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Age-constrained therapsid tracks from a mid-latitude upland (Permian–Triassic transition, Los Menucos Complex, Argentina)

Paolo Citton [a,*], Silvina de Valais [a], Ignacio Díaz-Martínez [a], Santiago N. González [a], Gerson A. Greco [a], Carlos Cónsole-Gonella [b], Giuseppe Leonardi [c,d]

[a] *Instituto de Investigación en Paleobiología y Geología (IIPG), CONICET - Universidad Nacional de Río Negro, Avenida J.A. Roca 1242, CP 8332, General Roca, Río Negro, Argentina*
[b] *Instituto Superior de Correlación Geológica (INSUGEO), Universidad Nacional de Tucumán - CONICET, Miguel Lillo 205, CP 4000, San Miguel de Tucumán, Tucumán, Argentina*
[c] *Istituto Cavanis, Sestiere Dorsoduro, 898, Rio Terrà Foscarini, CP 30123, Venezia, Italy*
[d] *Departamento de Geologia, Instituto de Geociências, Universidade Federal do Rio de Janeiro, Av. Athos da Silveira Ramos 274, Rio de Janeiro, RJ, Brazil*

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ABSTRACT

The Los Menucos Complex (North Patagonian Massif, Río Negro province, Argentina) has been long regarded as Late Triassic in age. A *Dicynodontipus*-dominated record is historically known from this complex and particularly from the Puesto Tscherig locality. Here we report the Puesto Vera site, where a new track-bearing horizon was discovered within a 73-m-thick volcano-sedimentary succession. Footprints from this site are morphologically similar to those from Puesto Tscherig and resemble footprints classically referred to the ichnogenus *Dicynodontipus*, thus we assigned the new material to *Dicynodontipus* isp. The new ichnological material is age constrained to a time interval between the Changhsingian (Lopingian, Permian) and the Olenekian (Early Triassic), on the basis of recently obtained U–Pb radiometric datings from two ignimbrites, respectively at the base and top of the Puesto Vera stratigraphic section. Interestingly, the *Dicynodontipus* record from the Los Menucos Complex is older than previously supposed. The inherent chronostratigraphy is consistent with the temporal occurrence of the ichnotaxon, which to date has a global distribution spanning from the Wuchiapingian (Lopingian, Permian) of northern Italy to the early Middle Triassic of Germany. Taking into account the most recent datings as well as previous literature about the geology and paleontology of Los Menucos, the new age-constrained finding turns out to encompass the Permian–Triassic transition and mirror a tetrapod fauna dwelling in a mid-latitude, highland paleoenvironment of southwestern Gondwana.

1. Introduction

The *Dicynodontipus* footprints from the volcano-sedimentary Los Menucos Complex (hereafter LMC; central North Patagonian Massif, Río Negro province, Argentina; Cucchi et al., 2001) constitute- a significant tetrapod track record from southern South America (Casamiquela, 1964; Leonardi and de Oliveira, 1990; Melchor and de Valais, 2006). Footprints reported from two historical quarries of Puesto Tscherig (Tscherig Farm), named 'Cantera Vieja' (Old Quarry) and 'Cantera Nueva' (New Quarry), were the basis for the establishment of several ichnotaxa (Casamiquela, 1964, 1975). The whole material was later revised, and some ichnotaxa were considered synonyms of *Dicynodontipus* or represented by *Dicynodontipus*-like tracks (Melchor and de Valais, 2006). Likewise, the ichnotaxon '*Shimmelia chirotheroides*' Casamiquela (1964) was first considered a *nomen nudum* (Melchor and de Valais, 2006) and subsequently a *nomen dubium* (de Valais, 2008), as well as the ichnotaxa '*Rogerbaletichnus aguilerai*' Casamiquela (1964) and '*Ingenierichnus sierrai*' Casamiquela (1964) (see de Valais, 2008).

A Late Triassic age was proposed for the LMC based on tetrapod tracks (Casamiquela, 1975) and paleoflora (Artabe, 1985a, b; Labudía et al., 2002) assemblages, and was subsequently calculated with radiometric datings (Rapela et al., 1996; Lema et al., 2008). The alleged unitary Late Triassic age for the whole LMC was recently questioned and an older age was proposed for the *Dicynodontipus* footprints bearing levels (Citton et al., 2018; Díaz-Martínez et al., 2019). In the meantime, new zircon U–Pb ages became available from different localities of LMC,

* Corresponding author.
E-mail address: pcitton@unrn.edu.ar (P. Citton).

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including the new ichnosite presented here, and indicated a Lopingian to Early Triassic age (Falco et al., 2018; Luppo et al., 2018; Falco, 2019). Although these datings have corrected the geochronology of part of the LMC, up to date, the ages could not be directly assigned to *Dicynodontipus* footprints, being the track-bearing levels not constrained by age from absolute dating below and above (de Valais et al., 2020).

Here we present a further ichnosite within the Puesto Vera (Vera Farm), from which footprints were never reported before. The material consists of several footprints, which we refer to as *Dicynodontipus* isp. The new finding is crucial in disentangling the chronostratigraphical issue of the *Dicynodontipus* ichnofauna, given that the footprints are precisely positioned in the stratigraphic succession and are time-constrained by two U–Pb datings obtained from two ignimbrites (Falco, 2019; see Falco et al., 2020 for a radiometric age from the topmost ignimbrite; see also Falco et al., 2018), below and above the track-bearing horizon. Thus, the age of the *Dicynodontipus* record from Los Menucos is lowered by about 30 million years at the Permian–-Triassic transition. The new evidence allows to likely tie also the track-bearing levels from the Tscherig sites, confirming the older age for the whole record, to properly re-locate the *Dicynodontipus* footprints in the global ichnological record and recapitulate, based on available literature, the terrestrial environment in which trackmakers lived.

2. Material and methods

The new ichnosite (S 40° 41′ 07.7''; W 068° 16′ 27.4''; 945 m a.s.l.) is located in the Puesto Vera locality, less than 30 km northwest from the Los Menucos town, Río Negro province, Argentina (Figs. 1 and 2A). The material is preserved on a surface pertaining to a 73-m-thick stratigraphical section with mean bed attitude of N200°/10° (dip direction/dip angle). High-resolution digital photogrammetry was performed to digitally preserve the material and to achieve a more objective representation of track features and disposition. The images selected for photogrammetric processing were acquired using a reflex digital camera with 35 mm and 50 mm focal lengths, resolution 6000 × 4000 and pixel size ranging of 3.84 × 3.84 μm.

In order to correctly scale the calculated models, a metric reference marker was applied on the surface. Three-dimensional models were converted to colour topographic profiles using the software Paraview (version 5.4.1). Overall footprint length and width were measured following Leonardi (1987) and later checked on three-dimensional meshes.

The track-bearing succession from Los Menucos has a long nomenclatural history that derives from the seminal work of Stipanicic (1967). Several lithostratigraphic schemes were proposed since then until very recently (Labudía and Bjerg, 2001; Cucchi et al., 2001; Lema et al., 2008; Martínez Dopico et al., 2017; Luppo et al., 2018; Falco et al., 2020 and references therein). Nevertheless, lithostratigraphy is beyond the aim of this report and it does not affect the discussion of the material presented here. Therefore, we generically refer to the entire succession as Complex, adopting the nomenclature used in the geological map of the area ('Hoja Geológica 4169 - II, Los Menucos' in Cucchi et al., 2001).

Institutional abbreviations: CICRN - Centro de Investigaciones Científicas de Río Negro, Viedma, Río Negro province, Argentina; MLP - Museo de La Plata, La Plata, Buenos Aires province, Argentina; MPA - Museo Municipal de Ciencias Naturales 'Carlos Darwin', Punta Alta, Buenos Aires province, Argentina; MPCA - Museo Provincial Carlos Ameghino, Cipolletti, Río Negro province, Argentina.

