VERTEBRATE TRACKS OF THE RÍO NEGRO PROVINCE, PATAGONIA, ARGENTINA: STRATIGRAPHY, PALAEOBIOLOGY AND ENVIRONMENTAL CONTEXTS

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MANUSCRITO ACEPTADO

ABSTRACT

To date, the tetrapod ichnological record in the Río Negro province, Argentina, is known from six areas from the Permo-Triassicto Neogene. Tetrapod tracks have been identified in different palaeoenvironments and geodinamic contexts. The oldest track record is represented by the therapsid tracks from the Los Menucos Group. A prevailing *Dicynodontipus* and *Dicynodontipus*-like footprints, Lopingian-Early Triassic in age, comes from the Tscherig and Puesto Vera localities, while *Pentasauropus* tracks, presumably Late Triassic in age,were recognized in the Yancaqueo locality. A tridactyl track-bearing level, still unpublished (related to El Refugio Formation, Middle-Upper Triassic), has been found in the Puesto Prado farm, in the Arroyo de la Ventana area. Some tracks classified as cf. *Anomoepus* and undetermined tridactyl tracks have been identified in the Perdomo farm(Marifil Volcanic Complex). The Late Cretaceous (Cenomanian) record is represented by the ornithopod, sauropod and theropod tracks from the Candeleros Formation (Ezequiel Ramos Mexía area). Moreover, cf. Iguanodontipodidae, sauropod and avian tracks from the Anacleto and Allen Formations characterise the latest Cretaceous (Campanian-early Maastrichtian) of the Paso Córdoba area.Avian tracks were also reportedfromthe Ingeniero Jacobacci area, from the Angostura Colorada Formation (upper Campanian-lower Maastrichtian), andfrom the Río Negro Formation (upper Miocene-lower Pliocene) along the shoreline of the province. In this area, tens of tracksites and several ichnotaxa have been studied. In regard of palaeoenvironments, ichnosites are constrained to three main sedimentary settings: fluvio-volcaniclastic, fluvial/fluvial-aeolian and shallow marine systems. Finally, a brief discussion about palaeobiology and heritage issues is provided.

Keywords: *Ichnological compilation, Palaeozoic, Mesozoic. Cenozoic, Río Negro province*

MANUSCRITO ACEPTADO

RESUMEN

Hasta la fecha, el registro icnológico de la provincia de Río Negro se conoce en seis áreas que van desde el Pérmico al Neógeno. Las huellas de tetrápodos han sido identificadas en diferentes contextos paleoambientes y geodinámicos. El registro más antiguo son las huellas de terápsidos del Grupo Los Menucos. Las huellas de *Dicynodontipus* y *Dicynodontipus*-like, dominantes, provienen del Lopingiano-Triásico Inferior, de las localidades de Tscherig y Puesto Vera, mientras que las huellas de *Pentasauropus*, probablemente del Triásico Superior, provienen de la localidad de Yancaqueo. Un nivel con una huella tridáctila, aún inédito (relacionado con la Formación El Refugio, Triásico Medio- Superior), ha sido hallado en el Puesto Prado, área de Arroyo de la Ventana. En Puesto Perdomo (Complejo Volcánico Marifil) se identificaron huellas como cf. *Anomoepus* y tridáctilas indeterminadas. El registro del área de Ezequiel Ramos-Mexía está representado por huellas ornitopodianas, sauropodianas y teropodianas, provenientes de la Formación Candeleros (Cretácico Superior, Cenomaniano). Además, huellas avianas, sauropodianas y cf. Iguanodontipodidae caracterizan el Cretácico final (Campaniano-Maastrichtiano inferior) en el área de Paso Córdoba. En el área de Ingeniero Jacobacci se reportaron huellas avianas de la Formación Angostura Colorada (Campaniano superior-Maastrichtiano inferior), como así también de la Formación Río Negro (Mioceno superior-Plioceno inferior), en la parte costera de la provincia. En esta misma área, se han estudiado decenas de afloramientos y varios icnotaxones. Respecto al paleoambiente, los sitios icnológicos están limitados a tres entornos sedimentarios principales: sistemas fluvio-volcaniclástico, fluvial/fluvio-eólico y marino somero. Finalmente, se provee una breve discusión sobre temas paleobiológicos y patrimoniales.

MANUSCRITO ACEPTADO

Palabras clave: *Recopilación icnológica, Paleozoico, Mesozoico, Cenozoico, provincia de Río Negro*

INTRODUCTION

The study of the vertebrate tracks from Argentina has its origin with the description of *Rigalites ischigualastianus* von Huene, 1931, from the Los Rastros Formation (Middle Triassic), San Juan province. Since then, several researchers have studied the vertebrate local ichnofauna, and some of the most outstanding works were made by Lull (1942), Rusconi (1952) and Casamiquela (1964). In this context, the ichnological contributions of the Río Negro province constituted one of the incipient lines of knowledge of trace fossils in Argentina, after seminal works by Casamiquela (1964, 1975).

Until present day, the tetrapod tracks from the Río Negro province, represented by a diverse imprint record from continental and transitional palaeoenvironments, although with no fish traces, spans a time interval from the Late Permian to the Pliocene (*e.g.*, Casamiquela 1964, 1996, Leonardi 1994, Melchor and de Valais 2006, Aramayo 2007, Calvo and Ortíz 2011, Domnanovich *et al*. 2008, Carmona *et al*. 2012, Díaz-Martínez *et al*. 2018). Six areas with multiple track-bearing levels are known since several decades ago, although some of the ichnosites have just been studied in the last years, or have been briefly mentioned in the literature and then no new scientific contribution has been referred from those localities (Fig. 1). Thus, the aim of this work is to present an updated compilation of the tetrapod track record from the Río Negro province, Patagonia, Argentina, assessing also their chronostratigraphical and palaeoenvironmental contexts.

GEOLOGICAL SETTING OF AREAS WITH ICHNOSITES

MANUSCRITO ACEPTADO

To date, in the Río Negro province, tetrapod tracks are mentioned and/or reported from six different areas, namely from: Los Menucos depocentre, the Arroyo de la Ventana, Ingeniero Jacobacci, Ezequiel Ramos Mexía lake and Paso Córdoba areas, and from the shoreline of the Río Negro province (Fig.1).

Los Menucos area

The Los Menucos area is located at the centre of the province. The homonym depocentre hosts a succession dominated by volcanic, intrusive sub-volcanic and volcaniclastic rocks with subordinate epiclastic sedimentary deposits (*e.g.*, Stipanicic *et al.* 1968, Cucchi *et al.* 2001, Labudía and Bjerg 2001, Lema *et al.* 2008) exposed in the North Patagonian Massif. The entire succession, formalised as Los Menucos Group (Labudía and Bjerg 2001), testifies the Permian and Triassic magmatism of the eastern North Patagonia during the post-orogenic stage of the Gondwanic Cycle (González *et al.* 2016, 2017).

The Los Menucos Group unconformably lies, through a non-conformity, on Lower Cambrian low grade metamorphic rocks (Martínez-Dopico *et al*. 2017). The upper limit of the unit is marked by an erosive unconformity, above which Upper Cretaceous continental and marine deposits or Tertiary basalts rest (Labudía and Bjerg 2001). Within the Los Menucos Group, two formations are included: the Vera Formation at the base, that is historically the track-bearing unit, and the Sierra Colorada Formation on top (Labudía and Bjerg 2001).

The Vera Formation comprises volcanic ashes, tuffs, pyroclastic flow deposits and volcanic breccias, with conglomerates, sandstones and pelites intercalated (Labudía and Bjerg 2001, 2005). Sedimentation took place inside small basins bordered by regional and local faults (Labudía and Bjerg 2001), and it was strongly influenced by the volcanic activity,

MANUSCRITO ACEPTADO

affecting alluvial plain and floodplains furrowed by ephemeral rivers and small lacustrine palaeoenvironments under a seasonal climate (Gallego 2010).

The fossil record of the Vera Formation comprises a very rich palaeoflora (*i.e.*, *Dicroidium* type flora, see Artabe 1985a,b), spinicaudatans ("conchostracans" sensu Gallego 2010) and abundant tetrapod tracks (Casamiquela 1964, 1975, 1987, Leonardi and de Oliveira 1990, Leonardi 1994, Manera de Bianco and Calvo 1999, Domnanovich and Marsicano 2006, Melchor and de Valais 2006, de Valais 2008, Domnanovich *et al.* 2008). The vertebrate skeletal fauna is only represented by remains of an amiiform fish (Bogan *et al*. 2013).

Based on the palaeoflora, different Triassic ages were proposed for the Vera Formation (Stipanicic 1967, Artabe *et al*. 1985a,b, Stipanicic and Methol 1972, 1980). Gallego (2010) proposed an early Late Triassic age based on the clam shrimp *Menucoestheria wichmanni*. Casamiquela (1964) indicated that the tetrapod fauna from Los Menucos is younger than the Late Triassic and older than the Late Jurassic; more recently, Citton *et al*. (2018) suggested an at least Early and Late Triassic age for different levels of the Vera Formation based on the tetrapod track global record.

