Late Triassic pentadactyl tracks from the Los Menucos Group (Río Negro province, Patagonia Argentina) and their bearing on Gondwanan trackmakers' autopod ial posture

autopodial

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The Los Menucos locality in Patagonia, Argentina, bears a quite well-known ichnofauna ~~resulting~~ mostly represented by small therapsid footprints. Within this ichnofauna, large pentadactyl footprints are also represented but to date were relatively under investigated. These footprints are here analyzed and discussed ~~by~~ from a palaeobiological (i.e. trackmaker identification) standpoint. Besides the classical methodology applied in tetrapod ichnology, the high resolution Digital Photogrammetry method was performed to achieve a more objective representation of footprint three-dimensional morphologies. Waiting for a future ichnotaxonomical revision of the Argentinian material, the footprints under study are compared with *Pentasauropus*, a well-known ichnotaxon established from the Upper Triassic lower Elliot Formation (Stormberg Group) of the Karoo Basin (Lesotho, Southern Africa). Some track features suggest a therapsid-grade synapsid as the potential trackmaker, to be sought among anomodont dicynodonts (probably Kannemeyeriiformes). While the interpretation of limb~~s~~ posture in the producer of *Pentasauropus* tracks from the Los Menucos locality agrees with that described from the dicynodont body fossil record, the autopodial posture does not completely. The relative distance between the impression of the digital (ungual) bases and the distal edge of the pad trace characterizing the studied tracks likely indicates a subunguligrade foot posture in static stance but plantiportal during the dynamics of locomotion. The reconstructed posture may have implied an arched configuration of the articulated metapodials and at least of the proximal phalanges, as well as little movement capabilities of the metapodials. A subunguligrade-plantiportal foot is a novelty among dicynodonts and, considering the large but not gigantic dimensions of the putative trackmakers, it was likely promoted independently ~~from the~~ by body size, ~~however~~ representing a pre-requisite for such evolutionary paths. ~~By~~ From a biochronological standpoint, *Pentasauropus* ~~results~~ represents a reliable Late Triassic marker and enables confirm~~ing~~ation of the ~~Upper~~ Late

Triassic age for the ~~concerning~~ -TRACK- bearing levels of the Los Menucos Group, as well as probably for other *Pentasauropus*-bearing units in Argentina.

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Abstract

The Los Menucos locality in Patagonia, Argentina, bears a quite well-known ichnofauna resulting mostly represented by small therapsid footprints. Within this ichnofauna, large pentadactyl footprints are also represented but to date were relatively under investigated. These footprints are here analyzed and discussed by a palaeobiological (i.e. trackmaker identification) standpoint. Besides the classical methodology applied in tetrapod ichnology, high resolution Digital Photogrammetry method was performed to achieve a more objective representation of footprint three-dimensional morphologies. Waiting for a future ichnotaxonomical revision of the Argentinian material, footprints under study are compared with *Pentasauropus*, a well-known ichnotaxon established from the Upper Triassic lower Elliot Formation (Stormberg Group) of Karoo Basin (Lesotho, Southern Africa). Some track features suggest a therapsid-grade synapsid as potential trackmaker, to be sought among anomodont dicynodonts (probably Kannemeyeriiformes). While the interpretation of limbs posture in the producer of *Pentasauropus* tracks from Los Menucos locality agree with that described from the dicynodont body fossil record, the autopod posture does not completely. The relative distance between the impression of the digital (ungual) bases and the distal edge of the pad trace characterizing the studied tracks likely indicates a subunguligrade foot posture in static stance but plantiportal during dynamic of locomotion. The reconstructed posture may have implied an arched configuration of the articulated metapodials and at least of the proximal phalanges, as well as little movement capabilities of metapodials. A subunguligrade-plantiportal foot is a novelty among dicynodonts and, considering the large but not gigantic dimensions of the putative trackmakers, it was likely promoted independently from the body size, however representing a pre-requisite for such evolutionary paths.

By a biochronological standpoint, *Pentasauropus* results a reliable Late Triassic marker and enables confirming the Upper Triassic age for the concerning bearing levels of the Los Menucos Group, as well as probably for other *Pentasauropus* bearing units in Argentina.

Keywords: *Pentasauropus*, Tracks, Therapsids, Dicynodonts, Triassic, Gondwana, Los Menucos, Patagonia, Trackmakers

INTRODUCTION

Tetrapod tracks and traces are valuable fossils informing about anatomy (e.g. Carpenter, 1992), functional adaptations (e.g. Baird, 1980), motion (e.g. Gatesy et al., 1999; Avanzini, Piñuela & García-Ramos, 2011; Romano, Citton & Nicosia, 2016) and ethology (e.g. Currie & Sarjeant, 1979; Barnes & Lockley, 1994; Lockley et al., 2016) of extinct animals, greatly expanding the potential of information that is often precluded ~~to~~ from the body-fossil record. The detailed analysis of tetrapod footprints is therefore dramatically significant for the chance of integrating and, if necessary, revising data derived from the tetrapod record based on osteological specimens.

The scientific study of tetrapod footprints in Argentina is relatively recent compared to that of Europe (Duncan, 1831) and North America (Hitchcock, 1836), dating back to the first half of the twentieth century (von Huene, 1931). The first, great contribution to the field of tetrapod ichnology in Argentina is that of Casamiquela (1964), who devoted himself to the study of Triassic and Jurassic tetrapod tracks from Patagonia. The work of Casamiquela was followed by other important contributions, mainly represented by fieldwork~~s~~ and the collection of important tetrapod ichnofaunas from the Ischigualasto-Villa Unión Basin (Romer, 1966) and Cuyo Basin (Bonaparte, 1966), and by the extensive catalog of tetrapod ichnofaunas from South America provided by Leonardi (1994). Apart from the different ichnological records, the only comprehensive ichnotaxonomical revision of Triassic tetrapod ichnofaunas from Argentina was conducted by Melchor & de Valais (2006), who re-discussed eight ichnofaunas spanning the whole Triassic. Among these, the well-known Los Menucos ichnofauna was largely studied in the distant and recent past (Casamiquela, 1964, 1975, 1987; Leonardi & de Oliveira, 1990;

Leonardi, 1994; Domnanovich & Marsicano, 2006; Melchor & de Valais, 2006; de Valais, 2008; Domnanovich et al., 2008; Díaz-Martínez & de Valais, 2014), ~~resulting~~ and is dominated by small therapsid footprints. The bulk of this ichnofauna was historically attributed to different new ichnotaxa by Casamiquela (1964, 1974), ~~which~~ who coined *Gallegosichnus garridoi*, *Calibarichnus ayestarani*, *Palaciosichnus zettii*, *Ingenierichnus sierrai*, *Rogerbaletichnus aguilerai*, *Stipanicichnus bonettii* and *Shimmelia chiroteroides*. These ichnotaxa have been ~~posteriorly~~ revised by Melchor & de Valais (2006), ~~which~~ who considered the ichnogenera *Gallegosichnus* Casamiquela, 1964, *Calibarichnus* Casamiquela, 1964, *Palaciosichnus* Casamiquela, 1964 and *Stipanicichnus* Casamiquela, 1975 to be synonyms of *Dicynodontipus* and proposed the abandonment of *Ingenierichnus sierrai* Casamiquela, 1964, *Rogerbaletichnus aguilerai* Casamiquela, 1964 and *Shimmelia chirotheroides* Casamiquela, 1964 due to the poor~~ly~~ preservation of the material. Leaving out the report of ~~an~~ undetermined chirotheroids tracks (de Valais, 2008), a single track referred to as *Rhynchosauroides* and large pentadactyl footprints mentioned as *Pentasauropus* sp. (Domnanovich et al., 2008) constitute up to know the only other well-represented tetrapod track record from the Los Menucos area. However, with respect to *Dicynodontipus*, large pentadactyl footprints were under investigated, as well as a detailed ichnological study focused on track-trackmaker relationships was never performed until now.

