

Late Permian-Early Jurassic vertebrate tracks from patagonia: Biochronological inferences and relationships with southern african realms

Ignacio Díaz-Martínez^{a,b,*}, Paolo Citton^{a,b}, Silvina de Valais^{a,b}, Carlos Cónsole-Gonella^{a,c},
Santiago N. González^{a,b}

^a Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

^b Instituto de Investigación en Paleobiología y Geología (IIPG, Universidad Nacional de Río Negro-CONICET), Av. Roca 1242, General Roca, 8332, Río Negro, Argentina

^c Instituto Superior de Correlación Geológica (INSUGEO, Universidad Nacional de Tucumán-CONICET), Miguel Lillo 205, 4000, Tucumán, Argentina

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ABSTRACT

In recent years, new studies about vertebrate tracks found in the late Permian-Triassic Los Menucos Complex and Early Jurassic Marifil Volcanic Complex (Río Negro province, Patagonia, Argentina) have been published. In those studies, the chronostratigraphic information of each track-bearing unit has been discussed and the relationships between the record from Patagonia and southern Africa have been highlighted. With the aim of deepening both subjects, the biochronological and palaeobiogeographical information of the main ichnotaxa found in the lower Mesozoic units of Patagonia, *Dicynodontipus*, *Pentasauropus* and *Anomoepus*-like tracks, have been analysed. Moreover, the updated chronological data from the Vera Formation, Los Menucos Complex, in the Tschering and Yancaqueo farm areas, and from the Marifil Volcanic Complex near Perdomo farm, have been studied. The entire biochronological, chronological and tectonic evidence suggests that within the Los Menucos Complex there are two sequences: a lower one, Wuchiapingian-Olenekian in age, near the Tschering farm and bearing *Dicynodontipus* tracks, and an upper sequence of Anisian-Rhaetian (?Norian) age, in the Yancaqueo farm and bearing *Pentasauropus* tracks. This suggests that the rocks historically defined as Vera Formation have different ages in different areas and span a longer time interval than previously thought. In the case of the *Anomoepus*-like tracks found in the Marifil Volcanic Complex, the biochronological and geological data are consistent with an Early Jurassic age. According to ichnological information and geological background we propose a correlation between Patagonia and southern Africa constrained in three main phases: 1. Lopingian to Early Triassic, Vera Formation (Tschering farm) and Balfour Formation, respectively; 2. Middle to Late Triassic, Vera Formation (Yancaqueo farm) and lower Elliot Formation, respectively; and 3. Early Jurassic, Marifil Volcanic Complex and upper Elliot Formation, respectively. In addition, this correlation is supported by a similarity in palaeoclimatic settings that allow inferring a homogeneous distribution of trackmakers in both realms of southern Gondwana. Finally, the palaeobiogeographic information of the studied ichnotaxa and their putative trackmakers is consistent and shows an extensive distribution, during a geotectonic moment with most of the continents assembled forming Pangaea.

1. Introduction

The tetrapod track record gives invaluable information about the producers, such as identity, anatomy, locomotion, and behaviour (e.g., Bird, 1954; Ostrom, 1972; Leakey and Hay, 1979; Sarjeant, 1981; Wilson and Carrano, 1999; Moreno et al., 2012). It contributes to the reconstruction of the palaeocommunity and its palaeoecological characteristics (e.g., Leonardi, 1989; de Valais, 2011; Díaz-Martínez et al.,

2018), and it complements the osteological fossil record (e.g., Casamiquela, 1964; Sarjeant and Mossman, 1978; Leonardi and Sarjeant, 1986; Brusatte et al., 2011; Apesteguía et al., 2011; Romano et al., 2016; Citton et al., 2019).

Moreover, vertebrate tracks provide valuable biochronological and palaeobiogeographic information. For instance, there are some Permian and Triassic ichnotaxa that are found in almost all worldwide rocks of a bounded age (e.g., Lockley et al., 1998; Klein and Haubold, 2007; Hunt

* Corresponding author. Instituto de Investigación en Paleobiología y Geología (IIPG, Universidad Nacional de Río Negro-CONICET), Av. Roca 1242, General Roca, 8332, Río Negro, Argentina.

E-mail addresses: inaportu@hotmail.com (I. Díaz-Martínez), pcitton@unrn.edu.ar (P. Citton), sdevalais@yahoo.com.ar (S. de Valais), carlosconsole@csnat.unt.edu.ar (C. Cónsole-Gonella), sgonzalez@unrn.edu.ar (S.N. González).

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and Lucas, 2007; Lucas, 2007; Klein and Lucas, 2010; Díaz-Martínez et al., 2015). This is the case for *Protochirotherium*, which is considered as late Induan-late Olenekian in age (biochron 1, *sensu* Klein and Haubold, 2007 or biochron *Protochirotherium*, *sensu* Klein and Lucas, 2010), though its record extends to the Lopingian (Bernardi et al., 2017a; Conti et al., 1977; Marchetti et al., 2019a).

In recent years, new and updated information about the Triassic-Early Jurassic vertebrate track record from Patagonia has been published. For instance, some revisions about the Triassic tracks from Argentina, including the ones from Patagonia, were carried out (e.g., Domnanovich and Marsicano, 2006; Melchor and de Valais, 2006). Moreover, a new Lower Jurassic dinosaur track-bearing locality from the Marifil Volcanic Complex has been presented and described by Díaz-Martínez et al. (2017). Finally, the Triassic ichnotaxon *Pentasauropus* from the Los Menucos Complex, which was mentioned for the first time by Domnanovich et al. (2008), has been recently revised by Citton et al. (2018). In some of these papers, the relationships between tetrapod tracks from Patagonia and southern Africa, and the biochronological and geochronological information of the analysed ichnotaxa and their sites, have been discussed. Nevertheless, there is no contribution that delves into these topics and there is a lack of chronostratigraphic knowledge of the track-bearing units in Argentina (Citton et al., 2018) respect others recognised worldwide.

Therefore, the aim of this contribution is to discuss the ichnological and geological data of the Patagonian Triassic-Lower Jurassic vertebrate track-bearing outcrops with special emphasis on the palaeobiogeographical and biochronological information. In addition, the relationship between the realms is analysed.

2. Geological setting

The uppermost Permian to Jurassic magmatism in eastern North Patagonia has been linked to an extensional event related to a post-orogenic stage after the final assembly of Pangaea (González et al., 2016, 2017a,b).

In Patagonia, the Triassic sedimentary continental rocks are represented by several units, such as the Paso Flores Formation, the El Tranquilo Formation or the Los Menucos Complex, while the Lower Jurassic is present by the Las Leoneras Formation or the Marifil Volcanic Complex. In this contribution, only those vertebrate track-bearing units will be analysed, namely the Los Menucos Complex and Marifil Volcanic Complex, both located in the central to eastern North Patagonian Massif (Río Negro province, Argentina) (Figs. 1 and 2).

2.1. Los Menucos Complex

The Los Menucos Complex crops out in the central North Patagonian Massif (Fig. 1). It includes Permian-Triassic volcanic and intrusive subvolcanic, and volcanoclastic and epiclastic sedimentary rocks (Stipanovic et al., 1968; Cucchi et al., 2001; Labudía and Bjerg, 2001; Lema et al., 2008; Luppo et al., 2018; Falco et al., 2018; Fig. 1). The structure of the Los Menucos area shows a SE-plunging anticlinal affecting the rocks from the Los Menucos Complex, whose core is near the Los Menucos town (Giacosa et al., 2007). This magmatism has been related to an extensional event, which in turn is connected to the post-orogenic stage of the Gondwanic Cycle (Falco et al., 2018). Otherwise, in regard to this calc-alkaline nature, the Los Menucos magmatism could be interpreted as related to a retro-arc depocentre (Spalletti et al., 1999). Labudía and Bjerg (2001) named the rhyolitic ignimbrites, mesosilicic lavas and subordinate Triassic sedimentary rocks exposed around the Los Menucos town as the Los Menucos Complex. The thickness of the unit is from 5 m to 130 m thick (Labudía and Bjerg, 2001), or more than 2000 m for the Los Menucos Volcanic Complex (*sensu* Lema et al., 2008).

The Los Menucos Complex is divided into the Vera Formation (Labudía and Bjerg, 2001) at the base and the Sierra Colorada

Formation (Stipanovic et al., 1968) on top. The Vera Formation is composed of conglomerates, sandstones and pelites, with intercalations of volcanic ashes, tuffs and tuffites, dacitic pyroclastic flow products and volcanic breccias (Labudía and Bjerg, 2001, 2005). It holds palaeoflora ("*Dicroidium*-type flora"), crustacean and tetrapod tracks (Citton et al., 2018, and references therein). Labudía and Bjerg (2001) suggested that sedimentation took place mainly in alluvial plain, floodplain, ephemeral river and small lacustrine environments that were strongly influenced by explosive volcanic activity. Moreover, Gallego (2010) pointed out that the epiclastic rocks were deposited under a seasonal climate with alternating periods of dry and wet conditions. Recently, Falco and Hauser (2018) claimed that the sedimentary rocks from the Puesto Tschering farm (Fig. 1) were formed during multi-episodic debris flows and/or hyperconcentrated flows to diluted currents, originated from re-sedimentation of a non-welded volcanoclastic deposit, and by settling and traction in standing water bodies. On the other hand, the Sierra Colorada Formation is essentially made of pyroclastic bed-rocks (ash-fall and density current deposits) and sub-volcanic intrusive bodies. It is dated at 222 ± 2 Ma with the Rb/Sr isochron method obtained from the volcanoclastic rocks overlying the Vera Formation (Norian, Late Triassic; Rapela et al., 1996) from the Puesto Vera farm (the place where was defined the Vera Formation). This age was historically proposed as the top of the Vera Formation and supported by the *Dicroidium*-type flora and the tetrapod ichnofauna, although no radiometric constraints were obtained from the uppermost level of the Vera Formation.

Some biochronological proposals have also been published. For instance, taking into account the taphoflora-bearing unit, it was assigned to the Upper Triassic by Stipanovic and Methol (1972, 1980), to the Middle Triassic by Artabe (1985a,b), and to the Lower Triassic by Stipanovic (1967). Gallego (2010) suggested that the presence of the crustacean *Menucoestheria* in the Vera Formation indicated a Late Triassic age. Based on the ichnological record, Casamiquela (1964) had pointed out that Los Menucos tracks were younger than Late Triassic but older than Late Jurassic. Citton et al. (2018) suggested that the tracks from the Los Menucos area indicated two different ages, Early and Late Triassic.

Recent U-Pb isotopic dating has provided different ages for the Los Menucos Complex rocks. Luppo et al. (2018) presented Lopingian to Early Triassic ages at the base of the volcanic sequence, northwest Los Menucos (257 ± 2 Ma, 252 ± 2 and 248 ± 2 Ma). In the same sense, Falco et al. (2018) presented U-Pb crystallization ages from pyroclastic rock-beds from the Los Menucos Complex in the Puesto Álvarez (256 ± 0.7 Ma), near the Tschering farm (252 ± 2 Ma), in the Puesto Vera (248 ± 2 Ma). According to these data, the age of the Los Menucos Complex range between 257 ± 2 Ma to 248 ± 2 Ma. Falco et al. (2018) considered the variety of isotopic ages as evidence of episodic volcanic activity during the Permo-Triassic in the Los Menucos area (Fig. 2).

