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

Paolo Citton [Corresp., 1, 2], **Ignacio Díaz-Martínez** [1, 2], **Silvina de Valais** [1, 2], **Carlos Cónsole-Gonella** [1, 3]

[1] CONICET

[2] Instituto de Investigación en Paleobiología y Geología (IIPG), General Roca, Argentina

[3] Instituto Superior de Correlación Geológica (INSUGEO), Tucumán, Argentina

Corresponding Author: Paolo Citton
Email address: pcitton@unrn.edu.ar

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.

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

Paolo Citton[1,2], Ignacio Díaz-Martínez[1,2], Silvina de Valais[1,2], Carlos Cónsole-Gonella[1,3]

[1]CONICET

[2]Instituto de Investigación en Paleobiología y Geología (IIPG), General Roca, Río Negro province, Argentina

[3]Instituto Superior de Correlación Geológica (INSUGEO), Miguel Lillo 205, Tucumán, Argentina

Corresponding Author:

Paolo Citton

Av. Roca 1242, General Roca, Río Negro province, 8332, Argentina

Email address: pcitton@unrn.edu.ar

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 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 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 fieldworks and 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 dominated by small therapsid footprints. The bulk of this ichnofauna was historically attributed to different new ichnotaxa by Casamiquela (1964, 1974), which 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 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 poorly 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 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 trackmaker, shedding lights 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 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 subordinated Triassic sediments

142 exposed around of the Los Menucos town, in the north-western sector of the Nord Patagonian
143 Massif (Río Negro province, Argentina; Fig. 1).

144 This lithostratigraphic unit can lie unconformably, through a non-conformity, on the low
145 grade metamorphic complex of the Colo Niyeu Formation, Lower Cambrian in age (Martínez
146 Dopico et al., 2017). Or, according to Labudía & Bjerg (2005, but see Luppo et al., 2017 for a
147 contrasting stratigraphic assessment), on granitoids of the Permo-Triassic La Esperanza Plutonic
148 Complex. The upper limit of the Los Menucos Group is marked by an erosive unconformity,
149 above which Upper Cretaceous continental and marine deposits or Tertiary basalts crop out
150 (Labudía & Bjerg, 2001). Within the Los Menucos Group two lithostratigraphic units were
151 defined, namely the Vera Formation and the Sierra Colorada Formation (Labudía & Bjerg,
152 2001). This subdivision, though on the basis of different nomenclatural ranks, followed that of
153 Miranda (1969) who recognized two informal members, one volcanic and the other sedimentary
154 and pyroclastic ("Sedimentitas Keuperianas" sensu Stipanicic et al., 1968) within the Los
155 Menucos Formation as defined by Stipanicic (1967).

156 The Vera Formation is mainly composed of volcanic and continental deposits and
157 typically displays rocks indicative of both volcanics and sedimentary processes (Labudía &
158 Bjerg, 2001). The sedimentary succession, ranging from 2 to 150 meters in thickness, is mainly
159 represented by brownish to yellowish conglomerates, made of metamorphic and volcanic clasts
160 up to 15 centimeters in diameter, white to greenish sandstones and reddish brown to red pelites
161 (Labudía & Bjerg, 2001). These sediments were laid down inside small basins bordered by
162 regional and local faults with attitude NE-SW, E-W and NW-SE (Labudía & Bjerg, 2001).
163 Volcanic ashes, tuffs and tuffites, dacitic pyroclastic flows products and volcanic breccias are
164 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 volcanoclastic 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 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 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 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 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 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. 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 interpretative 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, 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 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, Falkingham & Richter, 2016) and the convex hyporeliefs are natural casts (sensu Marty, Falkingham & Richter, 2016).

In general, the tracks studied here are moderate 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 evidences 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 content (wet, moisture 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 impessions. 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. (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 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 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 a lesser extent, digit IV imprints, can be affected by the same extramorphology, even if in such cases the trailing traces it is never as developed as in the medial digit traces.

A brief account on differential depth of 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, 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. Digit V trace, when preserved, results 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 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 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 inwardly rotated with respect to 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 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,

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).

Remarks. These footprints from 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 Karroo Basin in Subeng and other localities, such

394 as Morobong, Seaka, Subeng, Maseru and Maphutseng, of Lesotho (Southern Africa). Five
395 ichnospecies were originally included in the ichnogenus, namely *Pentasauropus erectus*,
396 *Pentasauropus incredibilis*, *Pentasauropus maphutsengi*, *Pentasauropus morobongensis* and
397 *Pentasauropus motlejoi*, which remained unchanged in the subsequent formal listing
398 (Ellenberger, 1970, 1972). Material from the Ellenberger Collection referred to this ichnogenus,
399 presently housed at the University of Montpellier (France), is represented by four cast of those
400 originally mentioned as *Pentasauropus incredibilis* (LES 054 1-3, LES 054 4), one cast of
401 *Pentasauropus morobongensis* (LES 005) and one cast of *Tetrasauropus gigas* (LES 038), plus
402 some missing specimens (see D'Orazi Porchetti & Nicosia, 2007, and reference therein for a
403 complete assessment of inventory numbers).
404 After the original and subsequent publications of Ellenberger (1955, 1970, 1972), the
405 ichnogenus was deemed as valid by Olsen & Galton (1984), Lockley & Meyer (2000) and
406 D'Orazi Porchetti & Nicosia (2007). The latter have been emended the ichnogenus diagnosis to
407 appoint the type ichnospecies and considered synonymous the five ichnospecies as
408 *Pentasauropus incredibilis* (reason for choosing *P. incredibilis* as the type ichnospecies can be
409 found in D'Orazi Porchetti & Nicosia, 2007). The differences in track patterns were considered
410 as originated by dimensional constraints and/or behavioural factors and, at the same time,
411 considering that the main footprint characters (e.g. number and arrangement of digits,
412 heteropody) did not justify ichnospecies separation (D'Orazi Porchetti & Nicosia, 2007).
413 Moreover, agreeing with Lockley & Meyer (2000), the same authors located the tracks originally
414 referred to as *Tetrasauropus gigas* into *Pentasauropus*.
415 Following the emended ichnogeneric diagnosis, the arcuate pattern of manus and pes
416 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 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 footprint ~~will been undergone and described 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 Ornitischian) 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 fitting between the

439 skeletal autopodia of Triassic dicynodonts and the manus and pes digit structures of
440 *Pentasauropus*, apart from the strong homopody and the limbs posture (see also Walter, 1986).
441 The studied material from Los Menucos locality, taking into account the handful of
442 features that can be recognized from tracks, allowed corroborating some previous interpretation
443 about trackmaker identity. At the same time, the attempt to identify a putative trackmaker opens
444 the way for new inferences about autopods posture.
445 Limbs posture kept by *Pentasauropus* trackmakers during the cycle of locomotion can be
446 tentatively inferred from trackway patterns, parameters and ratio (Peabody, 1948, 1959; Kubo &
447 Benton, 2009; Kubo & Ozaki, 2009) even if this interpretation is often far from being simple and
448 linear (Crompton & Jenkins, 1973). The ratio trackway width:stride length and stride
449 length:gleno acetabular distance, that were calculated from available trackways, indicate a semi-
450 erect posture for the trackmaker hind limbs, possibly up to erect, that however partially contrasts
451 with measured pace angulations that define wide gauge trackways, and a prevalent sprawling
452 posture for the fore limbs.
453 *Pentasauropus* producers, based on the type specimens, were characterized by a very low
454 heteropody, as suggested by the almost identical morphology and comparable dimensions of fore
455 and hind prints, consistently with what previously stated by other authors (e.g. Lockley & Meyer,
456 2000; D'Orazi Porchetti & Nicosia, 2007).
457 Digit traces are considered compatible with broad ungual phalanges characterized by
458 rounded tips. Their morphological variability most likely depends from substrate conditions at
459 time of impression and, as soon discussed, from the dynamic of locomotion of the producers.
460 Very low heteropody, number of digits, morphology of unguals and with a lesser extent
461 limbs posture enable to corroborate previous interpretations and suggest a dicynodont as most

462 probable trackmaker of *Pentasauropus*. Among dicynodonts, a quite confident match can be
463 found with Kannemeyeriiformes [see, for example, the descriptions and reconstructions of the
464 autopods of *Dinodontosaurus* by Morato (2006:fig. 30), *Tetragonias njalilus* by Cruickshank
465 (1967:fig. 17) and by Fröbisch (2006:fig. 9)].

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

485

486 **DISCUSSION**

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

491 Some ichnological features indicate the producer of *Pentasauropus* to be sought among
492 anomodont dicynodonts of the clade Kannemeyeriiformes (Fröbisch, 2009). The Anomodontia is
493 a clade of extinct, cosmopolitan therapsid synapsids representing the major primary consumers
494 (Watson & Romer, 1956; Mancuso et al., 2014) in terrestrial Permian and Triassic ecosystems
495 (Fröbisch, 2009), which were able to profit by different resources (i.e. coriaceous plants) with
496 respect to other earlier herbivores through derived jaw joint and horny 'beaks' (Angielczyk,
497 2004). Within this clade, the Dicynodontia constituted a very diversified group of Permian and
498 Triassic tetrapods of different body size and ecology, among which large, ground-welling
499 animals were represented (Fröbisch, 2009). By the Early Triassic, after a dramatic decline in
500 diversity at the end of the Permian, Dicynodontia experienced a second radiation represented by
501 members of the clade Kannemeyeriiformes, among the largest herbivores in many Triassic
502 ecosystems (Bonaparte, 1971, 1981; Fröbisch, 2006 and references therein; Domnanovich &
503 Marsicano, 2012; Mancuso et al., 2014).

504 The occurrence of the Dicynodontia in Argentina, among other therapsid clades,
505 encompasses the whole Triassic Period and ~~resulted characterized by~~ a distinct faunal
506 provinciality during the Middle and Late Triassic, most likely to be related to biogeographic
507 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).

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. 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 lying above the Ischigualasto Formation and has 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 *Pentasauropus* trackmaker finds a match with the osteological data provided by the therapsid record (e.g. King, 1981a; Fröbisch, 2006) and allows 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).

553 The observation of osteological material in non-mammalian therapsids has also benefited
554 from functional analyses of the locomotor apparatus (e.g. Pearson, 1924; Kemp, 1982; Walter,
555 1986). For example, Kemp (1978) proposed a dual-gait condition, intermediate between the
556 plesiomorphic gait of amniotes (Sumida & Modesto, 2001) and the mammalian erect gait, for the
557 therocephalian *Regisaurus jacobi*. This hypothesis contemplates that therapsids were capable of
558 switching from a sprawling posture to an advanced upright one as a function of speed, due to a
559 moveable articulation between the astragalus and the calcaneum (i.e. cruro-tarsal). This condition
560 has proved to be not possible for derived dicynodonts, such as *Kingoria nowacki*, a Permian
561 emydopid with a fully adducted posture of propodials (King, 1985), and for kannemeyeriiformes
562 dicynodonts, all characterized by an ankle joint inhibiting extensive rotational movements
563 needed for dual-gait locomotion (Fröbisch, 2006). In dicynodont anomodonts, the forelimb step
564 cycle was performed in abducted (i.e. sprawling) posture, whereas the hind limb step cycle
565 passed from a primitive abducted posture in earlier dicynodonts, such as *Robertia broomiana*
566 (see King, 1981b) to an adducted (i.e. erect) posture in more derived taxa (Walter, 1986), such as
567 *Dicynodon trigonocephalus* and *Tetragonias njalilus* (e.g. King, 1981a; Fröbisch, 2006). Such
568 different configurations of fore and hind limb postures were explained in terms of different
569 functions, for example for supporting the heavy anterior half of the body (King, 1981a) and
570 performing a powerful forward thrust (Kemp, 1980; King, 1981a).
571 If the interpretation of limbs posture in the producer of the *Pentasauropus* tracks from
572 Los Menucos find a general agreement with what described from body-fossils, that regarding
573 autopods posture does not completely, especially if some implications are taken into account. As
574 stated before, the alleged autopodial structure inferred from these *Pentasauropus* tracks is
575 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 fleshy pad, no other bony element of producer 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 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, 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 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 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 metapodials and could have dictated the observed relative position of 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.