An ichnological analysis based on this material from the Triassic Los Menucos Group of Patagonia Argentina is here proposed and discussed in terms of palaeobiology and identity of the trackmaker, shedding light~~s~~ on the autopodial anatomy of footprint-related Gondwanan producers and their dynamics of locomotion.

GEOLOGICAL SETTING

Continental deposits of Triassic age in Argentina ~~were~~ accumulated in different basins in the northwestern region (La Rioja province), the Cuyo region (Mendoza, San Juan and San Luis provinces) as well as in the Patagonia region, namely in the Macizo del Deseado (northern sector of the Santa Cruz province) and in the eastern, central and western sectors of the North Patagonian Massif (Río Negro province). These elongated, narrow rift basins with a prevalent NW-SE and NNW-SSE trends were developed during Permian and Triassic periods and witness an early evidence of the breakup of the western margin of south-west Gondwana, which occurred towards the end of the Triassic and the beginning of the Jurassic (Kokogian et al., 1999; Franzese & Spalletti, 2001; Barredo et al., 2012).

The Triassic tetrapod track record of southern South America is exclusive ~~of~~ to three basins, namely the Ischigualasto-Villa Unión Basin (San Juan and La Rioja provinces; e.g. Romer, 1966; Melchor et al., 2001, 2003; Melchor & de Valais, 2006), the Cuyo Basin (Mendoza and San Juan provinces; e.g.Bonaparte, 1966; Romer, 1966; Marsicano & Barredo, 2004; de Valais et al., 2006; de Valais, 2007), located at a palaeolatitude ranging between 35-37°S (Prezzi, Vizán & Rapalini, 2001) and the Los Menucos Basin (Río Negro province; e.g. Casamiquela, 1964, 1975; Manera de Bianco & Calvo, 1999; Domnanovich & Marsicano, 2006; Domnanovich et al., 2008; Díaz-Martínez & de Valais, 2014), at about 45°S (Prezzi, Vizán & Rapalini, 2001). In the northern basins the record encompasses most of the Triassic Period, while in the Los Menucos Basin sedimentation would have taken place in the Late Triassic (Spalletti, 1999).

After the first works of Stipanicic (1967), Stipanicic et al. (1968) and Stipanicic & Methol (1972, 1980), the Los Menucos Group (also as 'Complejo Los Menucos' - Los Menucos Complex in Cucchi, Busteros & Lema, 2001) was established by Labudía & Bjerg (2001) to indicate dacitic to rhyolitic ignimbrites, mesosilicic lavas and subordinate~~d~~ Triassic sediments exposed around ~~of the~~ Los Menucos town, in the north-western sector of the Nord Patagonian Massif (Río Negro province, Argentina; Fig. 1).

This lithostratigraphic unit can lie unconformably, through a non-conformity, on the low grade metamorphic complex of the Colo Niyeu Formation, Lower Cambrian in age (Martínez Dopico et al., 2017). Or, according to Labudía & Bjerg (2005, but see Luppo et al., 2017 for a contrasting stratigraphic assessment), on granitoids of the Permo-Triassic La Esperanza Plutonic Complex. The upper limit of the Los Menucos Group is marked by an erosive unconformity, above which Upper Cretaceous continental and marine deposits or Tertiary basalts crop out (Labudía & Bjerg, 2001). Within the Los Menucos Group two lithostratigraphic units were defined, namely the Vera Formation and the Sierra Colorada Formation (Labudía & Bjerg, 2001). This subdivision, though on the basis of different nomenclatural ranks, followed that of Miranda (1969) who recognized two informal members, one volcanic and the other sedimentary and pyroclastic ("Sedimentitas Keuperianas" sensu Stipanicic et al., 1968) within the Los Menucos Formation as defined by Stipanicic (1967).

The Vera Formation is mainly composed of volcanic and continental deposits and typically displays rocks indicative of both volcanic~~s~~ and sedimentary processes (Labudía & Bjerg, 2001). The sedimentary succession, ranging from 2 to 150 meters in thickness, is mainly represented by brownish to yellowish conglomerates, made of metamorphic and volcanic clasts up to 15 centimeters in diameter, white to greenish sandstones and reddish brown to red pelites (Labudía & Bjerg, 2001). These sediments were laid down inside small basins bordered by regional and local faults with attitud~~e~~s NE-SW, E-W and NW-SE (Labudía & Bjerg, 2001). Volcanic ashes, tuffs and tuffites, dacitic pyroclastic flows products and volcanic breccias are intercalated with epiclastics (Labudía & Bjerg, 2001). Sedimentation took place mainly in alluvial plain, floodplains, ephemeral rivers and small lacustrine palaeoenvironments (Labudía & Bjerg, 2001), in a seasonal climate condition with alternating periods of dry and wet conditions (Gallego, 2010). Sedimentary and volcan~~o~~iclastic levels within the Vera Formation are characterized by a very rich palaeoflora, the so-called "*Dicroidium* type flora", which is very common within tuffaceous mudstone (Stipanicic, 1967; Stipanicic & Methol, 1972; Artabe, 1985a, b; Labudía et al., 1995; Labudía & Bjerg, 2001), and by an abundant tetrapod fauna. This fauna is represented by tetrapod tracks (Casamiquela, 1964, 1975, 1987; Leonardi & de Oliveira, 1990; Leonardi, 1994; Domnanovich & Marsicano, 2006; Melchor & de Valais, 2006; de Valais, 2008; Domnanovich et al., 2008; Díaz-Martínez & de Valais, 2014) preserved on sandstones with poorly ~~selected~~ sorted grains and with a variable content of tuffaceous breccias. Skeletal fauna, for the time being represented by remains of an amiiform fish (Bogan et al., 2013), is very scarce.

The Sierra Colorada Formation is essentially made of ignimbritic volcanic rocks (Labudía & Bjerg, 2001). Different dates are available for the Los Menucos Group: Rapela et al. (1996) dated rocks pertaining to the Sierra Colorada Fm. at 222 ± 2 Ma (Norian, Late Triassic) with the Rb/Sr isochron method, while Lema et al. (2008) dated it at 206.9 ± 1.2 Ma (Rhaetian, Late Triassic) with the Ar/Ar method. Unfortunately, these dates, which were made on rocks pertaining to the Sierra Colorada Formation, ~~and not allow to~~ do not radiometrically constrain ~~also~~ the Vera Formation. For this lithostratigraphic unit, on the basis of the "*Dicroidium* flora" and the tetrapod ichnofauna (i.e. *Dicynodontipus* and *Pentasauropus*, see below) both coming from this sedimentary facies (Stipanicic, 1967), ~~an Upper~~ a Late Triassic age was proposed.