Volcaniclastic rocks of the Sierra Colorada Formation were firstly dated in 222± 2 Ma (Norian, Late Triassic) with the Rb/Sr isochron method (Rapela *et al.* 1996), while Lema *et al*. (2008) dated at 206.9 ± 1.2 Ma (Rhaetian, Late Triassic) with the Ar/Ar method. More recent radiometric ages constrained the Los Menucos Group between 257 ± 2 Ma (Wuchiapingian, Lopingian, Permian) and 248 ± 2 Ma (Olenekian, Early Triassic) (Falco *et al.* 2018, Luppo *et al.* 2018), making the Los Menucos Group coeval with the La Esperanza plutono-volcanic Complex, as it has already been stressed by González *et al*. (2017).

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Arroyo de la Ventana area

The Marifil volcanic Complex records an important magmatic event in the eastern North Patagonian Massif that occurred from the Middle Triassic to the Middle Jurassic (Malvicini and Llambías 1974, Pankhurst *et al.* 1998, and references therein). The Marifil volcanic Complex comprises large volume of rhyodacitic to rhyolitic ignimbrites with minor rhyolitic and andesitic lava flow deposits to which sedimentary lenses are intercalated (Cortés 1981). The Marifil volcanic Complex has been recently related to two different geotectonic phases, i) the first occurred during the Early-Middle Triassic under an extensional tectonic regime linked to the collapse of the Gondwanan orogeny, so it would not be part of Marifil volcanic Complex (González *et al.* 2017), and ii) the second, during the Early Jurassic, characterised by a continental-intraplate extensional regime related to the thermal activity of the Karoo plume (González *et al.* 2017). The rocks related to the former pertain to two lithostratigraphic units: the La Monasa Formation, comprising volcanic and subvolcanic rocks, and the Puesto Piris Formation, comprising epiclastic and volcaniclastic deposits. Radiometric ages obtained with U-Pb and LA-ICP-MS methods from volcanic and subvolcanic rocks from the La Monasa Formation indicated late Early and Middle Triassic ages (247.22 ± 0.46 Ma and 243. 6 ± 1.7 Ma, respectively; González *et al.* 2014).

The second geotectonicphase corresponds with the Early Jurassic acidic volcanism and it is represented by the Marifil volcanic Complex s.s. (González *et al.* 2017), comprising volcanic and subvolcanic products and associated interbedded sedimentary rocks. Andesitic rocks at the Marifil volcanic Complex base have been dated at 221 Ma (Carnian, Late Triassic), whileRb-Sr and Ar-Ar ages from pyroclastic rocks have ranged between the middle Pliensbachian (188 Ma) and the middle Toarcian (178 Ma), and altogether with the rhyolitic composition, have enabled to include the Marifil volcanic Complex in the Chon Aike Large Silicic Igneous Province (Pankhurst *et al.* 2000).

MANUSCRITO ACEPTADO

Puesto Prado site.This site was recently discovered and it is still unpublished. The new ichnosite is located near Arroyo de la Ventana, 55 km west of Sierra Grande, Río Negro province, in a farm owned by the Prado family. The site lacks of a detailed stratigraphic-sedimentologic analysis yet. A preliminary study of the track-bearing rocksuggested that the track-bearing level most likely belongs to the El Refugio Formation (equivalent to the Puesto Piris Formation *sensu* González *et al*. 2017).

Puesto Perdomo site. The Puesto Perdomo ichnosite is located in the Perdomo farm, 50 km southwest of Sierra Grande town (Díaz-Martínez *et al*. 2017b,c). The track-bearing slabs come from a flagstone quarry, where a 30 metre-thick succession, dominated by pyroclastic acidic flow deposits with thin volcaniclastic lenses, crops out.These slabs are composed of coarse-grained, light-pinkish sandstone with quartz, k-feldspar and pyroclastic material (*i.e.*, ash and pumice fragments). The sedimentation, strongly controlled by the volcanism, occurred in an incipient fluvial system, characterised by small palaeochannels infilled by arenaceous sediments. In the area, the succession underlies the rhyolitic ignimbrites dated at 188 Ma in age (Rb–Sr age, *in* Pankhurst and Rapela 1995), thus the epiclastic lenses are assigned to the Early Jurassic (pre-middle Pliensbachian) gap of the Marifil Volcanism (Cortés 1981, Pankhurst and Rapela 1995).

MANUSCRITO ACEPTADO

Ezequiel Ramos Mexía lake area

The Ezequiel Ramos Mexía lake is a dam built in the Limay river valley in between the Neuquén and Río Negro provinces, north Patagonia, Argentina. In this area, several extraordinarily fossiliferous lithostratigraphic units, belonging to the Neuquén Group, are exposed. The Neuquén Group comprises nine formations pertaining to three subgroups, namely the Candeleros, Huincul and Cerro Lisandro formations (Río Limay Subgroup), the Portezuelo and Plottier Formations (Río Neuquén Subgroup), and the Bajo de la Carpa and

Anacleto Formations (Río Colorado Subgroup) (Leanza *et al*. 2004, but see Garrido 2010 for a different nomenclatural assessment).

The track record from this area comes from the basal unit Candeleros Formation, which overlays the Rayoso Formation (Garrido 2010), and mainly it consists of massive coarse- to medium-grained sandstones and conglomerates, with intercalations of thin siltstone beds indicative of fluvial to alluvial plain, aeolian and playa-lake environments (Garrido 2010, Candia Halupczok *et al*. 2018 and references therein). The Candeleros Formation is considered Cenomanian in age (Leanza *et al*. 2004, and references therein), and corroborated by U-Pb detrital zircons ages (Tunik *et al*. 2010, Di Giulio *et al*. 2012, 2015).

Shoreline of the Río Negro side sites. The depositional studies of the Candeleros Formation in the Ezequiel Ramos Mexía lake area have suggested aeolian and playa-lake palaeoenvironments (Spalletti and Gazzera 1994). On the other hand, in the lower part of the Candeleros Formation, where the tetrapod tracks are preserved, Calvo and Gazzera (1989) pointed out the presence of floodplains associated with swamp deposits and poorly developed ephemeral channels.

Southwest slope of the Planicie de Rentería area. Candia Halupczok *et al*. (2018) suggested that the tracks were impressed in deposits of the Kokorkom palaeodesert, more specifically, on wet and dry interdune and within draa slipface deposits. The palaeontological record is mainly composed of an ample variety of vertebrates: lepidosaurs, snakes, crocodyliforms, theropods, sauropods, mammals and fishes (see Apesteguía *et al*. 2001, Candia Halupczok *et al*. 2018, and references therein).

Paso Córdoba area

In the Paso Córdoba area, three lithostratigraphical units, namely the Bajo de la Carpa, Anacleto (Neuquén Group) and Allen (Malargüe Group) Formations, constitute a continental

MANUSCRITO ACEPTADO

succession characterised by mainly fluvial deposits and subordinated aeolians and lacustrine ones (see Paz *et al*. 2014, Díaz-Martínez *et al*. 2018). The locality is characterised by a rich vertebrate fossiliferous content (*e.g.,* Pol 2005, Martinelli and Vera 2007, Ezcurra and Mendez 2009, Calvo and Ortíz 2011, Álvarez *et al*. 2016, Díaz-Martínez *et al*. 2015). Ichnological localities are located within the "Área Natural Municipal Protegida Paso Córdoba", on the side of the Negro river, near the Paso Córdoba town, 15 km south of General Roca city, at north of the province.

Vertebrate tracks are commonly found in strata belonging to two lithostratigraphic units:the Anacleto Formation (lower Campanian) and the Allen Formation (upper Campanian-lower Maastrichtian). In the Paso Córdoba area, the Anacleto Formation is related to a meandering fluvial, mainly floodplains (Díaz-Martínez *et al*. 2018), to shallow lacustrine system, represented by offshore and shoreface deposits, with associated deltaic systems (Paz *et al*. 2014). In turn, the Allen Formation records an eolian system related to coastal dunes (Armas and Sanchez 2013, 2015, Paz *et al*. 2014). The transitional contact between these units sometimes difficults positioning some ichnological records within lithostratigraphic schemes.

Ingeniero Jacobacci area

The track-bearing lithostratigraphic units in the Ingeniero Jacobacci area (south-centre of the Río Negro province), are the Angostura Colorada and the Río Negro Formations.

The Angostura Colorada Formation was established by Volkheimer (1973) to indicate a complex of continental sedimentary rocks exposed in the North Patagonian Massif, northeast of the Lipetrén locality, nearby Ingeniero Jacobacci town, up to Comallo town. The unit is composed of a rift-related succession made of conglomerates, sandstones and pelites

MANUSCRITO ACEPTADO

(González *et al*. 1999) and it was previously subdivided into three informal members indicative of alluvial fan, fluvial braided and floodplain facies associations (Manassero 1997).

The body fossil record is restricted to titanosaur sauropods, with the species *Aeolosaurus rionegrinus* and other remains (Powell 2003, Zurriaguz *et al*. 2018), and palynomorphs (Náñez 1983). The age of the Angostura Colorada Formation is regarded as upper Campanian-Maastrichtian based on its stratigraphic position and the content of palynomorphs (Volkheimer 1973, Coira 1979, Náñez 1983, Manassero and Maggi 1995). The tetrapod track record from this unit is characterised by avian tracks.