3. Geological setting

The large Choiyoi Magmatic Province developed during the mid-Cisuralian to Early Triassic times (Sato et al., 2015 and references therein) within the active southwestern Gondwana margin and related to the Gondwanide orogeny (Rapela and Llambías, 1985; Cawood and Buchan, 2007; Martínez Dopico et al., 2017; Lovecchio et al., 2020; see Fig. 2B).

Igneous rocks of the North Patagonian Massif (northern Patagonia), including the LMC, record on the whole the Choiyoi magmatism since its incipient stage up to the postorogenic extensional phase related to the collapse of the Gondwanide orogen (Leanza, 2009; Sato et al., 2015; González et al., 2016, 2017 and references therein).

The mainly volcanic LMC lies on pre-Permian metamorphic rocks and Permian granitoids and is covered by Upper Cretaceous sedimentary rocks and Paleogene to Neogene basalts (Cucchi et al., 2001; Labudía and Bjerg, 2001; Lema et al., 2009) (Fig. 2C). In the Los Menucos area, the succession, about 2000–3000 m thick (Lema et al., 2009), is exposed through a SE-plunging synclinal, the Piche synform (Giacosa et al., 2007) (Fig. 2C). The succession mainly comprises acidic (rhyolitic-dacitic) pyroclastic deposits with minor intercalations of volcanogenic clastic beds and andesitic lava flows (Labudía and Bjerg, 2001; Lema et al., 2009; Falco et al., 2020). Acidic dikes cutting the succession are part of the LMC (Cucchi et al., 2001; Lema et al., 2009; Luppo et al., 2018). Sedimentary rocks are mainly composed of sandstones and mudstones with minor conglomerates intercalations, which are deposited in lenses with reduced areal distribution (Llambías, 1999). Sedimentation was influenced by the volcanic activity and epiclastic frequently derived from re-sedimentation of non-welded volcaniclastic deposits (Labudía and Bjerg, 2001; Falco et al., 2020). The deposition of these epiclastic deposits took place in ephemeral, incipient low gradient streams, as well as in small lakes (Kokogián et al., 2001; Falco and Hauser, 2017).

Casamiquela (1964) assigned an age younger than Late Triassic and older than Late Jurassic to the tetrapod track record from Los Menucos. Later, the same author reinterpreted the ichnological record as Late Triassic in age (Casamiquela, 1975). A Late Triassic age was then calculated by means of radiometric datings from the uppermost part of the LMC (i.e. Sierra Colorada Formation in Labudía and Bjerg, 2001), using respectively Rb/Sr isochron method (222 ± 2 Ma; Rapela et al., 1996) and Ar/Ar method (206.9 ± 1.2 Ma; Lema et al., 2008). The age was also supported by some paleofloristic data (Labudía et al., 2002 and references therein) and remained unchanged in further paleontological studies (e.g. Domnanovich and Marsicano, 2006; Melchor and de Valais, 2006; Domnanovich et al., 2008). Recently, zircon U–Pb ages became available from different volcanic deposits of the LMC (Luppo et al., 2018), including rocks exposed both at Puesto Tscherig and Puesto Vera (Falco et al., 2018, 2020; Falco, 2019), overall indicating ages spanning from the Lopingian to the Early Triassic.

3.1. The Puesto Vera stratigraphic section

The Puesto Vera stratigraphic section, where the track-bearing horizon has been discovered, is the northernmost type locality of the LMC (Falco et al., 2020 and references therein). There, a 73-m thick succession is exposed (Fig. 2D). The partially covered base of the section (S 40° 41′ 06.1''; W 068° 16′ 26.7″) is constituted by a massive, whitish ignimbrite, consistent with the compositional variability of other ignimbrites of the area (dacitic to rhyolitic in composition; see Labudía and Bjerg, 2001). About twenty meters of sandy fluvial channel deposits, with subordinate fine-grained laminated sandstone and mudstones with imprints of *Dicroidium*-type flora (Artabe, 1985a, b) rest above the ignimbrite through an erosive contact. A tabular, fining upward and laminated fine tuff bed interpreted as an ash-fall deposit of 2 m in thickness lies above and bears the footprints reported here, at about 57 m from the base of the section (Fig. 2D). The top section (S 40° 41′ 09.1''; W 068° 16′ 27.9″) is constituted by three high-grade ignimbrites. U–Pb absolute ages, respectively obtained from the basal and the third ignimbrite at the top of the Puesto Vera section (Falco, 2019; see also Falco et al., 2018, 2020) enabled us to constrain footprints to a Changhsingian—Olenekian time interval (Fig. 2D).

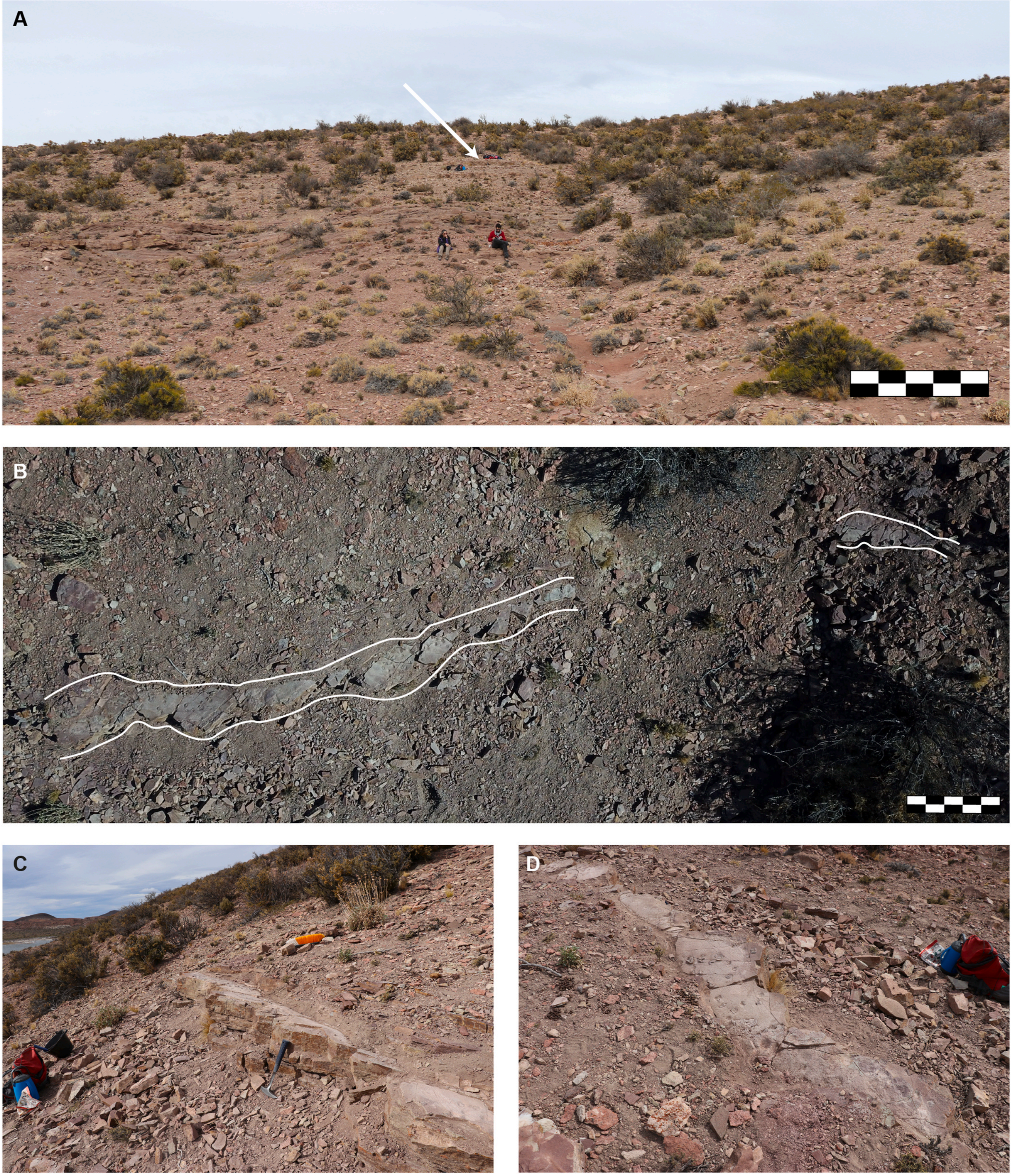

Fig. 1. (Color online) A. Panoramic view of the succession cropping out at Puesto Vera. White arrow indicates the stratigraphic position of the track-bearing horizon. B. Aerial photograph of the track-bearing surface taken from a quad-copter UAV during ichnological survey at Los Menucos area. A solid white line indicates the track-bearing surface. C, D. Different views of the track-bearing layers at Puesto Vera during cleaning of the surface. Scale bars equal to 10 m (A), 1 m (B). Hammer (33 cm long) and bags for scale in (C) and (D), respectively.