More recent results, obtained from the basal, middle and upper portion of a 6 km thick geological section trough the Los Menucos Group (Luppo et al., 2017, figs. 1 and 2), indicate an age of 257 ± 2 Ma (Wuchiapingian, Late Permian) for a rhyolitic ignimbrite, 252 ± 2 Ma

(Changhsingian, Late Permian) for an andesite and 248 ± 2 Ma (Olenekian, Early Triassic) for a dacitic ignimbrite (Luppo et al., 2017). These new data predate the main volcanic activity to an about ca 10 Ma period between the Late Permian and the Early Triassic, making the Los Menucos Group coeval with the La Esperanza Plutono-Volcanic Complex (Luppo et al., 2017) and conflicting with previous geological and chronostratigraphical reconstructions.

MATERIAL AND METHODS

The present study is based on the direct analysis of track-bearing slabs MPCA 27029-1/5, MPCA 27029-9, MPCA 27029-16, MPCA 27029-21 and MPCA 27029-33 presently stored at the Museo Provincial Carlos Ameghino (Cipolletti, Río Negro province, Argentina), MMLM 1 and MMLM 2 stored at the Museo Municipal de Los Menucos (Los Menucos, Río Negro province, Argentina) and MMLM 075-1 (ex MRPV 1987P.V.06 *in* Domnanovich et al., 2008, hereafter MMLM 075-1), currently deposited at the Museo Provincial María Inés Kopp (Valcheta, Río Negro province, Argentina). Except for the specimen MMLM 075-1, the material under study was to date unpublished. A Few other slabs, both with and without label, are stored at the Museo Provincial Carlos Ameghino but were not considered in this study due to faint preservation of the tracks.

The provenance of the track-bearing slabs can be traced back to the ex cantera de Felipe Curuil, estancia Yancaqueo, west of the town of Los Menucos (Domnanovich et al., 2008), but a stratigraphic repositioning of the material is currently prevented.

In order to characterize the microfacies of the trampled sediments, two thin sections were obtained from the slab MPCA 27029-19, both parallel and perpendicular to the trampled surface. This is one of the slab bearing not well preserved tracks but identical, from a sedimentological standpoint, to the studied material. For the description of thin sections, Mackenzie, Donaldson & Guilford (1982) and Scasso & Limarino (1997) were taken as a reference. Thin sections are presently stored at the Museo Provincial Carlos Ameghino in Cipolletti (Río Negro province, Argentina) and labelled as MPCA 27029/19.1 (parallel to the trampled surface) and MPCA 27029/19.2 (perpendicular to the trampled surface).

On the whole, about 60 footprints were analyzed. For each slab, tracks were numbered using Arabic numerals and, when referring to single tracks in the text, they are indicated as /number following the slab label (e.g. MPCA 27029-1/4 where MPCA 27029-1 and number 4 indicate slab and single track, respectively). Studied material mainly consist of isolated sets or incomplete trackways. Measurements related to trackmaker body dimension were obtained from the slabs MPCA 27029-1, MPCA 27029-9, MPCA 27029-16 and MPCA 27029-21. On single tracks, which as after discussed are mainly represented by digit traces, measurement of footprint width was taken. Also, track features and differential depth of impression allowed in some cases to recognize footprint identity, side of the trackway when incompletely preserved, or tracks belonging to different trackways (e.g. MMLM 075-1), and element orientations. Measurements of the footprints were performed according to guidelines introduced by Leonardi (1987).

Track outlines were represented through interpre~~ta~~tive drawings. High resolution Digital Photogrammetry was undertaken to achieve a more objective representation of track three-dimensional morphology. This method is based on Structure from Motion (SfM) (Ullman, 1979) and Multi View Stereo (MVS) (Seitz et al., 2006) algorithms and produces high quality dense point clouds. Recently, different software solutions for Digital Photogrammetry were discussed (e.g. Falkingham, 2012; Cipriani et al., 2016) and the method was largely adopted in the field of the tetrapod ichnology (e.g. Breithaupt, et al. ~~Matthews & Noble~~, 2004; McCrea et al., 2015; Citton et al., 2016, 2017; Díaz-Martínez et al., 2016; Díaz-Martínez, González & de Valais, 2017). To model the studied specimens, the software package Agisoft PhotoScan Pro (Educational License), which enables creating 3D textured meshes by means of semi-automatic processing of images (Mallison & Wings, 2014), was used.

The images selected for photogrammetric process were acquired using a Nikon Coolpix P520 camera with 4.3-7.6 focal length, resolution 4896x3672 and pixel size ranging from 1.25x1.25 μm and 1.27x1.27 μm. Camera altitude ranges from 26.2 cm (MPCA 27029-4) to 63.8 cm (MPCA 27029-3); ground resolution varies from 0.0753 mm/pix (MPCA 27029-4) to 0.183 mm/pix (MPCA 27029-3); RMS reprojection error ranges from 0.145637 pix (MPCA 27029-1) to 0.273984 pix (MPCA 27029-21); mean key point size varies from 2.28824 pix (MPCA 27029-21) to 3.99373 pix (MPCA 27029-1). In order to correctly scale the calculated model, 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).

Institutional abbreviations.

LES - Laboratoire de Paléontologie, Institut de Sciences de l'Evolution of the University of Montpellier II collection, Montpellier, France; MPCA - Museo Provincial Carlos Ameghino, Cipolletti, Río Negro province, Argentina; MMLM - Museo Municipal de Los Menucos, Los Menucos, Río Negro province, Argentina; MRPV - Museo Provincial María Inés Kopp, Valcheta, Río Negro province, Argentina.

TRACK RECORD

Sedimentological observations

Track-bearing slabs consist of yellowish to greenish, medium to mainly coarse grained and poorly sorted volcaniclastic sandstone lacking to the unaided eye ~~of~~ any sedimentary structures, neither on the surface nor in cross-section.

The observed texture ranges from inequigranular/equigranular (Figs. 2A, 2B) to predominantly equigranular (Fig. 2C). Phenocrysts, mainly subhedral and anhedral, range in dimension from 0,5 mm to 1,5 mm and show in one case incipient orientation. Phenocrysts are represented mainly by plagioclase, quartz, alkaline feldspar, biotite, amphibole (hornblende), orthopyroxene (enstatite) and calcite floating in a mafic, glassy matrix.

The highly epiclastic texture observed at the base of the trampled surface (thin section MPCA 27029/19.2), mainly represented by fragments of quartz and some lithics displaying attrition and rounded to sub-angular shape, suggesting sedimentary reworking of an original tuff of probable dacitic composition. The texture observed in the thin section MPCA 27029/19.1 instead indicates a scarce sedimentary reworking (Fig. 2D). In section, a faint normal gradation can be observed most likely indicating short sedimentation events; on the whole, the track-bearing slabs can be related to a proximal fluvial environments.

