pinheiro FL, Da Rosa ÁAS, Martinelli AG, Schultz CL, Silva-Neves E, Modesto SP. 2017. Biostratigraphic reappraisal of the Lower Triassic Sanga do Cabral Supersequence from South America, with a description of new material attributable to the parareptile genus *Procolophon*. *Journal of South American Earth Sciences* 79:281–296 DOI 10.1016/j.jsames.2017.07.012.

Domnanovich NS, Marsicano CA. 2006. Tetrapod footprints from the Triassic of Patagonia: reappraisal of the evidence. *Ameghiniana* 43(1):55–70.

Domnanovich NS, Tomassini R, Manera de Bianco T, Dalponte M. 2008. Nuevos aportes al conocimiento de la icnofauna de tetápodos del Triásico Superior de Los Menucos (Complejo Los Menucos), provincia de Río Negro, Argentina. *Ameghiniana* 45(1):211–224.

Dudgeon P. 1878. Note on a new fossil foot-print from the Permian sandstone of Dumfriesshire. *Proceedings of the Royal Society of Edinburgh* 9:154–155 DOI 10.1017/s037016460003203x.

Ekdale AA, Bromley RG. 2012. Eolian environments. In: Knaust D, Bromley RG, eds. *Trace Fossils as Indicators of Sedimentary Environments*. Amsterdam: Elsevier, 419–437.

Ellenberger P. 1984. Données complémentaires sur la zonation ichnologique du Permien du Midi de la France (Bassins de Lodève, Saint-Affrique et Rodez). *Comptes Rendus de l'Académie des Sciences* 299(9):581–586.
Faccini UF. 2000. Estratigrafia do Permo–Triássico do Rio Grande do Sul: estilos deposicionais versus espaço de acomodação. D. Phil. thesis, Universidade Federal do Rio Grande do Sul.

Falkingham PL. 2014. Interpreting ecology and behaviour from the vertebrate fossil track record. *Journal of Zoology* 292(4):222–228 DOI 10.1111/jzo.12110.

Falkingham PL, Bates KT, Margetts I, Manning PL. 2011. The ‘Goldilocks’ effect: preservation bias in vertebrate track assemblages. *Journal of the Royal Society Interface* 8(61):1142–1154 DOI 10.1098/rsif.2010.0634.

Falkingham PL, Hage J, Bäker M. 2014. Mitigating the Goldilocks effect: the effects of different substrate models on track formation potential. *Royal Society Open Science* 1(3):140225 DOI 10.1098/rsos.140225.

Falkingham PL, Margetts L, Manning PL. 2010. Fossil vertebrate tracks as paleopenetrometers: confounding effects of foot morphology. *Palaios* 25(6):356–360 DOI 10.2110/palo.2009.p09-164r.

Faul H, Roberts WA. 1951. New fossil footprints from the Navajo(?) Sandstone of Colorado. *Journal of Paleontology* 25(3):266–274.

Fernandes MA, Carvalho IS. 2008. Revisão diagnóstica para a icnoespécie de tetrapode Mesozóico *Brasilichnium elusivum* (Leonardi, 1981) da Formação Botucatu, Bacia do Paraná, Brasil. *Ameghiniana* 45(1):167–173.

Fichter J. 1994. Permische Sauierfährten–Ein Diskussionsbeitrag zu der Bearbeitungsproblematik der Tetrapodenfährten des Cornberger Sandsteins (Perm, Deutschland) und des Coconino Sandsteins (Perm, USA). Philippiya 7(1):61–82.

Francischini H, Dentzien-Dias PC, Fernandes MA, Schultz CL. 2015. Dinosaur ichnofauna of the Upper Jurassic/Lower Cretaceous of the Paraná Basin (Brazil and Uruguay). *Journal of South American Earth Sciences* 63:180–190 DOI 10.1016/j.jsames.2015.07.016.

Francischini H, Dentzien-Dias P, Guerra-Sommer M, Menegat R, Santos JOS, Manfroi J, Schultz CL. 2018. A middle Permian (Roadian) lungfish aestivation burrow from the Rio do Rasto Formation (Paraná Basin, Brazil) and associated U-Pb dating. *Palaios* 33(2):69–84 DOI 10.2110/palo.2017.050.

Fröbisch J. 2003. Locomotion of *Tetragonias njalilus* (Therapsida: Anomodontia)–A functional analysis of the pelvic girdle and hind limb. Undergraduate thesis, Rheinschen-Friedrich-Wilhelms Universität zu Bonn.