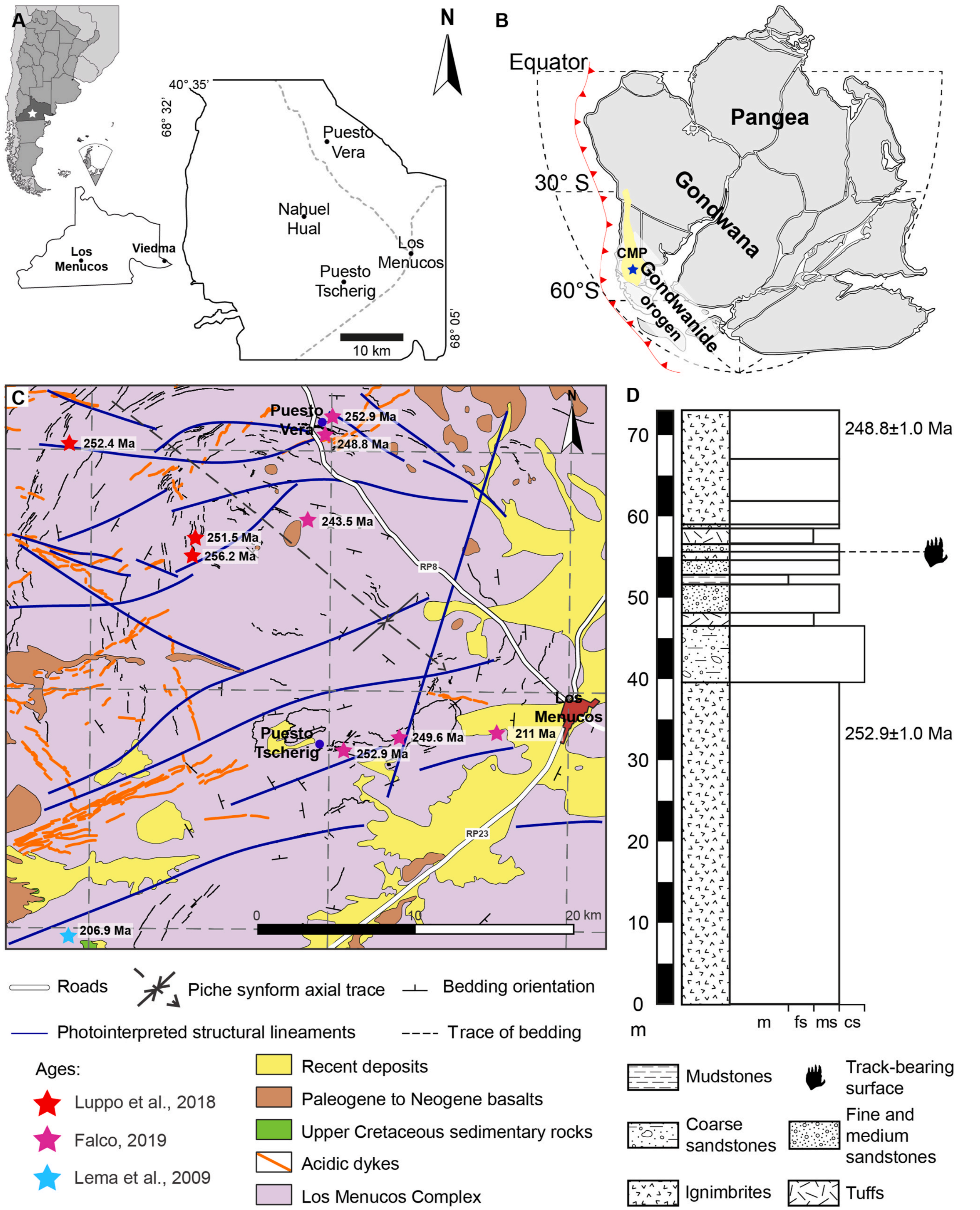

Fig. 2. (Color online) A. Location map of the Los Menucos area (North Patagonian Massif, Río Negro province, Argentina). B. Simplified paleo-tectonic map of southwestern Gondwana at the end of the Paleozoic (about 250 Ma), highlighting the geographical extension of the Choiyoi Magmatic Province (CMP) within the Gondwanide orogen (from Lovecchio et al., 2020, redrawn and slightly modified). Blue star indicates the study area. C. Geological sketch map of the area (blue points indicate Puesto Tscherig and Puesto Vera ichnological sites). D. Stratigraphical section at Puesto Vera. Grain size scale: mud (m), fine-grained sand (fs), medium-grained sand (ms) and coarse-grained sand (cs).

4. Ichnology

4.1. Description of the material

Tracks consist of sub-circular and sub-triangular concave epireliefs with very shallow to absent expulsion rims (Fig. 3). Most of the tracks are full of the overlying rock. On the basis of interpreted footprints main axes, three partial trackways were recognized (Fig. 3). The manus impression is positioned anteriorly and at a short distance from the pes impression; in a few cases the pes impression slightly overlaps the manus impression. Pace angulation values, coupled with the relative arrangement of manus and pes impressions and the slight manus overlapping likely indicate a walking gait of the producers.

Manus and pes imprints are quite homopodic; the better detailed tracks appear longer (overall length ranging from 3.2 cm to 4.3 cm, with an average length of 3.4 cm) than wide (overall width ranging from 2.5 cm to 4.0 cm, with an average width of 3.1 cm), plantigrade, pentadactyl, and characterized by a triangular sole trace, narrow in its proximal portion and distally expanded (Fig. 3A–C). Digit traces are not completely preserved distally; the digital bases of the central digits are roughly aligned, while the base of the digit V appears to be posteriorly shifted. When less detailed, the sole trace is sub-circular in shape, losing the proximal 'V' shaped morphology.

4.2. Remarks

The poor detail of most of the tracks from Puesto Vera does not allow to observe clear anatomical features of the producer's autopodia. However, some better detailed specimens (e.g. Fig. 3A–C) can be compared with those from Puesto Tscherig, matching the variability that characterizes the record from that locality (Fig. 4). So, the main features of Puesto Vera specimens (i.e. pentadactyly, triangular sole trace, morphology and relative position of digit impressions) are similar to the tracks from Puesto Tscherig, commonly referred to *Dicynodontipus* (see Melchor and de Valais, 2006; de Valais, 2008, both for further details). However, the absence of both, a clear series of manus-pes imprints and complete digit traces, hampers a more inclusive ichnotaxonomic assignment than *Dicynodontipus* isp.