Track preservation

The vertebrate tracks studied herein are preserved as concave epireliefs (MPCA 27029-1 and MMLM 075-1) and convex hyporeliefs (MPCA 27029-2; MPCA 27029-3; MPCA 27029-4; MPCA 27029-5; MPCA 27029-9; MPCA 27029-16; MPCA 27029-21; MPCA 27029-33; MMLM 1 and MMLM 2). MMLM 075-1 is composed of four slabs, two as casts -with negative epichnial tracks, labeled as MMLM 075-1/1a, /2 and /3a- and two as their moulds -with positive hypichnial tracks, labeled as MMLM 075-1/1b and 3/b. There are no evidences of any layer between the casts and the moulds and the shape of both concave epireliefs and convex hyporeliefs are exactly complementary (Fig. 3). Therefore, and taking into account that the tracks preserved similarly (i.e. sub-circular/sub-ovoidal to pointed digit impressions; roughly sub-circular to elliptical pad tracks; very thin displacement rims in the pad and well-marked in the digit impressions), in our opinion the concave epireliefs are true tracks (sensu Marty~~,~~ et al., ~~Falkingham & Richter~~, 2016) and the convex hyporeliefs are natural casts (sensu Marty, et al. ~~Falkingham & Richter~~, 2016).

In general, the tracks studied here are moderately well preserved (grade 1 sensu Belvedere & Farlow, 2016), and the true tracks are not elite tracks (sensu Lockley, 1991). In addition, they are not modified true tracks (sensu Marty, Falkingham & Richter, 2016) because they lack ~~of~~ evidence~~s~~ of physiochemical (e.g. weathering) and/or by biological influences after they were made. Thereby, the shape of these tracks is mainly conditioned by the substrate consistency (grain size and water content). Recently, Falk et al. (2017) performed neoichnological experiments ~~in~~ which compared the shape of several tracks impressed in three different sediments (fine, medium and coarse sand) with three different moisture contents (wet, moist~~ure~~ and dry). They concluded that wet and dry coarse sediments preserve tracks without fine details, but moisture coarse sediment might preserve the overall track shape and details as claw impressions. As ~~it~~ has been previously commented, the tracking surface is a medium to coarse sandstone, and tracks have depth digit impressions with extruded rims. Therefore, and according to Falk et al.'s (2017) experiments, the trackmakers most likely walked on humid, not waterlogged nor dry, coarse sediments with a moderately plastic behaviour, able to record the main anatomical features of the autopods.

Description. All the discussed slabs are illustrated in Figs. 4-9. The studied footprints from the Los Menucos ichnosite are manus and pes tracks with very low heteropody, both of them mainly preserved as tetradactyl, although pentadactyl tracks are present (MPCA 27029-1/4/6, MPCA 27029-2/2, MPCA 27029-4/2, MPCA 27029-16/10, MPCA 27029-33/2, MMLM 075-1) (Figs. 4, 5E-5H, 7A-7D, 8) as well as tridactyl ones, in which the central digits are those impressed (MPCA 27029-9/2, MPCA 27029-16/8, MPCA 27029-21/3, MMLM 1/1, MMLM 2/3) (Figs. 6E-6H, 7, 9). Position of the manus impression can be at the middle of a pes stride or lying closer to the previous pes impression or to the subsequent. Digit traces are commonly arranged to shape an arcuate pattern that is convex anteriorly, according to which the digit III trace (the central one) or digit III and IV traces are the most advanced. In several cases, the digit imprints are ~~representing~~ the only element constituting the tracks; variability affecting the number of digits can be obvious on the same slab and within the same manus-pes set (e.g. MPCA 27029-21, MMLM 2; Figs. 7E-7H, 9E-9H). In the material under study the degree of curvature of the arcuate pattern is variable and appears more pronounced in some smaller tracks (e.g. MPCA27029-16/7/9/10; Figs. 7A-7D) than in larger ones (e.g. MPCA 27029-1/4, MMLM 075-1, MMLM 2/2; Figs. 4, 8E-8H, 9E-9H). Apart from degree of curvature, the general morphology remains consistent despite dimensional differences, that are here interpreted as most likely pertaining to different ontogenetic stages of the same type of producer.

Digit traces show two distinct morphologies: in some cases they are characterized by a sub-circular/sub-ovoidal morphology (e.g. MPCA 27029-9, MPCA 27029-16, MPCA 27029-21; Figs. 6E-6H, 7), while in other cases digit traces are markedly pointed (e.g. MPCA 27029-2, MPCA 27029-4, MPCA 27029-5, MPCA 27029-33; Figs. 4E-4H, 5E-5H, 6A-6D, 8A-8D). This two morphologies can co-exist on the same slab and within the same set or trackway, thus pertaining to the spectrum of internal variability of the ichnotaxon. When pointed, the most medial digit traces (i.e. digit I or II imprints), both of manus and pes tracks, can be affected by trailing marks. These extramorphological features (see Peabody, 1948, for the concept of extramorphology in tetrapod ichnology) qualitatively range from weakly hinted and short (e.g. MPCA 27029-1/6, MPCA 27029-2/1, MPCA 27029-3/1/2, MPCA 27029-4/2, MPCA 27029-5, MPCA 27029-9/4/6; Figs. 4, 5, 6) to highly sharp and long (e.g. MMLM 075-1, MMLM 1 and MMLM 2; Figs. 8E-8H, 9) and are mostly inward oriented with respect to the hypothetical, reconstructed, trackway midline. Also, digit III and, ~~with~~ to a lesser extent, digit IV imprints, can be affected by the same extramorphology, even if in such cases in the trailing traces it is never as developed as in the medial digit traces.

A brief account o~~n~~f the differential depth of the studied tracks is deemed necessary, in order to hypothesize trackmaker functionality and deepen the discussion about zoological attribution following in the next section, as recently discussed for other tetrapod tracks (e.g. Romano ~~, Citton & Nicosia~~ et al., 2016; Citton et al., 2017). In the studied material, central digits are commonly the most deeply and uniformly impressed, both in manus and pes tracks (e.g. MPCA 27029-4, MPCA 27029-5, MMLM 1; Figs. 5F-5G, 6B-6C, 9B-9C). When a certain degree of variability is observed, digit III and IV imprints are the most deeply imprinted (e.g. MPCA 27029-1, MPCA 27029-3, MPCA 27029-16; Figs. 4B-4C, 5B-5C, 7B-7C), followed by digit II and I imprints. The ~~D~~digit V trace, when preserved, ~~results~~ is only faintly imprinted on the substrate (e.g. MMLM 075-1, but see MPCA 27029-16/9/10 for a different configuration of depth of impression; Figs. 7B-7C, 8F-8G).

Behind digit traces, a roughly sub-circular to elliptical pad trace can be preserved (e.g. MPCA 27029-1/2/4/5/6, MPCA 27029-5, MPCA 27029-16/10, MMLM 075-1, MMLM 1/2/4, MMLM 2/1; Figs. 4A-4D, 6A-6D, 7A-7D, 8E-8H, 9), lying at a short distance from the base of the central digit traces and commonly contacting the most medial and lateral digit imprints (e.g.

MPCA 27029-1; Figs. 4A-4D). This trace is separated from central digit traces ahead by a non impressed area, which appears as a groove or as a ridge depending on the mode of preservation (concave epirelief or convex hyporelief), tapering towards the most medial and lateral digit imprints. This should not be confused with displacement areas of similar morphology, which are instead related to digit traces (i.e. thrust of digit at the end of the cycle of locomotion; Fig. 10), where the non impressed area is absent (e.g. MPCA 27029-2, MPCA 27029-3/1/4, MPCA 27029-4, MPCA 27029-9/3/5, MPCA 27029-21/4, MPCA 27029-33/1/2/3, MMLM 2/3; Figs. 4E-4H, 5, 6E-6H, 7E-7H, 8A-8D, 9E-9H).