Fröbisch J. 2006. Locomotion in derived dicynodonts (Synapsida, Anomodontia): a functional analysis of the pelvic girdle and hind limb of *Tetragonias njalilus*. *Canadian Journal of Earth Sciences* 43(9):1297–1308 DOI 10.1139/e06-031.

Fröbisch J, Reisz RR. 2009. The Late Permian herbivore *Suminia* and the early evolution of arboreality in terrestrial vertebrate ecosystems. *Proceedings of the Royal Society B: Biological Sciences* 276(1673):3611–3618 DOI 10.1098/rspb.2009.0911.

Fúlfaro VJ, Gama E Jr, Soares PC. 1980. *Revisão Estratigráfica da Bacia do Paraná*. São Paulo: Paulipetro.

Gand G, Demathieu G, Ballestra F. 1995. La palichnifauna de vertébrés tétrapodes du Permien Supérieur de L’Estérel (Provence, France). *Palaeontographica Abteilung* 235:97–139.

Gand G, Garric J, Demathieu G, Ellenberger P. 2000. La palichnifauna de vertébrés tétrapodes du Permien Supérieur du Bassin de Lodève (Languedoc-France). *Palaeovertebrata* 29(1):1–82.

Gilmore CW. 1926. Fossil footprints from the Grand Canyon. *Smithsonian Miscellaneous Collections* 77(9):1–41.
Gilmore CW. 1927. Fossil footprints from the Grand Canyon: second contribution. Smithsonian Miscellaneous Collections 80:1–78.

Gubin YM, Golubev VK, Bulanov VV, Petuchov SV. 2003. Pareiasaurian tracks from the Upper Permian of Eastern Europe. Palontologicheskii Zhurnal 37(5):67–76.

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

Harkness R. 1851. Notice of some new footsteps in the Bunter Sandstone of Dumfriesshire. Annals and Magazine of Natural History 8(44):90–95 DOI 10.1080/03745486109494966.

Haubold H. 1965. Therapsiden- und Rhynchocephalen-Fährten aus dem Buntsandstein Südhüringens. Hercynia 3(2):147–183.

Haubold H. 1971a. Die Tetrapodenfährten des Buntsansteins in der Deutschen Demokratischen Republik und in Westdeutschland und ihre Äquivalente in der gesamten Trias. Paläontologische Abhandlungen A 4:395–548.

Haubold H. 1971b. Ichnia amphibiorum et reptiliorum fossilium. In: Kuhn O, ed. Handbuch der Paläoherpetologie. Jena: Gustav Fischer Verlag, 1–124.

Haubold H, Hunt AP, Lucas SG, Lockley MG. 1995. Wolfcampian (Early Permian) vertebrate tracks from Arizona and New Mexico. New Mexico Museum of Natural History and Science Bulletin 6:135–165.

Haughton S. 1864–1866. Notes on animal mechanics: No. 6. On the muscular anatomy of the crocodile. Proceedings of the Royal Irish Academy 9:268–277.

Heyler D, Lessertisseur J. 1963. Pistes de Tétrapodes permiens dans la région de Lodève (Hérault). Mémoire du Museum National d'Histoire Naturelle, Paris 11:125–221.

Holz M, França AB, Souza PA, Iannuzzi R, Rohn R. 2010. A stratigraphic chart of the Late Carboniferous/Permian succession of the eastern border of the Paraná Basin, Brazil, South America. Journal of South American Earth Sciences 29(2):381–399 DOI 10.1016/j.jsames.2009.04.004.

Hopson JA. 1995. Patterns of evolution in the manus and pes of non-mammalian therapsids. Journal of Vertebrate Paleontology 15(3):615–639 DOI 10.1080/02724634.1995.10011252.

Hornstein F. 1876. Entdeckung von Tierfährten im Buntsandstein von Karlshafen. Neues Jahrbuch für Mineralogie 923:923–924.

Hunt AP, Lucas SG. 2006. The taxonomic status of Navahopus falcipollex and the ichnofauna and ichnofacies of the Navajo Lithosome (Lower Jurassic) of Western North America. New Mexico Museum of Natural History and Science Bulletin 37:164–169.

Hunt AP, Lucas SG. 2007. Tetrapod ichnofacies: a new paradigm. Ichnos 14(1–2):59–68 DOI 10.1080/10420940601006826.