2.2. Marifil Volcanic Complex

The Marifil Volcanic Complex (Malvicini and Llambías, 1974; Cortés, 1981) is a widespread volcanic and volcanoclastic unit cropping out along the east side of the North Patagonian Massif from El Gualicho to Península Camarones, across Valcheta and Sierra Grande (Patagonia, Argentina). This unit includes volcanic and subvolcanic rocks and volcanogenic and epiclastic sediments (see an updated synthesis in González et al., 2017a).

Although the radiometric ages of these rocks start in the Middle Triassic and continue until the Middle Jurassic, González et al. (2017a) pointed out that there are two main groups of ages for this range between Valcheta and Sierra Grande towns: Middle Triassic (Cortés, 1981; Genovese, 1995; González et al., 2014, 2017b), and Early Jurassic (Rapela and Pankhurst, 1993; Pankhurst and Rapela, 1995; Strazzere et al., 2019). Younger ages (Middle Jurassic) were obtained southwards

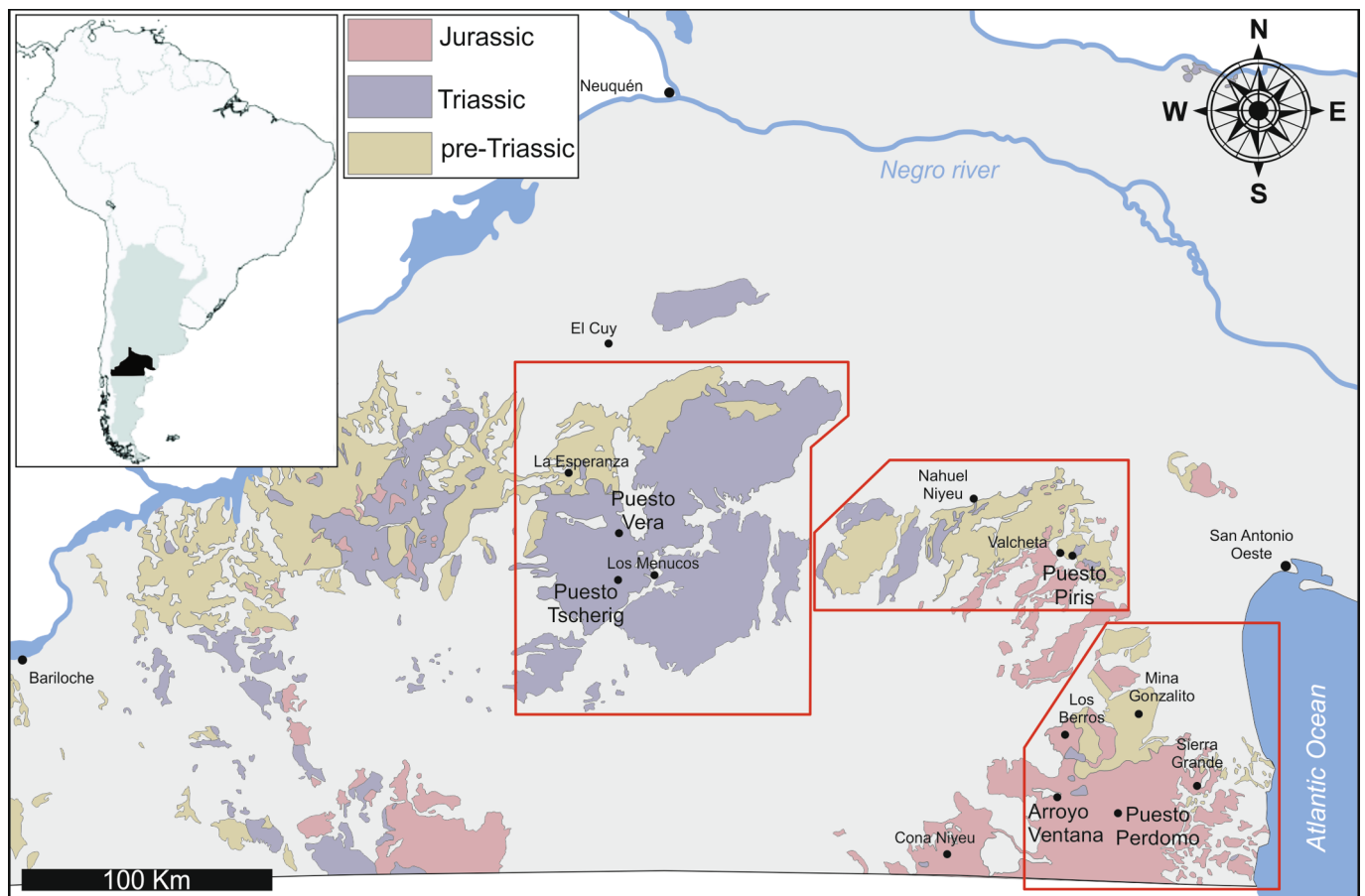


Fig. 1. Schematic geological map from Río Negro Province in the North Patagonian Massif indicating the outcrops of the pre-Permian, Permo-Triassic and Jurassic rocks. The red dots mark the ichnological localities (modified from González et al., 2017a).

in Península Camarones and Dique Ameghino (Féraud et al., 1999; Pankhurst et al., 2000). According to González et al. (2017a), only the Jurassic rocks correspond to the Marifil Volcanic Complex, while the Triassic units should be separated from it.

The Marifil Volcanic Complex overlies Triassic rocks that were previously considered as its base. These Triassic units overlie Paleozoic rocks and are composed of Olenekian-Anisian (247.22 ± 0.2 Ma) andesitic lavas covered by epiclastic rocks (González et al., 2017b). These rocks were related to the La Porfiá, El Refugio and Puesto Piris formations (Nuñez et al., 1975; Cortés, 1981; González et al., 2017a). Recently, González et al. (2017a) suggested that all the epiclastic and volcano-sedimentary rocks that underlie the acid Jurassic rocks of the Marifil Volcanic Complex correspond to the Puesto Piris Formation. This unit was defined by Nuñez et al. (1975) for epiclastic rocks at the base of Mesozoic volcanic-sedimentary sequences laying on Palaeozoic units. This formation is a 150 m to 550 m-thick sequence that has a grain-decreasing tendency and includes thick beds of conglomerate at the base grading to sandstones, limestones and siltstones at the top of the sequence (Nuñez et al., 1975; Strazzere et al., 2019). These rocks have been related to the evolution of high-energy fluvial currents to low-energy fluvial and lacustrine (Strazzere et al., 2019). Based on its stratigraphic position, the Puesto Piris Formation was proposed as Triassic in age (Nuñez et al., 1975).

The upper sequence, the Marifil Volcanic Complex (in the sense by González et al., 2017a) is thicker than the previous units and it is dominated by pyroclastic and volcanogenic deposits with minor epiclastic intercalations (Nuñez et al., 1975; Cortés, 1981). In the last facies, Early Jurassic vertebrate footprints from the Perdomo area were described by Díaz-Martínez et al. (2017). These interbedded epiclastic bed-rocks are 20–50 m thick coarse-to medium grained sandstones and

siltstones. They show parallel and cross lamination indicating medium to low tractive energy in a fluvial system. The levels of fine grain-size present vegetal remains which could be related to very-low energy periods of deposition. The age constrains for these rocks are based on their fossil content and stratigraphic position. Lower Jurassic, sub-volcanic intrusive bodies (Toarcian to Pliensbachian, see González et al., 2017b, for a summary of isotopic ages) are intruded in the Marifil Volcanic Complex indicating a pre-Toarcian age for the sequence.

Meanwhile, the Middle Triassic sequence has been linked to the mesosilicic magmatism related to the postorogenic stage of the Gondwanic Cycle (González et al., 2014, 2016, 2017b), and the Early Jurassic upper sequence is associated to the extrusive processes of the Chon Aike Large Silicic Igneous Province which, in turn, is related to the Karoo Plume (Pankhurst et al., 1998, 2000). In this context, taking into account that they are two distinctive processes, González et al. (2017a) suggested that the Marifil Volcanic Complex has no genetic relationships with either the Middle Triassic mesosilicic magmatism or the Puesto Piris Formation (Fig. 2).

3. Late Permian-Early Jurassic vertebrate tracks from patagonia

3.1. *Los Menucos* vertebrate tracks

The Los Menucos tracks were extensively studied with regard to their ichnotaxonomical and palaeobiological aspects (Casamiquela, 1964, 1975, 1987; Leonardi and de Oliveira, 1990; Leonardi, 1994; Melchor and de Valais, 2006; de Valais, 2008; Domnanovich et al., 2008; Citton et al., 2018). This record consists almost exclusively of footprints referable to *Dicynodontipus* (Fig. 3A) and *Pentasauropus* (Fig. 3B) (Melchor and de Valais, 2006; Domnanovich et al., 2008;

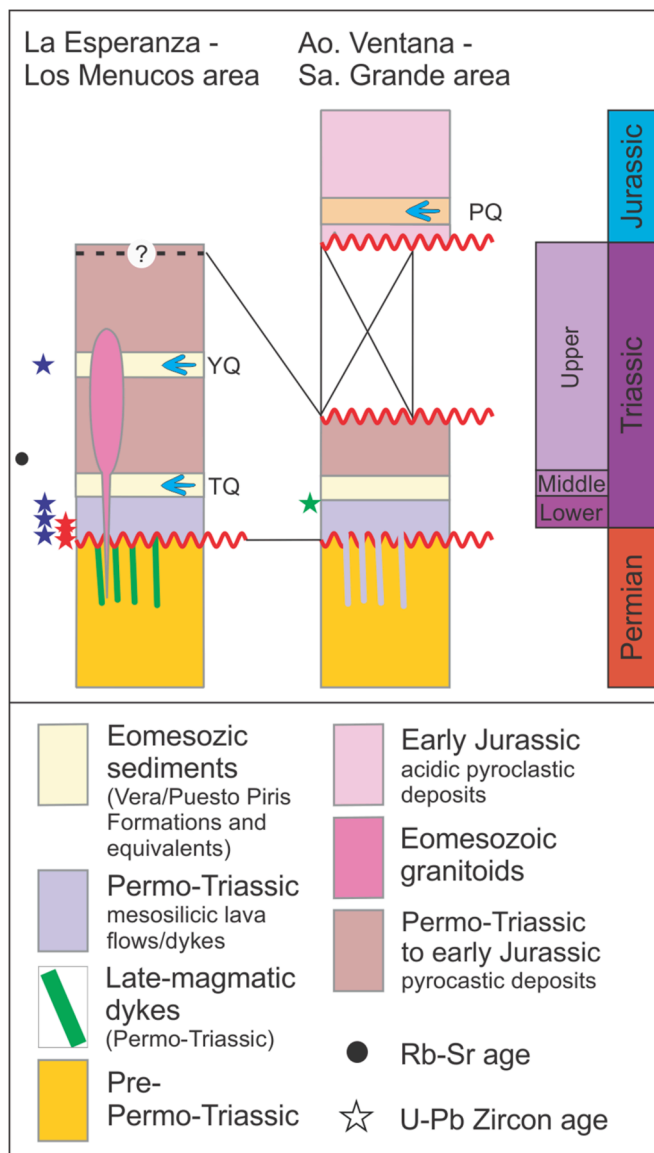


Fig. 2. Schematic stratigraphic columns from the Los Menucos Complex and Marifil Volcanic Complex. The lines between columns indicate possible correlation for these units. Black dot Rb-Sr whole rock age from Rapela et al. (1996); red stars U-Pb SHRIMP from Luppo et al. (2018); blue stars U-Pb LA-ICP-MS from Falco et al. (2018); green star U-Pb LA-ICP-MS from González et al. (2017a,b). YQ, Yancaqueo quarry; TQ, Tscherig quarry; and PQ, Perdomo quarry.