The pad trace behind digit traces is ~~result to be~~ more impressed centrally or centro-laterally and distally (i.e. close to the non impressed area behind digit traces, MPCA 27029-1, MMLM 075-1, MMLM 1; Figs. 4B-4C, 8F-8G, 9B-9C).

The axis of pes tracks is commonly inward~~ly~~ rotated with respect to the trackway midline but it can also be parallel to the trackway midline (e.g. MPCA 27029-9, 27029-16), while manus tracks show a wider range of variability, being both inwardly and outwardly rotated with respect to the trackway midline (e.g. MPCA 27029-1 and MMLM2, respectively). When possible, measurements and ratios were taken; measurements were performed taking into account digit III as a homologous point, both for manus and pes tracks. Pace length on manus tracks was measured on specimen MPCA 27029-1, ~~resulting~~ 42.2 cm and 33.3 cm; specimen MPCA 27029-9, ~~resulting~~ 28.5 cm; specimen MPCA 27029-16, resulting 21 cm and 15 cm. Pace length on pes tracks was measured on specimen MPCA 27029-1, ~~resulting~~ 41.7 cm and 40.5 cm; specimen MPCA 27029-9, ~~resulting~~ 37 cm and 32.5 cm; specimen MPCA 27029-16, ~~resulting~~ 22.5 cm; specimen MPCA 27029-21, ~~resulting~~ 37 cm, 34 cm and 34.5 cm. Stride length on manus tracks was measured on specimen MPCA 27029-1, ~~resulting~~ 59.5 cm; specimen MPCA 27029-16,

(2)

resulting 28.5 cm; specimen MMLM 1, resulting 52 cm; specimen MMLM 2, resulting 40.5 cm. Stride length on pes tracks was measured on specimen MPCA 27029-1, resulting 62.4 cm; MPCA 27029-3, resulting 63.5 cm; specimen MPCA 27029-9, resulting 45.5 cm; specimen MPCA 27029-21, resulting 37.5 cm and 41 cm; specimen MPCA 27029-33, resulting 63.5 cm; specimen MMLM 075-1, resulting 57.3 cm. External trackway width resulted 50 cm for MPCA 27029-1; 36 cm for MPCA 27029-9; 32 cm for MPCA 27029-16; 38.5 cm for MPCA 27029-21. Pace angulation on pes tracks was measured and it results ranging from 62° (MPCA 27029-21) to 99° (MPCA 27029-1); pace angulation measured on manus tracks results slightly more variable, ranging between 64° (MPCA 27029-21) and 101° (MPCA 27029-1). The ratio trackway width:stride length (pedes) resulted 0.80 (MPCA 27029-1), 0.79 (MPCA 27029-9), 1.03(MPCA 27029-21). Gleno-acetabular distance was measured on specimens MPCA 27029-1, 27029-9, 27029-16 and, tentatively, 27029-21 and resulted 46.2 cm, 40 cm, 26 cm and 36.2 cm, respectively. The ratio stride length:gleno-acetabular distance was calculated for specimens MPCA 27029-1, MPCA 27029-9, MPCA 27029-16 and MPCA 27029-21, resulting respectively 1.29 (calculated considering manus tracks) and 1.35 (calculated considering pes tracks); 1.14 (calculated considering pes tracks); 1.10 (calculated considering manus tracks) and 1.03 (calculated considering pes tracks).

②

Remarks. These footprints from the Los Menucos ichnosite are characterized by having the following features: manus and pes tracks with low heteropody, up to five digit imprints aligned forming an arch convenx anteriorly directed, a central or central-lateral pad trace.

The ichnogenus *Pentasauropus* Ellenberger, 1970 was established on the basis of material collected and described some years before (Ellenberger, 1955) from the Upper Triassic lower Elliot Formation (Stormberg Group) of the Karroo Basin in Subeng and other localities, such as Morobong, Seaka, Subeng, Maseru and Maphutseng, of Lesotho (Southern Africa). Five ichnospecies were originally included in the ichnogenus, namely *Pentasauropus erectus*, *Pentasauropus incredibilis*, *Pentasauropus maphutsengi*, *Pentasauropus morobongensis* and *Pentasauropus motlejoi*, which remained unchanged in the subsequent formal listing (Ellenberger, 1970, 1972). Material from the Ellenberger Collection referred to this ichnogenus, presently housed at the University of Montpellier (France), is represented by four cast of those originally mentioned as *Pentasauropus incredibilis* (LES 054 1-3, LES 054 4), one cast of *Pentasauropus morobongensis* (LES 005) and one cast of *Tetrasauropus gigas* (LES 038), plus some missing specimens (see D'Orazi Porchetti & Nicosia, 2007, and reference therein for a complete assessment of inventory numbers).

After the original and subsequent publications of Ellenberger (1955, 1970, 1972), the ichnogenus was deemed as valid by Olsen & Galton (1984), Lockley & Meyer (2000) and D'Orazi Porchetti & Nicosia (2007). ③ The latter have been emended the ichnogenus diagnosis to appoint the type ichnospecies and considered synonymous the five ichnospecies as *Pentasauropus incredibilis* (the reason for choosing *P. incredibilis* as the type ichnospecies can be found in D'Orazi Porchetti & Nicosia, 2007). The differences in track patterns were considered as originated by dimensional constraints and/or behavioural factors and, at the same time, considering that the main footprint characters (e.g. number and arrangement of digits, heteropody) did not justify ichnospecies separation (D'Orazi Porchetti & Nicosia, 2007). Moreover, agreeing with Lockley & Meyer (2000), the same authors ~~located~~ reassigned the tracks originally referred to as *Tetrasauropus gigas* into *Pentasauropus*.

Following the emended ichnogeneric diagnosis, the arcuate pattern of manus and pes tracks derives from the five clear equally spaced claw or ungual traces (those of imprints of digit

II, III and IV are the largest), representing in some cases the entire track. In other cases a roughly rounded sole pad is observed behind claw or ungual traces (LES 053 A, B, C in Ellenberger, 1972, pl. IV and V and LES 038). The axis of the pes impression is always inwardly rotated, while that of the manus impression can range from slightly inwardly rotated (LES 052 B and LES 053 A) to slightly outwardly rotated (LES 038 and LES 052 A).

The specimens from Los Menucos are provisionally compared with tracks referred to as *Pentasauropus* on the basis of their general features. However, a comprehensive and updated ichnotaxonomic treatment of these footprints will been under~~gone~~ taken and ~~described~~ presented elsewhere.

Zoological attribution

Several attempts to identify a trackmaker for the original ichnospecies erected within *Pentasauropus* have been previously made: *Pentasauropus incredibilis* was attributed to a "Theromorphe" or to a large amphibian (Ellenberger & Ellenberger, 1958: p. 67). Some years later, a "basal melanorosaurid" (or a basal ornithischian) was suggested as putative trackmaker of "*Pentasauropus morobongensis*", while a melanorosaurid was proposed for "*Pentasauropus motlejoi*", *P. incredibilis* and "*P. maphutsengi*", and a possible ornithischian for "*P. erectus*" (sensu Ellenberger, 1970). Moreover, an anapsid or a basal sauropod were proposed as putative trackmakers for "*P. motlejoi*", *P. incredibilis* and "*P. erectus*" (sensu Ellenberger, 1972). Haubold (1974, 1984) referred *Pentasauropus* to a sauropod or therapsid trackmaker. A dicynodont trackmaker for the ichnogenus was also proposed by Olsen & Galton (1984), Anderson, Anderson & Cruickshank (1998), Galton & Heerden (1998, attributing *Pentasauropus* to large anomodont dicynodonts) and Lockley & Meyer (2000). Finally, D'Orazi Porchetti & Nicosia (2007) accepted the attribution to a dicynodont, observing a good fitt~~in~~g between the skeletal autopodia of Triassic dicynodonts and the manus and pes digit structures of *Pentasauropus*, apart from the strong homopody and the limb~~s~~ posture (see also Walter, 1986).