Hunt AP, Lucas SG. 2016. The case for archetypal vertebrate ichnofacies. Ichnos 23(3–4):237–247 DOI 10.1080/10420940.2016.1164153.

Hunt AP, Santucci VL, Lockley MG, Olson TJ. 1993. Dicyonodont trackways from the Holbrook Member of the Moenkopi Formation (Middle Triassic: Anisian), Arizona, USA. New Mexico Museum of Natural History and Science Bulletin 3:213–218.

Huxley TH. 1877. The crocodilian remains found in the Elgin sandstones with remarks on the ichnites of Cummingstone. Memoir of the Geological Survey of the United Kingdom 3:1–52.

International Committee for Zoological Nomenclature (ICZN). 1999. International Code for Zoological Nomenclature. London: The International Trust for Zoological Nomenclature, Nature History Museum.
Jackson SJ, Whyte MA, Romano M. 2009. Laboratory-controlled simulations of dinosaur footprints in sand: a key to understanding vertebrate track formation and preservation. *Palaios* 24(4):222–238 DOI 10.2110/palo.2007.p07-070r.

Jackson SJ, Whyte MA, Romano M. 2010. Range of experimental dinosaur (*Hypsilophodon foxii*) footprints due to variation in sand consistency: how wet was the track? *Ichnos* 17(3):197–214 DOI 10.1080/10420940.2010.510026.

Jalil N-E, Janvier P. 2005. Les pareiasaures (Amniota, Parareptilie) du Permien supérieur du Bassin d’Argana, Maroc. *Geodiversitas* 27(1):35–132.

Jardine W. 1850. Note to Mr. Harkness’s paper “On the position of the impressions of footsteps in the Bunter sandstones of Dumfries-shire”. *Annals and Magazine of Natural History* 6:208–209.

Jardine W. 1853. The Ichnology of Annandale or illustrations of footmarks impressed on the New Red Sandstone of Corncokie Muir. Edinburgh: W.H. Lizzars.

Jenkins FA. 1970. Cynodont postcranial anatomy and the “prototherian” level of mammalian organization. *Evolution* 24(1):230–252 DOI 10.2307/2406730.

Jenkins FA. 1971. The postcranial skeleton of African cynodonts. *Bulletin of the Peabody Museum of Natural History* 36:1–216.

Kemp TS. 1982. *Mammal-like Reptiles and the Origin of Mammals*. London: Academic Press.

King GM. 1985. The postcranial skeleton of *Kingoria nowacki* (von Huene) (Therapsida: Dicynodontia). *Zoological Journal of the Linnean Society* 84(3):263–289 DOI 10.1111/j.1096-3642.1985.tb01801.x.

King GM. 1990. *The Dicynodonts: A Study in Palaeobiology*. London: Chapman and Hall.

King GM. 1991. The aquatic *Lystrosaurus*: a palaeontological myth. *Historical Biology* 4(3–4):285–321 DOI 10.1080/08912969009386547.

King MJ, Sarjeant WAS, Thompson DB, Tresise G. 2005. A revised systematic ichnotaxonomy and review of the vertebrate footprint Ichnofamily Chirotheriidae from the British Triassic. *Ichnos* 12(4):241–299 DOI 10.1080/10420940591009312.

Klein H, Lucas SG, Voigt S. 2015. Revision of the ?Permian–Triassic tetrapod ichnogenus *Procolophonichnium* Nopcsa 1923 with description of the new ichnospecies *P. lockleyi*. *Ichnos* 22(3–4):155–176 DOI 10.1080/10420940.2015.1063490.

Klein H, Niedźwiedzi G. 2012. Revision of the Lower Triassic tetrapod ichnofauna from Wióry, Holy Cross Mountains, Poland. *New Mexico Museum of Natural History & Science Bulletin* 56:61–62.

Klein H, Niedźwiedzi G, Voigt S, Lagnaoui A, Hminna A, Saber H, Schneider JW. 2013. The tetrapod ichnogenus *Protochirotherium* Fichter and Kunz 2004, a characteristic Early Triassic morphotype of Central Pangea. *Ichnos* 20(1):24–30 DOI 10.1080/10420940.2012.757699.

Krapovickas V, Mancuso AC, Arcucci A, Caselli A. 2010. Fluvial and eolian ichnofaunas from the Lower Permian of South America (Patquı’a Formation, Paganzo Basin). *Geologica Acta* 8(4):449–462.