This could explain the different depth of 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.

Statically subunguligrade, functionally plantiportal posture was described in several mammals regardless of body-weight (see Michilsens et al., 2009) but also can represents 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.

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 *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 on 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. (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* footprint 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), 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 out to be a Late Triassic marker. This constrain allows to confirm an Upper 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 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 most probable producer, and a relation with the 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 indicates a derived subunguligrade foot in static posture, if compared with

691 the plesiomorphic plantigrade foot posture of other synapsids, in which the wrist and the ankle
692 directly contact the ground. However, the foot likely acted as plantiportal during locomotion and
693 a large cushion of connective tissue behind the basipodials and partially metapodials can be
694 proposed for the heavy-footed producers of *Pentasauropus*, allowing to decrease the stress
695 transferred to the bones and spread it on a larger area during the touch-down and weight-bearing
696 phase of the locomotion cycle.

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

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

712

713 **ACKNOWLEDGEMENTS**

I. Cerda and C. Muñóz of the Museo Provincial Carlos Ameghino (Cipolletti, Río Negro province, Argentina), D. Ramos and S. Mercado of the Museo Municipal de Los Menucos (Los Menucos, Río Negro province, Argentina) and R. Rial of the Museo Provincial María Inés Kopp (Valcheta, Río Negro province, Argentina) are kindly acknowledged for having made access to Los Menucos material possible and for their assistance during museum operations. Umberto Nicosia is sincerely thanked for having reviewed an advanced draft of the manuscript.

REFERENCES

Abdala F, Marsicano CA, Smith RMH, Swart R. 2013. Strengthening Western Gondwanan correlations: A Brazilian Dicynodont (Synapsida, Anomodontia) in the Middle Triassic of Namibia. *Gondwana Research* 23 (3): 1151–1162. DOI: 10.1016/j.gr.2012.07.011

Anderson JM, Anderson HM, Cruickshank ARI. 1998. Late Triassic ecosystems of the Molteno/Lower Elliot biome of Southern Africa. *Palaeontology* 41: 387–421.

Angielczyk KD. 2004. Phylogenetic evidence for and implications of a dual origin of propaliny in anomodont therapsids (Synapsida). *Paleobiology* 30: 268–296. DOI: 10.1666/0094-8373(2004)030<0268:PEFAIO>2.0.CO;2

Artabe AE. 1985a. Estudio sistemático de la tafoflora triásica de Los Menucos, provincia de Río Negro, Argentina. Parte I. *Ameghiniana* 22(1-2): 3–22.

Artabe AE. 1985b. Estudio sistemático de la tafoflora triásica de Los Menucos, provincia de Río Negro, Argentina. Parte II. *Ameghiniana* 22(3-4): 197–212.

Avanzini M, Piñuela L, García-Ramos JC. 2011. Late Jurassic footprints reveal walking kinematics of theropod dinosaurs. *Lethaia* 45(2): 238–252. DOI: 10.1111/j.1502-3931.2011.00276.x

737 Baird D. 1980. A prosauropod dinosaur trackway from the Navajo Sandstone (Lower Jurassic) of
738 Arizona. In: Jacobs LL, ed. *Aspect of Vertebrate History: essay in honor of Harris*
739 *Colbert*. Flagstaff Museum of Northern Arizona Press, 219–230.
740 Barnes FA, Lockley MG. 1994. Trackway evidence for social sauropods from the Morrison
741 Formation, Eastern Utah (USA). *Gaia* 10: 37–41.
742 Barredo S, Chemale F, Ávila JN, Marsicano C, Ottone EG, Ramos VA, 2012. Tectono–sequence
743 stratigraphy and U–Pb zircon ages of the Rincón Blanco depocenter, northern Cuyo rift,
744 Argentina. *Gondwana Research* 21: 624–636. DOI: 10.1016/j.gr.2011.05.016
745 Belvedere M, Farlow JO. 2016. A Numerical Scale for Quantifying the Quality of Preservation
746 of Vertebrate Tracks. In: Falkingham PL, Marty D, Richter A, eds. *Dinosaur tracks: the*
747 *next steps*. Bloomington: Indiana University, Press, 93–98.
748 Bogan S, Taverne L, Agnolin F. 2013. First Triassic and oldest record of a South American
749 amiiform fish: *Caturus* sp. from the Los Menucos Group (lower Upper Triassic), Río
750 Negro province, Argentina. *Geologica Belgica* 16(3): 191–195.
751 Bonaparte JF. 1966. Cronología de algunas formaciones triásicas argentinas. *Revista de la*
752 *Asociación Geológica Argentina* 21: 20–38.
753 Bonaparte JF. 1969. Dos nuevas "faunas" de reptiles triásicos de Argentina. In: *First Gondwana*
754 *Symposium*, Mar del Plata 1967: Abstract book, 283–306.
755 Bonaparte JF. 1971. Annotated list of the South American Triassic tetrapods. *Symposium on*
756 *Gondwana Stratigraphy. Proceedings and Papers, Pretoria* 2: 665–682.
757 Bonaparte JF. 1981. Nota sobre una nueva fauna del Triasico Inferior del Sur de Mendoza,
758 Argentina, correspondiente a la zona de *Lystrosaurus* (Dicynodontia-Proterosuchia). In:
759 *Congreso Latino-Americano de Paleontologia*, Abstract book, 277–288.

760 Bonaparte JF. 1982. Faunal replacement in the Triassic of South America. *Journal of Vertebrate*
761 *Paleontology* 2: 362–371. DOI: 10.1080/02724634.1982.10011938
762 Boonstra LD. 1967. An early stage in the evolution of the mammalian quadrupedal walking gait.
763 *Annals of the South African Museum* 50: 27–42.
764 Breithaupt BH, Matthews NA, Noble TA. 2004. An integrated approach to three dimensional
765 data collection at dinosaur tracksites in the Rocky Mountain West. *Ichnos* 11: 11–26.
766 DOI: 10.1080/10420940490442296
767 Carpenter K. 1992. Behavior of hadrosaurs as interpreted from footprints in the "Mesaverde"
768 Group (Campanian) of Colorado, Utah, and Wyoming. *Contributions to Geology,*
769 *University of Wyoming* 29(2): 81–96.
770 Casamiquela RM. 1964. Estudios icnológicos. Problemas y métodos de la icnología con
771 aplicación al estudio de pisadas mesozoicas (Reptilia, Mammalia) de la Patagonia.
772 Talleres Gráficos Colegio Industrial Pío IX, Buenos Aires.
773 Casamiquela RM. 1974. Nuevo material y reinterpretación de las icnitas mesozoicas
774 (Neotriásicas) de Los Menucos, Provincia de Rio Negro (Patagonia). In: *1° Congreso*
775 *Argentino de Paleontologia y Biostratigrafia*, Tucumán, Argentina 1974: Abstract book,
776 555–580.
777 Casamiquela RM. 1987. Novedades en icnología de vertebrados en la Argentina. In: *10º*
778 *Congreso Brasileiro de Paleontologia*, Rio de Janeiro, Brazil: Abstract book 1, 445–456.
779 Charig AJ. 1980. Differentiation of lineages among Mesozoic tetrapods. *Mémoires de la Société*
780 *Géologique de France N.S.* 59: 207–210.
781 Cipriani A, Citton P, Romano M, Fabbi S. 2016. Testing two open-source photogrammetry
782 software as a tool to digitally preserve and objectively communicate significant

783 geological data: the Agolla case study (Umbria-Marche Apennines). *Italian Journal of*
784 *Geosciences*, 135(2): 199–209. DOI: 10.3301/IJG.2015.21
785 Citton P, Carluccio R, Nicolosi I, Nicosia U. 2017. Re-evaluation of *Chelichnus tazelwürmi*, a
786 non mammalian therapsid-grade track from the Upper Permian Arenaria di Val Gardena.
787 *Historical Biology*, DOI: 10.1080/08912963.2017.1370586
788 Citton P, Nicolosi I, Carluccio R, Nicosia U. 2016. Unveiling trampling history through
789 trackway interferences and track preservational features: a case study from the
790 Bletterbach gorge (Redagno, Western Dolomites, Italy). *Palaeontologia Electronica*,
791 19.2.20A: 1–20. palaeo-electronica.org/content/2016/1499-bletterbach-gorge-trackways
792 Cox CB. 1962. Preliminary diagnosis of *Ischigualastia*, a new genus of dicynodont from
793 Argentina. *Breviora*, 156: 8–9.
794 Crompton AW, Jenkins Jr. FA. 1973. Mammals from Reptiles: a review of mammalian origins.
795 *Annual Review of Earth Planetary Science*, 1: 131–155. DOI:
796 10.1146/annurev.ea.01.050173.001023
797 Cruickshank ARI. 1967. A new dicynodont genus from the Manda Formation of Tanzania
798 (Tanganyika). *Journal of Zoology*, 153: 163–208. DOI: 10.1111/j.1469-
799 7998.1967.tb04059.x
800 Cucchi R, Busteros A, Lema H. 2001. Hoja Geológica 4169 - II, Los Menucos, Provincia de Río
801 Negro. IGRM-SEGE-MAR Boletín, 265: 1–105. Buenos Aires.
802 Currie PJ, Sarjeant WAS. 1979. Lower Cretaceous dinosaur footprints from the Peace River
803 Canyon, British Columbia, Canada. *Palaeogeography, Palaeoclimatology,*
804 *Plalaeoecology*, 28: 103–115. DOI: 10.1016/0031-0182(79)90114-7

805 D'Orazi Porchetti S, Nicosia U. 2007. Re-examination of some large Early Mesozoic tetrapod
806 footprints from the African collection of Paul Ellenberger. *Ichnos*, 14(3-4): 219–245.
807 DOI: 10.1080/10420940601049990
808 de Valais S. 2008. Icnología de tetrápodos triásicos y jurásicos de Argentina: aportes al origen de
809 las aves y los mamíferos. D. Phil Thesis, Universidad de Buenos Aires, Facultad de
810 Ciencias Exactas y Naturales.
811 de Valais S, Melchor RN, Bellosi E. 2006. New large vertebrate footprints from the Cerro de Las
812 Cabras Formation (Middle Triassic), Mendoza province. *Ameghiniana* 43 (suppl.): 34R.
813 Díaz-Martínez I, de Valais S. 2014. Estudio de la variabilidad en la conservación de huellas de
814 tetrápodos del Triásico Superior de Los Menucos, Río Negro, Argentina. *Ameghiniana* 52
815 (suppl. 1): 8.
816 Díaz-Martínez I, González SN, de Valais S. 2017. Dinosaur footprints in the Early Jurassic of
817 Patagonia (Marifil Volcanic Complex, Argentina): biochronological and
818 palaeobiogeographical inferences. *Geological Magazine*: 1–9. DOI:
819 10.1017/S0016756817000103
820 Díaz-Martínez I, Suarez-Hernando O, Martínez-García BM, Larrasoaña JC, Murelaga X. 2016.
821 First bird footprints from the lower Miocene Lerín Formation, Ebro Basin, Spain.
822 *Palaeontologia Electronica* 19.1.7A: 1–15. palaeo-electronica.org/content/2016/1417-
823 early-miocene-bird-footprints
824 Domnanovich NS, Marsicano C. 2006. Tetrapod footprints from the Triassic of Patagonia:
825 reappraisal of the evidence. *Ameghiniana* 43(1): 55–70.