Footprints from Puesto Vera can be morphologically compared with specimens reported from the Pirambóia Formation (Lopingian–Induan) of Brazil and assigned to *Dicynodontipus* isp. by Francischini et al. (2018). The material under study also shows some analogies with the material described from the Rio do Rasto Formation of Brazil (Leonardi et al., 2002), subsequently used to establish the new ichnospecies *Dicynodontipus penugnu* (Silva et al., 2012; see Díaz-Martínez et al., 2019 for discussion). Our material shares with the above-mentioned footprints from Brazil the overall morphology of the sole pad, digit traces length and manus-pes set arrangement. The studied material shares the shape of the sole pad impression, and the relative lengths and bases of digit impressions with footprints assigned to *Dicynodontipus geinitzi* from the Lopingian Arenaria di Val Gardena Formation (Conti et al., 1977). The only substantial difference regards the larger size of the material from northern Italy. Tracks assigned to cf. *Dicynodontipus* isp. were reported from the Induan Palingkloof Member (Balfour Formation) of

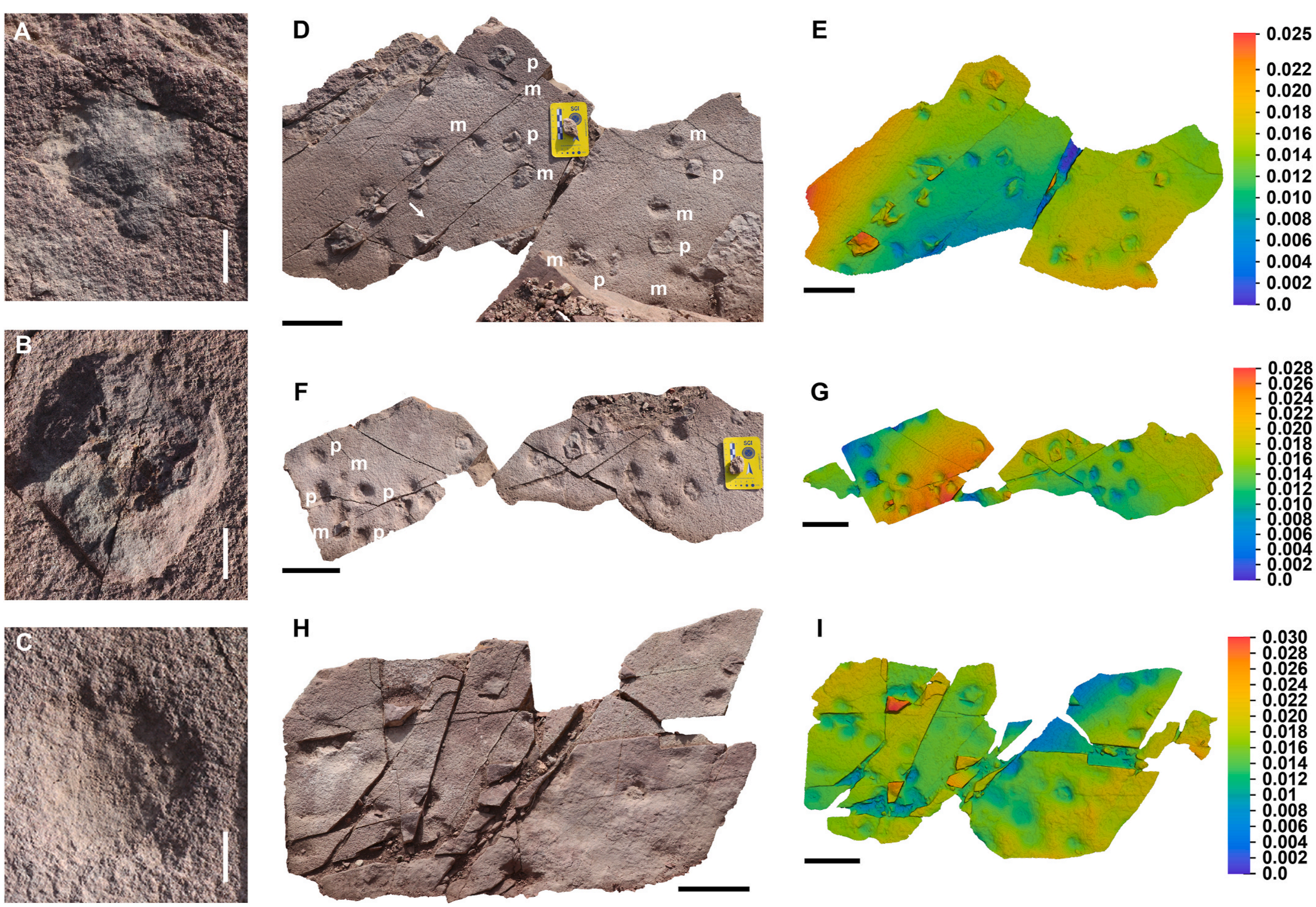

Fig. 3. (Color online) A-C. Footprints, probably pedes, on different portions of the track-bearing surface. D-I. Close up on the track-bearing surface (D, F, H) and related digital elevation models (E, G, I; scale in meters). p and m refer to pes and manus impressions, respectively, probable constituting trackways. Scale bars equal to 1 cm (A–C) and 10 cm (D–I).