Krapovickas V, Mángano MG, Buatois LA, Marsicano CA. 2016. Integrated ichnofacies models for deserts: recurrent patterns and megatrends. *Earth-Science Reviews* 157:61–85 DOI 10.1016/j.earscirev.2016.03.006.

Krapovickas V, Marsicano CA, Mancuso AC, de la Fuente MS, Ottone EG. 2014. Tetrapod and invertebrate trace fossils from aeolian deposits of the lower Permian of central-western Argentina. *Historical Biology* 27(7):827–842 DOI 10.1080/08912963.2014.904857.

Kuhn O. 1963. *Ichnia tetraradorum. Fossilium Catalogus I. Animalia pars 101. S’* Gravenhage: Junk.

Kümmel SB, Frey E. 2012. Digital arcade in the autopodia of Synapsida: standard position of the digits and dorsoventral excursion angle of digital joints in the rays II-V. *Palaeobiodiversity and Palaeoenvironments* 92(2):171–196 DOI 10.1007/s12549-012-0076-6.
Lavina EL. 1992. Geologia sedimentar e paleogeografia do Neopermiano e Eotriássico (intervalo Kazanian–Scythiano) da Bacia do Paraná. D. Phil. thesis, Universidade Federal do Rio Grande do Sul.

Lavina EL, Faccini UF, Ribeiro HJS. 1993. A Formação Pirambóia (Permo–Triássico) no estado do Rio Grande do Sul. Acta Geologica Leopoldensia 38(16):179–197.

Leonardi G. 1980. On the discovery of an abundant ichno-fauna (vertebrates and invertebrates) in the Botucatu Formation s.s. in Araraquara, São Paulo, Brazil. Anais da Academia Brasileira de Ciências 52(3):559–567.

Leonardi G. 1981. Novo ichnogênero de tetrápode mesozoico da Formação Botucatu, Araraquara, SP. Anais da Academia Brasileira de Ciências 53:793–805.

Leonardi G. 1987. Glossary and Manual of Tetrapod Footprint Palaeoichnology. Brasília: Departamento Nacional de Produção Mineral.

Leonardi G. 1994. Annotated Atlas of South America Tetrapod Footprints (Devonian to Holocene). Brasília: Companhia de Pesquisa de Recursos Minerais.

Leonardi G, Oliveira FH. 1990. A revision of the Triassic and Jurassic tetrapod footprints of Argentina and a new approach on the age and meaning of the Botucatu Formation footprints (Brazil). Revista Brasileira de Geociências 2(K1–4):216–229.

Leonardi G, Sedor FA, Costa R. 2002. Pegadas de répteis terrestres na Formação Rio do Rasto (Permiango Superior da Bacia do Paraná), Estado do Paraná, Brasil. Arquivos do Museu Nacional 60(3):213–216.

Leonardi P, Conti MA, Leonardi G, Mariotti N, Nicosia U. 1975. Pachypes dolomiticus n. gen. n. sp.; Pareiasaur footprint from the “Arenaria di Val Gardena” (Middle Permian) in the Western Dolomites (N. Italy). Atti della Accademia Nazionale dei Lincei, serie VIII 57(3–4):221–232.

Lockley MG. 2011. The ichnotaxonomic status of Brasilichnium with special reference to occurrences in the Navajo Sandstone (Lower Jurassic) in the Western USA. New Mexico Museum of Natural History and Science Bulletin 53:306–315.

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. New Mexico Museum of Natural History and Science Bulletin 6:225–233.

Lockley MG, Tedrow A. 2009. Are Bipedopus, Semibipedopus, Lacertipus, Navahopus and Brasilichnium distinct ichnogenera? Reevaluating Jurassic tracks from the Western USA. Journal of Vertebrate Paleontology 29:136A.

Loope DB. 1986. Recognizing and utilizing vertebrate tracks in cross section: Cenozoic hoofprints from Nebraska. Palaios 1(2):141–151 DOI 10.2307/3514507.

Loope DB, Rowe CM. 2003. Long-lived pluvial episodes during deposition of the Navajo Sandstone. Journal of Geology 111(2):223–232 DOI 10.1086/345843.

Lucas SG. 2009. Timing and magnitude of tetrapod extinctions across the Permo-Triassic boundary. Journal of Asian Earth Sciences 36(6):491–502 DOI 10.1016/j.jseaes.2008.11.016.

Lucas SG. 2017. Permian tetrapod extinction events. Earth-Science Reviews 170:31–60 DOI 10.1016/j.earscirev.2017.04.008.