The Angostura Colorada Formation transitionally passes to the Coli Toro Formation, which concordantly rests above (Volkheimer 1973, Coira 1979, Náñez 1983, Spalletti 1988). Originally, the Coli Toro Formation was named to indicate gray, fine-grained sandstones and shales rich in micaceous minerals, which are exposed in the North Patagonian Massif, underlying the Roca Formation, at about 50 km northeast of Ingeniero Jacobacci town (Bertels 1969).

Around Ingeniero Jacobacci town, Casamiquela (1969) recognized sandstone slabs with avian tracks preserved on them, referable to a fluvial and lacustrine environments from the Río Negro Formation (see description below). In this area, according to the geological sections provided by Casamiquela (1969: fig. 1), the unit is above the so-called “Estratos con Dinosaurios” and below the Plio-Pleistocene sedimentary rocks. Close to the avian tracks, Casamiquela (1969) suggested the presence of *Megatheridium* remains.

Shoreline of the Río Negro province

The Río Negro Formation (Andreis 1965) is extensively exposed in the most eastern portions of the Río Negro and Buenos Aires provinces, along sea-cliffs and alluvial plains (Aramayo 2007, Carmona *et al*. 2012) but was also reported from inner regions of the La

MANUSCRITO ACEPTADO

Pampa province (Melchor 2009) and in several areas of the Andes cordillera, in the Neuquén, Río Negro and Chubut provinces (*e.g.,* Casamiquela 1969, González Díaz and Nullo 1980, Bilmes *et al*. 2017). This formation has probably been deposited in an intracratonic basin, and the stratigraphic basin patterns are related to structural highs that controlled the sedimentation (Zavala and Freije 2000).

The Río Negro Formation comprises Neogene epiclastic and volcaniclastic deposits (Andreis 1965). On the basis of radiogenic dates and fossil mammal remains, the age of the formation is currently assigned to the interval upper Miocene-lower Pliocene (Zinsmeister *et al*. 1981, Aramayo 1987, Alberdi *et al*. 1997).

This formation is divided into three members (Zavala and Freije 2001) which extensively crop out along the shoreline of the Río Negro Province and contain many track-bearing levels (*e.g.,* Casamiquela 1969, Aramayo 2007, Carmona *et al*. 2012, Melchor *et al*. 2013). The lower member of eolian sandstones and mudstones accumulated in large dunes and dry-wet interdunes (Zavala and Freije 2000). The middle one is characterised by bioclastic sandstones and dark gray mudstone intervals deposited in a shallow-marine palaeoenvironment (Zavala and Freije 2001). Finally, the upper member is composed of eolian sandstones at the base to palaeosols to tuff levels at the top (see Carmona *et al*. 2012).

Along the shoreline of the Río Negro Province there are several and well exposed outcrops of this unit, displaying remarkable tetrapod tracks content that distributed in these three members (*e.g.,* Casamiquela 1969, Aramayo 2007, Carmona *et al*. 2012, Melchor *et al*. 2013).

MANUSCRITO ACEPTADO

MATERIALS AND METHODS

For this contribution, we are taking into account, on one hand, both unpublished and already published material, and on the other hand, both collected and *in situ* specimens.

The general ichnological concepts and descriptions of the tracks follow the criteria of Leonardi (1987) and Bertling *et al*. (2006). We consider the preservational scheme of the traces as epirelief (Seilacher 1964) or epichnia (Martinsson 1970), when preserved at the stratum top, and hyporelief (Seilacher 1964) or hypichnia (Martinsson 1970), when preserved at the stratum base, and additionally, concave as negative or in a depression in cross-section and convex as positive or a protuberance in cross-section.

Most of the photographs used herein have been taken by the authors, both *in situ* and in the collections; otherwise, it will be informed in each case.

Institutional abbreviations (all collections from Argentina). CICRN: Centro de Investigaciones Científicas de Río Negro, Viedma, Río Negro province; MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", CABA; MJG: Museo Jorge H. Gerhold, Ingeniero Jacobacci, Río Negro province; MLP: Museo de La Plata, La Plata, Buenos Aires province; MMLM: Museo Municipal de Los Menucos, Los Menucos, Río Negro province; MPA: Museo Punta Alta, Punta Alta, Buenos Aires province; MPCA: Museo Provincial Carlos Ameghino, Cipolletti, Río Negro province; MRPV: Museo Regional Provincial de Valcheta, Valcheta, Río Negro province; P.ICHN.U.N.S.: Palaeoichnology repository, Universidad Nacional del Sur, Bahía Blanca, Buenos Aires province.

MANUSCRITO ACEPTADO

ICHNOLOGICAL RECORD

Los Menucos area

Materials. All the specimens have been collected from the Los Menucos Group. 1) from the Tscherig locality, 12 km southwest of the Los Menucos town: *Dicynodontipus* and

Dicynodontipus-like: collected specimens: MLP 60-XI-31-4, 60-XI-31-6, 60-XI-31-7, 60-XI-31-8, 60-XI-31-9, 66-XI-15-1, 66-XI-15-2, 66-XI-15-3, 93-XII-13-1, 93-XII-13-2, 93-XII-13-3, MACN 18198 (and a plaster cast with no collection number, housed in the MJG), CICRN 1-X-72-3 (removed from a pavement in Bariloche, Río Negro province, currently housed in the MLP), several slabs CICRN with no collection number, MPA 76-605-I-E, 76-606-I-E, 76-607-I-E, 76-608-I-E, 76-609-I-E, 76-610-I-E, 76-611-I-E, 76-612-I-E, 76-613-I-E, 76-614-I-E, 76-615-I-E, 76-616-I-E, 76-617-I-E, 76-618-I-E, 76-619-I-E, 76-620-I-E, 76-621-I-E, 76-622-I-E, 76-623-I-E, 76-624-I-E, 76-625-I-E, 76-626-I-E, 76-627-I-E, MPA 76-628-I-E, MPCA 27029 (30 track-bearing slabs with the same collection number), at least 21 slabs without label in the MJG; indeterminate chirotherid track: MLP 60-XI-31-1, 60-XI-31-2 (removed from a pavement in Bariloche city, Río Negro province); at least one track-bearing level with *in situ* specimens; several track-bearing slabs on the pavements in Bariloche, Los Menucos and Ingeniero Jacobacci cities, in the Río Negro province, and San Martín de los Andes town, in the Neuquén province; *Rhynchosauroides*: MPA 85-366-I-E MD-99-6 (Casamiquela 1964, 1975, Leonardi 1994, Domnanovich and Marsicano 2006, Melchor and de Valais 2006, Domnanovich *et al*. 2008); 2) from the Yancaqueo locality, 8 km east of the Los Menucos town: *Pentasauropus*: MPCA 27029-1/5, 27029-9, 27029-16, 27029-21, 27029-33, MMLM 1, 2, 075-1 (ex MRPV 1987P.V.06, *in* Domnanovich *et al*. 2008); 3) from the Vera locality, 25 km northeast of the Los Menucos town: at least one track-bearing level with several *in situ* specimens (Citton *et al*. 2019); and 4) from not precise site mentioned, near the Los Menucos town: *in situ* large tracks (Manera de Bianco and Calvo 1999, Melchor and de Valais 2006) (Fig. 2).

Description. 1) *Dicynodontipus* and *Dicynodontipus*-like tracks (Fig. 2a-c). These tracks are preserved both as negative and positive epirelief with a quadrupedal disposition (*e.g.*, Casamiquela 1964, 1975, Leonardi 1994, Melchor and de Valais 2006, Domnanovich *et al*.

MANUSCRITO ACEPTADO

2008). The manus is positioned anteriorly and at a short distance from the pes impression but can also be extensively overstepped. Trackways are commonly narrows. Manus and pes impressions show the same general shape, and are plantigrade and pentadactyl. The digit impressions are short, forwardly oriented, being the digit IV the longest, and the digit V slightly laterally and posteriorly shifted. A broad sub-circular to sub-triangular sole/palm pad lies behind digit traces.

*Rhynchosauroides*isp. This track, preserved as positive hyporelief, was referred to *Rhynchosauroides* isp. by Domnanovich *et al*. (2008). It is pentadactyl, with digit length increasing from the digit I to the digit IV trace, with digit V trace being the shorter and roughly aligned with the digit I trace.

"*Shimmelia chirotheroides*". Both the holotype MLP 60-XI-31-2 and the paratype MLP 60-XI-31-2 are probably undertracks. Domnanovich and Marsicano (2006) suggested that manus and pes impressions would not belong to the same set. The footprint is pentadactyl, with four anteriorly directed digit imprints and one, probably the V digit impression, laterally directed. The hand print is tetradactyl, as large as the pes print.

2) *Pentasauropus* (Fig. 2d-f). They consist of homopodic fore- and hind-prints predominantly represented only by the digit traces, left by a large, quadrupedal producer. The axis of pes tracks is commonly inwardly rotated with respect to trackway midline but it can also be parallel to the trackway midline, while manus tracks show a wider range of variability. Even if the footprints are often tridactyl or tetradactyl, complete fore- and hind-prints are pentadactyl. Digit V trace, when preserved, is the smallest and can be slightly shifted posteriorly. Digit traces are characterised by a roughly sub-circular morphology and, in some cases, their tips are pointed and associated to drag traces more developed in the most medial elements (*i.e.*, digit I and digit II traces). Moreover, these traces are commonly arranged to shape an arcuate, anteriorly convex pattern according to which the trace of digit III or those of

MANUSCRITO ACEPTADO

digit III and IV are the most advanced. Behind the digit traces, a circular to ovoidal sole/palm pad is preserved as separated from the central digits by a non-impressed area (Citton *et al*. 2018).