826 Domnanovich NS, Marsicano C. 2012. The Triassic dicynodont *Vinceria* (Therapsida,
827 Anomodontia) from Argentina and a discussion on basal Kannemeyeriiformes. *Geobios*
828 45: 173–186. DOI: 10.1016/j.geobios.2011.03.003
829 Domnanovich NS, Tomassini R, Manera de Bianco T, Dalponte M. 2008. Nuevos aportes al
830 conocimiento de la icnofauna de tetrápodos del Triásico Superior de Los Menucos
831 (Complejo Los Menucos), provincia de Río Negro, Argentina. *Ameghiniana*, 45(1): 221–
832 224.
833 Duncan H. 1831. An account of the tracks and footmarks of animals found impressed on
834 sandstone in the quarry of Corncockle Muir, in Dumfriesshire. *Transactions of the Royal*
835 *Society of Edinburgh*, 11: 194–209. DOI: 10.1017/S0080456800021906
836 Ellenberger P. 1955. Note préliminaire sur les pistes et les restes osseux de Vertébrés du
837 Basutoland (Afrique du Sud). *Comptes Rendus Hebdomadaires des Séances de*
838 *l'Académie des Sciences*, Paris, 240: 889–891.
839 Ellenberger P. 1970. Les niveaux paléontologiques de premiére apparition des mammiféres
840 primordiaux en Afrique du Sud et leur ichnologie. Establissement de zones
841 stratigraphique détaillées dans le Stormberg du Lesotho (Afrique du Sud) (Trias superior
842 a Jurassique). *Proceedings and Papers II Gondwana Symposium*, 1970: 343–370.
843 Ellenberger P. 1972. Contribution à la classification des Pistes de Vertébrés du Trias: Les types
844 du Stormberg d'Afrique du Sud (I). *Paleovertebrata, Memoire Extraordinaire*,
845 Montpellier: 152 p.
846 Ellenberger F, Ellenberger P. 1958. Principaux types de pistes de vertébrés dans les couches du
847 Stormberg au Basutoland (Afrique du Sud) (Note préliminaire). *Comptes-Rendus*
848 *sommaire des Séances de la Société géologique de France*: 65–67.

849 Falk AR, Hasiotis ST, Gong E, Lim J-D, Brewer ED. 2017. A new experimental setup for
850 studying avian neoichnology and the effects of grain size and moisture content on tracks:
851 trials using the domestic chicken (*Gallus gallus*). *Palaios* 32 (11): 689–707.
852 Falkingham PL. 2012. Acquisition of high resolution three-dimensional models using free,
853 opensource, photogrammetric software. *Palaeontologia Electronica* 15 (1): 1–15. palaeo-
854 electronica.org/content/93-issue-1-2012-technical-articles/92-3d-photogrammetry
855 Franzese JR, Spalletti LA. 2001. Late Triassic-Early Jurassic continental extension in
856 southwestern Gondwana: tectonic segmentation and pre-break-up rifting. *Journal of*
857 *South American Earth Sciences* 14: 257–270. DOI: 10.1016/S0895-9811(01)00029-3
858 Fröbisch J. 2006. Locomotion in derived dicynodonts (Synapsida, Anomodontia): a functional
859 analysis of the pelvic girdle and hind limb of *Tetragonias njalilus*. *Canadian Journal of*
860 *Earth Sciences* 43: 1297–1308. DOI: 10.1139/e06-031
861 Fröbisch J. 2009. Composition and similarity of global anomodont-bearing tetrapod faunas.
862 *Earth-Science Reviews* 95: 119–157. DOI:10.1016/j.earscirev.2009.04.001
863 Gallego OF. 2010. A new crustacean clam shrimp (Spinicaudata: Eosestheriidae) from the Upper
864 Triassic of Argentina and its importance for ‘conchostracan’ taxonomy. *Alcheringa: An*
865 *Australasian Journal of Palaeontology* 34: 179–195. DOI: 10.1080/03115510903546152
866 Galton PM, Heerden van J. 1998. Anatomy of the prosauropod dinosaur *Blikanasaurus*
867 *cromptoni* (Upper Triassic, South Africa), with notes on the other tetrapods from the
868 Lower Elliot Formation. *Paläontologische Zeitschrift* 72: 163–177. DOI:
869 10.1007/BF02987824

870 Gatesy SM, Middleton KM, Jenkins Jr FA, Shubin NH. 1999. Three-dimensional preservation of
871 foot movements in Triassic theropod dinosaurs. *Nature* 399: 141–144. DOI:
872 10.1038/20167
873 Gould SJ, Vrba ES. 1982. Exaptation - a missing term in the science of form. *Paleobiology* 8(1):
874 4–15. DOI: 10.1017/S0094837300004310
875 Haubold H. 1974. *Die fossilien Saurierfährten*. A. Ziemsen, Wittenberg.
876 Haubold H. 1984. *Saurierfährten*. Die Neue Brehm-Bucherei, A. Ziemsen Verlagl, Wittenberg
877 Lutherstadt.
878 Hitchcock E. 1836. Ornithichnology - description of the foot marks of birds (Ornithichnites) on
879 New Red Sandstone in Massachusetts. *American Journal of Science* 29: 307–340.
880 Huene F. von. 1931. Die fossilen Fährten im Rhät von Ischigualasto in Nordwest-Argentinien.
881 *Palaeobiologica* 4: 99–112.
882 Hutchinson JR, Delmer C, Miller CE, Hildebrandt T, Pitsillides AA, Boyde A. 2011. From flat
883 foot to fat foot: structure, ontogeny, function, and evolution of elephant “sixth toes”.
884 *Science* 334: 1699–1703. DOI: 10.1126/science.1211437
885 Jenkins FA, Jr. 1971. The postcranial skeleton of African cynodonts. *Peabody Museum of*
886 *Natural History, Yale University, Bulletin* 36: 1–216.
887 Kemp TS. 1978. Stance and gait in the hindlimb of a therocephalian mammal-like reptile.
888 *Journal of Zoology* 186: 143–161. DOI: 10.1111/j.1469-7998.1978.tb03362.x
889 Kemp TS. 1980. The primitive cynodont *Procynosuchus*: structure, function and evolution of the
890 post cranial skeleton. *Philosophical Transaction of the Royal Society of London B* 288:
891 217–258. DOI: 10.1098/rstb.1980.0001

892 Kemp TS. 1982. *Mammal-like reptiles and the origin of mammals*. Academic Press, London,
893 UK.
894 King GM. 1981a. The functional anatomy of a Permian dicynodont. *Philosophical Transaction*
895 *of the Royal Society of London B* 291: 243–322. DOI: 10.1098/rstb.1981.0001
896 King GM. 1981b. The post cranial skeleton of *Robertia broomiana*, an early dicynodont
897 (Reptilia, Therapsida) from the South African Karoo. *Annals of South African Museum*
898 84: 203–231.
899 King GM. 1985. The postcranial skeleton of *Kingoria nowacki* (von Huene) (Therapsida:
900 Dicynodontia). *Zoological Journal of the Linnean Society* 84: 263–298. DOI:
901 10.1111/j.1096-3642.1985.tb01801.x
902 Knoll F. 2004. Review of the tetrapod fauna of the "Lower Stormberg Group" of the main Karoo
903 Basin (southern Africa): implication for the age of the Lower Elliot Formation. *Bulletin*
904 *de la Societe géologique de France* 175(1): 73–83. DOI: 10.2113/175.1.73
905 Kokogian DA, Spalletti L, Morel E, Artabe A, Martínez RN, Alcober OA, Milana JP, Zavattieri
906 AM, Papù OH. 1999. Los depósitos continentales triásicos. In: Caminos R, Panza J, eds.
907 *Geología Argentina, Instituto de Geología y Recursos Minerales*. Buenos Aires, Anales,
908 29(15), 377–398.
909 Kubo T, Benton MJ. 2009. Tetrapod postural shift estimated from Permian and Triassic
910 trackways. *Palaeontology* 52: 1029–1037. DOI: 10.1111/j.1475-4983.2009.00897.x
911 Kubo T, Ozaki M. 2009. Does pace angulation correlate with limb posture? *Palaeogeography,*
912 *Palaeoclimatology, Paleoecology* 275: 54–58. DOI: 10.1016/j.palaeo.2009.02.001

913 Labudía CH, Bjerg EA. 2001. El Grupo Los Menucos: redefinición estratigráfica del Triásico
914 Superior del Macizo Nordpatagonico. *Revista de la Asociación Geologica Argentina* 56:
915 404–407.
916 Labudía CH, Bjerg EA. 2005. Geología del Grupo Los Menucos, Comarca Nordpatagónica,
917 Argentina. In: *16° Congreso Geológico Argentino*, La Plata, Argentina: Abstract book,
918 233–238.
919 Labudía CH, Llambías EJ, Rapela CW, Artabe AE. 1995. El Triásico de Los Menucos: procesos
920 volcánicos y sedimentarios. In: *2º Reunión del Triásico de Cono Sur*, Bahía Blanca,
921 Argentina: Abstract book, 17–21.
922 Lema H, Busteros A, Giacosa RE, Cucchi R. 2008. Geología del complejo volcánico Los
923 Menucos en el área tipo, Río Negro. *Revista de la Asociación Geológica Argentina* 63:
924 3–13.
925 Leonardi G. 1987. *Glossary and manual of tetrapod footprint palaeoichnology*. Brasilia:
926 Departamento Nacional da Produção Mineral.
927 Leonardi G. 1994. *Annotated atlas of South America tetrapod footprints (Devonian-Holocene)*.
928 Ministerio de Minas y Energia, Companhia de Pesquisa de Recursos Minerais, Brazil.
929 Leonardi G, de Oliveira FH. 1990. A revision of the Triassic and Jurassic tetrapod footprints of
930 Argentina and a new approach on the age and meaning of the Botucatu Formation
931 footprints (Brazil). *Revista Brasileira de Geociencias* 20: 216–229.
932 Lockley MG. 1991. *Tracking Dinosaurs. A new look at an ancient world.* Cambridge University
933 Press, Cambridge.
934 Lockley MG, McCrea RT, Buckley LG, Lim JD, Matthews NA, Breithaupt BH, Houck KJ,
935 Gierlinski GD, Surmik D, Kim KS, Xing L, Kong DY, Cart K, Martin J, Hadden G.

2016. Theropod courtship: large scale physical evidence of display arenas and avian-like scrape ceremony behaviour by Cretaceous dinosaurs. *Scientific Reports* 6:18952. DOI: 10.1038/srep18952

Lockley MG, Meyer CA. 2000. *Dinosaur Tracks and other fossil footprints of Europe*. Columbia University Press, New York.

Luppo T, López De Luchi MG, Rapalini AE, Martínez Dopico CI, Fanning CM. 2017. Geochronologic evidence of a large magmatic province in northern Patagonia encompassing the Permian-Triassic boundary. *Journal of South American Earth Sciences* (2017): 1–10. DOI: 10.1016/j.jsames.2018.01.003

Mackenzie WS, Donaldson CH, Guilford C. 1982. *Atlas of Igneous Rocks and Their Textures.* John Wiley, New York.

Mallison H, Wings O. 2014. Photogrammetry in Paleontology – a practical guide. *Journal of Paleontological Techniques* 12: 1–31.

Mancuso AC, Gaetano LC, Leardi JM, Abdala F, Arcucci AB. 2014. The Chañares Formation: a window to a Middle Triassic tetrapod community. *Lethaia* 47: 244–265. DOI: 10.1111/let.12055

Manera de Bianco T, Calvo JO. 1999. Hallazgo de huellas de gran tamaño en el Triásico de Los Menucos, provincia de Río Negro, Argentina. *Ameghiniana* 36 (Supplement): 14R.