Lucas SG, Hunt AP. 2006. Permian tetrapod footprints: biostratigraphy and biochronology. In: Lucas SG, Cassinis G, Schneider JW, eds. Non-Marine Permian Biostratigraphy and Biochronology. London: Geological Society of London, 179–200.
Lucas SG, Spielmann JA, Klein H, Lerner AJ. 2010. Ichnology of the Upper Triassic (Apachean) Redonda Formation, east-central New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 47:3–70.

Lull RS. 1918. Fossil footprints from the Grand Canyon of the Colorado. *American Journal of Science* 45(269):337–346 DOI 10.2475/ajs.s4-45.269.337.

Mancuso AC, Krapovickas V, Marsicano C, Benavente C, Benedito D, de la Fuente M, Ottone EG. 2016. Tetrapod tracks taphonomy in eolian facies from the Permian of Argentina. *Paläios* 31(8):374–388 DOI 10.1080/08912963.2015.1077077.

Manning PL. 2004. A new approach to the analysis and interpretation of tracks: examples from the Dinosauria. *Geological Society, London, Special Publications* 228(1):93–123 DOI 10.1144/gsl.sp.2004.228.01.06.

Marchetti L, Belvedere M, Mietto P. 2017. Lopingian tetrapod footprints from the Venetian Prealps, Italy: New discoveries in a largely incomplete panorama. *Acta Palaeontologica Polonica* 62(4):801–817 DOI 10.4202/app.00392.2017.

Marchetti L, Voigt S, Klein H. 2017. Revision of Late Permian tetrapod tracks from the Dolomites (Trentino-Alto Adige, Italy). Epub ahead of print 10 November 2017. *Historical Biology* 1–36 DOI 10.1080/08912963.2017.1391806.

Marsh OC. 1894. Footprints of vertebrates in the Coal Measures of Kansas. *American Journal of Science* 48(283):81–84 DOI 10.2475/ajs.s3-48.283.81.

Marsicano CA, Wilson JA, Smith RMH. 2014. A temnospondyl trackway from the Early Mesozoic of Western Gondwana and its implications for basal tetrapod locomotion. *PLOS ONE* 9(8):e103255 DOI 10.1371/journal.pone.0103255.

Mateus O, Marzola M, Schulp AS, Jacobs LL, Polcyn MJ, Pervov V, Gonçalves AO, Morais ML. 2017. Angolan ichnosite in a diamond mine shows the presence of a large terrestrial mammaliform, a crocodylomorph, and a sauropod dinosaur in the Early Cretaceous of Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 471:220–232 DOI 10.1016/j.palaeo.2016.12.049.

Matos SLF. 1995. O contato entre o Grupo Passa Dois e a Formação Pirambóia na borda leste da Bacia do Paraná no estado de São Paulo. M.Sc. thesis, Universidade de São Paulo.

Matos SLF, Coimbra AM. 1997. Sucessão de fácies na camada Porangaba, Grupo Passa Dois, Estado de São Paulo. *Revista Brasileira de Geociências* 27:377–386.

McCrea RT, Tanke DH, Buckley LG, Lockley MG, Farlow JO, Xing L, Matthews NA, Helm CW, Pemberton SG, Breithaupt BH. 2015. Vertebrate ichnopathology: pathologies inferred from dinosaur tracks and trackways from the Mesozoic. *Ichnos* 22(3–4):235–260 DOI 10.1080/10420940.2015.1064408.

McEachern JA, Bann KL, Gingras MK, Zonneveld J-P, Dashtgard SE, Pemberton SG. 2012. The Ichnofacies Paradigm. In: Knaust D, Bromley RG, eds. *Trace Fossils as Indicators of Sedimentary Environments*. Amsterdam: Elsevier, 103–138.

McKee ED. 1944. Tracks that go uphill. *Plateau* 16(4):61–72.

McKee ED. 1947. Experiments on the development of tracks in fine cross-bedded sand. *SEPM Journal of Sedimentary Research* 17(1):23–28 DOI 10.1306/d4269292-2b26-11d7-8648000102c1865d.

McKee ED, Douglass JR, Rittenhouse S. 1971. Deformation of lee-side laminae in eolian dunes. *Geological Society of America Bulletin* 82(2):359–378 DOI 10.1130/0016-7606(1971)82[359:dollie]2.0.co;2.