Citton et al., 2018). Some indeterminate chirotheroid tracks (Manera de Bianco and Calvo, 1999; de Valais, 2008) and a single track of *Rhynchosauroioides* (Domnanovich et al., 2008) have also been reported. All the authors pointed out that the tracks were found in the Vera Formation outcrops, mentioned as Upper Triassic in age (see above in 2. Geological context).

To date, the vertebrate tracks from the Los Menucos area come from two sites, the Tscherig farm, owning the “Cantera Nueva and Cantera Vieja” (New Quarry and Old Quarry, respectively) located about 15 km east of the Los Menucos town (Fig. 1), and the Yancaqueo farm -Felipe Curuil's ex quarry-, at about 10 km west from the Los Menucos town (Fig. 1). The tetrapod footprints referred to as *Dicynodontipus*, *Rhynchosauroioides* and indeterminate chirotheroid come from the Tscherig farm, while those referred to as *Pentasauropus* come from the Yancaqueo farm. The ichnotaxa belonging to each locality have never been found together in the same outcrop.

3.1.1. The Tscherig farm site

The first tracks from the Los Menucos town were discovered by Casamiquela in 1959 in the Ingeniero Jacobacci sidewalks, Río Negro province, which were placed there around 1940 (sensu Casamiquela, 1964). About one year later, in November 1960, Mr. Shimmel told Dr. Casamiquela about the presence of the same kind of track-bearing slabs of the sidewalks of Costanera Av. (currently 12 de Octubre Av.) in Bariloche city, Río Negro province (Casamiquela, 1964). Both the Jacobacci and Bariloche slabs have been collected from “Cantera Nueva” and “Cantera Vieja”, from the Tscherig farm, near the Los Menucos town (Casamiquela, 1964; Leonardi and de Oliveira, 1990). Some of those slabs, plus others more collected in later fieldtrips, are currently housed in the following Argentine repositories (see de Valais et al., in press, for a complete list of specimen numbers): Museo de La Plata, La Plata city, Buenos Aires province; Colección Paleontología de Vertebrados del Instituto Miguel Lillo, San Miguel de Tucumán, Tucumán province; Museo Municipal de Ciencias Naturales “Carlos Darwin”, Punta Alta, Buenos Aires province; Colección de Paleontología de Vertebrados del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, CABA; Museo Provincial “Carlos Ameghino”, Cipolletti city, Río Negro province; and, Museo Municipal de Ingeniero Jacobacci “Jorge H. Gerhold”, Ingeniero Jacobacci city, Río Negro province (Leonardi, 1994; de Valais, 2008).

Originally, the Tscherig farm tracks have been named by Casamiquela (1964) as *Gallegosichnus*, *Calibarichnus*, *Palaciosichnus*, *Ingenierichnus*, *Rogerbaletichnus* and *Shimmelia*, and by Casamiquela (1975) as *Stipanichichnus*. Subsequently, *Gallegosichnus*, *Calibarichnus*, *Palaciosichnus* and *Stipanichichnus* are considered as synonyms of *Dicynodontipus* (sensu Melchor and de Valais, 2006; Fig. 3A). The tracks represent a quadrupedal producer, with manus and pes impressions with the same general shape, plantigrade and pentadactyl. The digit impressions are short, anteriorly directed. The digit IV is the longest, the digit V is slightly laterally and posteriorly shifted. The ichnotaxa *Ingenierichnus*, *Rogerbaletichnus* and *Shimmelia* are based on poorly preserved material (Melchor and de Valais, 2006) and are considered as *nomina dubia* (de Valais, 2008; Díaz-Martínez and de Valais, 2014).

With regard to the large chirotheroid tracks (Manera de Bianco and Calvo, 1999), there is no published illustration to evaluate this record. The manus track classified as *Rhynchosauroioides* is well preserved. It is pentadactyl, and the digit impressions increase in length from I to IV, with digit V imprint as the shorter (Domnanovich et al., 2008).

3.1.2. The Yancaqueo farm site

The first ichnological materials from the Yancaqueo farm, some few *Pentasauropus*-bearing slabs, were studied by Domnanovich et al. (2008). Recently, Citton et al. (2018) reviewed both those materials, and several unpublished *Pentasauropus* tracks (Fig. 3B). The slabs are housed in the repositories of the Museo Provincial “Carlos Ameghino”, Cipolletti city; the Museo Municipal de Los Menucos, Los Menucos town; and, the Museo Regional “María Inés Kopp” Valcheta town, all of them in the Río Negro province (see de Valais et al., in press, for a list of specimen numbers).

Pentasauropus is represented by homopodic and pentadactyl fore- and hind-prints, even though incomplete tridactyl and tetradactyl preservation is possible. The footprints are predominantly represented only by the digit traces. In pentadactyl tracks, the trace of digit III and that of digit IV are the most projecting and the most deeply and uniformly imprinted. Digit V trace, when preserved, is the smallest. Digit traces are characterised by a roughly sub-circular morphology. In some cases, digit imprints are pointed and associated with drag traces, especially in the most medial ones (i.e., digit I and II). Behind digit imprints, a circular sole/palm pad trace can be preserved. It resulted separated from the central digit imprints by a non-impressed area, which tapers towards the most medial and lateral digit elements (see Citton et al., 2018).

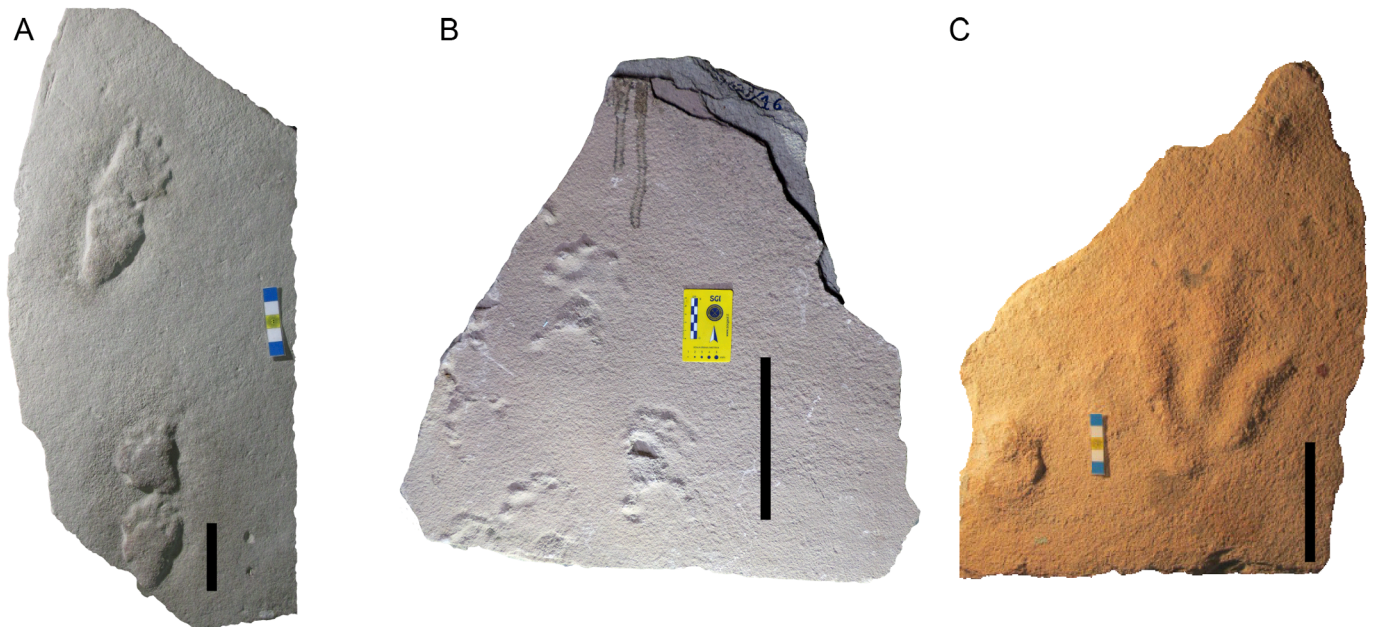


Fig. 3. Patagonian vertebrate tracks of the Los Menucos Complex (A–B) and the Marifil Volcanic Complex (C). A, *Dicynodontipus* isp. from the Tschering farm (Museo Municipal de Ingeniero Jacobacci “Jorge H. Gerhold”, no collection number). B, *Pentasauropus* isp. from the Yancaqueo farm (Museo Provincial de Cipolletti “Carlos Ameghino”, MPCA 27029–16). C, cf. *Anomoepus* from the Perdomo farm (Museo Regional Provincial de Valcheta “María Inés Kopp”, MRPV 430/P/13). Scale bars: A, 5 cm; B, 15 cm; C, 10 cm.

3.2. Marifil Volcanic Complex vertebrate tracks

During the 1950's, a new dinosaurian track-bearing ichnosite, located 50 km southwest of Sierra Grande (Río Negro province, Patagonia, Argentina), was found in the Lower Jurassic Marifil Volcanic Complex (Díaz-Martínez et al., 2017).

The tracks were collected by the Perdomo family from a flagstone quarry close to their homonym farm. Then, 50 years later, the material was donated to the Museo Regional Provincial “María Inés Kopp”, Valcheta town, Río Negro province, Argentina, where it is now housed and labelled MRPV 427/P/13, 428/P/13, 429/P/13, 430/P/13.1, 430/P/13.2 and 430/P/13.3 (Díaz-Martínez et al., 2017).

The Marifil Volcanic Complex vertebrate tracks, represented by cf. *Anomoepus* (Fig. 3C) and *Anomoepus*-like tracks, are less abundant and diverse than those from the Los Menucos Complex (Díaz-Martínez et al., 2017). Nevertheless, they provide valuable information, such as being the first evidence of an Early Jurassic vertebrate record from the Patagonia (Díaz-Martínez et al., 2017).

There are only four footprints, preserved as natural casts. They are tridactyl, subsymmetric, mesaxonic and longer than wide. The posterior margin impression is almost directly or directly aligned with the axis of digit III impression. The best preserved track MRPV 430/P/13 shows clear digital and metatarso-phalangeal pad impressions. Its digit impressions are long and elongated, anteriorly orientated, being the digit III the longest, and the digit IV slightly longer than digit II. In the digit II and III impressions, claw traces are recognised, laterally and anteriorly directed respectively (Díaz-Martínez et al., 2017).

4. Biochronological implications

Although the fact that the reliability of tetrapod footprints in stratigraphic and biochronological applications has been repeatedly questioned or diminished on different bases (Boy and Fichter, 1988; Lucas, 1998b, 2007), the use of vertebrate tracks in biochronology and biostratigraphy has been applied for decades and with different theoretical and methodological approaches (Ellenberger, 1983a, 1983b, 1984; Gand, 1987; Haubold, 1969, 1996, 2000; Lucas, 1998a, 1998b, 2004, 2005, 2006; Cassinis and Santi, 2005; Gand and Durand, 2006; Klein

and Haubold, 2007; Avanzini and Mietto, 2008; Klein and Lucas, 2010). The utility of tetrapod tracks for biostratigraphic correlations and biochronological subdivisions was already pointed out by Haubold and Katzung (1978), who proposed the term “palichnostratigraphy”. At the same time, Conti et al. (1977) suggested the use of tetrapod ichnoassociations to establish ichnofaunal units with a clear biochronological meaning. Avanzini et al. (2001a) suggested a biochronological scheme of different Permian and Triassic ichnofaunas worldwide.