Marsicano CA, Barredo SP. 2004. A Triassic tetrapod footprint assemblage from southern South America: palaeobiogeographical and evolutionary implications. *Palaeogeography, Palaeoclimatology, Palaeocology* 203: 313–335. DOI: 10.1016/S0031-0182(03)00689-8

957 Marsicano CA, Irmis RB, Mancuso AC, Mundil R, Chemale F. 2016. The precise temporal
958 calibration of dinosaur origins. *Proceedings of the National Academy of Sciences* 113 (3):
959 509–513. DOI: 10.1073/pnas.1512541112.
960 Martínez Dopico CI, López De Luchi MG, Rapalini AE, Hervé F, Fuentes F, Fanning CM,
961 Luppo T. 2017. U-Pb SHRIMPS dating of detrital zircon grains of the Colo Niyeu
962 Formation: extending to northern Patagonia the peri-Gondwana realm during the latest
963 Neoproterozoic to Cambrian. XX Congreso Geológico Argentino, Simposio 15: 66–72,
964 San Miguel de Tucumán.
965 Marty D, Falkingham PL, Richter A. 2016. Dinosaur Track Terminology: A Glossary of Terms.
966 In: Falkingham PL, Marty D, Richter A, eds. *Dinosaur tracks: the next steps*.
967 Bloomington: Indiana University, Press, 399–402.
968 McCrea RT, Tanke DH, Buckley LG, Lockley MG, Farlow JO, Xing L, Matthews NA, Helm
969 CV, Pemberton SG, Breithaupt BH. 2015. Vertebrate ichnopathology: pathologies
970 inferred from dinosaur tracks and trackways from the Mesozoic. *Ichnos* 22: 235–260.
971 DOI:10.1080/10420940.2015.1064408.
972 Melchor RN, Bellosi E, Genise JF. 2003. Invertebrate and vertebrate trace fossils from a Triassic
973 lacustrine delta: the Los Rastros Formation, Ischigualasto Provincial Park, San Juan,
974 Argentina. In: Buatois LA, Mangano MG, eds. *Icnología: hacia una convergencia entre*
975 *geología y biología*. Asociación Paleontológica Argentina, Publicación Especial 9: 19–
976 33.
977 Melchor RN, de Valais S. 2006. A review of Triassic tetrapod track assemblages from Argentina.
978 *Palaeontology* 49(2): 355–379. DOI: 10.1111/j.1475-4983.2006.00538.x

979 Melchor RN, Genise JF, Poiré DGG. 2001. Icnología de los depósitos continentales triásicos. In:
980 Artabe AE, Morel EM, Zamuner AB, eds. *El Sistema Triásico en Argentina*. Fundación
981 Museo de La Plata 'Francisco Pascasio Moreno', La Plata, 101–135.
982 Michilsens F, Aerts P, Van Damme R, D'Aout K. 2009. Scaling of plantar pressures in
983 mammals. *Journal of Zoology* 279: 236–242. DOI: 10.1111/j.1469-7998.2009.00611.x
984 Miranda J. 1969. *Reconocimiento geológico de la zona situada entre meseta de Rentería, Sierra*
985 *Colorada, Los Menucos, Maquinchao y Chasicó, provincia de Río Negro*. Informe
986 Yacimientos Petrolíferos Fiscales, Gerencia de Exploración. Buenos Aires.
987 Morato L. 2006. *Dinodontosaurus* (Synapsida, Dicynodontia): reconstituições morfológicas e
988 aspectos biomecânicos. Master Thesis, Universidade Federal do Rio Grande do Sul do
989 Porto Alegre, Instituto de Geociências, Área de Concentração Paleontologia.
990 Olsen PE, Galton PM. 1984. A review of the reptile and amphibian assemblages from the
991 Stormberg of southern Africa, with special emphasis on the footprints and the age of the
992 Stormberg. *Paleontologica Africana* 25: 87–110. http://hdl.handle.net/10539/16131
993 Ottone EG, Monti M, Marsicano CA, de la Fuente MS, Naipauer M, Armstrong R, Mancuso AC.
994 2014. Age constraints for the Triassic Puesto Viejo Group (San Rafael depocenter,
995 Argentina): SHRIMP U–Pb zircon dating and correlations across southern Gondwana.
996 *Journal of South American Earth Sciences* 56: 186–199. DOI:
997 10.1016/j.jsames.2014.08.008
998 Peabody FE. 1948. Reptile and Amphibian trackways from the Lower Triassic Moenkopi
999 Formation of Arizona and Utah. *Bulletin of the Department of Geological Sciences,*
1000 *Berkeley and Los Angeles* 27: 295–468.

1001 Peabody FE. 1959. Trackways of living and fossil salamanders. *University of California*
1002 *Publications in Zoology* 63: 1–72.
1003 Pearson HS. 1924. A dicynodont reptile reconstructed. *Proceedings of the Zoological Society of*
1004 *London* 94: 827–855. DOI:10.1111/j.1096-3642.1924.tb03317.x
1005 Prezzi C, Vizán H, Rapalini A. 2001. Marco paleogeográfico. In: Artabe AE, Morel EM,
1006 Zamuner AB, eds. *El Sistema Triásico en Argentina*. Fundación Museo de la Plata
1007 'Francisco Pascasio Moreno', La Plata, 255–267.
1008 Rapela CW, Pankhurst RJ, Llambías EJ, Labudia CH, Artabe AE. 1996. Gondwana magmatism
1009 of Patagonia: inner cordilleran calc-alkaline batholiths and bimodal volcanic provinces.
1010 In: *3° International Symposium on Andean Geodynamics, Saint Malo*, Extended Abstract
1011 book, 791–794.
1012 Romano M, Citton P, Nicosia U. 2016. Corroborating trackmaker identification through footprint
1013 functional analysis: the case study of *Ichniotherium* and *Dimetropus*. *Lethaia* 49: 102–
1014 116. DOI: 10.1111/let.12136
1015 Rogers RR, Arcucci A, Abdala F, Sereno PC, Forster CA, May CL. 2001. Paleoenvironment and
1016 taphonomy of the Chañares Formation tetrapod assemblage (Middle Triassic),
1017 northwestern Argentina: spectacular preservation in volcanogenic concretions. *Palaios* 16
1018 (5): 461–481. DOI: 10.1669/0883-1351(2001)016<0461:PATOTC>2.0.CO;2
1019 Romer AS. 1922. The locomotor apparatus of certain primitive and mammal-like reptiles.
1020 *Bulletin of the American Museum of Natural History* 46: 517–606.
1021 http://hdl.handle.net/2246/929
1022 Romer AS. 1956. *Osteology of the Reptiles*. Malabar (FL): Krieger Publishing Company.

1023 Romer AS. 1966. The Chañares (Argentina) Triassic reptile fauna; I. Introduction. *Breviora* 247:
1024 1–14.
1025 Rubidge BS, Hopson JA. 1996. A primitive anomodont therapsid from the base of the Beaufort
1026 Group (Upper Permian) of South Africa. *Zoological Journal of the Linnean Society* 117:
1027 115–139. DOI: 10.1111/j.1096-3642.1996.tb02152.x
1028 Scasso RA, Limarino CO. 1997. Petrología y diagénesis de rocas clásticas. *Asociación Argentina*
1029 *de Sedimentología, Publicación Especial* 1, 259 pp., Buenos Aires.
1030 Sciscio L, de Kock M, Bordy E, Knoll F. 2017. Magnetostratigraphy over the Triassic-Jurassic
1031 boundary in the main Karoo Basin. *Gondwana Research* 51: 177–192. DOI:
1032 10.1016/j.gr.2017.07.009
1033 Seitz SM, Curless B, Diebel J, Scharstein D, Szeliski R. 2006. A comparison and evaluation of
1034 multi-view stereo reconstruction algorithms. *Proceedings of the 2006 IEEE Computer*
1035 *Society Conference on Computer Vision and Pattern Recognition (CVPR"06) 0-7695-*
1036 *2597-0/06.*
1037 Sidor CA. 2001. Simplification as a trend in synapsid cranial evolution. *Evolution* 55(7): 1419–
1038 1442. DOI: 10.1554/0014-3820(2001)055[1419:SAATIS]2.0.CO;2
1039 Spalletti LA. 1999. Cuencas triásicas del Oeste argentino: origen y evolución. *Acta Geológica*
1040 *Hispánica* 32: 29–50.
1041 Stipanicic PN. 1967. Consideraciones sobre las edades de algunas fases magmáticas del
1042 Neopaleozoico y Mesozoico. *Revista de la Asociación Geológica Argentina* 22: 101–133.
1043 Stipanicic PN, González Díaz EF, Zavattieri AM. 2007. Grupo Puesto Viejo nom. transl. por
1044 Formación Puesto Viejo González Díaz, 1964–1967 nuevas interpretaciones
1045 paleontológicas, estratigráficas y cronológicas. *Ameghiniana* 44: 759–761.

1046 Stipanicic PN, Methol EJ. 1972. Macizo de Somún Curá. In: Leanza AF, ed. *Geología Regional*
1047 *Argentina*. Academia Nacional de Ciencias de Córdoba: 581–600. Córdoba.
1048 Stipanicic PN, Methol EJ. 1980. Comarca Norpatagónica. In: *Geología Regional Argentina*.
1049 Academia Nacional de Ciencias de Córdoba: 1071–1097. Córdoba.
1050 Stipanicic PN, Rodrigo F, Baulies OL, Martínez CG. 1968. Las formaciones pre-senonianas en el
1051 denominado Macizo Nordpatagónico y regiones adyacentes. *Revista de la Asociación*
1052 *Geológica Argentina* 23: 67–98.
1053 Sumida SS, Modesto SP. 2001. A phylogenetic perspective on locomotory strategies in early
1054 amniotes. *American Zoologist* 41: 586–597. DOI: 10.1093/icb/41.3.586
1055 Ullman S. 1979. The interpretation of structure from motion. *Proceedings of the Royal Society of*
1056 *London B* 203: 405–426. DOI: 10.1098/rspb.1979.0006
1057 Valencio DA, Mendia JE, Vilas JF. 1975. Palaeomagnetism and K–Ar ages of Triassic igneous
1058 rocks from the Ischigualasto-Ischichuca Basin and Puesto Viejo Formation, Argentina.
1059 *Earth and Planetary Science Letters* 26: 319–330. DOI: 10.1016/0012-821X(75)90007-2
1060 Walter LR. 1986. The limb posture of kannemeyeriid dicynodonts: functional and ecological
1061 consideration. In: Padian K, ed. *The Beginning of the Age of Dinosaurs*. Cambridge
1062 University Press, Cambridge: 89–97.
1063 Watson DMS, Romer AS. 1956. A classification of therapsid reptiles. *Bulletin of the Museum of*
1064 *Comparative Zoology* 114: 35–89.
1065 Zavattieri AM, Arcucci AB. 2007. Edad y posición estratigráfica de los tetrápodos del cerro
1066 Bayo de Potrerillos (Triásico), Mendoza, Argentina. *Ameghiniana* 44(1): 133–142.
1067 http://www.scielo.org.ar/scielo.php script=sci_arttext&pid=S0002-
1068 70142007000100009&lng=es&nrm=iso

1069

1070 **Figure captions**

1071 Figure 1 Location map and geological sketch of Los Menucos area (from Labudía & Bjerg,
1072 2005, redrawn and slightly modified).

1073 Figure 2 Thin sections (MPCA 27029/19.1 and MPCA 27029/19.2) of track-bearing slab MPCA
1074 27029-19. Inequigranular epiclastic texture with anhedral and subhedral phenocrysts at the
1075 base (A) and middle portion (B) of the track-bearing slab MPCA 27029-19. (C, D)
1076 Equigranular less epiclastic texture indicating a minor sedimentary reworking of the trampled
1077 surface.