McKeever PJ. 1994. A new vertebrate trackway from the Permian of Dumfries and Galloway. *Scottish Journal of Geology* 30(1):11–14 DOI 10.1144/sjg30010011.
McKeever PJ, Haubold H. 1996. Reclassification of vertebrate trackways from the Permian of Scotland and related forms from Arizona and Germany. *Journal of Paleontology* 70(6):1011–1022 DOI 10.1017/s0022336000038713.

Melchor RN, Sarjeant WAS. 2004. Small amphibian and reptile footprints from the Permian Carapacha Basin, Argentina. *Ichnos* 11(1–2):57–78 DOI 10.1080/10420940490428814.

Melchor RN, de Valais S. 2006. A review of Triassic tetrapod track assemblages from Argentina. *Palaeontology* 49(2):355–379 DOI 10.1111/j.1475-4983.2006.00538.x.

Mietto P, Muscio G. 1987. *Prochirotherium permicum* Leonardi, 1951 (Reptilia: ?Chirotheriidae) nelle Arenarie di Val Gardena della Carnia. *Atti del MuseoFriulano di Storia Naturale* 8(86):81–94.

Milàn J. 2006. Variations in the morphology of emu (*Dromaius novaehollandiae*) tracks reflecting differences in walking pattern and substrate consistency: ichnotaxonomic implications. *Palaeontology* 49(2):405–420 DOI 10.1111/j.1475-4983.2006.00543.x.

Milàn J, Bromley RG. 2006. True tracks, undertracks and eroded track, experimental work with tetrapod tracks in laboratory and field. *Palaeogeography, Palaeoclimatology, Palaeoecology* 231(3–4):253–264 DOI 10.1016/j.palaeo.2004.12.022.

Milàn J, Falkingham PL. 2016. Experimental and Comparative Ichnology. In: Falkingham PL, Marty D, Richter A, eds. *Dinosaur Tracks: The Next Steps*. Bloomington: Indiana University Press, 14–27.

Milàn J, Loope DB, Bromley RG. 2008. Crouching theropod and *Navahopus* sauropodomorph tracks from the Early Jurassic Navajo Sandstone of USA. *Acta Palaeontologica Polonica* 53(2):197–205 DOI 10.4202/app.2008.0203.

Modesto SP, Smith RMH, Campione NE, Reisz RR. 2011. The last “pelycosaur”: a varanopid synapsid from the *Pristerognathus* Assemblage Zone, Middle Permian of South Africa. *Naturwissenschaften* 98(12):1027–1034 DOI 10.1007/s00114-011-0856-2.

Morales M, Haubold H. 1995. Tetrapod tracks from the Lower Permian DeChelly Sandstone of Arizona: systematic description. *New Mexico Museum of Natural History and Science Bulletin* 6:251–261.

Morato L. 2006. *Dinodontosaurus* (Synapsida, Dicynodontia): reconstituições morfológicas e aspectos biomecânicos. M.Sc. thesis, Universidade Federal do Rio Grande do Sul.

Morato L, Schultz CL, Vega-Dias C, Silva FP, Kindlein W Jr. 2008. Discussing a myth: biomechanical comparisons between *Dinodontosaurus* (Synapsida, Dicynodontia) and extinct ground sloths. *Arquivos do Museu Nacional* 66(1):145–154.

Ogg JG. 2012. Triassic. In: Gradstein FM, Ogg JG, Schmitz M, Ogg G, eds. *The Geologic Time Scale 2012*. Amsterdam: Elsevier, 681–730.

Oliveira TV, Soares MB, Schultz CL. 2010. *Trucidocynodon riograndensis* gen. nov. et sp. nov. (Eucynodontia), a new cynodont from the Brazilian Upper Triassic (Santa Maria Formation). *Zootaxa* 2382:1–71.

Orlov YA. 1958. The carnivorous dinocephalians of the Isheevo fauna (titanosuchians). *Trudy Palaeontologicheskogo Instituta, Akademiya Nauk SSSR* 72:3–113.

Owen R. 1842. Report on British Fossil Reptiles: Part 2. Report of the British Association for the Advancement of Science. Plymouth: British Association for the Advancement of Science, 60–204.

Pacheco J. 1927. Relatório elucidativo do esboço da região compreendida entre o meridiano 4º, rio Itararé e os paralelos 23º34' e 28º38'. São Paulo: Relatório da Comissão Geográfica e Geológica.