3) There are at least 14 *in situ* tracks of about 5 cm in overall length, similar to those referable to as *Dicynodontipus*, but with very poor preservational quality (Fig. 2h) (Citton *et al*. 2019).

4) Manera de Bianco and Calvo (1999) have briefly described several large, *in situ* tracks, from different levels. There are a set with a strong heteropody, composed of a semicircular manus and a sub-triangular pes. Besides, there are nine circular to elliptical tracks with a quadrupedal disposition, and an isolated, kidney-shaped footprint. All of them have poor quality of preservation and no clear morphologic details can be distinguished.

Comments. 1) Tetrapod footprints from the Los Menucos basin were firstly recognized at the end of the 50s in the town of Ingeniero Jacobacci, where track-bearing slabs were used for flooring the pavements around the beginning of the 1940s (sensu Casamiquela 1964). Soon after, other slabs with similar footprints, still used for the paving of the pavements of Costanera Av. (currently 12 de Octubre Av.) in Bariloche city, were brought to the attention of Casamiquela (see Casamiquela 1964). According to this author and to Leonardi and de Oliveira (1990), all these slabs were extracted from two distinct quarries of the Tscherig farm, named “Cantera Vieja” and “Cantera Nueva” (Old Quarry and New Quarry, respectively), at about 15 km northwest of the Los Menucos town (Fig. 2g). Subsequent fieldtrips in the Los Menucos area returned many slabs with tetrapod tracks, which are currently housed in several Argentine repositories (see Materials).

Dicynodontipus and *Dicynodontipus*-like tracks.Originally, Casamiquela (1964, 1975) named several ichnotaxa based on the material from the Tscherig farm, of which “*Calibarichnus*”, “*Gallegosichnus*”, “*Stipanicichnus*” and “*Palaciosichnus*” were after

MANUSCRITO ACEPTADO

considered synonyms of *Dicynodontipus* or compared with this ichnotaxon (see Leonardi 1994, Melchor and de Valais 2006, de Valais 2008). Besides, "*Rogerbaletichnus aguilerai*" (MLP 60-XI-31-5) and "*Ingenierichnus sierrai*" (MLP 60-XI-31-3) were considered as *nomina dubia* (de Valais 2008, Díaz-Martínez and de Valais 2014). The producer of *Dicynodontipus* has been long attributed to therapsids (Leonardi and de Oliveira 1990, Melchor and de Valais 2006), particularly theriodonts (Domnanovich and Marsicano 2006) and dicynodonts (Francischini *et al*. 2018).

Rhynchosauroides isp. A single track from the Tscherig farm (MPA 85-366-I-E MD-99-6) was assigned to *Rhynchosauroides* isp. by Domnanovich *et al*. (2008). Actually, the authors of this contribution could not find this material in the MPA or in any other collection.

"*Shimmelia chirotheroides*". Originally, Casamiquela (1964) named as "*Shimmelia chirotheroides*" the specimens MLP 60-XI-31-1 and 60-XI-31-2, and later, three other track-bearing slabs have been associated to this ichnotaxon by Domnanovich and Marsicano (2006). However, based on the poor preservation of the tracks, the ichnospecies was considered as *nomen dubium* by de Valais (2008).

2) *Pentasauropus*. The Yancaqueo site, in the Yancaqueo farm -Felipe Curuil's ex quarry, is 8 km east of the Los Menucos town; it has provided tetrapod footprints referred to as *Pentasauropus*. After the description of a single slab bearing three *Pentasauropus* tracks (MMLM 075-1 ex MRPV 1987P.V.06 in Domnanovich *et al*. 2008), the whole record has been reviewed (Citton *et al*. 2018). Based on the gleno-acetabular distances obtained from trackway parameters, the producers of these tracks ranged between 45 cm and 1 m in overall body length. The main ichnological features indicate that the producer of *Pentasauropus* had to be sought among anomodont dicynodonts of the clade Kannemeyeriiformes, characterised by a prevalent sprawling up to possibly semi-erect posture of the forelimbs, and by a semi-erect up to erect posture of the hindlimbs (Citton *et al*. 2018).

MANUSCRITO ACEPTADO

3) More recently, a new track-bearing locality was discovered at about 25 km northwest of the Los Menucos town, in the Vera farm. The footprints from this site have been referred to as comparable to *Dicynodontipus*; however, up to date, the poor preservation prevents an ichnotaxonomic assignment until new studies are carried out.

4) Manera de Bianco and Calvo (1999) have related them with the prosauropods. These specimens are probably undertracks, with no morphological details, and the poor preservational quality prevents any conclusion with confidence.

MANUSCRITO ACEPTADO

Arroyo de la Ventana area

Materials. 1) Four dinosaur track-bearing slabs (MRPV427/P/13, 428/P/13, 429/P/13 and 430/P/13), from the Puesto Perdomo site, 50 km west of the Sierra Grande, from the Marifil volcanic Complex (see Díaz-Martínez *et al*. 2017b,c); and 2) one *in situ* track, from the Puesto Prado site, 55 km west of the Sierra Grande town, from an equivalent unit to the El Refugio Formation (Gonzalez *et al*. 2017) (Fig. 3a-b).

Description and comments. 1) The four dinosaur track-bearing slabs were found in the 1950's during the extraction works of flagstone quarry in the Perdomo farm (Díaz-Martínez *et al*. 2017b,c). They had been part of the floor of a grocery store during decades. After that, they were extracted and returned to the Perdomo farm. In the 2000's, Mr. Perdomo donated the four slabs to the Museo Regional Provincial de Valcheta, where are currently housed.

These tracks, preserved as positive hyporelief, are tridactyl, mesaxonic and roughly symmetrical. The metatarso-phalangeal pad is in line with the axis of digit III impression. The tracks are longer than wide (average 167 cm long, 122 cm wide). One track is better preserved than the others. In MVP430/P/13, the phalangeal pad impressions and claw traces are preserved. Because of the observed preservational variants due to taphonomy, MRPV430/P/13 was assigned to cf. *Anomoepus*, while MRPV427/P/13, 428/P/13 and

429/P/13 were designated as *Anomoepus*-like footprints (Fig. 3a) (Díaz-Martínez *et al*. 2017c). They have been attributed to an ornithischian origin (Díaz-Martínez *et al*. 2017c).

2) Recently, during fieldwork carried out by some of the authors of this contribution, a new ichnological locality has been discovered, the Puesto Prado site, near Sierra Grande town. The only specimen from Puesto Prado is a medium-sized *in situ* tridactyl footprint (Gónzalez *et al*. 2017), as long as wide, with relative thick digit impressions and wide divarication angle between the II-IV digit imprints (Fig. 3b). This record and ichnosite are currently under study.

Ezequiel Ramos-Mexía lake area

1) Shoreline of the Río Negro province side

Materials. 1) sauropodian and pterosaurian track-bearing surface, not precise site mentioned, about 25 km south of the Villa El Chocón town, from the Candeleros Formation (Novas 2009, Novas and Isasi 2019 pers.comm.); and 2) tetrapod track-bearing surface in the Salas site, about 10 km southeast of the Villa El Chocón town, from the Candeleros Formation (Apesteguía 2005, Apesteguía *et al*. 2010) (Fig. 3c-f).

Description and comments. Several tetrapod tracks and trackways, recorded on the shoreline of the Ezequiel Ramos Mexía lake of the Río Negro province, boundary with the Neuquén province, have been briefly mentioned, described or figured (Apesteguía 2005, Novas 2009, Apesteguía *et al*. 2010) or are still unpublished. The track bearing-levels are equivalent to those of the Neuquén province, where the famous footprints from the El Chocón area come from (*e.g.,* Calvo 1991, 1999, Leonardi 1994, Calvo and Mazzetta 2004, Calvo and Rivera 2018).

1) At least a very well-preserved trackway composed of large manus and pes tracks (Fig. 3f), has been mentioned from a place on the shoreline of the lake, about 25 km south of

MANUSCRITO ACEPTADO

the Villa El Chocón town (Novas 2009: p. 240). Based on the manus and pes track features composing this trackway, Novas (2009) have claimed that it corresponds to a different sauropodian ichnotaxa previously known, for instance *Sauropodichnus*, which has been named from equivalent levels (Calvo 1991, Calvo and Mazzetta 2004, Calvo and Rivera 2018). Surely, the detailed morphology of the manus-pes set imprints of the specimens will allow assigning them both ichnotaxonomically and taxonomically in future studies.

Besides, on the same surface, there are imprints related to pterosaurs, composed of tridactyl and asymmetrical manus prints and large and tetradactyl footprints (Novas and Isasi 2019 *pers. comm.*).

2) A well-preserved heteropodic manus-pes print set, related to rebbachisaurid sauropods, is mentioned and figured by Apesteguía (2005) and Apesteguía *et al*. (2010), although no further morphological details are provided (Figs. 3d-e). Besides, abundant isolated, tridactyl tracks have been recorded from the same levels (Apesteguía 2019 *pers. comm.*). They are longer than wide, relative thick digit impressions, and some of them display clear claw and digital pad traces (Fig. 3c). Till now, no ichnotaxonomic or taxonomic approximation has been done.