1078 Figure 3 Tracks mode of preservation. Convex hyporeliefs (A, C) fitting with concave epireliefs
1079 (B, D) preserved on slab MMLM 075-1 (true tracks and natural casts, respectively).

1080 Figure 4 Photos, three-dimensional representations and interpretative drawings of the studied
1081 material. (A) Track-bearing slabs MPCA 27029-1; (B) Solid three-dimensional model of (A);
1082 (C) Colour topographic profile and (D) interpretative drawing of (A). (E) Track-bearing slabs
1083 MPCA 27029-2; (F) Solid three-dimensional model of (E); (G) Colour topographic profile
1084 and (H) interpretative drawing of (E).

1085 Figure 5 Photos, three-dimensional representations and interpretative drawings of the studied
1086 material. (A) Track-bearing slabs MPCA 27029-3; (B) Solid three-dimensional model of (A);
1087 (C) Colour topographic profile and (D) interpretative drawing of (A). (E) Track-bearing slabs
1088 MPCA 27029-4; (F) Solid three-dimensional model of (E); (G) Colour topographic profile
1089 and (H) interpretative drawing of (E).

1090 Figure 6 Photos, three-dimensional representations and interpretative drawings of the studied
1091 material. (A) Track-bearing slabs MPCA 27029-5; (B) Solid three-dimensional model of (A);

1092 (C) Colour topographic profile and (D) interpretative drawing of (A). (E) Track-bearing slabs
1093 MPCA 27029-9; (F) Solid three-dimensional model of (E); (G) Colour topographic profile
1094 and (H) interpretative drawing of (E).
1095 Figure 7 Photos, three-dimensional representations and interpretative drawings of the studied
1096 material. (A) Track-bearing slabs MPCA 27029-16; (B) Solid three-dimensional model of
1097 (A); (C) Colour topographic profile and (D) interpretative drawing of (A). (E) Track-bearing
1098 slabs MPCA 27029-21; (F) Solid three-dimensional model of (E); (G) Colour topographic
1099 profile and (H) interpretative drawing of (E).
1100 Figure 8 Photos, three-dimensional representations and interpretative drawings of the studied
1101 material. (A) Track-bearing slabs MPCA 27029-33; (B) Solid three-dimensional model of
1102 (A); (C) Colour topographic profile and (D) interpretative drawing of (A). (E) Track-bearing
1103 slabs MMLM 075-1; (F) Solid three-dimensional model of (E); (G) Colour topographic
1104 profile and (H) interpretative drawing of (E).
1105 Figure 9 Photos, three-dimensional representations and interpretative drawings of the studied
1106 material. (A) Track-bearing slabs MMLM 1; (B) Solid three-dimensional model of (A); (C)
1107 Colour topographic profile and (D) interpretative drawing of (A). (E) Track-bearing slabs
1108 MMLM 2; (F) Solid three-dimensional model of (E); (G) Colour topographic profile and (H)
1109 interpretative drawing of (E).
1110 Figure 10 Morphological and extramorphological features identified on the studied material. (A)
1111 Pes track MPCA 27029-1/5 and (B) interpretative drawing. (C) Manus track MPCA 27029/2
1112 and (D) interpretative drawing.
1113 Figure 11 Palaeozoological attribution of pentadactyl tracks from Los Menucos (Patagonia,
1114 Argentina). Reconstruction of the proposed autopod posture of the *Pentasauropus* putative

1115 trackmaker (A) in dorsal (B) and lateral (C) view. Basipodials in green, metapodials in blue
1116 and acropodials in light blue. Redrawn and modified from Morato (2006: fig. 54c).

Figure 1

Location map and geological sketch of Los Menucos area (from Labudía & Bjerg, 2005, redrawn and slightly modified).

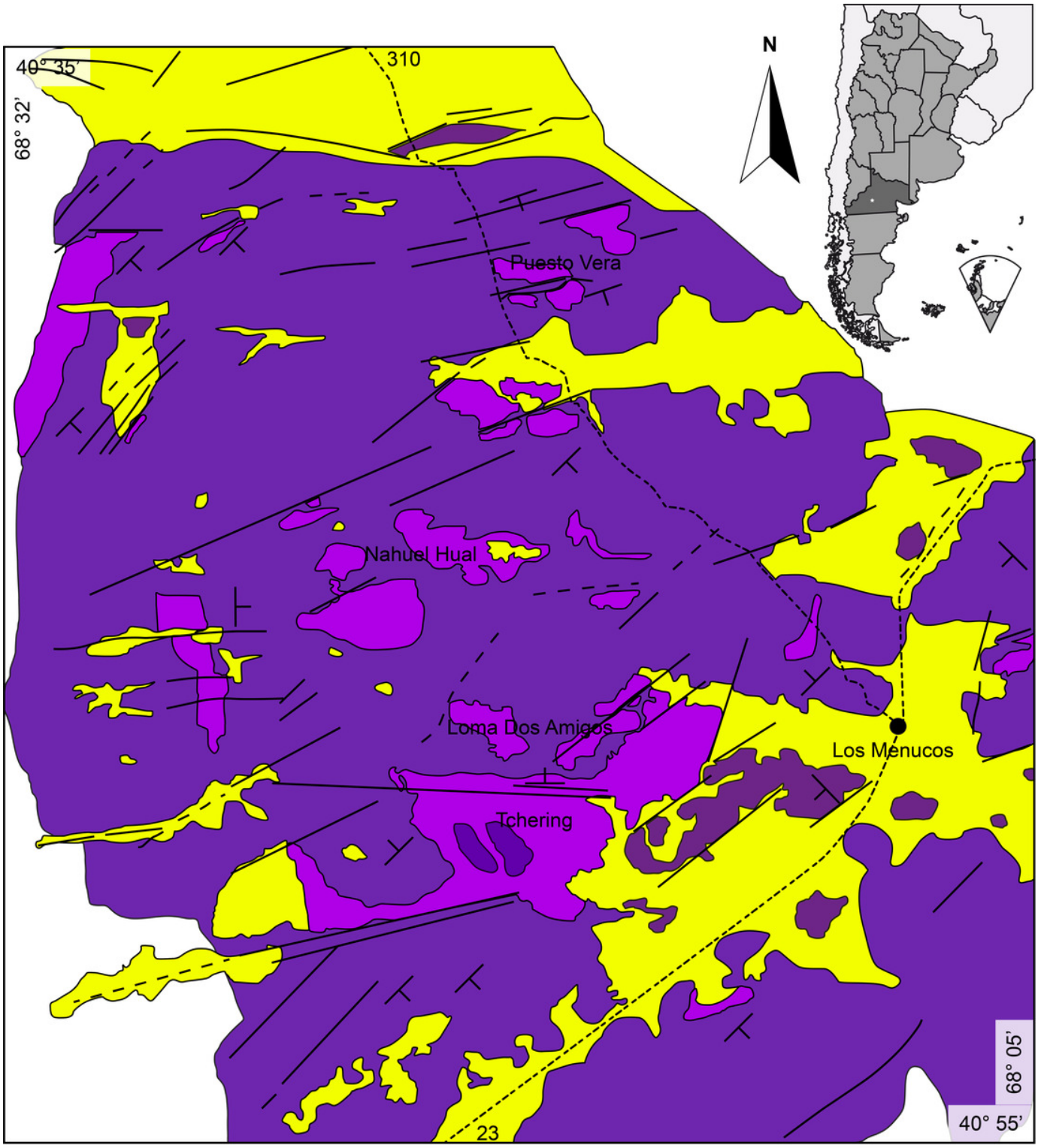
N
40° 35'
68° 32'
310
Puesto Vera
Nahuel Hual
Loma Dos Amigos
Tchering
Los Menucos
68° 05'
40° 55'
23
10 km
Scree and alluvial deposits
Sierra Colorada Fm
Vera Fm
Bed attitude
Fault
Inferred fault
Main road

Figure 2

Thin sections (MPCA 27029/19.1 and MPCA 27029/19.2) of track-bearing slab MPCA 27029-19.

Inequigranular epiclastic texture with anhedral and subhedral phenocrysts at the base (A) and middle portion (B) of the track-bearing slab MPCA 27029-19. (C, D) Equigranular less epiclastic texture indicating a minor sedimentary reworking of the trampled surface.

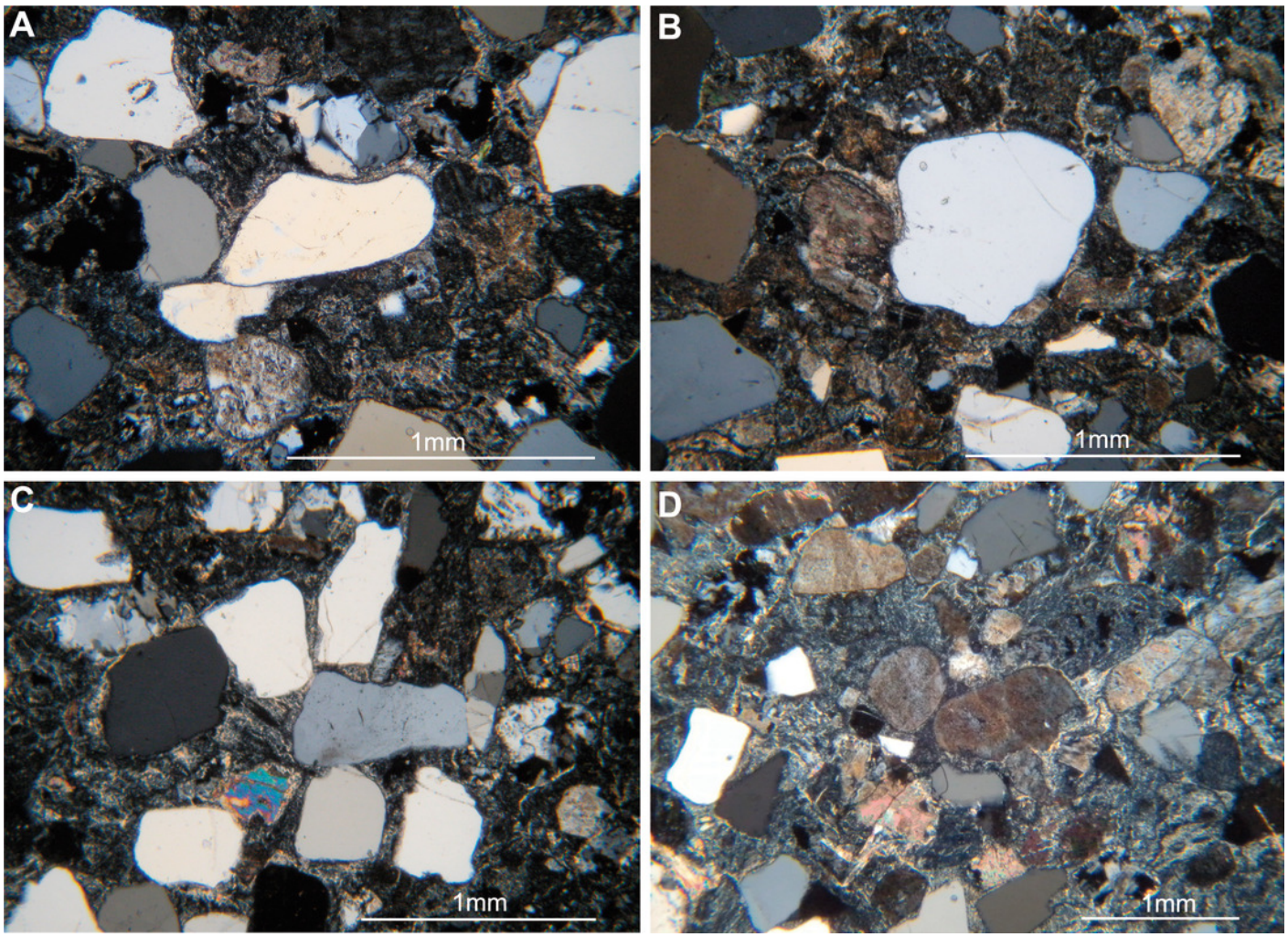

Figure 3

Tracks mode of preservation.