Peabody FE. 1948. Reptile and amphibian trackways from the Moenkopi Formation at Arizona and Utah. *University of California Publications, Department of Geological Sciences Bulletin* 27:195–468.
Pearson MR, Benson RBJ, Upchurch P, Fröbisch J, Kammerer CF. 2013. Reconstructing the diversity of early terrestrial herbivorous tetrapods. *Palaeogeography, Palaeoclimatology, Palaeoecology* 372:42–49 DOI 10.1016/j.palaeo.2012.11.008.

Porchetti SD, Bertini RJ, Langer MC. 2017. Proposal for ichnotaxonomic allocation of therapsid footprints from the Botucatu Formation (Brazil). *Ichnos* 25(2–3):192–207 DOI 10.1080/10420940.2017.1308929.

Porchetti SD, Wagensommer A. 2015. A vertebrate trackway from the Twyfelfontein Formation (Lower Cretaceous), Damaraland, Namibia. *Paleontologische Zeitschrift* 89(4):807–814 DOI 10.1007/s12542-015-0264-6.

Ray S. 2006. Functional and evolutionary aspects of the postcranial anatomy of dicynodonts (Synapsida, Therapsida). *Palaeontology* 49(6):1263–1286 DOI 10.1111/j.1475-4983.2006.00597.x.

Retallack GJ. 1996. Early Triassic therapsid footprints from the Sydney Basin, Australia. *Alcheringa: An Australasian Journal of Palaeontology* 20(4):301–314 DOI 10.1080/03115519608619473.

Retallack GJ, Smith RMH, Ward PD. 2003. Vertebrate extinction across Permian–Triassic boundary in Karoo Basin, South Africa. *Geological Society of America Bulletin* 115(9):1133–1152 DOI 10.1130/b25215.1.

Romer AS. 1976. *Osteology of Reptiles*. Third edition. Chicago: The University of Chicago Press.

Romer AS, Price LW. 1940. Review of the polyosauria. *Geological Society of America Special Papers* 28:1–534 DOI 10.1130/spe28-p1.

Rowe T, van den Heever JA. 1986. The hand of *Anteosaurus magnificus* (Dinocephalia: Therapsida) and its bearing on the origin of the mammalian manual phalangeal formula. *Suid-Afrikaanse Tydskrif vir Wetenskap* 82:641–645.

Rubidge BS, King GM, Hancox PJ. 1994. The postcranial skeleton of the earliest dicynodont *Eodicynodon* from the Upper Permian of South Africa. *Palaeontology* 37(2):397–408.

Rubidge BS, Sidor CA. 2001. Evolutionary patterns among Permo–Triassic therapsids. *Annual Review of Ecology Evolution and Systematics* 32(1):449–480 DOI 10.1146/annurev.ecolsys.32.081501.114113.
Rühle von Lilienstern H. 1939. Fährten und Spuren im Chirotherium-Sandstein von Südhüningen. Fortschritte der Geologie und Paläontologie 12:293–387.

Rühle von Lilienstern H. 1944. Eine Dicynodontierfährten aus dem Chirotheriumsandstein von Heßberg. Paläontologische Zeitschrift 23:368–385.

Sanford RM, Lange FW. 1960. Basin study approach for evaluation of Paraná miogeosyncline of South Brazil. American Association of Petroleum Geologists Bulletin 44(8):1316–1370.

Scherer CMS, Lavina ELC. 2005. Sedimentary cycles and facies architecture of aeolian-fluvial strata of the Upper Jurassic Guará Formation, southern Brazil. Sedimentology 52(6):1323–1341 DOI 10.1111/j.1365-3091.2005.00746.x.

Schmidt H. 1959. Die Cornberger Fährten im Rahmen der Vierfüßler-Entwicklung. Abhandlungen des Hessischen Landesamtes für Bodenforschung 28:137.

Scotese CR. 2002. PALEOMAP project. Available at http://www.scotese.com (accessed 6 April 2018).

Scott JJ, Renaut RW, Owen RB. 2010. Taphonomic controls on animal tracks at saline, alkaline Lake Bogoria, Kenya Rift Valley: impact of salt efflorescence and clay mineralogy. Journal of Sedimentary Research 80(7):639–665 DOI 10.2110/jsr.2010.057.

Silva RC, Carvalho IS, Fernandes ACS, Ferigolo J. 2008. Pegadas teromorfoídes do Triássico Superior (Formação Santa Maria) do Sul do Brasil. Revista Brasileira de Geociências 38(1):98–113 DOI 10.25249/0375-7536.200838198113.

Silva RC, Fernandes ACS. 2004. Revisão das pegadas fósseis de Archosauromorpha do Permiano superior do Brasil (Formação Corumbataí, Bacia do Paraná). Curitiba: Anais do I Congresso Brasileiro de Herpetologia.