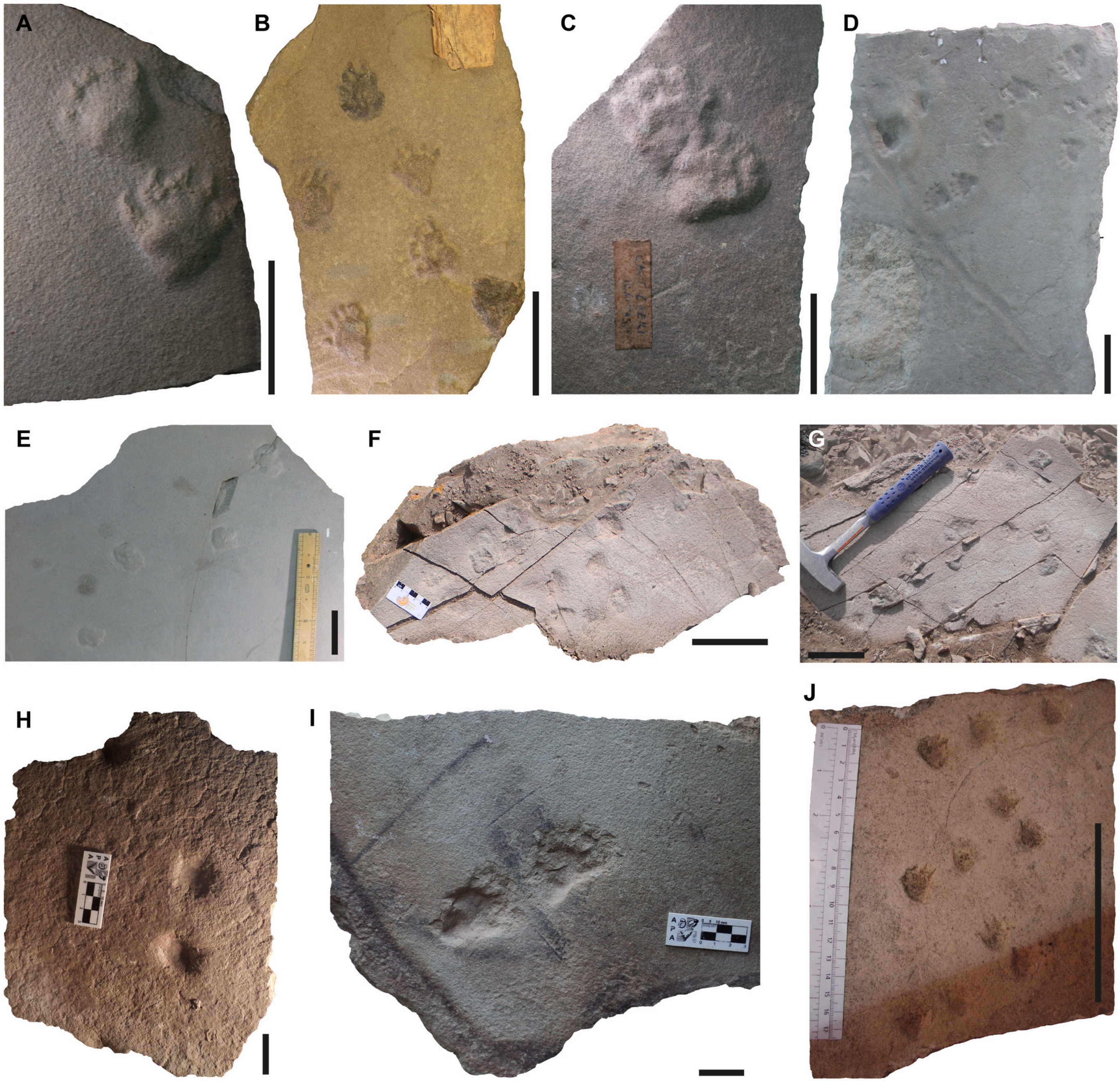

Fig. 4. (Color online) Footprints from Los Menucos (Río Negro province, Argentina). A-C. Highly detailed footprints referred to *Dicynodontipus*: MLP 60-XI-31-4 (A); MLP 60-XI-31-7 (B); MLP 66-XI-15-3 (C). D. Track-bearing slab without a label deposited in the 'Museo Antropológico e Histórico Jorge H. Gerhold' (Ingeniero Jacobacci, Río Negro province, Argentina). E. Track-bearing slab without a label, deposited in the 'Museo Antropológico e Histórico Jorge H. Gerhold' (Ingeniero Jacobacci, Río Negro province, Argentina). F-G. Footprints referred to *Dicynodontipus* from Puesto Vera (this work); uncollected material. H. MPCA 27029, deposited in the 'Museo Provincial Carlos Ameghino' (Cipolletti, Río Negro province, Argentina). I. MPA 76-606-I-E, deposited in the Museo de Punta Alta (Buenos Aires province, Argentina). J. CICRN 1-X-72-3, '*Stipanicichnus bonetti*' holotype, currently housed in the Museo de La Plata collection (La Plata city, Buenos Aires province, Argentina). Material in (A–E) and (H–J) from Tscherig Farm. Scale bars equal to 5 cm (A, C), 10 cm (B, D, E, F, G, J) and 3 cm (H–I).

South Africa (Marchetti et al., 2019). This material is different from the studied footprints after having seemingly longer digit impressions and a rounded sole pad.

5. Discussion

The age-constrained ichnological record from the mixed succession of Puesto Vera enabled us to assign a late Lopingian–Early Triassic time interval to the Los Menucos *Dicynodontipus* ichnofauna. In agreement with previous suggestions (Citton et al., 2018; Díaz-Martínez et al., 2019), footprints from the Puesto Vera and Puesto Tscherig are reconsidered in the framework of the global occurrence of the ichnogenus. Moreover, the terrestrial environment in which the *Dicynodontipus* producers lived during the Permian–Triassic transition is discussed based on previous literature.

5.1. *Dicynodontipus* global occurrence

The bulk of *Dicynodontipus* record is from the Early and early Middle Triassic (Anisian) of Germany (e.g. Rühle von Lilienstern, 1944;

Haubold, 1966, 1971a, b; Fichter et al., 1999; Klein and Lucas, 2018).

From Lopingian and Lopingian–Induan strata, as above mentioned, *Dicynodontipus* has also been reported, respectively, from northern Italy (Conti et al., 1975, 1977) and Brazil (Leonardi et al., 2002; Francischini et al., 2018). The material from the Arenaria di Val Gardena Formation, which is Lopingian (Permian) in age (Bernardi et al., 2017, and references therein), most likely comes from Changhsingian horizons (see Marchetti et al., 2020).

Footprints referred to as '*Dicynodontipus*' from the Middle Triassic Cerro de las Cabras Formation of the Cuyana Basin (Mendoza, Argentina) were reported by Marsicano et al. (2004). We consider other tracks reported from the same unit not detailed enough to attempt a confident ichnotaxonomical assignment, even comparing the whole morphology of the material with that characterizing *Dicynodontipus* (Leonardi and de Oliveira, 1990; Leonardi, 1994). More recently, Lagnaoui et al. (2019) reported from the Cerro de las Cabras Formation a single track referred to as cf. *Dicynodontipus* isp. From the photograph and interpretive drawing provided by the authors, this track resembles those referred to as *Pentasauropus* (see Ellenberger, 1970) but this matter has to be clarified after direct comparison. *Dicynodontipus* has been also reported from the Lopingian and Lower Triassic of South Africa, from the Lower Triassic of Australia, Spain and Poland, and from the Upper Triassic of Argentina. These occurrences have been recently questioned and we refer to Díaz-Martínez et al. (2019, and references therein) for a thorough discussion.

5.2. *Dicynodontipus* producer

Dicynodontipus footprints were attributed to producers to be sought among dicynodonts and theriodonts, or even eutheriodonts (e.g. Rühle von Lilienstern, 1944; Haubold, 1966, 1971a, b; Demathieu and Fichter, 1989; Leonardi and de Oliveira, 1990; Leonardi, 1994; Domnanovich and Marsicano, 2006; Avanzini et al., 2011; Francischini et al., 2018). From the standpoint of a hierarchic, enkaptic, synapomorphy-based approach for producer identification in tetrapod ichnology (the concept of 'footprint holomorphy' in Romano et al., 2016, and references therein), the material under study prevents achieving a systematic allocation of the footprints to a rank below to Order.

Ichnological features of Puesto Vera tracks mirroring anatomical characteristics of the producers mainly concern equalization of central digit impressions and the triangular morphology of the sole pad impression, which make the footprint more symmetrical as a whole. A greater dimensional uniformity of digits II–IV (i.e. equalization) and the more medial position of the base of the footprint, likely due to a change in basipodials' make-up, could be related to modifications characterizing the therapsid-grade autopodium with respect to non-therapsid grade synapsids (Romer, 1956; Hopson, 1995; Kummell and Frey, 2012; Citton et al., 2019). Thus, the material from Puesto Vera locality is here referred to producers to be sought among Therapsida.

5.3. The Los Menucos terrestrial paleoenvironment: state of the art and future perspectives

The Los Menucos succession was laid down in an upland setting at about 45°S paleolatitude (Prezzi et al., 2001) as part, regionally, of the Gondwanide mountain range (Rapela and Llambías, 1985; Martínez Dopico et al., 2017; see also Roscher et al., 2011, Fig. 1, p. 188, and references therein) in this area of southern South America during the latest Permian (Ziegler et al., 1997 in Roscher et al., 2011) and Early Triassic times (Veevers, 2004; Blakey, 2008).

An interesting point to be accounted, if the new geochronological ages are considered, concerns the significance of the paleofloral association from Los Menucos. The Los Menucos paleoflora has been considered indicative of the extratropical area of the Gondwana paleofloristic realm (Artabe et al., 2003; Spalletti et al., 2003). It would indicate an arid climatic phase (Spalletti et al., 2003), but with a certain degree of seasonality (Kokogián et al., 2001) consistent with a monsoon circulation (Parrish, 1993; Allen et al., 2020). Bodnar et al. (2021) recently revised the paleoflora from Los Menucos, distinguishing a lower taphoflora mainly composed of xeromorphic seed plants and dominated by cycads, and an upper taphoflora dominated by corystosperms. The first taphoflora is interpreted as a refuge and recovery vegetation during and after the end-Permian crisis, while the second one as the recuperation after the end-Permian crisis (Bodnar et al., 2021). The interpretation proposed by Bodnar et al. (2021) would support, implicitly, a certain degree of persistence of the floral taxa composing the first association. This in turn would indicate some niche continuity available for related plant-eating trackmakers across the Permian-Triassic transition.