In this way, *Protochirotherium* is usually recorded in late Induan-lower Olenekian rocks, as well as *Brachychirotherium* is a typical Upper Triassic ichnogenus (see Klein and Haubold, 2007; Klein and Lucas, 2010). But not all the Permian-Triassic ichnotaxa have restricted temporal distributions. The ichnogenus *Rhynchosauroides* has a broad temporal range, which spans from the Lopingian to the Late Jurassic (e.g., Klein and Lucas, 2010; Avanzini et al., 2010). According to Lucas (2007), the biochronology performed by tetrapod tracks has three main limiting factors: (1) invalid ichnotaxa based on extramorphological variants; (2) slow apparent evolutionary turnover rates; and (3) facies restrictions; we add a fourth factor, (4) precise geological and temporal information of the track-bearing levels.

In this section, the biochronological significance and the utility of the late Permian-Early Jurassic Patagonian tetrapod tracks will be discussed. For that, the ichnotaxa *Dicynodontipus*, *Pentasauropus*, and *Anomoepus*-like (sensu Díaz-Martínez et al., 2017) are analysed. Regarding *Rhynchosauroides*, this ichnogenus was not taken into account in this proposal due to its scarcity in the ichnosites from Patagonia and for its wide temporal range.

4.1. *Dicynodontipus* record

The chronostratigraphic distribution of *Dicynodontipus* based on bibliographic information spans from the Lopingian (Wuchiapingian) to the Late Triassic (Carnian) (see Table 1 for occurrences and related references).

The Lopingian record comprises: *Dicynodontipus geinitzi* (Hornstein, 1876) from the Arenaria di Val Gardena (western Dolomites, northern Italy) (Conti et al., 1977); *Dicynodontipus icelsi* from the Beaufort Group (South Africa) (de Klerk, 2002); *Dicynodontipus*-like from the upper

Table 1
Geographical and temporal distribution of *Dicynodontipus* tracks. *holotype.

Taxon	Age	Unit	Country	Reference
<i>D. geinitzi</i>	Wuchiapingian	Arenaria di Val Gardena	Italy	Conti et al. (1977)
<i>Dicynodontipus</i> isp.	Lopingian–Induan	Pirambóia Formation	Brazil	Francischini et al. (2018)
<i>D. icelsi</i> *	Late Permian	Beaufort Group	South Africa	de Klerk (2002)
<i>D. penugnu</i> *	Late Permian	Rio do Rasto Formation	Brazil	Silva et al. (2012)
<i>Dicynodontipus</i> -like	Late Permian	Upper Upper Red Unit	Spain	Mujal et al. (2017)
<i>Dicynodontipus</i> ispp.	? Wuchiapingian–Olenekian (this work)	Vera Formation	Argentina	Melchor and de Valais (2006)
cf. <i>Dicynodontipus</i> isp.	Induan	Balfour Formation	South Africa	Marchetti et al. (2019b)
<i>Dicynodontipus</i> isp.	Olenekian	Detfurth Formation	Germany	Fichter et al. (1999)
<i>D. hildburghausensis</i> *	Olenekian–Anisian	Solling Formation	Germany	Lilienstern von (1944)
<i>D. bellambiensis</i> *	Earliest Triassic	Coal Cliff Sandstone	Australia	Retallack (1996)
<i>Dicynodontipus</i>	Early Triassic	Solling Formation	Germany	Haubold (1983)
<i>D. geinitzi</i> *	Early Anisian	Solling Formation	Germany	Lilienstern von (1944)
<i>Dicynodontipus</i> isp.	Anisian	Buntsandstein	Spain	Valdiserri et al. (2009)
<i>Dicynodontipus</i> isp.	Anisian	Eschenbach and Grafenwöhr formations	Germany	Klein and Lucas (2018)
<i>Dicynodontipus</i> ispp.	Late Anisian–late Ladinian (Tassi et al., 2015)	Cerro de las Cabras Formation	Argentina	Casamiuela (1964); Leonardi (1994); Melchor and de Valais (2006)
cf. <i>Dicynodontipus</i> isp.	Anisian–Ladinian	Cerro de las Cabras Formation	Argentina	Lagnaoui et al. (2019)
<i>Dicynodontipus</i> isp.	Carnian	Portezuelo Formation	Argentina	Marsicano and Barredo (2004); Melchor and de Valais (2006)
<i>D. protherioides</i> *	Carnian	Santa María Formation	Brazil	Costa da Silva et al. (2008)
<i>Dicynodontipus</i> isp.	Carnian	Santa María Formation	Brazil	Costa da Silva et al. (2008)

Upper Red Unit (Spain) (Mujal et al., 2017), *Dicynodontipus penugnu* from the Rio do Rasto Formation (Costa da Silva et al., 2012), and *Dicynodontipus* isp. (Francischini et al., 2018) from the Pirambóia Formation (both in Brazil). Recent works about the Wuchiapingian ichnofauna from Italy have supported the occurrence of *Dicynodontipus* (e.g., Avanzini et al., 2011; Bernardi et al., 2017a, 2017b; Marchetti et al., 2019a). Herein, we share the authors' opinion about the assignment of the tracks from Italy and the Pirambóia Formation of Brazil. The material referred as *Dicynodontipus penugnu* was instead recently questioned based on the preservation (Marchetti et al., 2019a), and *Dicynodontipus icelsi* has been located within the ichnogenus *Dolomitipes* under the new combination *Dolomitipes icelsi* (see Marchetti et al., 2019b, for further details). Moreover, the *Dicynodontipus* tracks published by Mujal et al. (2017) and referred to as *D. icelsi* are considered here as different to *Dicynodontipus*.

Globally, most of the tracks referred to the ichnogenus *Dicynodontipus* come from Lower Triassic and lower Middle Triassic (Olenekian–Anisian) deposits (see Table 1 for occurrences and related references). From this interval, tracks referred to as *Dicynodontipus* were reported from Germany where *D. hildburghausensis* Lilienstern von, 1944 was described (Lilienstern von, 1944; Fichter et al., 1999; Klein and Lucas, 2018, among others), Australia (Retallack, 1996), Argentina (Melchor and de Valais, 2006; de Valais, 2008), Spain (Valdiserri et al., 2009) and Poland (Klein and Niedźwiedzki, 2012). Retallack (1996) erected *Dicynodontipus bellambiensis* from the Lower Triassic Coal Cliff Sandstone of Australia. The material was recently considered as different from *Dicynodontipus* by Klein et al. (2015); the authors stated that the material is too poorly preserved to be reliably assigned to a ichnotaxon but it can be considered different from *Dicynodontipus* and more similar to the holotype of *Procolophonichnium nopcsai*. We agree that this material is not clear enough to attempt a reliable ichnotaxonomical attribution due to substrate properties during track registration and, therefore, we will not consider it in this work. Recently, material referred to as cf. *Dicynodontipus* isp. has been reported from the Induan Palingkloof Member (Balfour Formation) of South Africa (Marchetti et al., 2019b). The only set illustrated show footprints with a rounded sole pad and a long digit traces to be hardly comparable with the ichnogenus. The Spanish record (Valdiserri et al., 2009) is not figured in the publication, therefore it is not considered in this study. In Argentina, the tracks related to *Dicynodontipus* were reported from the Cerro de las Cabras Formation, Northern Mendoza province (Melchor and de Valais, 2006; de Valais, 2008; Lagnaoui et al., 2019), dated as

upper Anisian–upper Ladinian (Tassi et al., 2015) or Anisian–Ladinian (Lagnaoui et al., 2019). Although the general shape of the tracks published by Melchor and de Valais (2006) and de Valais (2008) from Mendoza resembles those of the ichnogenus, the digit impressions are different from the classical *Dicynodontipus* and, thus, their precise ichnotaxonomic identity should be discussed in the future. On the other hand, the track considered as cf. *Dicynodontipus* isp. by Lagnaoui et al. (2019) is poorly preserved, thus it is not considered in this study. Klein and Niedźwiedzki (2012) reported tracks deemed similar to *Dicynodontipus* from the Lower Triassic Wióry locality (Holy Cross Mountains, Poland), but the material is here considered too poorly preserved to be confidently assigned to the ichnogenus (see also Francischini et al., 2018).

The Late Triassic record related to this ichnogenus comprises tracks from Argentina (Melchor and de Valais, 2006) and Brazil (Costa da Silva et al., 2008). In Argentina, the tracks from the Carnian Portezuelo Formation (Marsicano and Barredo, 2004) are poorly preserved and thus not considered in this study, while the tracks from the Vera Formation are clearly *Dicynodontipus* but the Late Triassic age is questioned in this work. The material from Brazil, *Dicynodontipus protherioides* (Costa da Silva et al., 2008) has been synonymised with *Procolophonichnium* by Klein et al. (2015). In our opinion, this material is lacking in diagnostic features, particularly in the sole/palm impression, therefore we reject the attribution to *Dicynodontipus*.

Finally, if all dubious assignments are discarded, and the age of the Vera Formation is still under discussion, the temporal distribution of *Dicynodontipus* is restricted to the Lopingian (Wuchiapingian)–early Middle Triassic (early Anisian) time interval (see Fig. 4).

There are four proposed biochrons for the Lopingian–Middle Triassic interval, according to biochronological studies based on vertebrate tracks (e.g., Klein and Lucas, 2010; Conti et al., 2000):

- 1 Late Permian (Wuchiapingian, Lopingian), Bletterbach Faunal Unit (Conti et al., 2000; Avanzini et al., 2011) characterised by at least 13 ichnotaxa among which some with clear Triassic affinity are also present (see Bernardi et al., 2017a, 2017b); for the late Permian, Voigt and Lucas (2016) proposed the *Paradoxichnium* biochron;
- 2 latest Changhsingian–early Induan, dicynodont footprints biochron, associated with *Procolophonichnium*, *Rhynchosauroides*, *Capitosauroides* and *Prorotodactylus*;
- 3 late Induan–early Olenekian, *Protochirotherium* biochron with the associated forms *Rhynchosauroides*, *Procolophonichnium* and