2) Southwest slope of the Planicie de Rentería area

Materials. 1) tracks in cross-section and one in plan view, in the La Buitrera locality, about 35 km south of the Villa El Chocón town, from the Candeleros Formation (Candia Halupczok *et al*. 2018); and 2) one track, in the Cerro Policía locality, from about 55 km south of the El Chocón town, from the Candeleros Formation (Candia Halupczok *et al*. 2018).

Description and comments. On the southwest slope of the Planicie de Rentería, located about 45 km south of El Chocón city, tetrapod tracks have been recorded in the La Buitrera and Cerro Policía areas (Candia Halupczok *et al*. 2018).

MANUSCRITO ACEPTADO

1) Candia Halupczok *et al*. (2018) described tracks in cross-sections, preserved as negative epichnia, recorded in three different sedimentary associations, namely dune slipfaces, wet interdunes and sandsheet deposits. The tracks from the first association are characterised by being usually laterally symmetrical and displaying a depth of up to 10 cm and a width of up to 15 cm, and those tracks from the other two facies are up to 25 cm wide, with a depth from 15 to 25 cm. None of these imprints displays any necessary features to make a taxonomical or ichnotaxonomical assignment (Candia Halupczok *et al*. 2018).

Besides, there is a tridactyl, symmetrical footprint as long as wide (100 cm long, 100 cm wide), with equidistant digit imprints of about 30 cm long, and a total divarication angle between digit impressions II-IV of 65º. Candia Halupczok *et al*. (2018) attributed it to ornithopods.

2) A tridactyl, symmetrical footprint of 35 cm long and 42 cm wide, with equidistant digit imprints (35 cm long, 10 cm wide) and the divarication angle between digit II and IV impression of 54º, has been recorded in the Cerro Policía locality, and as the previous track, has been vinculated with ornithopod producers (Candia Halupczok *et al*. 2018).

In our opinion, both tridactyl tracks are very poorly preserved and almost no detail can be distinguished. Surely, future studies in the area will allow to elucidate these questions.

Paso Córdoba area

Materials. 1) six track-bearing strata, including tracks in cross-section, three collected tracks with provisional field number PC-1-A, B and C (currently in the Museo Patagónico de Ciencias Naturales, General Roca city, Río Negro province), from the Cañadón del Desvío site, limit of the Valle de la Luna Rojo, southeast of Paso Córdoba, from the Anacleto and Allen Formations (Díaz-Martínez *et al*. 2018); 2) avian track-bearing level, exact locality unknown, near the Valle de la Luna Amarillo, east of Paso Córdoba, from the Allen

MANUSCRITO ACEPTADO

Formation (Ortíz *et al*. 2013); 3) dinosaur track-bearing surface, in the Pasarela site, southeast of the Paso Córdoba town, from the Allen Formation (Calvo and Ortíz 2013); and 4) several track-bearing levels, exact localities unknown, from the Anacleto and Allen Formations (Calvo and Ortíz 2011, Paz *et al*. 2014, Ortíz and Calvo 2017, Díaz-Martínez *et al*. 2017a) (Fig. 4).

Description. 1) The material from the Cañadón del Desvío have been described by Díaz-Martínez *et al*. (2018) (Figs. 4a, c). The track-bearing levels are mentioned, in ascending order, as PC-1-10.2, PC-1-15.9, PC-1-20.5, PC-1-23.3, PC-1-23.7, and PC-1-24.3.

PC-1-10.2: with footprints on a bedding-plane preserved mainly as negative epichnia, two of them preserved in cross-section as well. The tracks are at least eleven, semicircular to circular of about 30-50 cm diameter. Some of the footprints have abundant wrinkle structures, interpreted as microbial mat.

PC-1-15.9: with several cross-section tracks of about 20 cm depth.

PC-1-20.5: where the footprints are on a bedding-plane, preserved as negative epichnia. They are circular to subcircular depressions of about 20-30 cm diameter, representing a trampled area. There are wrinkle structures, similar to those in PC-1-10.2, evidencing microbial mats.

PC-1-23.2: the three collected tracks, preserved as positive hypichnia or natural casts, PC-1-A, B and C, come from this level. Two of the tracks are tridactyl, mesaxonic, sub-symmetrical pes, slightly longer than wide (PC-1-A: 25 cm long, 28 cm wide; PC-1-B: 27 cm long, 29 cm wide). The digit impressions are short and wide, with blunt ends, and the heel impression is large and rounded. The third footprint (PC-1-C) displays an unclear contour of the track, and it seems to be laterally symmetrical, wider than long (33 cm long and 28 cm wide), possibly pentadactyl with very short digit imprints.

MANUSCRITO ACEPTADO

PC-1-23.7: with two different track-bearing levels. The specimens are preserved as cross-section, both as true tracks and natural casts. The most interesting specimen is a natural cast, of about 12 cm in depth, with no morphological features, but with large, parallel traces produced by the pedal integument when the autopod was moving into the substrate. The rest of tracks are poorly preserved, but the high density indicates an intense trampling.

PC-1-24.3: with the tracks on bedding plane, and some of them as cross-section as well. In the tracking surface, the tracks are semicircular concave depressions of about 25 cm diameter, with wrinkle structures interpreted as microbial mat.

2) Ortíz *et al*. (2013) have described some avian tracks from a new locality, near the Negro river, at east of Paso Córdoba. The footprints are tridactyl, small, with slender digit imprints, basally not in touch. The digit III impression is the longest, and the total divarication angle is from 100º to 120º.

3) The dinosaur tracks, at least seven ornithopod trackways accounting for 13 footprints, are large, tridactyl and mesaxonic; the digit imprints are wide, with rounded ends and with equidistant lengths; digits converging proximally into a broad heel trace (Calvo and Ortíz 2013).

4) There are several surfaces and localities with tetrapod tracks mentioned in the literature (Calvo and Ortíz 2011, Paz *et al*. 2014, Ortíz and Calvo 2017, Díaz-Martínez *et al*. 2017a), but none of them is clear enough about the exact geographic site (Figs. 4b-c). The specimens mentioned are: 1- tracks assigned to small Hadrosauridae, wider than long; hand and pes prints related with medium-sized Sauropoda Titanosauridae; and small avian tracks, from the Allen Formation (Calvo and Ortíz 2011); 2- small avian footprints, with slender digit impressions, and large dinosaur tracks in cross-section, probably sauropodian, from the Anacleto and Allen Formations (Paz *et al*. 2014); 3- avian tracks, compared to *Barrosopus slobodai*, hand and pes prints assigned to medium-sized Sauropoda Lithostrotia, and tracks

MANUSCRITO ACEPTADO

related to medium-sized Hadrosauridae, from the Allen Formation (Ortíz and Calvo 2017); and 4- several tracks, even in cross-section and with skin traces, tetradactyl and tridactyl avian tracks, and tridactyl footprints attributed to large ornithopods, from the Anacleto and Allen Formations (Díaz-Martínez *et al*. 2017a, 2018).

Comments. The first tetrapod ichnological records from the Paso Córdoba area are known since the report of tracks from the Anacleto and Allen Formation (Calvo and Ortíz 2011, 2013, Ortíz *et al*. 2013). Since then, many other track-bearing localities and levels have been discovered, some of them published or mentioned in the literature (Paz *et al*. 2014, Ortíz and Calvo 2016, Díaz-Martínez *et al*. 2017a, 2018) and many others remain still unpublished (Figs. 4b-e).

1) The tetrapod tracks described by Díaz-Martínez *et al*. (2018) lack clear anatomic features. Therefore, they were not assigned to any ichnotaxon with confidence. Two of them (PC-1-A and B) are tridactyl, mesaxonic and sub-symmetrical and they were classified as cf. Iguanodontopodidae. The rest are poorly preserved and they were considered as indeterminate vertebrate tracks.

2) Ortíz *et al*. (2013) compared these avian footprints with *Barrosopus slobodai* from the Campanian Sierra Barrosa Formation, Neuquén (see Coria *et al*. 2002, for further details).

3) Based on the track morphology, Calvo and Ortíz (2013) claimed that the specimens are related to ornithopod dinosaurs, more probably to hadrosaurs.

4) The different track record mentioned and described in the literature (*i.e.*, Calvo and Ortíz 2011, Ortíz *et al*. 2013, Ortíz and Calvo 2017, Díaz-Martínez *et al*. 2017a) reaffirms the ichnological potential of the Paso Córdoba area.

Ingeniero Jacobacci area

MANUSCRITO ACEPTADO

Materials. 1) An avian track-bearing slab, CICRN 15-IV-78-1 (currently housed in the repository of the Museo di Storia Naturale of Venice, Italy) and other *in situ* slabs, from Montonilo place, about 60 km northeast of Ingeniero Jacobacci town (Casamiquela 1987, 1996, Leonardi 1994, Díaz-Martínez *et al*. 2015), from the Angostura Colorada Formation; 2) several *in situ* avian track-bearing levels and avian track-bearing slabs sited in one pavementof the city (Díaz-Martínez *et al*. 2015), from the María Luisa farm, near Ingeniero Jacobacci, from the Angostura Colorada Formation; and 3) one track-bearing slab, MJG 263, and one probably natural cast of a "Rheidae" track, MJG 304 (Casamiquela 1996, Leonardi 1994), from the Bajo Colorado, exact locality unknown, near Ingeniero Jacobacci town, from the Río Negro Formation (Fig. 5).