Convex hyporeliefs (A, C) fitting with concave epireliefs (B, D) preserved on slab MMLM 075-1 (true tracks and natural casts, respectively).

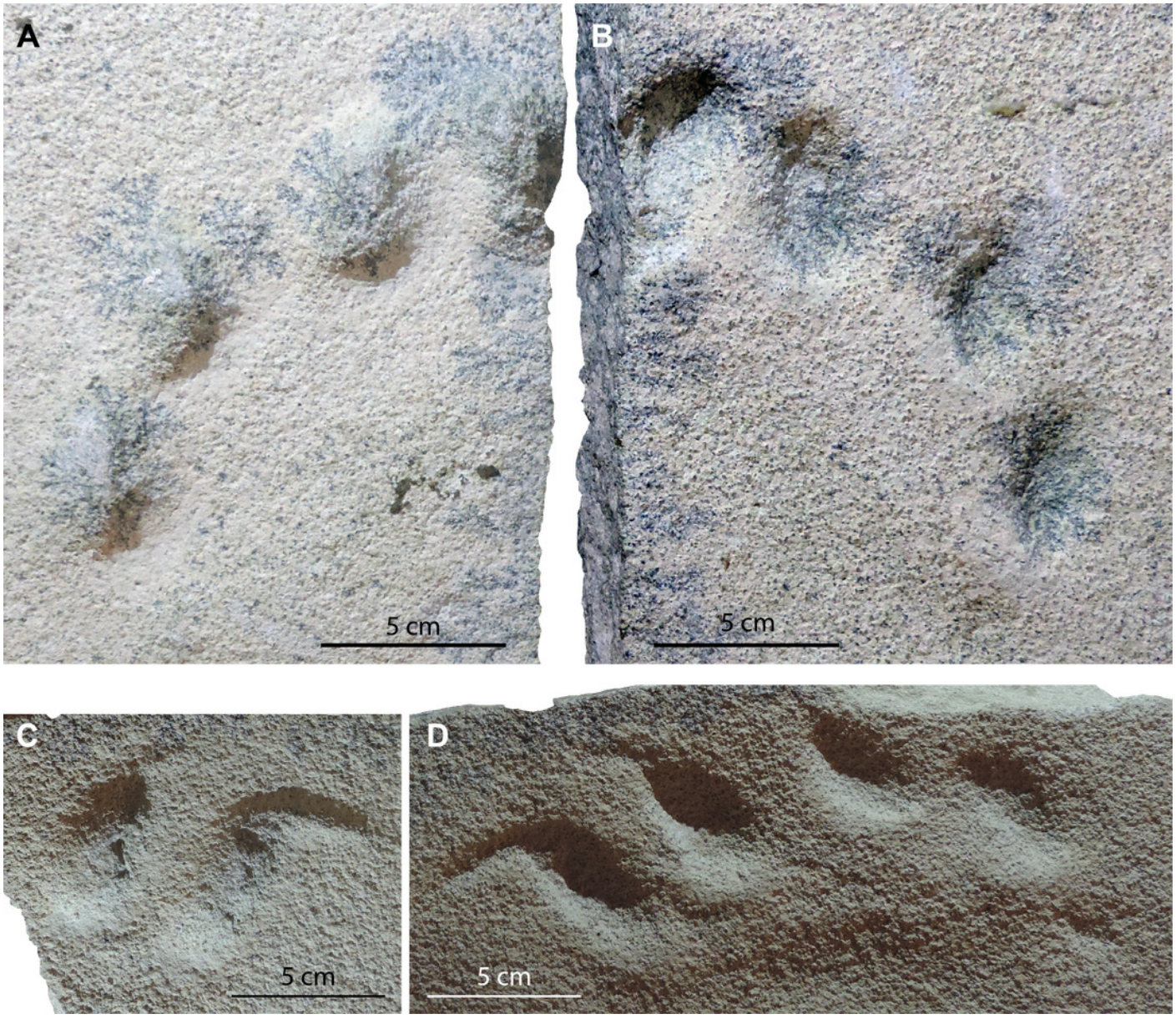

Figure 4

Photos, three-dimensional representations and interpretative drawings of the studied material.

(A) Track-bearing slabs MPCA 27029-1; (B) Solid three-dimensional model of (A); (C) Colour topographic profile and (D) interpretative drawing of (A). (E) Track-bearing slabs MPCA 27029-2; (F) Solid three-dimensional model of (E); (G) Colour topographic profile and (H) interpretative drawing of (E).

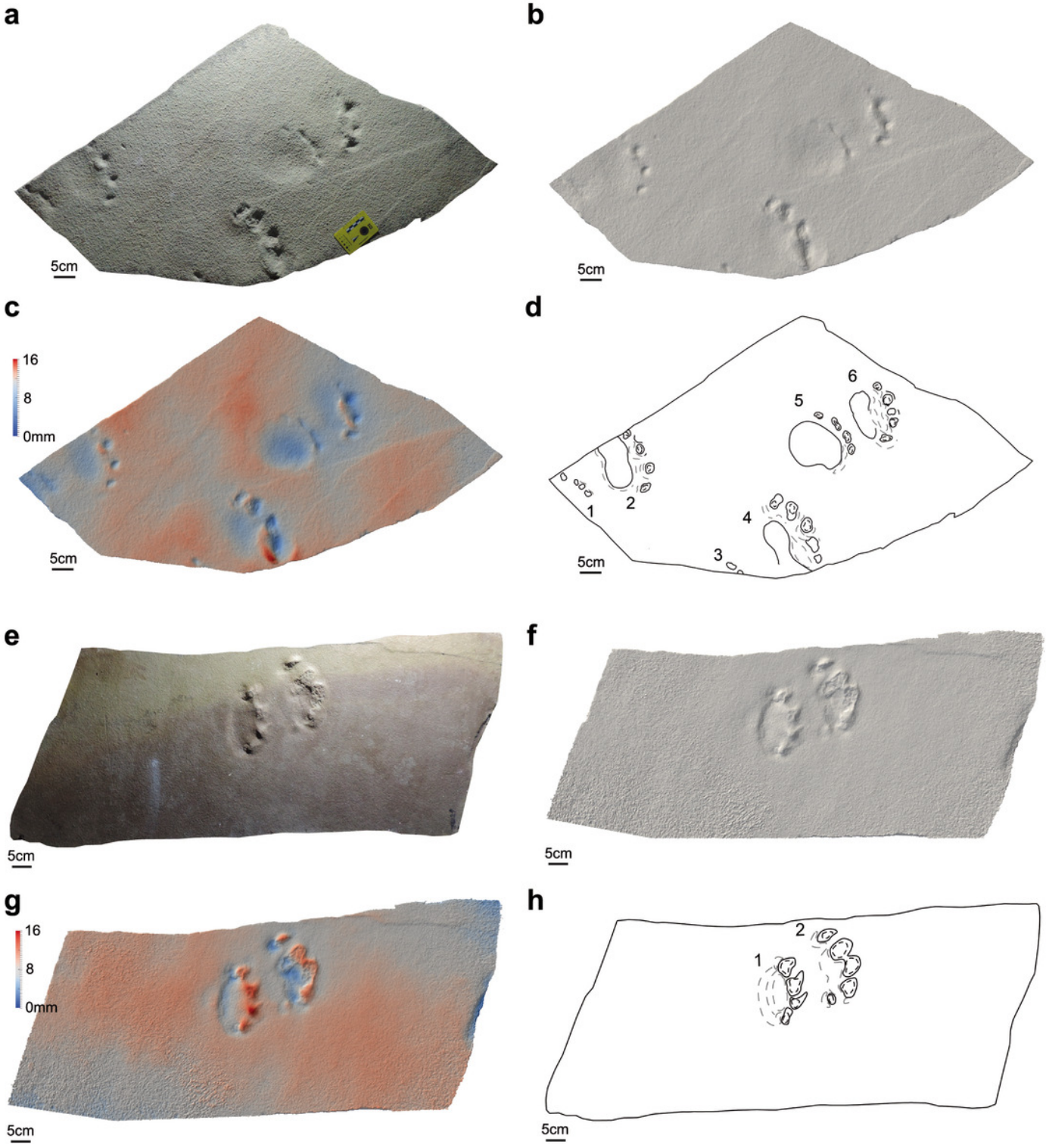
a
5cm
b
5cm
c
16
8
0mm
5cm
d
1
2
3
4
5
6
5cm
e
5cm
f
5cm
g
16
8
0mm
5cm
h
1
2
5cm

Figure 5

Photos, three-dimensional representations and interpretative drawings of the studied material.

(A) Track-bearing slabs MPCA 27029-3; (B) Solid three-dimensional model of (A); (C) Colour topographic profile and (D) interpretative drawing of (A). (E) Track-bearing slabs MPCA 27029-4; (F) Solid three-dimensional model of (E); (G) Colour topographic profile and (H) interpretative drawing of (E).

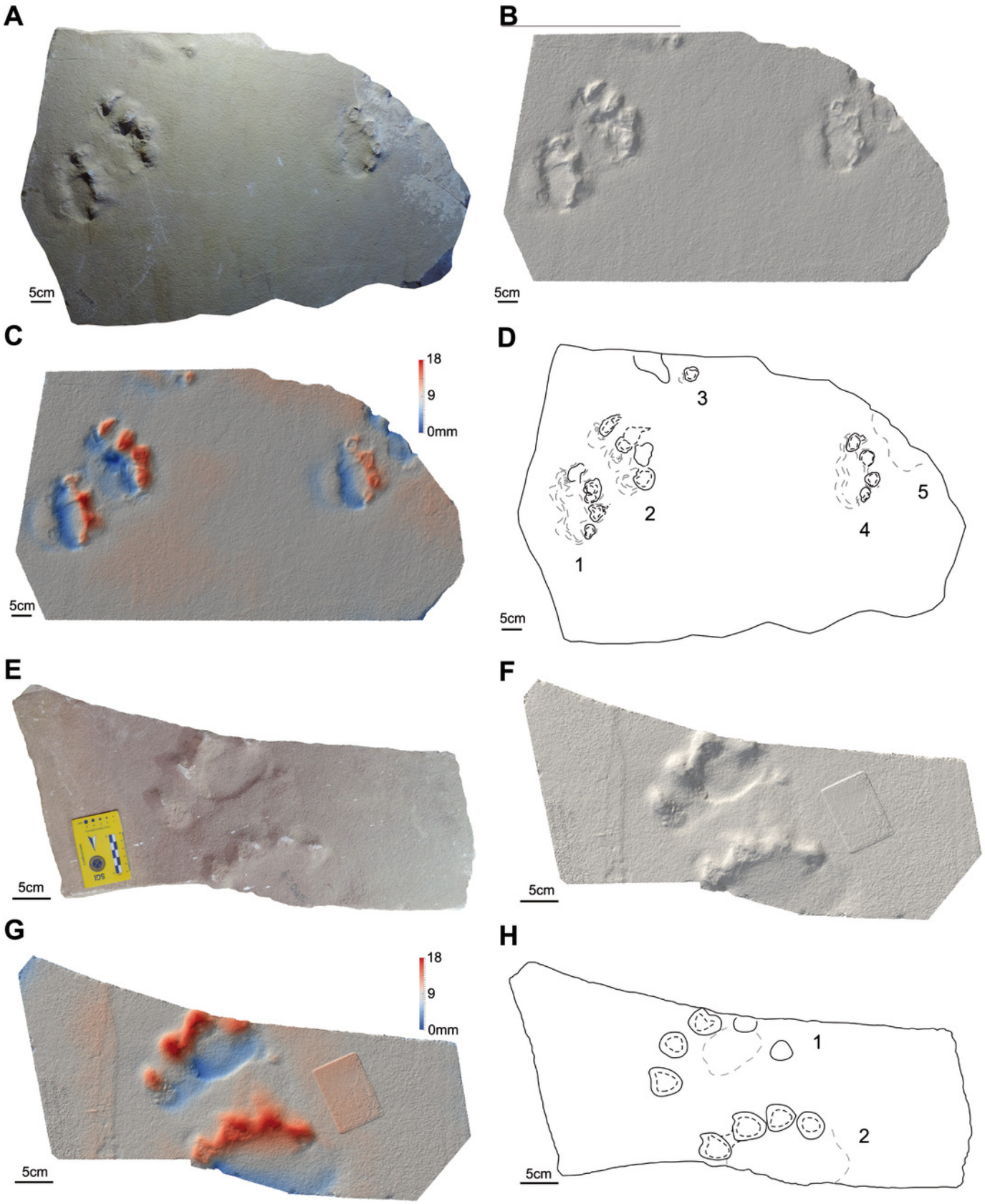
A
5cm
B
5cm
C
18
9
0mm
5cm
D
3
2
1
5
4
5cm
E
5cm
F
5cm
G
18
9
0mm
5cm
H
1
2
5cm

Figure 6

Photos, three-dimensional representations and interpretative drawings of the studied material.