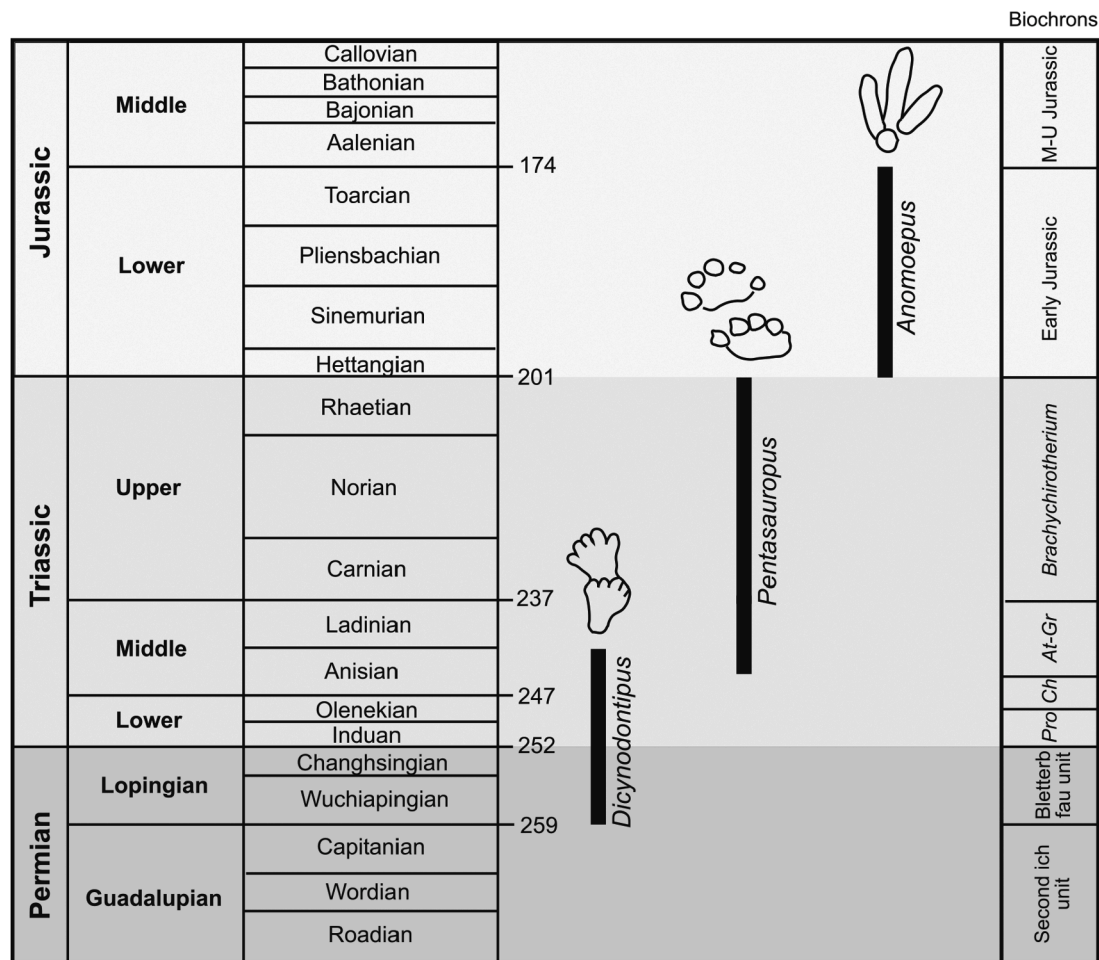


Fig. 4. Stratigraphic distribution of *Dicynodontipus*, *Pentasauropus* and *Anomoepus*-like ichnotaxa in the Permian-Jurassic global biochrons and characteristic assemblages (Gand and Durand, 2006; Klein and Lucas, 2010). It is based on the ichnotaxonomical discussion of section 4. Biochronological implications. Abbreviations: ich., ichnological; Bletterb. fau., Bletterbach faunal; Pro., *Protochirotherium*; Ch., *Chirotherium*; At., *Atreipus*; Gr., *Grallator*; M-U., Middle-Upper.

temnospondyl footprints;

4 late Olenekian-early Anisian, *Chirotherium barthii* biochron with *C. sickleri*, *Rotodactylus*, *Isochirotherium* and *Synaptichnium*, together with *Rhynchosauroides*, *Procolophonichnium*, dicynodont and temnospondyl footprints. Although the temporal distribution of *Dicynodontipus* is widespread, it could be an important ichnotaxon to take into account for the future biochronological and biostratigraphical studies in Lopingian-Middle Triassic basins.

4.2. *Pentasauropus* record

The temporal distribution of *Pentasauropus*, according to the published information, ranges from Middle Triassic (Anisian or late Anisian) to Late Triassic (Rhaetian) (see Table 2). The type ichnospecies, *P. incredibilis* Ellenberger (1970), was established on the basis of material coming from the Upper Triassic lower Elliot Formation, considered recently as Norian-Rhaetian in age (Sciscio et al., 2017), of the Karoo Basin of Lesotho (Southern Africa) (Ellenberger, 1955, 1970, 1972; see D'Orazi Porchetti and Nicosia, 2007 for an ichnotaxonomical discussion). Outside southern Africa, tracks tentatively referred as *Pentasauropus* were reported from the Upper Triassic Chinle Group of Utah (Lockley and Hunt, 1995; Hunt-Foster et al., 2016) and Colorado (Gaston et al., 2003), both in the USA. Moreover, some localities with tracks associated with *Pentasauropus* have been found in Argentina. For instance, in the Triassic Vera Formation (see the Geological setting section) about 60 footprints assigned to *Pentasauropus* have been studied (Domnanovich et al., 2008; Citton et al., 2018). Moreover, some

tracks from the Carnian Portezuelo Formation, southern San Juan Province, Argentina (Marsicano and Barredo, 2004) have been referred to this ichnotaxon (de Valais, 2008). Finally, the new ichnotaxon *Pentasauropus argentinae* (Lagnaoui et al., 2019) and tracks similar to *Pentasauropus* (see de Valais et al., 2006; de Valais, 2008) were recorded in the Middle Triassic Cerro de Las Cabras Formation. Based on geochronological and biochronological data, this unit is considered as late Anisian-late Ladinian in age (Tassi et al., 2015) or Anisian-Ladinian (Lagnaoui et al., 2019), although K/Ar radiometric ages obtained in a basic sill intruded in the unit yielded suggest the possibility of a Carnian age (235 ± 5 Ma, in Ramos and Kay, 1991; see Spalletti et al., 1999 for further interpretations).

We consider that all the tracks presented above are *Pentasauropus* in shape. Although this record is not abundant, almost all of them were found in Upper Triassic rocks with the exception of tracks from the Middle Triassic (late Anisian-late Ladinian) Cerro de las Cabras Formation (see Fig. 4). For this temporal distribution two biochrons were proposed according to Klein and Lucas (2010): 1- the biochron *Grallator-Atreipus* (late Anisian-Ladinian) in association with the pentadactyl footprints of *Sphingopus* and *Parachirotherium*; and 2- the biochron *Brachychirotherium* together with the presence of *Atreipus*, *Grallator* and *Eubrontes* with an early Carnian-late Rhaetian temporal distribution.

4.3. *Anomoepus*-like ichnotaxa

Anomoepus-like ichnotaxa (i.e., *Anomoepus Hitchcock*, 1845,

Table 2
Geographical and temporal distribution of *Pentasauropus* tracks. *holotype.

Taxon	Age	Unit	Country	Reference
<i>Pentasauropus argentiniae</i> *	Anisian-Ladinian	Cerro de las Cabras Formation	Argentina	Lagnaoui et al. (2019)
cf. <i>Pentasauropus</i>	Late Anisian- late Ladinian (Tassi et al., 2015)	Cerro de las Cabras Formation	Argentina	de Valais et al. (2006)
<i>Pentasauropus</i> isp.	Late Anisian- late Rhaetian (?Norian, this work)	Vera Formation	Argentina	Marsicano and Barredo (2004); Domnanovich et al. (2008); Citton et al. (2018)
Tracks referred to as <i>Pentasauropus</i>	Carnian	Portezuelo Formation	Argentina	Citton et al. (2018)
May be referable to <i>Pentasauropus</i>	Carnian-Norian	Gettysberg Shale, Newark Supergroup	USA	Olsen and Galton (1984).
<i>Pentasauropus</i> isp.	Norian-Rhaetian	Rock Point Formation, Chinle Group	USA	Lockley and Hunt (1995); Gaston et al. (2003)
<i>Pentasauropus incredibilis</i> *	Norian-Rhaetian (Sciscio et al., 2017)	Lower Elliot Formation	Lesotho	Ellenberger (1955, 1970, 1972);

Moyenisauropus Ellenberger, 1970 and *Shenmuichnus* Li et al., 2012) present a wide temporal distribution, from Late Triassic to Middle Jurassic (Table 3), according to bibliographic data.

Anomoepus-like tracks have been found in Upper Triassic rocks of USA and Poland. The Late Triassic tracks from the USA were assigned as ?*Anomoepus* isp. by Baird (1964), and currently considered chirotheriid tracks by Lockley and Gierlínski (2006). The tracks from Poland that are considered as cf. *Anomoepus* isp. and cf. *Moyenisauropus* are poorly-preserved (Niedźwiedzki, 2011), so it is difficult to relate them with confidence to these ichnogenera (Díaz-Martínez et al., 2017).

The most abundant *Anomoepus*-like record came from the Lower Jurassic units. They were reported from the USA (Hitchcock, 1845; Olsen and Rainforth, 2003; Lockley and Gierlínski (2006); Dalman and Weems, 2013), Poland (Gierlínski, 1991; Niedźwiedzki and Pieńkowski, 2016); China (Xing et al., 2015, 2016a,b,c); Italy (Avanzini et al., 2001); Australia (Thulborn, 1994); Lesotho (Ellenberger, 1970) and Argentina (Díaz-Martínez et al., 2017). Almost all this material is confidently classified within the *Anomoepus*-like group with the exception of the tracks found in China, which have been assigned to *Anomoepus* isp. (Lockley and Matsukawa, 2009; Xing et al., 2015), but only illustrated by linear drawings and therefore it is difficult to corroborate their ichnotaxonomical affinity.

The Middle Jurassic record is composed of tracks from China and Morocco. Those classified as *Anomoepus* isp. from the Yima Formation (Xing et al., 2017a) and cf. *Anomoepus* from the Xintiangou Formation (Xing et al., 2017b), both from China, and *Anomoepus*-like from the Gettioua Formation of Morocco (Belvedere et al., 2011) are closer to an avian-like ichnotaxon than to *Anomoepus*, given that they have very slender digit impressions and narrow metatarsophalangeal pad impressions (Díaz-Martínez et al., 2017). Finally, Xing et al. (2015) proposed the new combination *Anomoepus tungchuanensis* (Young, 1966) (= "*Shensipus tungchuanensis*", from the Middle Jurassic Zhiluo Group, China). However, the original specimens are lost (sensu Xing et al., 2015), but in view of the published photographs, they seem poorly-preserved, so a confident conclusion seems to be difficult (Díaz-Martínez et al., 2017).

According to the reliable record, the temporal distribution of *Anomoepus*-like tracks is restricted to the Early Jurassic (see Fig. 4). Some authors pointed out the utility of *Anomoepus* to biochronological studies (e.g., Olsen and Rainforth, 2003; Lockley and Gierlínski, 2006). Lucas (2007) suggested that the Early Jurassic biochron is characterised by theropod-footprint dominated (ichnogenera *Eubrontes* and *Grallator*), but includes a few tracks (ichnogenera *Anomoepus*, *Moyenosauropus*, *Otozoum* and *Evazoum*) attributed to ornithopods, thyreophorans and sauropodomorphs. The *Anomoepus*-like ichnotaxa have the same temporal distribution as proposed for the Early Jurassic biochron, thus this kind of tracks is a good marker of this epoch.

5. Chronological inferences of the Triassic-Early Jurassic patagonian tetrapod tracks

All the tracks from Patagonia studied here come from quarries that were explored in the 1950–1980s of the 20th century. Although the bibliographical data allow relating the tracks with each quarry, the exact information about their stratigraphic position is uncertain.

The tracks found near to the Los Menucos town had been related with the Vera Formation. In several papers (e.g., Melchor and de Valais, 2006; Domnanovich et al., 2008, and references in both contributions), these tracks were considered as Carnian in age because of a Rb–Sr isochron for volcaniclastic rocks of the Sierra Colorada Formation indicating 222 ± 2 Ma (Rapela et al., 1996). The latter unit overlies the Vera Formation (see the Geological section for more detailed information), so the chronological data related to the tracks should be older than 222 ± 2 Ma. Recently, new U–Pb on zircon dating pointed out latest Permian-Early Triassic in age for the Vera Formation. Lupo et al. (2018) suggested that the taphoflora remains, belonging to the

Table 3
Geographical and temporal distribution of *Anomoepus*-like ichnotaxa. *holotype.