The studied material from the Los Menucos locality, taking into account the handful of features that can be recognized from tracks, allowed corroborat~~ing~~ion of some previous interpretation about trackmaker identity. At the same time, the attempt to identify a putative trackmaker opens the way for new inferences about autopod~~s~~al posture.

Limb~~s~~ posture kept by *Pentasauropus* trackmakers during the cycle of locomotion can be tentatively inferred from trackway patterns, parameters and ratios (Peabody, 1948, 1959; Kubo & Benton, 2009; Kubo & Ozaki, 2009) even if this interpretation is often far from being simple and linear (Crompton & Jenkins, 1973). The ratio trackway width:stride length and stride length:gleno acetabular distance, that were calculated from available trackways, indicate a semi-erect posture for the trackmaker hind limbs, possibly up to erect, that however partially contrasts with measured pace angulations that define wide gauge trackways, and a prevalent sprawling posture for the fore limbs. ④

Pentasauropus producers, based on the type specimens, were characterized by a very low heteropody, as suggested by the almost identical morphology and comparable dimensions of fore and hind prints, consistently with what was previously stated by other authors (e.g. Lockley & Meyer, 2000; D'Orazi Porchetti & Nicosia, 2007).

Digit traces are considered compatible with broad ungual phalanges characterized by rounded tips. Their morphological variability most likely depends from substrate conditions at the time of impression and, as soon discussed, from the dynamics of locomotion of the producers.

Very low heteropody, number of digits, morphology of unguals and ~~with~~ to a lesser extent limb~~s~~ posture enables to corroborate previous interpretations and suggest a dicynodont as the most probable trackmaker of *Pentasauropus*. Among dicynodonts, a quite confident match can be found with Kannemeyeriiformes [see, for example, the descriptions and reconstructions of the autopods of *Dinodontosaurus* by Morato (2006:fig. 30), *Tetragonias njalilus* by Cruickshank (1967:fig. 17) and by Fröbisch (2006:fig. 9)].

The limb~~s~~ posture as supposed from tracks fits ~~enough~~ well with that discussed for Triassic dicynodonts by Fröbisch (2006). The observed contrast between the pace angulation measured in hind prints and osteological data could be likely explained considering a lateral undulation of the vertebral column causing swing of the hips (Fröbisch, 2006: p. 1305). On the contrary, based on the body fossils, the autopod posture that can be inferred from the ichnological material quite differs from that inferable from Cruickshank's description (1967). In those *Pentasauropus* tracks with the impression of the sole or palm present, a negligible distance between the distal margin of sole/palm pad trace and the proximal margin of central digit traces, further reducing toward digits I and V, was observed. This feature most likely indicates that not all the foot bones contacted the ground during locomotion constraining, at the same time, the orientation of metapodial and basipodial elements, and most likely also that of the more proximal phalanges, in the articulated autopod. Thus, the reconstruction here proposed contemplates a more inclined position of pedal and manual elements in the autopods of *Pentasauropus* producers, moving significantly away from the classic plantigrade posture proposed for therapsids. The sub-circular to elliptical pad trace behind digit traces is consequently considered compatible with an extended fleshy pad below basipodials and likely metapodials of the producer autopods. This fleshy pad actively contacted the ground likely during the touch-down and weight-bearing phase, while the final stroke was performed by acropodials and in particular by the central ones from a functional standpoint.

DISCUSSION

Tracks from Los Menucos Group compared to the ichnogenus *Pentasauropus* allowed us to verify previous ichnological interpretation based on the reference material from Lesotho and enabled us to corroborate identification of a putative trackmaker, shedding light on its dynamics of locomotion and autopodial posture.

Some ichnological features indicate the producer of *Pentasauropus* to be sought among anomodont dicynodonts of the clade Kannemeyeriiformes (Fröbisch, 2009). The Anomodontia is a clade of extinct, cosmopolitan therapsid synapsids representing the major primary consumers (Watson & Romer, 1956; Mancuso et al., 2014) in terrestrial Permian and Triassic ecosystems (Fröbisch, 2009), which were able to profit by different resources (i.e. coriaceous plants) with respect to other earlier herbivores through a derived jaw joint and horny 'beaks' (Angielczyk, 2004). Within this clade, the Dicynodontia constituted a very diversified group of Permian and Triassic tetrapods of different body size and ecology, among which large, ground-welling animals were represented (Fröbisch, 2009). By the Early Triassic, after a dramatic decline in diversity at the end of the Permian, Dicynodontia experienced a second radiation represented by members of the clade Kannemeyeriiformes, among the largest herbivores in many Triassic ecosystems (Bonaparte, 1971, 1981; Fröbisch, 2006 and references therein; Domnanovich & Marsicano, 2012; Mancuso et al., 2014).

The occurrence of the Dicynodontia in Argentina, among other therapsid clades, encompasses the whole Triassic Period and ~~resulted~~ was characterized by a distinct faunal provinciality during the Middle and Late Triassic, most likely to be related to biogeographic separation controlled by the fragmented configuration of Pangaea (Fröbisch, 2009).

Two distinct faunas from the Puesto Viejo Formation, from the Mendoza province, characterized by kannemeyeriiformes in the lower portion of the lithostratigraphic unit and *Cynognathus* in the upper one, were recognized by Bonaparte (1981; see also Abdala et al., 2013), which correlated with the South African *Lystrosaurus* AZ (the lower fauna) and with *Cynognathus* AZ (the upper fauna) age, respectively.

Based on radiometric data (Valencio et al., 1975), the minimum ages of the fossiliferous beds of the Puesto Viejo Formation were fixed at 232±4 and 238 Ma (latest Ladinian-middle Carnian according to the International Chronostratigraphic Chart - v2017/2). Recently, a early Carnian age (Ottone et al., 2014) has been confirmed for the Puesto Viejo Group (Stipanicic et al., 2007) and correlation between this lithostratigraphic unit and the Chañares Formation has been proposed (Marsicano et al., 2016). (5)

The dicynodont *Vinceria andina* was discovered from the Río Mendoza Formation by Bonaparte (1969). Zavattieri & Arcucci (2007) described kannemeyeriid dicynodonts and indeterminate eucynodonts form the same unit. The therapsid-bearing unit could be referred to an Induan-Anisian age on the basis of macroplants, or to a Ladinian-early Carnian age on the basis of pollen. A late Anisian age has been recently suggested by Fröbisch (2009, based on Fernando Abdala, pers. comm., 2006), while Zavattieri & Arcucci (2007) proposed an age not older than the late Middle Triassic. (6) Two dicynodont genera, *Dinodontosaurus* and *Jachaleria* (see Fröbisch, 2009 for taxonomical assessment) were reported from the Ischichuca Formation, generally regarded as Ladinian in age (Rogers et al., 2001). The dicynodont *Ischigualastia jenseni* was reported from the Carnian Ischigualasto Formation by Cox (1962), and represents a member of an endemic fauna (Fröbisch, 2009). Finally, the youngest Argentine fauna is that represented by the dicynodonts from the Los Colorados Formation, which lie ~~lying~~ above the Ischigualasto Formation and has ve been referred to an early Norian age (Fröbisch, 2009).