(A) Track-bearing slabs MPCA 27029-5; (B) Solid three-dimensional model of (A); (C) Colour topographic profile and (D) interpretative drawing of (A). (E) Track-bearing slabs MPCA 27029-9; (F) Solid three-dimensional model of (E); (G) Colour topographic profile and (H) interpretative drawing of (E).

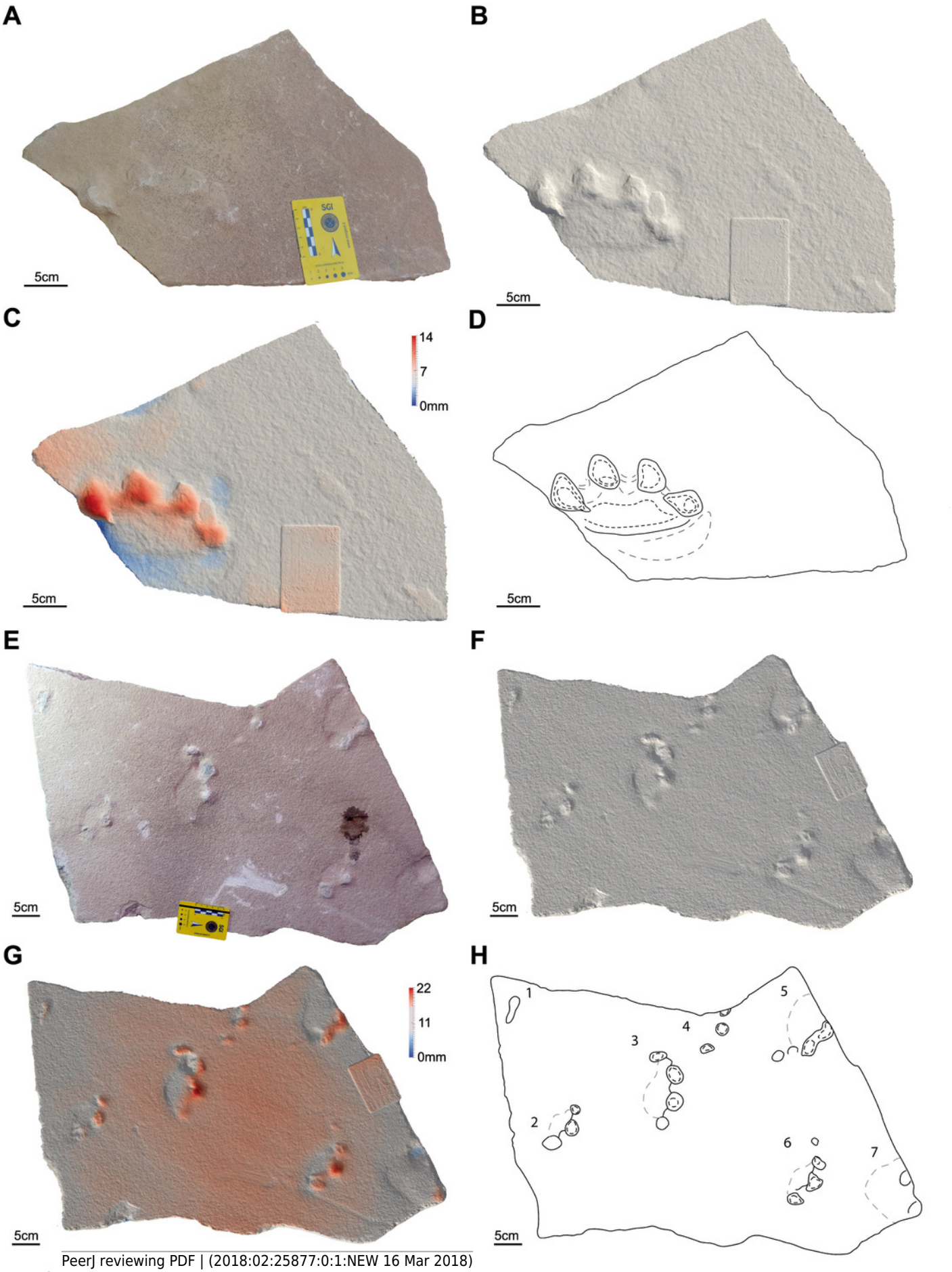
A
5cm
B
5cm
C
14
7
0mm
5cm
D
5cm
E
5cm
F
5cm
G
22
11
0mm
5cm
H
1
2
3
4
5
6
7
5cm

Figure 7

Photos, three-dimensional representations and interpretative drawings of the studied material.

(A) Track-bearing slabs MPCA 27029-16; (B) Solid three-dimensional model of (A); (C) Colour topographic profile and (D) interpretative drawing of (A). (E) Track-bearing slabs MPCA 27029-21; (F) Solid three-dimensional model of (E); (G) Colour topographic profile and (H) interpretative drawing of (E).

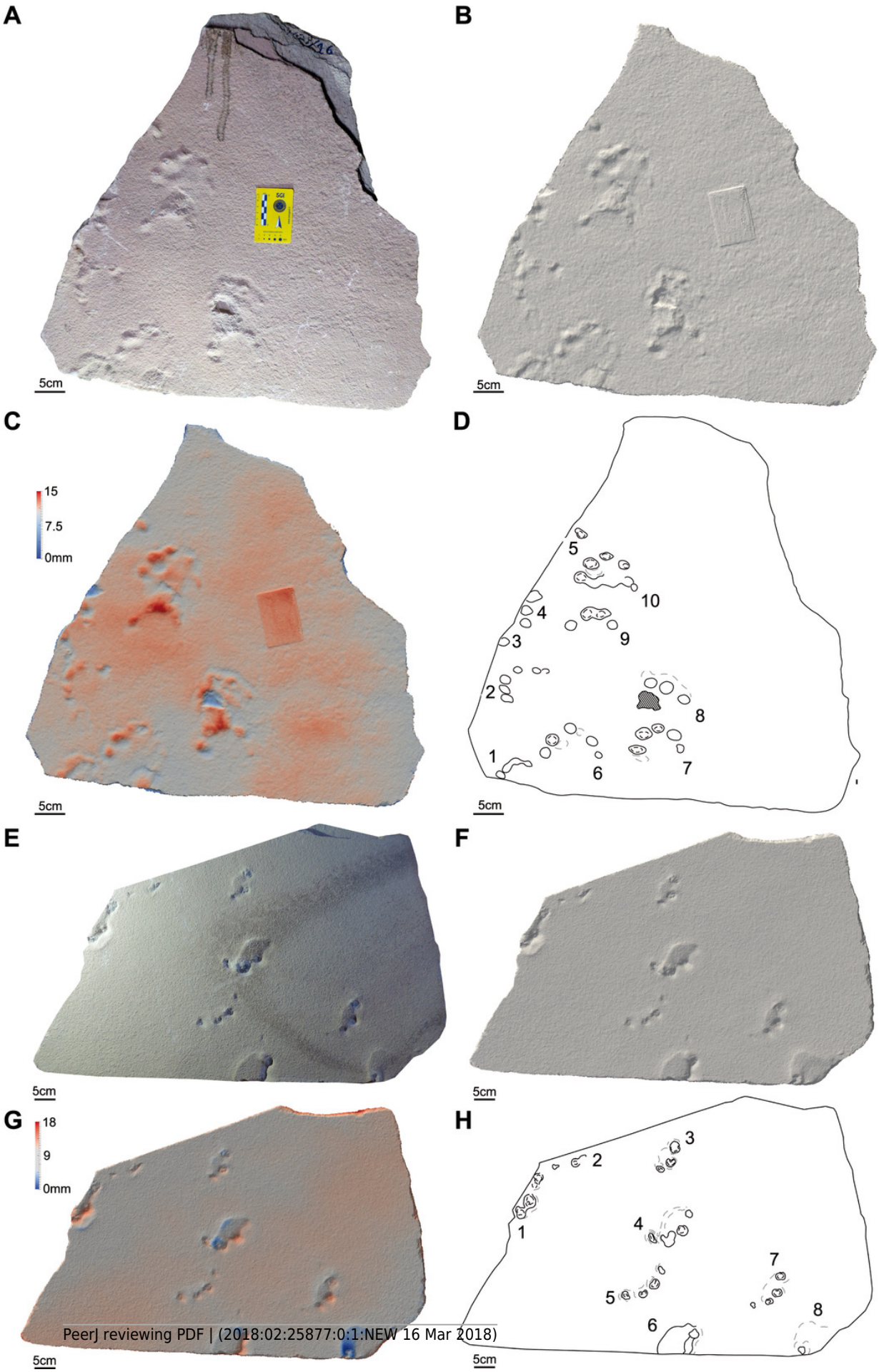
A
5cm
B
5cm
C
15
7.5
0mm
5cm
D
5
10
4
9
3
2
8
1
6
7
5cm
E
5cm
F
5cm
G
18
9
0mm
5cm
H
3
2
1
4
7
5
8
6
5cm

Figure 8

Photos, three-dimensional representations and interpretative drawings of the studied material.

(A) Track-bearing slabs MPCA 27029-33; (B) Solid three-dimensional model of (A); (C) Colour topographic profile and (D) interpretative drawing of (A). (E) Track-bearing slabs MMLM 075-1; (F) Solid three-dimensional model of (E); (G) Colour topographic profile and (H) interpretative drawing of (E).