In this framework, assessing the paleobiological and the biochronological significance of the entire tetrapod track record from Los Menucos could represent a further constraint to refine our knowledge about the stratigraphy of the area, especially on the light of the recent interpretations about the paleoflora. In fact, in addition to therapsid producers of *Dicynodontipus*, a single specimen assigned to *Rhynchosauroides* isp. by Domnanovich et al. (2008) would indicate a type of producer to be sought within Diapsida, even if more footprints are needed to corroborate and possibly refine the attribution. The same applies for footprints referred to as '*Shimmelia chirotheroides*' (tracks possibly related to archosauriform producers), '*Rogerbaletichnus aguilerai*' and '*Ingenierichnus sierrai*' (related to Squamata *sensu* Casamiquela, 1984), whose significance is currently hampered due to the lack of diagnostic features (Díaz-Martínez and de Valais, 2014). To date, tetrapod body-fossil remains are virtually absent, having been found the first indeterminable bone by two of us (I. D.-M. and G. G.). Attempt to disentangling the paleobiological significance of the tetrapod track record from Los Menucos is important to discuss the ichnofauna with respect to one of the most severe life crisis in terrestrial vertebrate evolution related to terrestrial ecosystems collapse (Dal Corso et al., 2020), and compare it to Lopingian (Bernardi et al., 2017) and/or Early Triassic ichnofaunas and paleofaunas (Retallack et al., 2011; Romano et al., 2020). An interesting point that can be mentioned concerns the producers' paleoecology. Dwelling in an upland setting characterized by active acidic volcanism during atmospheric gas crises at the Permian–-Triassic transition, and considering oxygenation levels (Berner, 2002) close to the limit for vertebrate life, most likely the Los Menucos trackmakers had adaptations to hypoxic environments, as repeatedly stressed for land vertebrates during the Permian–Triassic transition in lowlands (Retallack et al., 2003; Retallack, 2021; but see Lucas, 2017 for a contrasting hypothesis).

6. Conclusions

The *Dicynodontipus* record from the Los Menucos Complex, up to date considered to be Late Triassic in age, is included in a volcano-sedimentary succession that includes the Permian–Triassic transition, spanning from the Lopingian to the middle Olenekian according to new geochronological ages constraining tetrapod tracks. The record represents a further window on mid latitude tetrapod faunas (based on higher taxa) of southwestern Gondwana. Footprints are attributed to therapsid-grade synapsid producers dwelling mid latitude, upland environments of the Gondwanide range that were severely affected by intense volcanism in a dry, seasonal paleoclimate. New paleontological findings will be pivotal in order to possibly attempt an even more refined stratigraphy, shed new light on the tetrapod record and its significance in the context of the end Permian mass extinction and/or the Early Triassic recovery of life.