Taxon	Age	Unit	Country	Reference
? <i>Anomoepus</i> isp.	Norian	Sloan Canyon Formation	USA	Baird (1964)
cf. <i>Anomoepus</i> isp.	(?late Norian–Rhaetian	Tomanová Formation	Poland	Niedźwiedzki (2011)
cf. <i>Moyenisauripus</i> isp.	(?late Norian–Rhaetian	Tomanová Formation	Poland	Niedźwiedzki (2011)
<i>Anomoepus pienkovskii</i> *	Early Hettangian	Przysucha Ore-bearing Series	Poland	Gierliński (1991)
<i>Moyenisauropus karaszewskii</i> *	Early Hettangian	Przysucha Ore-bearing Series	Poland	Gierliński (1991)
<i>Moyenisauropus</i> isp.	Early Hettangian	Przysucha Ore-bearing Series	Poland	Gierliński (1991)
<i>Anomoepus lacertoideus</i>	Hettangian	East Berlin Formation	USA	Dalman and Weems (2013)
cf. <i>Anomoepus</i> isp.	Late Hettangian	Przysucha Formation	Poland	Niedźwiedzki and Pieńkowski (2016)
<i>Moyenisauropus natator</i> *	Hettangian-early Sinemurian (Sciscio et al., 2017)	Upper Elliot Formation	Lesotho	Ellenberger (1970)
<i>Anomoepus</i> isp.	Hettangian- early Sinemurian	Calcari Grigi Formation	Italy	Avanzini et al. (2001)
<i>Anomoepus shingi</i>	Hettangian-Sinemurian	Wingate, Kayenta and Navajo formations	USA	Lockley and Gierliński (2006)
<i>Anomoepus scambus</i> *	Early Jurassic	Turners Falls and lower Portland formations	USA	Hitchcock (1845); Olsen and Rainforth (2003)
<i>Anomoepus</i> cf. <i>A. gracillimus</i>	Early Jurassic	Precipice Sandstone	Australia	Thulborn (1994)
<i>Shenmuichnus youngteihardorum</i> *	Early Jurassic	Fuxian Formation	China	Li et al. (2012)
<i>Shenmuichnus wangi</i> *	Early Jurassic	Lufeng Formation	China	Xing et al. (2016a)
<i>Anomoepus</i> isp.	Early Jurassic	Lufen Formation	China	Xing et al. (2016b)
<i>Anomoepus</i> isp.	Early Jurassic sensu Wang et al. (2016)	Yanan Formation	China	Xing et al. (2015)
<i>Anomoepus</i> isp.	Early Jurassic	Fengjiahe Formation	China	Xing et al. (2016c)
cf. <i>Anomoepus</i>	Early Jurassic	Marifil Volcanic Complex	Argentina	Díaz-Martínez et al. (2017)
<i>Anomoepus</i> isp.	Early-Middle Jurassic	Xintiangou Formation	China	Lockley and Matsukawa (2009)
<i>Anomoepus</i> -like	Bajocian/Bathonian	Guettoua Formation	Morocco	Belvedere et al. (2011)
<i>Anomoepus tungchuanensis</i>	Middle Jurassic	Zhiluo Group	China	Xing et al. (2015)
<i>Anomoepus</i> isp.	Middle Jurassic	Yima Formation	China	Xing et al. (2017a)
cf. <i>Anomoepus</i>	Middle Jurassic	Xintiangou Formation	China	Xing et al. (2017b)

Vera Formation according to Labudía and Bjerg (2001), are stratigraphically intercalated between samples of 252 ± 2 Ma and 248 ± 2 Ma. Moreover, Falco et al. (2018) analysed two samples, one from near to the Tschering farm and the other from the Puesto Vera farm, which indicated ages of 252 ± 1 Ma and 248 ± 1 Ma respectively. Other westernmost samples were analysed by both authors indicating ages of 257 ± 2 Ma and 256 ± 0.7 Ma (Falco et al., 2018; Luppo et al., 2018). All these ages were calculated from pyroclastic flow deposits so they could be considered as maximum depositional ages for the sedimentary process and a near-eruptive age for the volcanic activity. The ages obtained by Luppo et al. (2018) and Falco et al. (2018) are very similar, and considered as Wuchiapingian-Olenekian in age (according to the International Chronostratigraphic Chart, 2018; Cohen et al., 2013, updated). The biochronological information obtained from the *Dicynodontipus* tracks (Lopingian-early Middle Triassic), which were found in the Tschering farm, is consistent with the current geochronological data. Therefore, it is possible that the Vera Formation and the *Dicynodontipus* tracks have a tentative age of Wuchiapingian-Olenekian, about 257–242 Ma (Lopingian- Early Triassic).

Otherwise, the tracks classified as *Pentasauropus* found at the Yancaqueo farm have also been related to the Vera Formation (Domnanovich et al., 2008). This area lacks precise geochronological information, being the closest measured point in the Cerro de Las Minas, located 5 km west, of 211 ± 1 Ma, Norian in age (Falco et al., 2018). From a structural point of view, the Piche synform (Giacosa et al., 2007) repeats the Vera Formation in Puesto Vera dipping southwards and in the Tschering farm dipping eastwards, defining a SE-plunging syncline fold. The Cerro de Las Minas area, Norian in age, is found in the centre of this structure with a very low dipping angle and it is possible to compare with those cropping out in Yancaqueo farm. Also in this case the age is in agreement with the global record of *Pentasauropus*, and the rocks around the Yancaqueo farm (Norian?) and constituting the core of the syncline are much younger than those cropping out at the Tschering locality (west of the Los Menucos town). The starting point of the deposition of the original Vera Formation had to be most likely anticipated with respect to the historical interpretation during the Lopingian-Early Triassic time interval.

Far from radiometric dating failures, these age discrepancies allow

us to infer a hiatus between Changhsingian-Olenekian to Middle-Late Triassic aged deposits. In this regard, it is possible to assess the existence of two allounits separated by discontinuities. On the basis of the environmental setting of the Vera Formation (Labudía and Bjerg, 2001), it can be useful to elucidate discontinuities with possible regional significance. These authors described fluvial to alluvial systems along with pyroclastic flows. Conglomerates are a frequent component, probably linked with progressive discordances. Although the elucidation of the regional distribution of these discontinuities is far from the scope of this contribution, the described data support the existence of at least two allounits of different ages: one ranging from the lattermost Permian to Early Triassic (Tschering farm area); and the other for the Middle-Late Triassic (Yancaqueo farm area).

In the case of both the Tschering and the Yancaqueo farms they are in different lithostratigraphic units, the first one would belong to the Vera Formation because it is equivalent to the Puesto Vera, where the formation was originally defined. Thereby, the Yancaqueo farm could be part of the Upper Triassic Sierra Colorada Formation, or part of an undescribed unit depending on the lithological features. New lithostratigraphic and geochronological studies are needed in the Los Menucos area, and especially in the Yancaqueo farm, in order to try to solve this discussion.

The case of the Marifil Volcanic Complex is less problematic than the Los Menucos Complex as far as concerns the chronological information of the track-bearing levels. As suggested above, González et al. (2017a) separated the Lower Jurassic Marifil Volcanic Complex from the Middle Triassic magmatism and sedimentation. The tracks were found near the Perdomo farm in epiclastic rocks intercalated with pyroclastic and volcanogenic deposits from the Marifil Volcanic Complex (Díaz-Martínez et al., 2017). These rocks have been considered as pre-Toarcian in age considering Rb–Sr and Ar–Ar dating in the same unit of 188 Ma and 178 Ma (Pankhurst et al., 2000). This temporal range is coherent with the biochronological information of *Anomoepus*, considered as Early Jurassic.

6. Relationships with southern african realm

It is usual that palaeontological works about Gondwanan early

Mesozoic fossil record discuss phylogenetic correlations between South America and South Africa (e.g., Olsen and Galton, 1984; Knoll, 2005; Rauhut and López-Arbarello, 2008; Martínez, 2009; Apaldetti et al., 2011; McPhee et al., 2017). In Patagonia, there are few outcrops within this temporal range, but the relationships with the record from southern Africa are also analysed (e.g., Pol and Powell, 2007; Pol et al., 2011). Indeed, the similarities between the ichnological record from both places have also been studied (e.g., Díaz-Martínez et al., 2017; Citton et al., 2018; Lagnaoui et al., 2019), which coincides with the improved knowledge of this record in recent years (Abrahams et al., 2017; Bordy et al., 2017; Rampersadh et al., 2018; Sciscio et al., 2016, 2017). In order to better understand this type of correlations during the latest Permian–Early Jurassic, the similarities and differences regarding the geology, environment and ichnological fossil record between Patagonia and southern Africa are described.

6.1. Brief Karoo Basin background

In terms of the geological correlation of the ichnological record discussed here, it is appropriate to review the stratigraphy and palaeoenvironmental settings of the latest Permian–Early Jurassic basins of southern Africa.

The Karoo Supergroup (late Carboniferous–Early Jurassic) in southern Africa involves a complex group of basins that, although they share a mainly common history, each one has distinct characteristics in terms of tecto-sedimentary and palaeoenvironmental evolution (Johnson et al., 1996, and references therein). The size, thickness and inherent complexity of the overall basin and minor basins or sub-basins that comprise the Karoo Supergroup (Catuneanu et al., 1998) has a counterpart in uncertainty regarding the nomenclature of these various basins (Johnson et al., 1996). The maximum preserved thickness of the Karoo Basin megasequence is about 6 km (Catuneanu et al., 1998), comprising a set of varied palaeoenvironments including glacial to deep marine, deltaic, fluvial, wadi-playa lake, and aeolian (Smith, 1990, Smith et al., 1993). Thus, the revision of the entire stratigraphic record of the Karoo Basin is far from our present scope, and therefore, we will focus on the units that comprise the ichnofossils discussed in this contribution, namely some aspects of the lithostratigraphy of the Beaufort Group (late Permian–Carnian?) (after Johnson et al., 1996; Catuneanu et al., 1998; Rubidge et al., 2000, and references therein) and the “Stormberg” Group (Carnian–Pliensbachian?) (after Knoll, 2005; Bordy et al., 2005, and references therein).

Although the “Stormberg” label is informal in origin, it is still accepted and widely used (Knoll, 2005). Within the main Karoo Basin, a section displaying the transition from bottom to the top of these mentioned crops out in the northeastern sector (i.e., Memel area of South Africa *sensu* Johnson et al., 1996). As it is understood by consensus, the Stormberg Group retains the original definition of Dunn (1878) who divided the sedimentary rocks between the Guadalupian–Early Triassic Beaufort and the Jurassic Drakensberg Groups in three “stages”, from bottom to top: Coal Measures, Red Beds, and Cave Sandstone (see reviews in Knoll, 2005; and Bordy et al., 2005). These three units comprise respectively the Molteno, Elliot and Clarens formations (Knoll, 2005; Bordy et al., 2005). These names are mainly maintained across the basin. So, the label of Stormberg Group needs to be maintained in order to allow the correlation of the stratigraphic units in the upper part of the Karoo Supergroup, as suggested by Bordy et al. (2005).

In an overall sense, the Beaufort Group and overlying Molteno and Elliot formations of the Stormberg Group consist almost entirely of fining upwards fluvial sediments (Johnson et al., 1996). The sedimentology of the Elliot Formation suggests a predominantly fluvio-lacustrine system for the unit, with a change in conditions from the lower Elliot Formation to the upper Elliot Formation represented by a migration between meandering rivers to ephemeral rivers and lakes (Bordy et al., 2004; Rampersadh et al., 2018).