Description. 1) The slab CICRN 15-IV-78-1 is a yellowish-pink coarse-grained sandstone, of about 42 cm by 45 cm, preserving several tracks and traces in positive hyporelief (Fig. 5c). Originally, Casamiquela (1996) mentioned and described two new ichnotaxa: 1- *Tridigitichnus inopinatus* is represented by a tridactyl footprint, with short and wide digit imprints, proximally not in touch, and a tentatively associated hand print. It was assigned to small hadrosaurs with doubt. 2- *Patagonichnornis venetiorum*, with avian affinity, is represented by at least five tridactyl, mesaxonic tracks, with slender digit imprints directed forward, with no evidence of webbing trace or digit I impression, wider than long (averaging 65.0 mm long, 96.0 mm wide), with divarication angle between digit impressions II and IV of about 145º.

2) The footprints from the María Luisa site (Fig. 5a,b), both the avian track-bearing slabs conforming the pavement of a particular house (Fig. 5d,e) and the still *in situ* track in the outcrops, display two different morphologies (Díaz-Martínez *et al*. 2015). They are tridactyl and mesaxonic, with slender digit imprints, with no evidence of webbing trace or digit I impression. The morphology A is composed of three isolated, laterally symmetric

MANUSCRITO ACEPTADO

tracks, wider than long (averaging 81.0 mm long and 108.4 mm wide), with an average divarication angle between digit impressions II-IV of 150º. The morphotype B includes two small, laterally asymmetric, isolated footprints (averaging 38.2 mm long and 41.3 mm wide), with an average divarication angle between digit impressions II-IV of 109º.

3) The slab MJG 263 has at least four avian footprints preserved as negative epichnia (Fig. 5f). The tracks are tridactyl, mesaxonic, and approximately as wide as long (average of 25.7 mm long and 28.0 mm wide). The digit imprints are very slender, proximally not in touch, and distally acuminated. These footprints had been considered as avian tracks by Casamiquela (1969) and Leonardi (1994).

The specimen MJG 304 is a 3-D natural sandy cast, briefly mentioned by Casamiquela (1987:449, 1996:89) (Fig. 5g). It is 12.6 cm long and 6.8 cm in maximum width. It seems to display a central digital imprint and two lateral minor ones, all of them broad and robust, with pad or digital traces, and practically parallel to each other. The distal tips of the three digit impressions are broken.

Comments. 1) In the seventies, one slab with avian footprints have been collected from Montonilo place, about 65 km at northeast of Ingeniero Jacobacci town, in the centre-west of the province (Basaglia *et al*. 1980, Casamiquela 1987, 1996, Leonardi 1994). Currently, the slab is housed in the Museo di Storia Naturale of Venice, Italy, thanks to G. Ligabue, President of the Fundación Veneciana, who supported the fieldtrip to collect the slab. Besides, *sensu* Leonardi (1994), in some moment, it has been on a pavement, probably from Ingeniero Jacobacci, given that it still has remains of cement. Based on the traces preserved in the slab CICRN 15-IV-78-1, the names *Patagonichnornis venetiorum* and *Tridigitichnus inopinatus* were mentioned for the first time by Casamiquela (1987: p. 449 and 448, respectively) with no description of the traces, but brief references of the purported producers. The ICZN (Art. 13.1) does not validate an ichnotaxon published after 1930 without its corresponding

MANUSCRITO ACEPTADO

description, therefore these names are considered as *nomina nuda*. This does not disqualify them from being used later as valid names, such as Casamiquela (1996) did, satisfying the requirements of the ICZN, conforming the valid names *Patagonichnornis venetiorum* Casamiquela, 1996 and *Tridigitichnus inopinatus* Casamiquela, 1996. Leonardi (1994) questioned the quality of *T. inopinatus* and kept it as *nomen nudum*. *P. venetiorum* was considered as *nomen nudum* by Coria *et al*. (2002) and Díaz-Martínez *et al*. (2015), but because of unawareness of the correct naming by Casamiquela (1996). Actually, these ichnotaxa are under study and more details will be published in future contributions.

2) The avian track-bearing slabs from the María Luisa site are paving a pavement in the centre of Ingeniero Jacobacci since many decades ago. After some fieldtrips by the authors of this contribution, ichnological levels have been discovered in the farm, being currently under study (Díaz-Martínez *et al*. 2015).

3) The tracks preserved in MJG 263 have been already briefly mentioned as related to an avian origin (Casamiquela 1969:301, 1974:265, 1996:89, Leonardi 1994:35, Melchor 2009:209), while the specimen MJG 304 has been compared to a Rheidae track by Casamiquela (1987:449, 1996:89). However, in both cases, no further morphological detail was given. After studying MJG 304, based on its morphology, it may not be a vertebrate trace, and new findings could help to disentangle this issue.

Both specimens have been mentioned as coming from the Río Negro Formation (upper Miocene-lower Pliocene), based on the lithology, although no data about the exact provenance place have been provided. The lithostratigraphic unit of provenance of this material is dubious, seeing that it could be identified with both units, the Río Negro and Coli Toro Formations, based on different geological mappings (Gonzalez *et al*. 1999, Bilmes *et al*. 2013, 2017) and the field data and geological sections provided by Casamiquela (1969).

MANUSCRITO ACEPTADO

Shoreline of the Río Negro province

Material. Several track-bearing surfaces (fallen slabs and *in situ* tracksites), from about 30 km of a marine beach area between the second descent of El Faro and La Lobería localities, near Balneario El Cóndor (*e.g.*, Angulo and Casamiquela 1982, Leonardi 1994, Aramayo 2007, Carmona *et al*. 2012, Melchor *et al*. 2013); three plaster casts, P.ICHN.U.N.S. 100 to 102 (Aramayo 2007) (Fig. 6).

Description. *Megatherichnum*. An *in situ* eight-track trackway, preserved as negative epichnia, has been assigned to *Megatherichnum oportoi* Casamiquela, 1974 by Aramayo (2007). The tracks are elliptical in shape, longer than wide (average 50 cm long, 30 cm wide), and wider in the anterior surface. The digit III imprint displays a clear claw trace.A conspicuous rim, generally anterior and laterally located, is observed. The producer of *Megatherichnum* has been attributed to ground sloths (*e.g.*, Casamiquela 1974, Aramayo 2007) with a bipedal locomotion. Besides, two isolated tracks preserved in a fallen slab as positive hypichnia and at least six *in situ* tracks in negative epichnia, have been mentioned as ?*Megatherichnum oportoi* (sensu Angulo and Casamiquela, 1982).

Cf. *Mylodontidichnium* isp. It consists of an *in situ* trackway made up of ten tracks, preserved as negative epichnia, and one plaster cast, P.ICHN.U.N.S. 100 (Aramayo 2007). The tracks are sub-elliptical in shape, longer than wide (average 30 cm long, 15 cm wide), while the posterior area is narrower than the anterior one (Aramayo 2007). They preserve a clear claw impression in the anteromedial surface. It has been related to a bipedal ground sloth (Aramayo 2007).

Falsatorichnum cannabius Casamiquela 1982 *in* Angulo and Casamiquela (1982). The holotype is a trackway with three tracks preserved as positive hyporelief (Angulo and Casamiquela 1982). Moreover, there are two other trackways assigned to this ichnospecies. The tracks are elliptical and longer than wide (about 35 cm long, 22 cm wide). The erosion

MANUSCRITO ACEPTADO

could erase the medial notch, thus the shape can be ellipsoidal or sub-ellipsoidal as well. *Sensu* Angulo and Casamiquela (1982), they are morphologically similar to *Megatherichnum*, but different in size (*Falsatorichnum* half than *Megatherichnum*) (Angulo and Casamiquela 1982). The authors suggest that the trackmaker of these tracks is a bipedal ground sloth.

Porcellusignum conculcator Casamiquela 1982 *in* Angulo and Casamiquela (1982).It includes tens of tracks found in a fallen slab, preserved as negative epirelief. They are homopodic tridactyl manus and pes tracks with blunt claw traces. According to Angulo and Casamiquela (1982), *Porcellusignum conculcator* are probably associated with hydrochoerid mammals.

Macrauchenichnus rector Casamiquela, 1982 *in* Angulo and Casamiquela (1982). Two tridactyl tracks in a fallen slab, preserved as negative epirrelief, are the holotype. Angulo and Casamiquela (1982) assigned abundant material to this ichnotaxon, the bigger ones being about 18 cm long and 16 cm wide, and its producer has been attributed to macrauchenids mammals.