Within this panorama and accepting the proposed palaeozoological attribution, *Pentasauropus* tracks represent a valuable datum further confirming the occurrence of dicynodonts in the Triassic of Argentina and greatly increasing the knowledge of the therapsid faunas from south-western Gondwana. Especially, what concern their locomotion and functionality of fore and hind feet, that commonly are faintly investigated due to the relative paucity of findings in the body fossil record.

The inferred posture of the *Pentasauropus* trackmaker finds a match with the osteological data provided by the therapsid record (e.g. King, 1981a; Fröbisch, 2006) and allows a corroborating interpretation derived from body-fossils observation. Contrarily to what was stated in the past about therapsid posture (Charig, 1980; Bonaparte, 1982), therapsid-grade limb osteology was characterized by several important modifications from a functional standpoint, mainly indicating a more parasagittal stance of the limbs (Romer, 1956; Boonstra, 1967; Jenkins, 1971), especially if compared with the prevalent limb posture of non-therapsid synapsids ('pelycosaurs'), which had massive limb girdles, with broad, shallow, laterally facing glenoid and acetabulum indicative of a prevailing sprawling posture. Some of these modifications are: i) the scapula and the glenoid for what concerns the fore limbs, allowing the elbow to inwardly rotate and bring the humerus closer to the sagittal plane (Walter, 1986); and, ii) the iliac blade and femoral head for what concerns the hind limbs, the first expanding anteriorly and allowing the insertion of a larger iliofemoralis muscle into the great trochanter of the femur, and thus enabling femoral retraction, and the second one bending medially and attaining a more parasagittal position of the propodial (Romer, 1922; Walter, 1986).

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The observation of osteological material in non-mammalian therapsids has also benefited from functional analyses of the locomotor apparatus (e.g. Pearson, 1924; Kemp, 1982; Walter, 1986). For example, Kemp (1978) proposed a dual-gait condition, intermediate between the plesiomorphic gait of amniotes (Sumida & Modesto, 2001) and the mammalian erect gait, for the therocephalian *Regisaurus jacobi*. This hypothesis contemplates that therapsids were capable of switching from a sprawling posture to an advanced upright one as a function of speed, due to a moveable articulation between the astragalus and the calcaneum (i.e. cruro-tarsal). This condition has proved to be not possible for derived dicynodonts, such as *Kingoria nowacki*, a Permian emydopid with a fully adducted posture of the propodials (King, 1985), and for kannemeyeriiforme~~s~~ dicynodonts, all characterized by an ankle joint inhibiting extensive rotational movements needed for dual-gait locomotion (Fröbisch, 2006). In dicynodont anomodonts, the forelimb step cycle was performed in abducted (i.e. sprawling) posture, whereas the hind limb step cycle passed from a primitive abducted posture in earlier dicynodonts, such as *Robertia broomiana* (see King, 1981b) to an adducted (i.e. erect) posture in more derived taxa (Walter, 1986), such as *Dicynodon trigonocephalus* and *Tetragonias njalilus* (e.g. King, 1981a; Fröbisch, 2006). Such different configurations of fore and hind limb postures were explained in terms of different functions, for example for supporting the heavy anterior half of the body (King, 1981a) and performing a powerful forward thrust (Kemp, 1980; King, 1981a).

If the interpretation of limb~~s~~ posture in the producer of the *Pentasauropus* tracks from Los Menucos finds a general agreement with what has been described from body-fossils, that regarding autopods posture does not completely, especially if some implications are taken into account. (8) As stated before, the alleged autopodial structure inferred from these *Pentasauropus* tracks is dictated by the relative distance between the base of digital (ungual) traces and the distal edge of the sub-circular pad trace, which has been referred to a fleshy pad behind the basipodial. The observed track morphology seems to imply that, except for acropodial and the fleshy pad, no other bony element of the producer's autopods were imprinted on the substrate, consequently indicating that they were likely raised in position. Such a configuration is considered valid for the foot bones in a static-state and would fall at least within a subunguligrade posture, implying that the phalanges were the only bony pedal elements contacting the ground in a static stance. However, if the three-dimensional footprint morphology is considered (i.e. ungual traces and pad trace behind them) concurrently with spatial data regarding pad trace/digit trace distance, it is evident that the unguals were not the only pedal elements performing the cycle of locomotion. Thus, the foot cannot be regarded as subunguligrade ~~by~~ from a dynamic point of view. During locomotion, the body weight of *Pentasauropus* producers was not carried only by phalanges but most likely, the entire foot supported the load (Fig. 11). Thus, ~~by~~ from a functional standpoint, the autopod posture of the *Pentasauropus* trackmaker can be regarded as plantiportal (sensu Michilsens et al., 2009). Such a posture could have been accompanied by an arched configuration of the articulated metapodials and at least of the proximal phalanges. ¶ Metacarpals forming an arched configuration in end view when articulated were described in a specimen of *Tetragonias njalilus* (Cruickshank, 1967), and this kind of configuration could had been accompanied by little movement capabilities (Rubidge & Hopson, 1996) of the metapodials and could have dictated the observed relative position of the ungual traces. A manual/pedal structure like the one here hypothesized could had maintain a large surface contacting the ground by means of cartilaginous elements and fleshy cushions on which the basipodials rested, ensuring a supportive role of the whole autopods during the cycle of locomotion and particularly during the maximum load. Digit traces were formed by acropodials deeply penetrating into the substrate during the final weight-bearing phase, kick-off and thrust. ⑨

This could explain the different depth of the impression that is observed in completely preserved tracks. Among digits the series II-IV, and with a lesser extent digit I, played a major role in performing the end of the cycle of locomotion. Trailing traces affecting the material under study could be formed for external limb rotation during foot recovery, starting from a straight or slightly inwardly turned resting position of the autopods. ⑩

¶ Statically subunguligrade, functionally plantiportal posture ~~was~~ has been described in several mammals regardless of body-weight (see Michilsens et al., 2009) but also can represent~~s~~ a functional strategy, co-occurrent with a graviportal structure of the limbs, in fat-footed, giant animals like some members of the Family Elephantidae comprising the extant elephants. In these animals, apart from connective tissues, a significant functional role is ensured by sesamoid bones expanded into 'digit-like' structures (Hutchinson et al., 2011). These structures, which can have cartilaginous precursors, absorb part of the body load moving away the stress from the toes during locomotion (Hutchinson et al., 2011). Radial sesamoid bones have evolved convergently in numerous tetrapod clades and represent an evident example of evolutionary exaptations, i.e. 'features that now enhance fitness but were not built by natural selection for their current role' (Gould & Vrba, 1982). Cruickshank (1967) has tentatively identified two sesamoid ossifications in the fore autopod of *Tetragonias njalilus*, one fused to the ventral surface of the radiale, and other associated with a terminal phalanx but were never related to a function involving load-support during locomotion. By contrast, Sidor (2001) stated that sesamoid ossifications occur in crown-group mammals (i.e. represented by the most recent common ancestor of all living mammals and its descendants, living or not) and are unknown in earlier synapsids. ⑪

¶ Subunguligrade-plantiportal foot implies a complex set of associated characters in the autopodial anatomy of the *Pentasauropus* producers and represents a novelty among dicynodonts. Taking into account the large but not gigantic dimensions of the putative trackmakers [(e.g. Morato (2006) estimates a body mass between 23- 32 kg for juveniles of *Dinodontosaurus* and exceeding 300 kg for adults, while Mancuso et al. (2014) indicate a body mass of 362 kg for *Dinodontosaurus platyceps* and 170 kg for *Dinodontosaurus brevirostris*)], most likely the subunguligrade-plantiportal autopod posture was promoted in these dicynodonts regardless of the body-dimension, not necessarily implying an increase in body size but being a pre-requisite for lineages experiencing such an evolutionary path.