Silva RC, Fernandes ACS. 2005. Morfologia funcional das pegadas fósseis de Archosauromorpha da Formação Corumbataí (Neopermiano–Eotriássico da Bacia do Paraná). Aracaju: Anais do XIX Congresso Brasileiro de Paleontologia.

Silva RC, Sedor FA, Fernandes ACS. 2012. Fossil footprints from the Late Permian of Brazil: an example of hidden biodiversity. Journal of South American Earth Sciences 38:31–43 DOI 10.1016/j.jsames.2012.05.001.

Silva RC, Sedor FA, Monteiro-Filho ELA. 2012. Pegadas fósseis de Tetrapoda da Bacia do Paraná, Brasil. In: Monteiro-Filho ELA, Aranha JMR, eds. Revisões em Zoologia I. Curitiba: SEMA/PR, 239–253.

Soares AP, Soares PC, Holz M. 2008. Correlações estratigráficas conflitantes no limite Permo–Triássico no sul da Bacia do Paraná: o contato entre duas sequências e implicações na configuração espacial do Aquífero Guarani. Pesquisas em Geociências 35(2):115–133.

Soares PC. 1975. Divisão estratigráfica do Mesozóico no Estado de São Paulo. Revista Brasileira de Geociências 5(4):229–251.

Soares PC, Soares AP, Bettú DF. 2014. Formação da sequência triássico-jurássica na Bacia do Paraná. Boletim de Geociências da Petrobrás 22(1):135–160.

Souza A, Sinelli O, Gonçalves NMM. 1971. Nova ocorrência fossilífera na Formação Botucatu. In: Anais do XXV Congresso Brasileiro de Geologia, São Paulo, 281–295.

Szalay FS. 1993. Pedal evolution of mammals in the Mesozoic: tests for taxic relationships. In: Szalay FS, Novacek MJ, McKenna MC, eds. Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials. New York: Springer-Verlag, 108–128.
Thulborn RA. 1990. *Dinosaur Tracks*. London: Chapman and Hall.

Tohver E, Schmieder M, Lana C, Mendes PST, Jourdan F, Warren L, Riccomini C. 2018. End-Permian impactogenic earthquake and tsunami deposits in the intracratonic Paraná Basin of Brazil. Epub ahead of print 2 January 2018. *Geological Society of America Bulletin* DOI 10.1130/B31626.1.

Turek V. 1989. Fish and amphibian trace fossils from Westphalian sediments of Bohemia. *Palaeontology* 32(3):623–643.

Valentini M, Conti MA, Nicosia U. 2008. Linking tetrapod tracks to the biodynamics, paleobiogeography, and paleobiology of their trackmakers: *Pachypes dolomiticus* Leonardi et al. 1975, a case study. *Studi Trentini di Scienze Naturali, Acta Geologica* 83:237–246.

Valentini M, Nicosia U, Conti MA. 2009. A re-evaluation of *Pachypes*, a pareiasaurian track from the Late Permian. *Neues Jahrbuch für Geologie und Paläontologie–Abhandlungen* 251(1):71–94 DOI 10.1127/0077-7749/2009/0251-0071.

Vega-Dias C, Schultz CL. 2004. Postcranial material of *Jachaleria candelariensis* Araújo and Gonzaga 1980 (Therapsida, Dicynodontia), Upper Triassic of Rio Grande do Sul, Brazil. *PaleoBios* 24(1):7–31.

Voigt S, Berman DS, Henrici AC. 2007. First well-established track-trackmaker association of Paleozoic tetrapods based on *Ichniotherium* trackways and diadectid skeletons from the Lower Permian of Germany. *Journal of Vertebrate Paleontology* 27(3):553–570 DOI 10.1671/0272-4634(2007)27[553:fwtaop]2.0.co;2.

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). *Journal of African Earth Sciences* 57(5):470–478 DOI 10.1016/j.jafrearsci.2009.12.003.

Washburne CW. 1930. Geologia do Estado de São Paulo. *Boletim da Comissão Geográfica e Geológica do Estado de São Paulo* 22:1–282.

Watson DMS. 1913. The limbs of *Lystrosaurus*. *Geological Magazine* 10(06):256–258 DOI 10.1017/s0016756800126445.

Watson DMS. 1960. The anomodont skeleton. *Transactions of the Zoological Society of London* 29(3):131–209.