Caballichnus impersonalis Casamiquela, 1982 *in* Angulo and Casamiquela (1982).The holotype is a several trackways-bearing fallen slab, preserved as negative epirelief. However, there are more specimens assigned to this ichnotaxon (Angulo and Casamiquela 1982). The tracks are homopodic and monodactyl, with half-moon shape in the anterior area. They present conspicuous displacement rims in the anterior part. The track length varies from 13 cm to 22 cm. The authors related *Caballichnus* to equid mammals.

cf. *Porcellusignum* isp. The tracks are preserved as negative epirelief at the top of trampled surfaces in some fallen blocks. The pes tracks are tridactyl (9 cm wide, 8.5 cm long) and the manus tracks are tetradactyl (10 cm wide, 9.5 cm long), all of them wider than long. Aramayo (2007) related these tracks to hydrochoerid rodents.

MANUSCRITO ACEPTADO

Aramayo (2007) described two trackways and two isolated tracks of undetermined ungulates. The first trackway has 19 tracks, preserved as negative epirelief, circular and 22 cm of diameter. The other trackway, of six tracks, and the isolated imprints are subcircular (average 13.5 cm long; 11 cm wide). The producer of these tracks has been attributed to proterotherid mammals by Aramayo (2007).

A trackway accounting six pentadactyl tracks, related to a digitigrade mammal, was described by Aramayo (2007). The tracks are wider than long (average 9.6 cm long, 7.5 cm wide), with clear III-V digit impressions. Aramayo (2007) has related this trackway with a carnivorous marsupial, similar in size at least with *Thylacosmilus* sp.

Besides, two types of avian tracks have been described (Aramayo 2007). The first one is tridactyl, with the central digit imprint longer than the lateral ones, the divarication angle between II-III greater than between III-IV, and longer than wide (mean, 25 cm long; 17 wide). These tracks have been related to phorusrhacid birds. The other avian tracks are also tridactyl, with the digit III impression slightly longer than II and IV, with interdigital web impression. Aramayo (2007) related them to flamingo birds.

Carmona *et al*. (2012) figured some avian, mammal and indeterminated tracks, but they are neither described nor classified. The avian footprints are tetradactyl, mesaxonic and longer than wide (about 20 cm long). The axis of digit I impression corresponds with the axis of digit III imprint, which is the longest. The mammal tracks, preserved in a trampled surface, are semicircular, slightly longer than wide (about 10 cm long) and have claw impressions. Probably, they were produced by a carnivore mammal. From the same tracksite, Melchor *et al*. (2013) cited the presence of *Mylodontidichnum* and *Porcellusignum* mammal tracks, as well as *Phoenicopterichnum* and other undetermined avian footprints.

Comments. The track-bearing outcrops are a continuous area of about 15 km long between the second descent of El Faro and La Lobería localities, near Balneario El Cóndor, with several

MANUSCRITO ACEPTADO

sites that have not always been clearly determined in the literature, and therefore, in this contribution, will not be distinguished from each other. These ichnological records have been widely mentioned for decades (*e.g.,* Angulo and Casamiquela 1982, Aramayo 2007, Aramayo *et al*. 2004, Carmona *et al*. 2012). However, they are long known by authorities, colleagues and locals, who even mention unpublished sites, such as Punta Mejillón,about 100km west from the Balneario El Cóndor (*e.g.,* Archuby 2016, 2019 *pers. comm*., Valle 2018, 2019 pers.comm.).

On the Atlantic shoreline in the Río Negro province, the tetrapod ichnological record of the homonymous formation is studied at least since the 1970's (Casamiquela 1974, Carmona *et al*. 2012, for further details). This formation is considered eolian associated with shallow marine deposits (Carmona *et al*. 2012), and most of the tracks were found in the eolian facies. It is noteworthy that xenarthran and ungulate tracks are related to this facies, while the avian and carnivores ones are both in eolian and marine facies.

MANUSCRITO ACEPTADO

DISCUSSION

Sedimentology and environmental background

Although the overall track record of the Río Negro province exhibits complexity in regard of different geological contexts, besides long geological/stratigraphic history (see Temporal and palaeobiological considerations), it is possible to assess certain particularities and even coincidences on sedimentary processes that controlled footprint distribution. Trampled strata are distributed in several basins, as described before. In regard of palaeoenvironmental issues, ichnosites are constrained to three main sedimentary settings: fluvio-volcaniclastic, fluvial/fluvial-aeolian, and shallow marine systems.

Fluvio - volcaniclastic systems. Tetrapod tracks from the Los Menucos depocentre (Vera Formation) and from the Puesto Perdomo site (Marifil volcanic Complex) are preserved in volcaniclastic sediments. Interestingly, in both localities the interplay between fluvial processes and volcanic activity performed a main role enhancing tracks preservation. In Los Menucos, two main patterns were observed. The typical footprint preservation pattern is related to surfaces made up of medium- to coarse-grained, poorly sorted volcaniclastic sandstones with a minimum sedimentary reworking, being inferred as a product of sedimentation in a proximal fluvial environment (Citton *et al*. 2018). On the other hand, at the Yancaqueo locality thin sections analysis data supported the idea of a process in which the fluvial reworking played a more important role, modifying a substrate originally composed by a dacitic tuff (Citton *et al*. 2018).

At Puesto Perdomo site the process was quite similar, with the difference that the main volcanic components are tuff ash and pumice fragments (Díaz-Martínez *et al*. 2017b,c), suggesting more distance from the volcanic source.

In such environments, the good quality of footprints preservation, like true tracks, trackways, and also detailed digit impressions with rim displacement marks (Díaz-Martínez *et al*. 2017, Citton *et al*. 2018), suggests a very narrow preservation window enabled by the early cementation of volcanic components.

Fluvial/fluvio -aeolian systems. Several localities at Río Negro province provide good examples of track distribution in such environments. These localities are Ingeniero Jacobacci, the Shoreline of the Ezequiel Ramos-Mexía lake, Paso Córdoba, and the Shoreline of Río Negro. In overall sense tracksites are mainly distributed in two distinct palaeoenvironments: floodplain deposits of meandering rivers to shallow lakes and/or wet interdune deposits of aeolian settings (*e.g.*, Díaz-Martínez *et al*. 2015, 2017b). This distribution is consistent with the background of such kind of environments. Trampled floodplain deposits were found at

MANUSCRITO ACEPTADO

Ingeniero Jacobacci (Angostura Colorada Formation), Paso Córdoba (Anacleto-Allen Formations transition) and the Shoreline of Río Negro (lower and upper members of Río Negro Formation). Particularly, within fluvial environments, floodplain facies exhibit abundant trace fossil associations considering global records (see review in Melchor *et al*. 2012).

The stabilization of trampled surfaces by microbial mats is a process that needs to be highlighted. At Paso Córdoba tracksite such kind of record was observed mainly in ephemeral pond facies (Díaz-Martínez *et al*. 2018).

In regard of interdune track records, these are distributed in the shoreline of the Ezequiel Ramos-Mexía lake (Candeleros Formation), at Paso Córdoba (Anacleto and Allen Formations transition) and along the shoreline of Río Negro (lower and upper members of the Río Negro Formation).These deposits are suggesting short preservation windows in facies dominated by current activity with dissimilar levels of pedogenization, and aeolian activity (see Zavala and Freije 2001, Díaz-Martínez *et al*. 2018).Although tracks were found in dry interdune facies, the better preservation quality belongs to the transition between dry and wet interdune (Zavala and Freije 2001). This can be explained because at this position, seasonal changes in the freshwater body extension, result in an alternance of periods of subaerial and subaqueous deposition in marginal areas (Zavala and Freije 2001). Thus, footprints registered during periods of emergence could be preserved by the subsequent fine draping settled during the high water level (Zavala and Freije 2001).This seasonal constrained window of preservation in these sites is supporting the idea of recurrent patterns in such environments.

Marginal marine systems. Marginal marine trampled surfaces were identified in the Río Negro Formation, and such strata are included within the middle member (Zavala and Freije 2000). The facies analysis suggested a shallow marine environment recording the transition between offshore to shoreface and foreshore settings, which is supported with the invertebrate

MANUSCRITO ACEPTADO

trace fossils content that display ichnogenera assigned to the *Cruziana-Skolithos* ichnofacies transition (Zavala and Freije 2000). In regard of tetrapod track records, interestingly the bird and mammal footprints are preserved immediately below and above the marine member, within MISS-bearing facies, suggesting a tidal flat setting (Carmona *et al*. 2012, Melchor *et al*. 2013). In these tidal flat facies, microbial mats allowed footprint preservation in a process involving two main steps, first giving plasticity and cohesiveness to trampled sands, and later and after buried, microbial mat decayment induced early cementation (see Carmona *et al*. 2012).

MANUSCRITO ACEPTADO

Ichnological record

Los Menucos area. Rodolfo Casamiquela's contributions about this topic are noteworthy. He named seven ichnotaxa based on the tracks from the Tscherig farm, in the Los Menucos area (Casamiquela 1964, 1975), namely: "*Calibarichnus"*, "*Gallegosichnus*", "*Stipanicichnus*" and "*Palaciosichnus*", considered as junior synonyms of *Dicynodontipus*, and "*Shimmelia chirotheroides*", "*Rogerbaletichnus aguilerai*" and "*Ingenierichnus sierra*", considered as *nomina dubia* (Leonardi 1994, Melchor and de Valais 2006, de Valais 2008). Díaz-Martínez *et al*. (2014) suggested that the trackmaker of the last two ichnotaxa is related to the producer of *Dicynodontipus*. Besides, a footprint assigned as *Rhynchosauroides* isp. and several undetermined quadrupedal tracks are also cited from this locality (Manera de Bianco and Calvo 1999, Domnanovich *et al*. 2008).