In the Beaufort Group the track-bearing unit is the Balfour

Formation (*Cistecephalus* Assemblage Zone *sensu de* Klerk, 2002). This unit is correlative to the west with the Oukloof Member of the Tekloof Formation (Turner, 1981). The palaeoenvironment is inferred as a fluvial deposit, consisting of floodplains of meandering rivers, which is consistent with the overall interpretation of the Balfour and Tekloof formations along the basin (Turner, 1981). The lower facies of the Beaufort Group at the southern Karoo Basin, along the contact with the underlying Ecca Group can be attributed to a deltaic system (Rubidge et al., 2000).

The scenario is quite similar for the Molteno and Elliot formations, both also dominated by fluvial system. The rivers were mostly of meandering type, with extensive floodplain muds predominating over lenticular channel sands, although the Molteno Formation rivers appear to have been deposited by braided low-sinuosity streams (Johnson et al., 1996). On the other hand, the Clarens Formation palaeoenvironmental situation is characterised by arid, aeolian conditions along fluvial and playa lake environments (Johnson et al., 1996; Bordy and Head, 2018).

6.2. Geological correlation

6.2.1. General considerations

With regard to the geological context mentioned before, the problem is related to the disparity between the age of the track-bearing units in Argentina and others recognised worldwide, mainly in regard to the correlation with Karoo occurrences. This is because until a few years ago, the tracks-bearing units from Patagonia were lacking appropriate geochronological dating and chronostratigraphic data. Some gaps still remain, principally related with the stratigraphic and chronologic position of these ichnological records. Most of these problems are linked with the complexity and disparity of the Patagonian and southern Africa geological realms caused by the break-up of Pangaea along the Permo-Triassic to Early Jurassic time lapse that produced an intricate mosaic of extensional basins (see Golonka, 2007). Whilst the Patagonia realm basins developed as small to medium regional scale in size (e.g., the Los Menucos Complex and the Marifil Volcanic Complex), the southern African depocentres occur within the large Karoo Supergroup Basin. Beyond these inherent characteristics, such as sizes and tectonics, the geological correlation of these basins commonly is hard to assess, because lithostratigraphic similarities between diachronic units and the lack of enough radiometric ages caused an overlapping of unit names. In addition, another problem regarding the lithostratigraphic correlation between track-bearing units in Patagonia and southern Africa is that their different tecto-sedimentary histories generated different settings.

6.2.2. Tectonic settings

The overall context of tectonic processes along the Permian–Triassic boundary is related with the break-up of the main part of Pangaea and continues with extensive rifting that occurred during the Triassic–Early Jurassic time (Golonka, 2007). The Pangaeian Rim of Fire was active during the Triassic and Jurassic, causing active volcanism, terrane accretion, and back-arc basin development (Golonka, 2007). In this context, the Karoo rifting between southern Africa and Antarctica is related with the impingement of the Karoo plume in the early Jurassic and the extrusion of flood basalts (Cox, 1992). The main Karoo Basin can be classified as a retro-arc foreland basin produced by northward subduction of oceanic lithosphere located south of the arc (Johnson et al., 1996; Catuneanu et al., 1998, and references therein). The bulk of the Ecca and Beaufort groups in the southern foredeep part of the basin were derived from the arc during the Permian, but the rapidly rising Cape Fold Belt along the basin margin contributed significantly to the basin fill during the Triassic and was the predominant source for the Molteno and Elliot formations (Johnson et al., 1996). To the western, in addition to this process and along the Patagonian realm, the basins were developed under the influence of the subduction of the proto-

Table 4
Geological correlation, ichnological record distribution and palaeoenvironments between Patagonia and Karoo realms.

Unit	Ichnofauna	Age	Palaeoenvironmental setting		References
Marifil Volcanic Complex	cf. <i>Anomoepus</i>	Early Jurassic	Fluvial systems with volcanoclastic supply	Fluvial system to aeolian settings	Díaz-Martínez et al., 2017; Olsen and Rainforth, 2003; Sciscio et al., 2017; this work
Vera Formation (Yancaqueo farm)	<i>Pentasauropus</i>	Late Anisian-Rhaetian (?Norian)	Fluvial systems with volcanoclastic supply	Fluvial systems in arid conditions	Citton et al., 2018; Sciscio et al., 2017 and references therein; this work
Vera Formation (Tschering farm)	<i>Dicynodontipus</i> “ <i>Dicynodontipus icelst</i> ”	Wuchiapingian-Olenekian Late Permian			

Pacific plate below the western margin of Gondwana and the progressive development of the western Gondwana magmatic arc (Franzese et al., 2003). Regarding the tectonic setting of the Los Menucos magmatism, the context is not fully understood, and models of a magmatic arc, slab break-off and extensional processes have been proposed (Luppo et al., 2018, and references therein). In regard to this, calc-alkaline volcanic rocks of the Los Menucos depocentre could be interpreted as evidence of coeval retro-arc magmatism (Spalletti et al., 1999). In the Cuyo Basin of Argentina, extensional processes generated continental deposits (Franzese et al., 2003).

6.2.3. Chronostratigraphic intervals

In Patagonia, the Lopingian-Early Triassic is represented by the Los Menucos Complex (Vera Formation), while in southern Africa, by the Beaufort Group (Beaufort Formation). Taking into account the age and as it has been stated before, the Vera Formation at the Tschering farm is Wuchiapingian-Olenekian. This unit is equivalent to the late Permian Beaufort Formation, which is within the zones of the synapsids *Daptocephalus*, *Dicynodon lacerticeps* and the therapsid *Whaitsia* (Turner, 1981). In both units, *Dicynodontipus* was identified (de Klerk, 2002; Melchor and de Valais, 2006; Marchetti et al., 2019b) but the assignation of Beaufort specimens is questioned.

Pentasauropus is recorded from the Yancaqueo farm rocks. Based on the above, as well by geochronological dating, this ichnogenus is indicative of a Middle-Late Triassic age (probably Norian) (Falco et al., 2018). This taxon is also part of the huge ichnological record of the lower Elliot Formation, suggesting the same age, namely Norian-Rhaetian (Sciscio et al., 2017).

In the central and eastern North Patagonia, the Permo-Triassic to Jurassic continental environments were dominated by volcanic activity. The effusive volcanic activity constructed and modeled the topography where small and restricted basins were formed and provided the main material to fill them. This scenario is quite different from other areas of Gondwana, such as the Karoo Basin, where large continental basins were developed. The overall palaeoclimatic and environmental settings for this interval suggest semiarid conditions. The southern semiarid belt of late Permian times in Pangaea is detectable with a sufficient confidence in southern areas of Africa and southern America (Zharkov and Chumakov, 2001). Extensive fluvial systems and playa lakes are a common scenario in the Karoo Basin (Johnson et al., 1996; Zharkov and Chumakov, 2001), a situation analogous to the Patagonian basins, but with an important volcanoclastic input (e.g., Labudía and Bjerg, 2001, 2005; Citton et al., 2018).

The Marifil Volcanic Complex and the Stormberg Group (upper Elliot and Clarens formations) represent the Early Jurassic in Patagonia and in southern Africa, respectively. The track-bearing strata of Marifil Volcanic Complex possess cf. *Anomoepus* isp. and *Anomoepus*-like tracks, whose biochronological information suggests an Early Jurassic age (Díaz-Martínez et al., 2017). This is consistent with the absolute dating, seeing that track-bearing surfaces are comprised in a time span between 188 and 178 Ma (Díaz-Martínez et al., 2017). On the correlation with the Karoo occurrences, some records of the ichnotaxon *Moyenisauropus* (*sensu* Ellenberger, 1970) in the upper Elliot (Hettangian-early Sinemurian *sensu* Sciscio et al., 2017) have been compared with *Anomoepus* (Olsen and Rainforth, 2003). Moreover, the age of southern African records allows the correlation with the Marifil Volcanic Complex (Díaz-Martínez et al., 2017).

The sedimentary deposits in Patagonia and Karoo are dominated by fluvial systems, even though in the Clarens Formation, they tend to aeolian/arid conditions (Johnson et al., 1996). At this time, the tectonic context of the break-up of Pangea and the establishment of the Weddell Sea culminated in the connection between the South American and southern African realms, ending the homogeneous distribution of trackmakers. The progressive aridification of southern Gondwana during the Early Jurassic has been linked to a foreland basin tectonics (Bordy et al., 2004).

Despite the size and geotectonic location of the analysed basins, which control the extension and quality of the fossil and sedimentary record, the late Permian to Jurassic ichnological record provides an interesting tool to perform correlations between Patagonia and southern Africa. A summary of these correlations is provided in Table 4.

7. Palaeobiogeographical considerations

It is important to have precise chronostratigraphic, geographical and taxonomical data to perform any palaeobiogeographical study. In this case, the information obtained in the previous sections has been used for this proposal. Thereby, the temporal range analysed here is from the latest Permian to the Early Jurassic (both inclusive) that includes very relevant episodes that happened in what concerns the whole history of the Earth. For instance, during the Lopingian epoch, several large continents and a number of micro-continents were already assembled forming the western Pangaea, although the eastern one was formed during the Late Triassic-Early Jurassic (e.g., Blakey and Wong, 2003, Blakey, 2008). While the onset of Pangaea break-up was initiated in the Early Triassic and continued and intensified at the beginning of the Norian (Golonka, 2007), in southern Pangaea almost all the landmass remained connected through the Triassic and Early Jurassic (Wilf et al., 2013). Finally, the widespread extension related to the southern Pangaea break-up and the opening of the Weddell Sea started during the Early Jurassic and reached the western margin of the South American plate (e.g., Franzese et al., 2003; Golonka, 2007). In this context, the palaeogeographic distribution of *Dicynodontipus*, *Pentasauropus* and *Anomoepus*-like tracks and their putative trackmakers has been discussed (Fig. 5).

As suggested before, the temporal distribution of valid *Dicynodontipus* specimens is restricted to the Lopingian (Wuchiapingian)-early Middle Triassic (early Anisian) time interval (see Fig. 4), and shows a diachronism. The oldest record is *Dicynodontipus geinitzi* from the low-latitude Wuchiapingian Arenaria di Val Gardena, Bletterbach section (Italy), whose record is characterised by the co-occurrence of Permian and Early Triassic ichnotaxa (see Ceoloni et al., 1988; Bernardi et al., 2017a, 2017b). In higher latitudes, *Dicynodontipus* tracks have been identified in the uppermost Permian and Lower Triassic outcrops of South America (Argentina, Melchor and de Valais et al., 2006; and Brazil, Francischini et al., 2018) (Fig. 5A). Finally, abundant specimens from the Early-Middle Triassic transition have been recognised in low-latitude rocks of Germany (Lilienstern von, 1944; Haubold, 1984; Klein and Lucas, 2018). *Dicynodontipus* trackmakers have been related with non-mammalian cynodonts (Haubold, 1971; Conti et al., 1977, 1997). According to the temporal calibrated phylogeny of Ruta et al. (2013) and Kammerer (2016), the clades that are present in the latest Permian-early Middle Triassic are the basal cynodonts, basal epicynodonts and basal charassognathids. Their members have been found in Upper Permian-Lower Triassic outcrops of South Africa, Zambia, Tanzania, Russia and Germany (Kammerer, 2016). Their age and their palaeogeographic position are similar to the *Dicynodontipus* ones, being two main areas with both kinds of remains: 1. high latitudes of southern Pangaea (South America and southern Africa), and 2. low latitudes of Pangaea (Italy-Germany-Russia).

The above data suggest that there is no latitudinal bias and both *Dicynodontipus* and its proposed trackmaker present a widespread Pangaeian distribution. It is possible that their absence in eastern continents is because the latter were not assembled into the rest of Pangaea yet.