Author statement

All authors equally participated to this manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Allen, B.J., Wignall, P.B., Hill, D.J., Saupe, E.E., Dunhill, A.M., 2020. The latitudinal diversity gradient of tetrapods across the Permo-Triassic mass extinction and recovery interval. Proceedings of the Royal Society B 287, 20201125.
Artabe, A.E., 1985a. Estudio sistemático de la tafoflora triásica de Los Menucos, provincia de Río Negro, Argentina. Parte I. Ameghiniana 22, 3–22.
Artabe, A.E., 1985b. Estudio sistemático de la tafoflora triásica de Los Menucos, provincia de Río Negro, Argentina. Parte II. Ameghiniana 22, 197–212.
Artabe, A.E., Morel, E.M., Spalletti, L.A., 2003. Caracterización de las provincias fitogeográficas triásicas del Gondwana extratropical. Ameghiniana 40, 387–405.
Avanzini, M., Bernardi, M., Nicosia, U., 2011. The Permo-Triassic tetrapod faunal diversity in the Italian Southern Alps. In: Dar, I.A., Dar, M.A. (Eds.), Earth and Environmental Sciences. InTech, London, UK, pp. 591–608.
Bernardi, M., Petti, F.M., Kustatscher, E., Franz, M., Hartkopf-Fröder, C., Labandeira, C. C., Wappler, T., van Konijnenburg-van Cittert, J.H.A., Peecook, B.R., Angielczyk, K. D., 2017. Late Permian (Lopingian) terrestrial ecosystems: a global comparison with new data from the low-latitude Bletterbach Biota. Earth Sci. Rev. 175, 18–43.
Berner, R.A., 2002. Examination of hypotheses for the Permo-Triassic boundary extinction by carbon cycle modeling. Proc. Natl. Acad. Sci. Unit. States Am. 99, 4172–4177.
Blakey, R.C., 2008. Gondwana paleogeography from assembly to breakup – a 500 my odyssey. GSA (Geol. Soc. Am.) Spec. Pap. (Reg. Stud.) 441, 1–28.
Bodnar, J., Coturel, E.P., Falco, J.I., Beltrán, M., 2021. An updated scenario for the end-Permian crisis and the recovery of Triassic land flora in Argentina. Hist. Biol. https://doi.org/10.1080/08912963.2021.1884245.
Casamiquela, R.M., 1964. Estudios icnológicos. Problemas y métodos de la icnología con aplicación al estudio de pisadas mesozoicas (Reptilia, Mammalia) de la Patagonia. Talleres Gráficos Colegio Industrial Pío IX, Buenos Aires.
Casamiquela, R.M., 1975. Nuevo material y reinterpretación de las icnitas mesozoicas (Neotriásicas) de Los Menucos. In: Provincia de Río Negro (Patagonia). Primer Congreso Argentino de Paleontología y Bioestratigrafía, Abstract book. Tucumán, Argentina, pp. 555–580.
Casamiquela, R.M., 1984. Los vertebrados mesozoicos. In: Ramos, V.A. (Ed.), Geología y Recursos Naturales de la Provincia de Río Negro. Asociación Geológica Argentina, Buenos Aires, pp. 527–538.
Cawood, P.A., Buchan, C., 2007. Linking accretionary orogenesis with supercontinent assembly. Earth Sci. Rev. 82, 217–256.
Citton, P., Carluccio, R., Nicolosi, I., Nicosia, U., 2019. Re-evaluation of *Chelichnus tazelwürmi*, a non mammalian therapsid-grade track from the Upper Permian Arenaria di Val Gardena. Hist. Biol. 31, 322–340.
Citton, P., Díaz-Martínez, I., de Valais, S., Cónsole-Gonella, C., 2018. Triassic pentadactyl tracks from the Los Menucos Group (Río Negro province, Patagonia, Argentina): possible constraints on the autopodial posture of Gondwanan trackmakers. PeerJ 6, e5358.
Conti, M.A., Leonardi, G., Mariotti, N., Nicosia, U., 1975. Tetrapod footprints, fishes and molluscs from the middle permian of the dolomites (N. Italy). Mem. Geopaleontol. Univ. Ferrara 3, 139–150.
Conti, M.A., Leonardi, G., Mariotti, N., Nicosia, U., 1977. Tetrapod footprints of the 'Val Gardena Sandstone' (North Italy). Their paleontological, stratigraphic and paleoenvironmental meaning. Palaeontogr. Ital. 70, 1–91.
Cucchi, R., Busteros, A., Lema, H., 2001. Hoja Geológica 4169-II, los Menucos, provincia de Río negro. IGRM-SEGEMAR Boletín 265, 1–105.
Dal Corso J, Mills, b.J.W., Chu, D., Newton, R.J., Mather, T.A., Shu, W., Wu, Y., Tong, J., Wignall, P.B., 2020. Permo–Triassic boundary carbon and mercury cycling linked to terrestrial ecosystem collapse. Nat. Commun. 11, 2962.
de Valais, S., 2008. Icnología de tetrápodos triásicos y jurásicos de Argentina: aportes al origen de las aves y los mamíferos.. PhD Thesis. In: Facultad de Ciencias Exactas y Naturales. Universidad de Buenos Aires, Buenos Aires, Argentina.
de Valais, S., Díaz-Martínez, I., Citton, P., Cónsole-Gonella, C., 2020. Vertebrate tracks of the Río negro Province. In: Bressan S., Graciela, Fernández E., Diana (Eds.), Patagonia, Argentina: stratigraphy, palaeobiology and environmental contexts. Revista de la Asociación Geológica Argentina, vol. 77. Asociación Geológica Argentina, pp. 402–426.
Demathieu, G., Fichter, J., 1989. Die Karlshafener Fährten im Naturkundemuseum der Stadt Kassel – ihre Beschreibung und Bedeutung. Philippia VI/2, 111–154.
Díaz-Martínez, I., Citton, P., de Valais, S., Cónsole-Gonella, C., González, S.N., 2019. Late Permian-Early Jurassic vertebrate tracks from Patagonia: biochronological inferences and relationships with southern African realms. J. Afr. Earth Sci. 160, 103619.
Díaz-Martínez, I., de Valais, S., 2014. Estudio de la variabilidad en la conservación de huellas de tetrápodos del Triásico Superior de Los Menucos, Río Negro, Argentina. Ameghiniana 52 (1), 8R.
Domnanovich, N.S., Marsicano, C., 2006. Tetrapod footprints from the Triassic of Patagonia: reappraisal of the evidence. Ameghiniana 43, 55–70.
Domnanovich, N.S., Tomassini, R., Manera de Bianco, T., Dalponte, M., 2008. Nuevos aportes al conocimiento de la icnofauna de tetrápodos del Triásico Superior de Los Menucos (Complejo Los Menucos), provincia de Río Negro, Argentina. Ameghiniana 45, 221–224.
Ellenberger, P., 1970. Les niveaux paléontologiques de premiére apparition des mammiféres primordiaux en Afrique du Sud et leur ichnologie. Establissement de zones stratigraphique détaillées dans le Stormberg du Lesotho (Afrique du Sud) (Trias superior a Jurassique). In: Proceedings and Papers II Gondwana Symposium, pp. 343–370.
Falco, J.I., 2019. Estratigrafía y evolución magmática del Grupo Los Menucos (Triásico), Provincia de Río Negro, Argentina.. Ph.D. Thesis Universidad Nacional del Sur, Bahía Blanca, Argentina, p. 267.
Falco, J.I., Hauser, N., 2017. Sedimentología y proveniencia de los depósitos de la Formación Vera (Grupo Los Menucos-Triásico) en el área del Puesto Tscherig, provincia de Río Negro, Argentina. Lat. Am. J. Sedimentol. Basin Anal. 24, 21–37.
Falco, J.I., Hauser, N., Uwe, R., 2018. Three magmatic events in the Los Menucos area of the central- North Patagonian Massif, Argentina?. In: 11th South American Symposium on Isotope Geology. Cochabamba, Bolivia. Colegio de Geólogos de Bolivia.
Falco, J.I., Bodnar, J., Del Río, D., 2020. Revisión Estratigráfica del Grupo Los Menucos, Pérmico tardío - Triásico temprano del Macizo Nordpatagónico, Prov. de Río Negro, Argentina. Rev. Asoc. Geol. Argent. 77, 1–48.
Fichter, J., Heggemann, H., Kunz, R., 1999. Neue beziehungsweise bisher nicht veröffentlichte Tetrapodenfährten-Lokalitäten im mittleren Buntsandstein Nordhessens und Südniedersachsens. Geol. Jahrb. Hessen 127, 33–55.
Francischini, H., Dentzien-Dias, P., Lucas, S.G., Schultz, C.L., 2018. Tetrapod tracks in permo–triassic eolian beds of southern Brazil (paraná basin). PeerJ 6, e4764.
Giacosa, R., Lema, H., Busteros, A., Zubia, M., Cucchi, R., Di Tommaso, I., 2007. Estructura del Triásico de la región norte del Macizo Nordpatagónico (40°-41° S, 67° 30'-69° 45'O), Río Negro. Rev. Asoc. Geol. Argent. 62, 355–365.
González, S.N., Greco, G.A., González, P.D., Sato, A.M., Llambías, E.J., Varela, R., 2016. Geochemistry of a triassic dyke swarm in the north patagonian Massif, Argentina. Implications for a postorogenic event of the permian Gondwanide orogeny. J. S. Am. Earth Sci. 70, 69–82.
González, S.N., Greco, G.A., Sato, A.M., Llambías, E.J., Basei, M.A., González, P.D., Díaz, P.E., 2017. Middle Triassic trachytic lava flows associated with coeval dyke swarm in the North Patagonian Massif: a postorogenic magmatism related to extensional collapse of the Gondwanide orogen. J. S. Am. Earth Sci. 75, 134–143.
Haubold, H., 1966. Therapsiden- und Rhynchocephalen- Fährten aus dem Buntsandstein Südthüringens. Hercynia 3, 147–183.
Haubold, H., 1971a. Die Tetrapodenfährten des Buntsandsteins: Paläontologische Abhandlungen A 4, 395–548.
Haubold, H., 1971b. Ichnia amphibiorum et reptiliorum fossilium. In: Kuhn, O. (Ed.), Handbuch der Palaoherpetologie encyclopedia of paleoherpetology. Gustav Fischer Verlag 18, Stuttgart, p. 124.
Hopson, J.A., 1995. Patterns of evolution in the manus and pes of non-mammalian therapsids. J. Vertebr. Paleontol. 15, 615–639.
Klein, H., Lucas, S.G., 2018. Diverse middle triassic tetrapod footprint assemblage from the muschelkalk of Germany. Ichnos 25, 162–176.
Kokogián, D., Spalletti, L., Morel, E., Artabe, A., Martínez, R., Alcober, O., Milana, J., Zavattieri, A., Papú, O., 2001. Estratigrafía del Triásico Argentino. In: Artabe, A.E., Morel, E., Zamuner, A. (Eds.), El Sistema Triásico en la Argentina. Fundación Museo de La Plata "Francisco P. Moreno". La Plata, Argentina, pp. 23–54.
Kummell, S., 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 IIIV. Palaeobiology and Palaeoenvironments 92, 171–196.
Labudía, C.H., Bjerg, E.A., 2001. El Grupo Los Menucos: redefinición estratigráfica del Triásico Superior del Macizo Nordpatagónico. Rev. Asoc. Geol. Argent. 56, 404–407.
Labudía, C.H., Llambías, E.J., Bjerg, E.A., Stipanicic, P.N., 2002. Formación Vera. In: Stipanicic, P.N., Marsicano, C.A. (Eds.), Léxico Estratigráfico de la Argentina, Volumen VIII, Triásico, Serie 'B' (Didáctica y Complementaria) 26. Asociación Geológica Argentina, Buenos Aires, pp. 295–296.
Lagnaoui, A., Melchor, R.N., Bellosi, E.S., Villegas, P.M., Espinoza, N., Umazano, A.M., 2019. Middle Triassic *Pentasauropus*-dominated ichnofauna from western