As final remarks, a brief account o~~n~~f the biochronologic significance of *Pentasauropus* is deemed necessary. As before stated, some apparent inconsistencies affect the stratigraphical positioning of the Los Menucos Group if the new radiometric data provided by Luppo et al. (6) (2017) are considered jointly to the occurrence of *Pentasauropus* tracks from sedimentary and volcanoclastic levels of the Vera Formation. The Vera Formation was considered for a long time as Upper Triassic in age based on some radiometric data obtained from the overlying Sierra Colorada Formation (Rapela et al., 1996). On the basis of the new isotopic ages, Luppo et al. (2017) concluded that the levels bearing the '*Dicroidium*'-type flora (Artabe, 1985a, b) are intercalated between deposits dated 252 ± 2 Ma (Changhsingian, Late Permian) and 248 ± 2 Ma (Olenekian, Early Triassic). These authors also suggested that the stratigraphic position of the deposits exposed in the Tchering quarry, near Los Menucos town, where part of the Los Menucos ichnofauna (mainly *Dicynodontipus* footprints, sensu Melchor & de Valais, 2006) was found, is not yet completely clear. Nevertheless, this quarry is spatially close to the geochronological data provided by Luppo et al. (2017). On the other hand, the Estancia Yancaqueo from which the *Pentasauropus* footprints come, is located west of Los Menucos town and lacks ~~of~~ detailed geochronological and geological studies.

If the global temporal distribution of *Pentasauropus* or *Pentasauropus*-like footprints is analyzed, ~~results that~~ all the geological units where these track were identified were considered as Middle Triassic or Late Triassic in age. In Lesotho, Southern Africa, *Pentasauropus* is traditionally reported from the lower Elliot Formation (Stormberg Group), which lies above the Carnian Molteno Formation. The lower Elliot Formation was considered Upper Triassic by Ellenberger (1970), Norian-Rhaetian by Olsen & Galton (1984) and Norian by Knoll (2004), (12) based on fossil remains, both bones and traces ones. Recently, the Elliot Formation (Lower and Upper) was discussed by means of magnetostratigraphy, and fixed as Upper Triassic - Lower Jurassic by Sciscio et al. (2017). The same authors also confirmed a Norian-Rhaetian age for the lower Elliot Formation, thus in agreement with previously relative data proposed on palaeontological bases, and correlated the unit with the Los Colorado Formation in the Ischigualasto-Villa Union Basin of Argentina (Sciscio et al., 2017). Thus, for the time being *Pentasauropus* turn s out to be a Late Triassic marker. This constrain t allows us to confirm ~~an Upper~~ a Late Triassic and most likely a Norian-Rhaetian age for the *Pentasauropus*-bearing sedimentary and volcaniclastic levels of the Vera Formation and challenge for a probable younger age for the *Pentasauropus*-bearing strata of Cerro de Las Cabras Formation and Portezuelo Formation. From this lithostratigraphic unit, tracks were mentioned as morphologically close to *Pentasauropus* (Marsicano & Barredo, 2004; Melchor & de Valais, 2006; de Valais, 2008).

As already stated, radiometric data available for the Los Menucos Group are in contrast with palaeofloristic and palaeoichnological ones. The latter, and in particular the occurrence of *Pentasauropus*, suggest an age earlier than that indicated by radiometric data and, if considered as a whole, would indicate a probable diachroneity and multiple ages of sedimentary deposits currently attributed to the Los Menucos Group. The current contrasting evidences between radiometric data and palaeontological ones also stress the importance of a detailed study of the stratigraphy of Los Menucos Group, which should be focused on the recognition of new track-bearing levels and on the study of stratigraphical relations between volcanic (including collection of geochronological data) and sedimentary deposits.

CONCLUSIONS

Large pentadactyl tracks from the Upper Triassic Vera Formation of the Los Menucos Group (Río Negro province, North Patagonia, Argentina) were studied and discussed in terms of palaeobiological attribution.

The tracks are currently referred to as *Pentasauropus* Ellenberger 1970, a typical Late Triassic ichnotaxon from the lower Elliot Formation (Stormberg Group) of Karoo Basin (Lesotho, Southern Africa).

Material under study allowed to more effectively appreciate ichnotaxon variability, as well as a few but important morphological and extramorphological features, which have proved to be significant for a better definition of the locomotor dynamics of the producer and particularly of its foot anatomy. Track and trackway parameters indicate, as suggested in the past, a dicynodont as the most probable producer, and a relationship with the ~~s~~South-American members of the clade Kannemeyeriiformes is here proposed. At the same time, a great affinity between this Gondwanan therapsid ichnofauna and that from South Africa is evident, as well as functional features of producers autopods are considered significantly similar and may be related to the same autopodial anatomy shared by the clade. A valuable feature is represented by the spatial relationship (i.e. distance) between the pad trace, both in fore and hind prints, and the relative digital bases, which indicate~~s~~ a derived subunguligrade foot in static posture, if compared with the plesiomorphic plantigrade foot posture of other synapsids, in which the wrist and the ankle directly contact the ground. However, the foot likely acted as plantiportal during locomotion and a large cushion of connective tissue behind the basipodials and partially metapodials can be proposed for the heavy-footed producers of *Pentasauropus*, allowing to decrease the stress transferred to the bones and spread it on a larger area during the touch-down and weight-bearing phase of the locomotion cycle.

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In modern animals, this kind of specialized foot can be equipped with co-opted sesamoid ossifications that have the role of stiffening the expanded foot pad. Sesamoid ossifications, although tentatively recognized in some dicynodonts, are not definitely ascertained in the non-mammalian therapsid grade body-fossil record. These structures however, as well as cartilaginous or tendinous precursors, cannot be proved but not even excluded a priori from the trackmaker foot anatomy and could be in future may be verified or discarded by taking advantage of new osteological and ichnological findings.

Finally, considering the widely accepted Late Triassic age of *Pentasauropus*, recently refined at the Norian-Rhaetian in the Karoo Basin, a Norian-Rhaetian age for the *Pentasauropus*-bearing sedimentary levels of the Los Menucos Group is most likely for the time being, in agreement with the previous datations on palaeontological bases but in contrast with radiometric data obtained from volcanics of the Los Menucos Group, which ultimately stress the importance of a detailed bio- and chronostratigraphic reconstruction of this lithostratigraphic unit. At the same time, a quite younger age for Cerro de Las Cabras Formation and Portezuelo Formation levels from which *Pentasauropus* has been described, can be tentatively proposed.

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