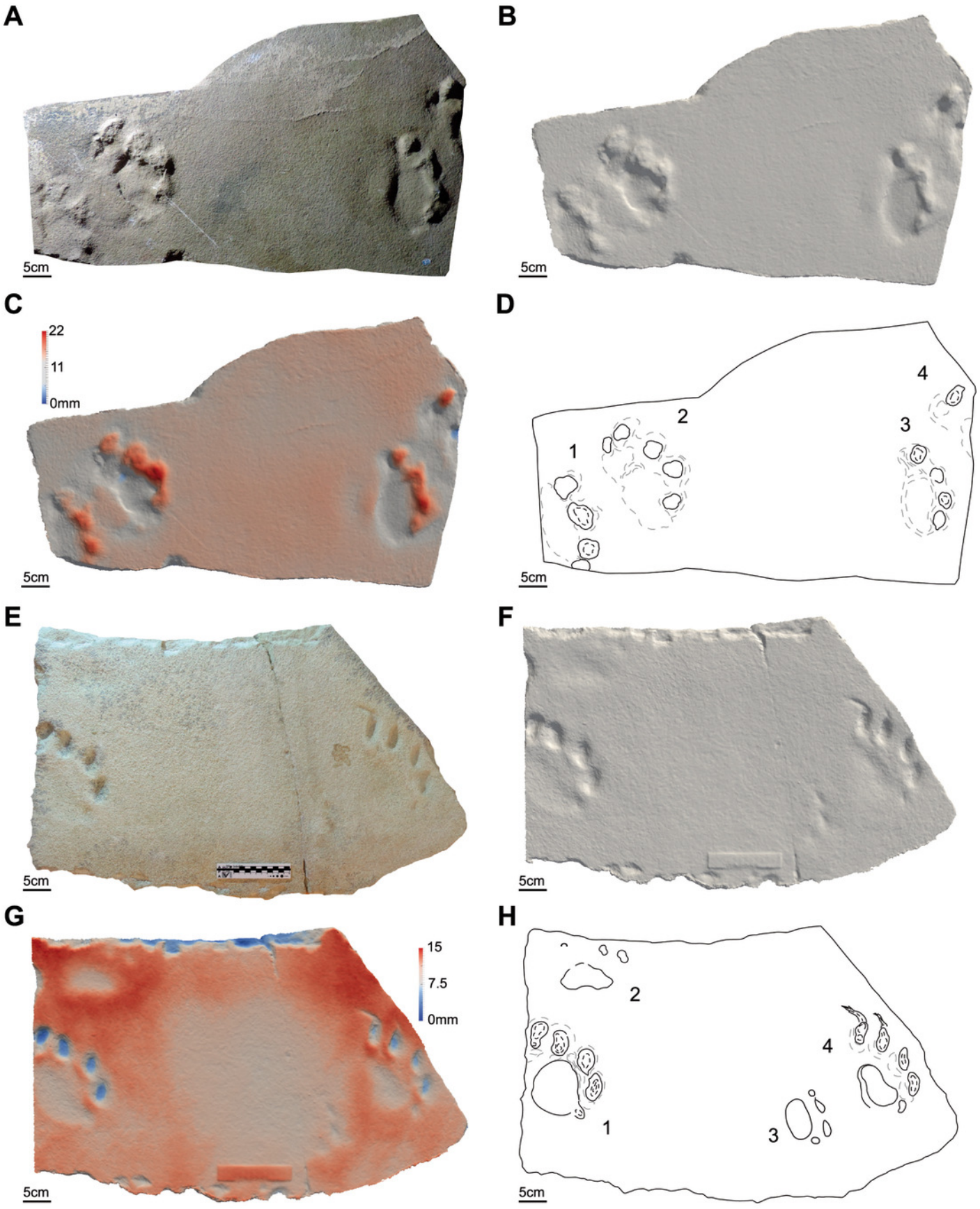
A
5cm
B
5cm
C
22
11
0mm
5cm
D
1
2
3
4
5cm
E
5cm
F
5cm
G
15
7.5
0mm
5cm
H
1
2
3
4
5cm

Figure 9

Photos, three-dimensional representations and interpretative drawings of the studied material.

(A) Track-bearing slabs MMLM 1; (B) Solid three-dimensional model of (A); (C) Colour topographic profile and (D) interpretative drawing of (A). (E) Track-bearing slabs MMLM 2; (F) Solid three-dimensional model of (E); (G) Colour topographic profile and (H) interpretative drawing of (E).

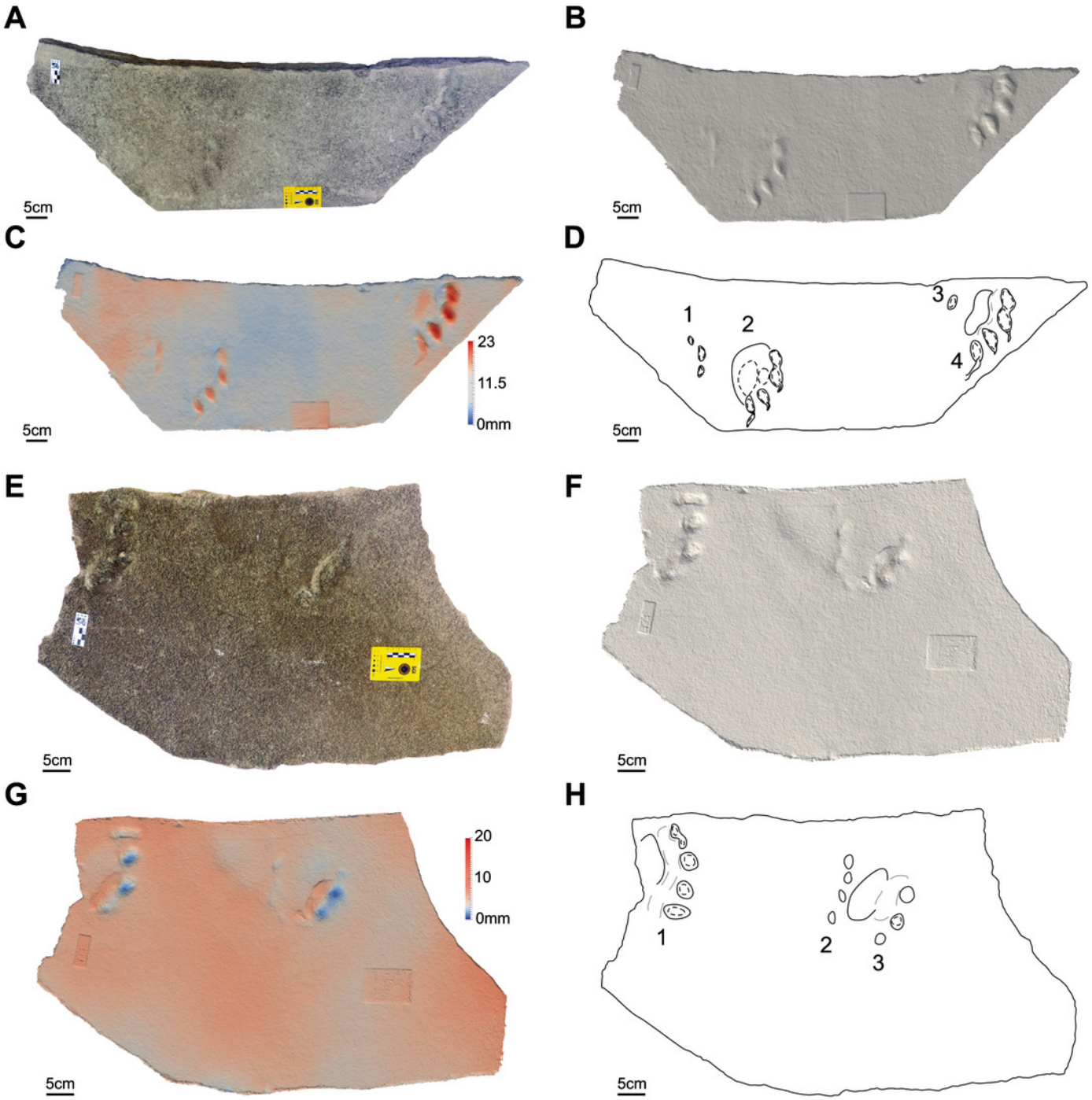
A
5cm
B
5cm
C
23
11.5
0mm
5cm
D
1
2
3
4
5cm
E
5cm
F
5cm
G
20
10
0mm
5cm
H
1
2
3
5cm

Figure 10

Morphological and extramorphological features identified on the studied material.

(A) Pes track MPCA 27029-1/5 and (B) interpretative drawing. (C) Manus track MPCA 27029/2 and (D) interpretative drawing.

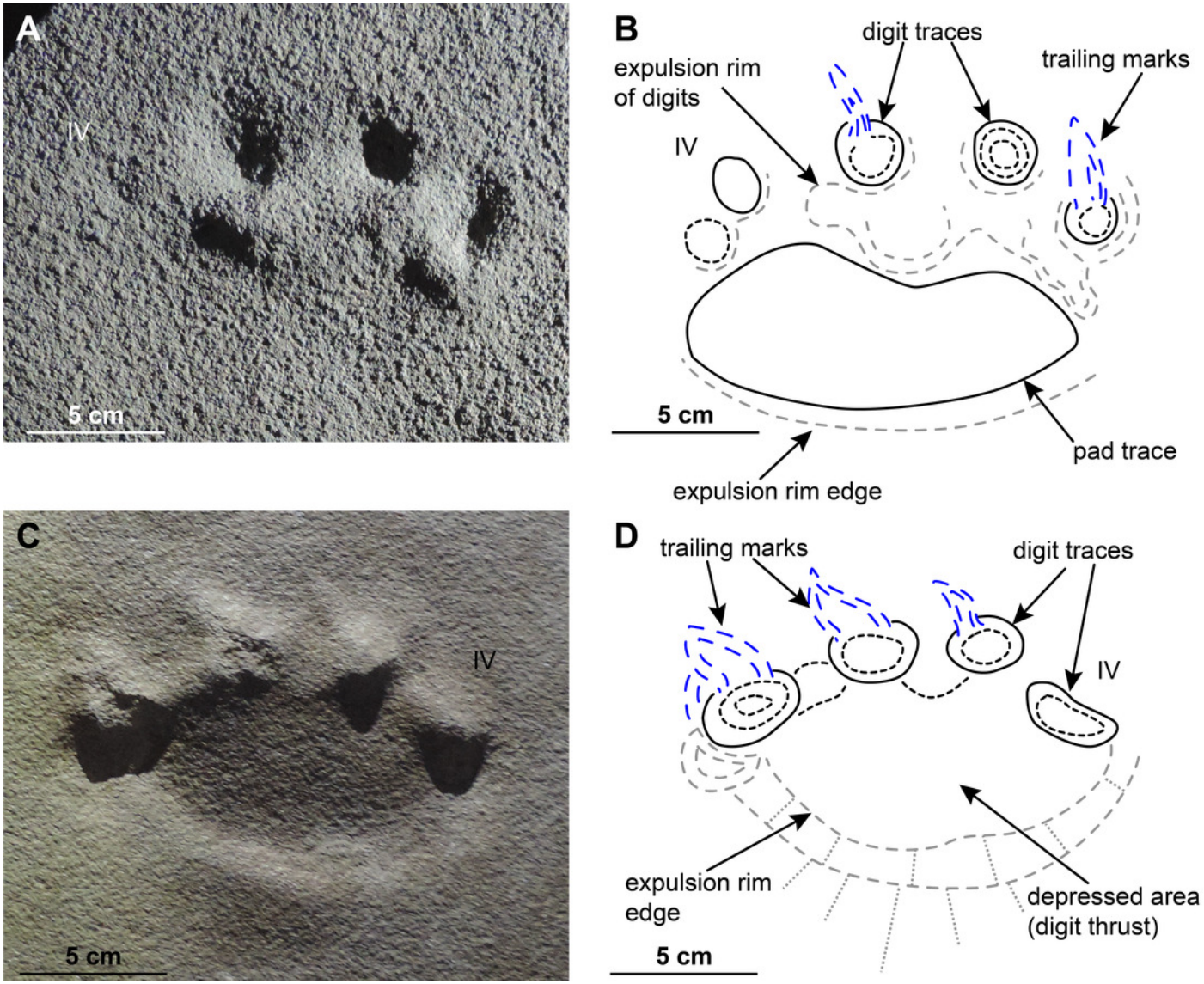

Figure 11

Palaeozoological attribution of pentadactyl tracks from Los Menucos (Patagonia, Argentina).

Reconstruction of the proposed autopod posture of the Pentasauropus *putative trackmaker (A) in dorsal (B) and lateral (C) view. Basipodials in green, metapodials in blue and acropodials in light blue. Redrawn and modified from Morato (2006: fig. 54c).*