Gondwana: ichnotaxonomy, palaeoenvironment, biostratigraphy and palaeobiogeography. Palaeogeogr. Palaeoclimatol. Palaeoecol 524, 41–61.
Leanza, H.A., 2009. Las principales discordancias del Mesozoico de la Cuenca Neuquina según observaciones de superficie. Revista del Museo Argentino de Ciencias Naturales 11, 145–184.
Lema, H., Busteros, A., Giacosa, R.E., Cucchi, R., 2008. Geología del complejo volcánico Los Menucos en el área tipo, Río Negro. Rev. Asoc. Geol. Argent. 63, 3–13.
Lema, H., Busteros, A., Giacosa, R.E., Cucchi, R., Zubía, M., Dalponte, M., Espejo, P., Di Tommaso, I., Franchi, M., 2009. Hojas Geológicas 4169-17 y 4169-18, Cerro Abanico y Colonia Ganzú Lauquén. Provincia de Río Negro. Servicio Geológico Minero Argentino. Instituto de Geología y Recursos Minerales. Boletín 380, Buenos Aires, p. 131.
Leonardi, G., 1987. Glossary and Manual of Tetrapod Footprint Palaeoichnology. Departamento Nacional da Produção Mineral, Brasilia, p. 117.
Leonardi, G., 1994. Annotated atlas of South America tetrapod footprints (Devonian-Holocene). In: Ministerio de Minas y Energia, Companhia de Pesquisa de Recursos Minerais, Brazil, p. 247.
Leonardi, G., de Oliveira, F.H., 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). Rev. Bras. Geociencias 20, 216–229.
Leonardi, G., Sedor, F.A., Costa, R., 2002. Pegadas de répteis terrestres na Formação Rio do Rasto (Permiano Superior da Bacia do Paraná), Estado do Paraná, Brasil. Archivos do Museu Nacional do Rio de Janeiro 60, 213–216.
Llambías, E.J., 1999. Las rocas ígneas gondwánicas. In: Caminos, R. (Ed.), Geología Argentina, vol. 29. Instituto de Geología y Recursos Minerales, Buenos Aires, pp. 349–376.
Lovecchio, J.P., Rohais, S., Joseph, P., Bolatti, N.D., Ramos, V.A., 2020. Mesozoic rifting evolution of SW Gondwana: a poly-phased, subduction-related, extensional history responsible for basin formation along the Argentinean Atlantic margin. Earth Sci. Rev. 203, 103–138.
Lucas, S.G., 2017. Permian tetrapod extinction events. Earth Sci. Rev. 170, 31–60.
Luppo, T., López De Luchi, M.G., Rapalini, A.E., Martínez Dopico, C.I., Fanning, C.M., 2018. Geochronologic evidence of a large magmatic province in northern Patagonia encompassing the Permian-Triassic boundary. J. S. Am. Earth Sci. 82, 346–355.
Marchetti, L., Klein, H., Buchwitz, M., Ronchi, A., Smith, R.M.H., De Klerk, W.G., Sciscio, L., Groenewald, G.H., 2019. Permian-Triassic vertebrate footprints from South Africa: ichnotaxonomy, producers and biostratigraphy through two major faunal crises. Gondwana Res. 72, 139–168.
Marchetti, L., Ceoloni, P., Leonardi, G., Massari, F., Mietto, P., Sacchi, E., Valentini, M., 2020. The Lopingian tetrapod ichnoassociation from Italy, a key for the understanding of low-latitude faunas before the end-Permian crisis. In: Romano, M., Citton, P. (Eds.), Tetrapod Ichnology in Italy: the State of the Art. Journal of Mediterranean Earth Sciences, vol. 12, pp. 31–52.
Marsicano, C.A., Arcucci, A.B., Mancuso, A., Caselli, A.T., 2004. Middle Triassic tetrapod footprints of southern South America. Ameghiniana 41, 171–184.
Martínez Dopico, C.I., Fanning, C.M., López de Luchi, M.G., Rapalini, A.E., Wemmer, K., Basei, M.A.S., 2017. Emplacement and temporal constraints of the Gondwanan intrusive complexes of northern Patagonia: La Esperanza plutono-volcanic case. Tectonophysics 712–713, 249–269.
Melchor, R.N., de Valais, S., 2006. A review of Triassic tetrapod track assemblages from Argentina. Palaeontology 49, 355–379.
Parrish, J.T., 1993. Climate of the supercontinent pangea. J. Geol. 101, 215–233.
Prezzi, C., Vizán, H., Rapalini, A., 2001. Marco paleogeográfico. In: Artabe, A.E., Morel, E.M., Zamuner, A.B. (Eds.), El Sistema Triásico en Argentina. Fundación Museo de la Plata 'Francisco Pascasio Moreno', La Plata, pp. 255–267.
Rapela, C.W., Llambías, E.J., 1985. Evolución magmática y relaciones regionales de los complejos eruptivos de La Esperanza, Provincia de Río Negro. Rev. Asoc. Geol. Argent. 1–2, 4–25.
Rapela, C.W., Pankhurst, R.J., Llambías, E.J., Labudía, C.H., Artabe, A., 1996. "Gondwana" magmatism of Patagonia: inner Cordilleran calc-alkaline batholiths and bimodal volcanic provinces. III International Symposium on "Andean Geodynamics" Extended Abstracts 791–794.
Retallack, G.J., 2021. Multiple Permian-Triassic life crises on land and at sea. Global Planet. Change 198, 103415.
Retallack, G.J., Smith, R.M.H., Ward, P.D., 2003. Vertebrate extinction across permian–triassic boundary in karoo basin, South Africa. Geol. Soc. Am. Bull. 115, 1133–1152.
Retallack, G.J., Sheldon, N.D., Carr, P.F., Fanning, M., Thompson, C.A., Williams, M.L., Jones, B.G., Hutton, A., 2011. Multiple Early Triassic greenhouse crises impeded recovery from Late Permian mass extinction. Palaeogeogr. Palaeoclimatol. Palaeoecol. 308, 233–251.
Romano, M., Citton, P., Nicosia, U., 2016. Corroborating trackmaker identification through footprint functional analysis: the case study of *Ichniotherium* and *Dimetropus*. Lethaia 49, 102–116.
Romano, M., Bernardi, M., Petti, F.M., Rubidge, B., Hancox, J., Benton, M.J., 2020. Early Triassic terrestrial tetrapod fauna: a review. Earth Sci. Rev. 210, 103331.
Romer, A.S., 1956. Osteology of the reptiles. In: Krieger Publishing Company. Florida, Malabar, p. 772.
Roscher, M., Stordal, F., Svensen, H., 2011. The effect of global warming and global cooling on the distribution of the latest Permian climate zones. Palaeogeogr. Palaeoclimatol. Palaeoecol. 309, 186–200.
Rühle von Lilienstern, H., 1944. Eine Dicynodontierfährten aus dem *Chirotherium* sandstein von Hebberg. Paläontol. Z. 23, 368–385.
Sato, A.M., Llambías, E.J., Basei, M.A.S., Castro, C.E., 2015. Three stages in the Late Paleozoic to Triassic magmatism of southwestern Gondwana, and the relationships with the volcanogenic events in coeval basins. J. S. Am. Earth Sci. 63, 48–69.
Silva, R.C., Sedor, F.A., Fernandes, A.C.S., 2012. Fossil footprints from the Late Permian of Brazil: an example of hidden biodiversity. J. S. Am. Earth Sci. 38, 31–43.
Spalletti, L.A., Artabe, A.E., Morel, E.M., 2003. Geological factors and evolution of southwestern Gondwana Triassic plants. Gondwana Res. 6, 119–134.
Stipanicic, P.N., 1967. Consideraciones sobre las edades de algunas fases magmáticas del Neopaleozoico y Mesozoico. Rev. Asoc. Geol. Argent. 22, 101–133.
Veevers, J.J., 2004. Gondwanaland from 650–500 Ma assembly through 320 Ma merger in Pangea to 185–100 Ma breakup: supercontinental tectonics via stratigraphy and radiometric dating. Earth Sci. Rev. 68, 1–132.
Ziegler, A.M., Hulver, M.L., Rowley, D.B., Martini, I.P., 1997. Permian world topography and climate. In: Martini, I.P. (Ed.), Late Glacial and Postglacial Environmental Changes; Quaternary, Carboniferous–Permian, and Proterozoic. Oxford University Press, New York, United States, pp. 111–142.