Palaeogeographically, the distribution of the *Pentasauropus* tracks is located in two areas: the high-latitude of southern Pangaea (Lesotho, Ellenberger, 1970; Argentina, Domnanovich et al., 2008; Citton et al., 2018; Lagnaoui et al., 2019), and the low-latitude of central Pangaea (North America, Olsen and Galton, 1984; Lockley and Hunt, 1995; Gaston et al., 2003) (Fig. 5B). As it has been commented before, almost all the *Pentasauropus* record is Late Triassic in age, except the Cerro de

las Cabras Formation tracks that are from the Middle Triassic.

On the whole, the producer of *Pentasauropus* had to be sought among dicynodont therapsids (Haubold, 1984; Olsen and Galton, 1984; Anderson et al., 1998; Lockley and Meyer, 2000; D'Orazi Porchetti and Nicosia, 2007), and most likely among kannemeyeriiform dicynodonts (Citton et al., 2018; Kammerer, 2018; Lagnaoui et al., 2019). Although the origin of this group roots in the Early Triassic (Maisch and Matzke, 2014), the clade is abundant from the Anisian (Kammerer et al., 2013). In fact, kannemeyeriiform dicynodonts would have distributed worldwide during the Middle Triassic (Fröbisch, 2009), including the Cerro de las Cabras Formation (Zavattieri and Arcucci, 2007). On the other hand, Late Triassic kannemeyeriiforms occur in low abundance and are probably geographically restricted (Kammerer et al., 2013). Only three Late Triassic records have been found outside South America: one from North America (USA, Lucas and Hunt, 1993; Lucas and Heckert, 2002); another from Africa (South Africa, Kammerer, 2018); and the third from Europe (Poland, Dzik et al., 2008; Sulej and Niedźwiedzki, 2019). The geographical distribution of the kannemeyeriiform osteological record is similar to the ichnological one with the addition of high-latitude remains from Poland. During the Late Triassic, the configuration of Pangaea allows the palaeofaunal interchange, and although the remains of *Pentasauropus* and kannemeyeriiforms are scarce, it could be considered widespread.

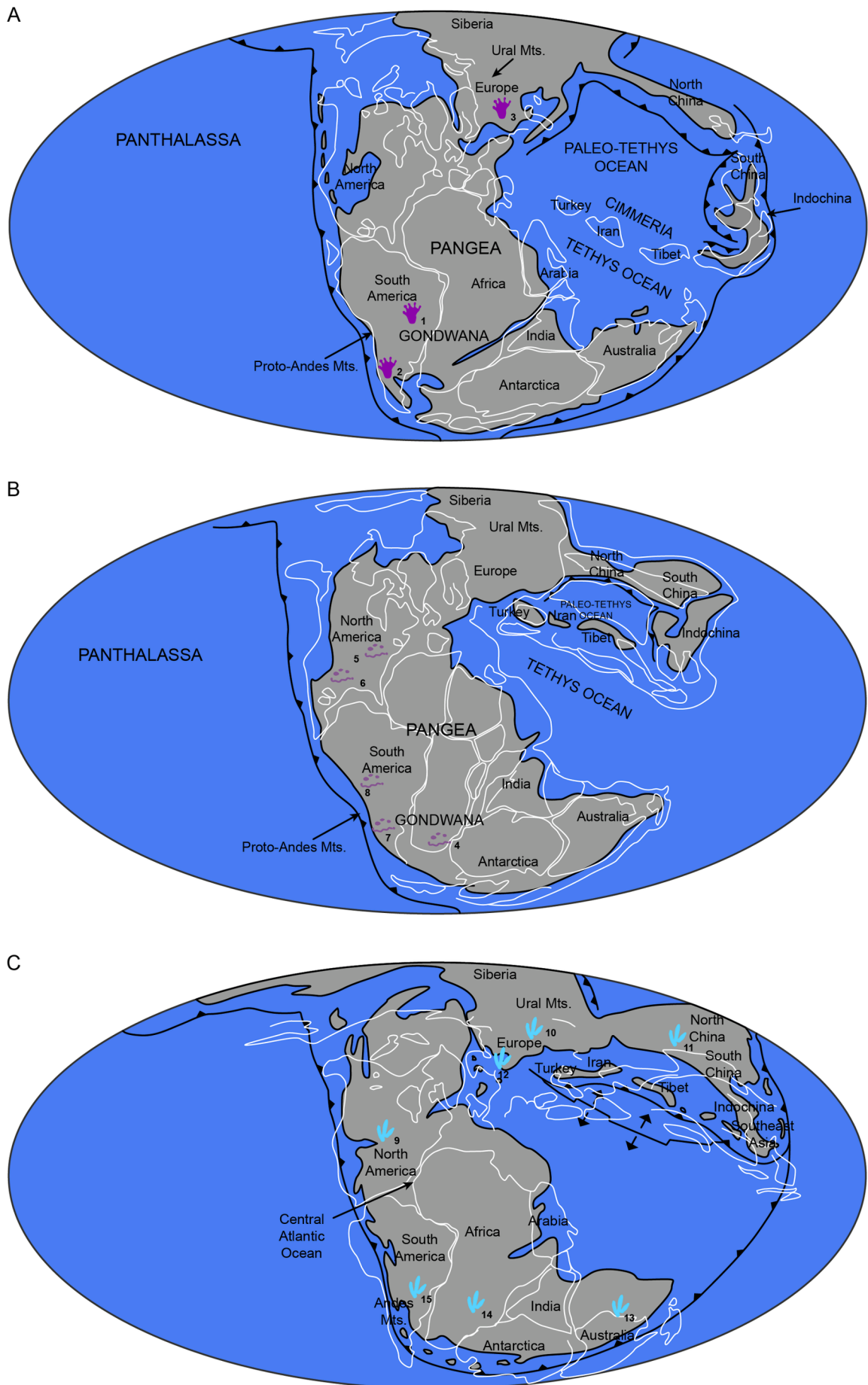
Anomoepus-like tracks have been found in Lower Jurassic rocks of almost all the continents and latitudes: South America (Díaz-Martínez et al., 2017); North America (Hitchcock, 1845; Lockley and Gierliński, 2006; Dalman and Weems, 2013); Africa (Ellenberger, 1970); Australia (Thulborn, 1994); Asia (Li et al., 2012; Xing et al., 2016a,b,c); and Europe (Gierliński, 1991; Niedźwiedzki and Pieńkowski, 2016) (Fig. 5C). In Gondwanaland, they have been recorded in Argentina, southern Africa and Australia, so it is possible we may find such tracks in Antarctica in the future.

Anomoepus was most likely produced by a relatively small, gracile, facultatively bipedal ornithischian (Olsen and Rainforth, 2003), *Moyenisauropus* by a basal thyreophoran (Gierliński, 1991) and *Shemuichnus* by a larger quadruped ornithischian (Li et al., 2012) or a basal thyreophoran (Xing et al., 2013). The geographical distribution of *Anomoepus*-like tracks is wider than the osteological record (see Boyd, 2015). For instance, Australia has not ornithischian bone remains from the Early Jurassic, but there are *Anomoepus*-like tracks (Thulborn, 1994). Moreover, the abundance of ornithischian tracks (e.g., Li et al., 2012; Xing et al., 2013) and the scarcity of ornithischian bone remains in the Early Jurassic of China (Irmis and Knoll, 2008) is noteworthy. On the other hand, in South America both bones and tracks are scarce, and there are no data of any Early Jurassic ornithischian remains from Antarctica.

During the Early Jurassic, Pangaea broke-up, being evident between North America and Eurasia, and incipient growing the Weddell Sea in the south of Gondwana (Brewer et al., 1996). Probably, the widespread distribution of the basal ornithischian clades was given before the break-up of Pangaea. After the Early Jurassic, it is difficult to find cosmopolite ichnotaxa and this could be associated with the formation of the new continents (see Lucas, 2007).

8. Conclusions

Combining biochronological, structural analysis and isotopic ages from the latest Permian-Early Jurassic track-bearing units of Patagonia, three sedimentary sequences different in age and ichnological record have been identified. Within the Los Menucos Complex, *Dicynodontipus* tracks, whose biochron represents a Lopingian (Wuchiapingian)-early Middle Triassic (early Anisian) time interval, have been recorded near to the Tschering farm in the Vera Formation. Recent dating suggest Wuchiapingian-Olenekian in age for these outcrops. Also in the Vera Formation, *Pentasauropus* tracks, which indicate a late Anisian-Rhaetian time interval, comes from the Yancaqueo farm that could be Norian in



(caption on next page)

Fig. 5. Palaeobiogeographic distribution of *Dicynodontipus*, *Pentasauropus* and *Anomoepus*-like taxa. A. Early Triassic *Dicynodontipus*: 1, Brazil (Francischini et al., 2018); 2, Argentina (de Valais, 2008); 3, Germany (Hornstein, 1876; Lillienstern von, 1944). B. Middle Triassic *Pentasauropus*: 4, Lesotho (Ellenberger, 1970); 5, USA (Olsen and Galton, 1984); 6, USA (Lockley and Hunt, 1995); 7, Argentina (Citton et al., 2018); 8, Argentina (Marsicano and Barredo, 2004). C. Early Jurassic *Anomoepus*-like ichnotaxa: 9, USA Hitchcock, 1845; 10, Poland (Gierlinski); 11, China (Xing et al., 2015, 2016a,b,c); 12, Italy (Avanzini et al., 2001b); 13, Australia (Thulborn, 1994); 14, Lesotho (Ellenberger, 1970); 15, Argentina (Díaz-Martínez et al., 2017). The *Dicynodontipus* from Italy (Conti et al., 1977) and *Pentasauropus* from Argentina (de Valais, 2008; Lagnaoui et al., 2019) are not in the palaeobiogeographic maps because are Wuchiapingian (Lopingian) and late Anisian-late Ladinian (Middle Triassic) in age respectively. Palaeogeographic maps retrieved from <http://www.scotese.com>.

age. Therefore, or the Vera Formations has a wide temporal range (from uppermost Permian-Early Triassic to Middle Triassic-latest Triassic) and it is possible the existence of two allouits separated by discontinuities, or the Tscherig farm and the Yancaqueo farm rocks are representing different lithostratigraphic units. The biochronological information of the *Anomoepus*-like tracks (Early Jurassic), from the Marifil Volcanic Complex, is consistent with the already published chronological data.

The summary of ichnological data and geological background allows us to propose a correlation between conspicuous units of Patagonia and southern African Karoo basins. This correlation is constrained to three main time-lapses: 1. Lopingian to Early Triassic, Vera Formation at the Tscherig farm and Balfour Formation; 2. Middle to Late Triassic, Vera Formation at the Yancaqueo farm and lower Elliot Formation; and 3. Early Jurassic, Marifil Volcanic Complex and upper Elliot Formation. In addition, this correlation is supported by similar palaeoclimatic settings that allow us to infer a homogeneous distribution of trackmakers in both realms of southern Gondwana.

Both the studied ichnotaxa and their proposed trackmakers allow us to infer similar palaeobiogeographical information. For instance, *Dicynodontipus* record and basal cynodonts were present in central and southern Pangaea during the last Permian-Early Triassic. *Pentasauropus* remains have been found in almost the same areas, southern and middle Pangaea, than their trackmakers, the kannemeyeriiform dicynodonts, in the late Middle Triassic-Late Triassic. Finally, the *Anomoepus*-like tracks were widespread and had more extensive geographical distribution than the basal ornithischians and basal thyreophorans bone remains. The studied record displays an extensive distribution, which could be predicted taking into account the geotectonic situation with most of the continents assembled forming the Pangaea.

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