On the other hand, the ichnotaxon *Pentasauropus* has been also identified, from the Yancaqueo farm, in the Los Menucos area (Domnanovich *et al*. 2008, Citton *et al*. 2018).

Puesto Perdomo site. The ichnological fieldworks in the Arroyo de la Ventana area are relative recent. Four tracks from the Perdomo site have been classified as cf. *Anomoepus* or *Anomoepus*-like footprints (Díaz-Martínez *et al*. 2017c). The studies in the Puesto Prado site are just in their early stages and only one *in situ* tridactyl track is known (Gónzalez *et al*. 2017).

Ezequiel Ramos-Mexía lake. The tracks from the Ezequiel Ramos Mexía area lack any ichnotaxonomical proposal. On the shoreline of the lake, a large surface with sauropodian and tridactyl tracks in the Salas site (Apesteguía 2005, Apesteguía *et al*. 2010, and 2019 *pers.comm*.) and a very well-preserved sauropodian trackway and many pterosaurian tracks, in a southernmost site (Novas 2009, Novas and Isasi 2019 *pers.comm.*) have been mentioned.

Several cross-section and plan view tracks have been recorded both in the La Buitrera and Cerro Policía localities, and some of them have been assigned to ornithopod dinosaurs (Candia Halupczok *et al*. 2018).

Paso Córdoba area. The Cañadón del Desvío site, near the Valle de la Luna Rojo, has provided six track-bearing levels, with footprints in cross-section and plan view, and three collected tracks (Díaz-Martínez *et al*. 2018). Two of the collected tracks, PC-1-A and B are classified as cf. Iguanodontopodidae, while the third one is a pentadactyl, indeterminate track; in many cases, evidence of microbial mat is recorded in the footprint surfaces (Díaz-Martínez *et al*. 2018).

There are several other ichnological localities mentioned in the literature, mainly with avian –even some of them are considered as cf. *Barrosopus slobodai*–, sauropodian and hadrosaurian tracks, from a site near the Valle de la Luna Amarillo and other places with an unknown exact location (Calvo and Ortíz 2011, 2013, Ortíz *et al*. 2013, Paz *et al*. 2014, Ortíz and Calvo 2017, Díaz-Martínez *et al*. 2017a).

Ingeniero Jacobacci area. Based on the traces preserved in a slab from the Montonilo site, *Patagonichnornis venetiorum* Casamiquela, 1996 and *Tridigitichnus inopinatus* Casamiquela, 1996 have been named, althought now both ichnotaxa are considered *nomina nuda* (Leonardi 1994, Coria *et al*. 2002, Díaz-Martínez *et al*. 2015).

MANUSCRITO ACEPTADO

The rest of the record consists in several avian tracks, including a putative “Rheidae” track (Casamiquela 1996, Leonardi 1994, Díaz-Martínez *et al*. 2015).

Shoreline of Río Negro province. This is the area with more ichnotaxa (Aramayo 2007). *Megatherichnum oportoi* was described by Aramayo (2007). Later, Casamiquela (*in* Angulo and Casamiquela 1982) named four new ichnotaxa: *Porcellusignum conculcator*, *Macrauchenichnus rector*, *Falsatorichnum cannabius* and *Caballichnus impersonalis*, but Melchor (2009) questioned the validity of the last two icnospecies. Moreover, Angulo and Casamiquela (1982) classified as ?*Megatherichnum oportoi* some other tracks. Another tracks have been assigned to *Mylodontidichnum* and cf.

Mylodontidichnium isp.,*Phoenicopterichnum*, and cf. *Porcellusignum* isp. (Aramayo 2007, Melchor *et al*. 2013). Finally, some artiodactyl, carnivorous and avian tracks were also found (Aramayo 2007, Carmona *et al*. 2012).

Temporal and palaeobiological considerations

The track record of the Río Negro province and their provenance units are summarized in Figure 7. The Los Menucos area returned predominantly two types of therapsid tracks that can be related to two distinct group of producers: theriodonts (Domnanovich and Marsicano 2006) and small-sized dicynodonts (Francischini *et al*. 2018) for the Lopingian-Early Triassic, while the kannemeyeriiformes are recorded in the ?Middle-Late Triassic (Citton *et al*. 2018).

The Early Jurassic is recorded in the Puesto Perdomo site (Arroyo de la Ventana area) from which the footprints of basal ornithischian dinosaurs were reported.

The “mid” Cretaceous tracks are represented by the Ezequiel Ramos Mexía dam record, which is dominated by sauropod, ornithopod and theropod tracks. On the other hand, the Paso Cordoba and Ingeniero Jacobacci areas represent the last Cretaceous fauna in the Patagonia after the entrance of North American immigrants (such as hadrosaurs or

MANUSCRITO ACEPTADO

ankylosaurs; *e.g.*, Leanza *et al*. 2004). The tetrapod ichnological record is dominated by different types of avian tracks, with hadrosaur and sauropod tracks less represented.

Finally, the Río Negro Formation tetrapod tracks are mainly characterised by avian and mammalian tracks. The avian ones have been related to small shorebirds, cariamid and flamingos. Among the large mammals, it should be noted the high presence of ground sloths, besides hydrochoerid and macrauchenids mammals. It is also cited the presence of hydrochoerid rodents and carnivorous marsupials. Aramayo (2007) pointed out that these ichnotaxa represent a faunistic autochtonous association before the entrance of North American immigrants, the "true carnivorous mammals", which will drive to extinction the mentioned marsupials and phorusrhacid birds.

A brief comment about the ichnological heritage of the Río Negro province

The ichnological record from the Río Negro province allows to make some consideration about the inherent heritage. Many of the specimens of the province (i.e., from the Tscherig and Yancaqueo localities,in the Los Menucos area, Puerto Perdomo and Puesto Prado sites, in the Arroyo de la Ventana area, and María Luisa site, in Ingeniero Jacobacci), were found during flagstone quarry activities (Fig. 2h). In most cases, these materials were directly recognized or by the quarry workers during the extraction or subsequently by no professionals –related to palaeontology– in, for instance, the city pavements (Fig. 5d,e). The track-bearing slabs, consequently, often are not accompanied by significant information, such as the stratigraphic level and lithostratigraphic unit of provenance, the sedimentological features of the trampled level, an analysis of the stratigraphic section, the associated fauna, among others. As a result, correctly relocate the material in the stratigraphic succession and attempt to interpret its preservational history can be a hard task.

MANUSCRITO ACEPTADO

A second aspect to consider concerns the tracksites and all the footprints that are in the field and can be damaged by weathering and/or geomorphological processes. Two striking examples are provided by the imprints from the Ezequiel Ramos Mexía lake and the Atlantic shoreline. In the first case, tetrapod tracks present a high-risk of vulnerability (*sensu* García Ortiz *et al*. 2014) due to dam floods. In the second case, the tracks are strongly affected by both tidal variations that increase the erosion process on the exposed surfaces and the collapse of the rocks from the cliffs (Figs. 6b, f).

It is especially important when the type and other referred material are still *in situ*; performing management tasks for their conservation will be crucial. It could be developed generating scientific plaster casts (such as the plaster casts made for preserving the Río Negro Formation specimens and housed in the P.ICHN.U.N.S.; see Aramayo 2007) or three-dimensional digital models through different methodologies (*e.g.,* digital photogrammetry and laser scanning).

CONCLUDING REMARKS

Since the 1960's, the ichnology of Río Negro province provided some of the seminal contributions of this discipline in Argentina. These works have been a main background from which modern contributions on vertebrate ichnology have developed.

The tetrapod track record from the Río Negro province comes from six different areas, each one with one or more track-bearing localities, spanning chronostratigraphically from thePermo-Triassicto Neogene. The track record is related to different palaeoenvironments and provides a good example of how certain environments can exhibit analogous ichnological patterns of distributions along space and time. The late Palaeozoic and Triassic record (Los Menucos and Arroyo de la Ventana areas) is related to proximal fluvial environments, in

MANUSCRITO ACEPTADO

which the sediment deposition was strongly controlled by the volcanic activity. The Cretaceous record (Ingeniero Jacobacci, Ezequiel Ramos-Mexía lake, and Paso Córdoba areas) is instead related to fluvial and aeolian environments, similarly to the Mio-Pliocene record (shoreline of the Rio Negro province) which is also characterised by footprints in shallow marine, coastal environments.

From a palaeobiological point of view, the described ichnological records from the Río Negro province is represented, at least, by two groups of therapsids in the late Permian-Early Triassic and Late Triassic epochs. A quite large biodiversity characterises the Cretaceous record, being represented sauropods, ornithopods, theropods, and even different birds. In addition, the Mio-Pliocene record is represented by footprints related to small shorebirds, cariamid and flamingos, large mammals such as ground sloths, macrauchenids, hydrochoerid rodents and carnivorous marsupials.

It is worth noting that some areas, like Los Menucos and the shoreline of the province, have been profusely mentioned in the literature, while other areas, like Ingeniero Jacobacci and Paso Córdoba, were less investigated. Other areas, such as Arroyo de la Ventana and the Ezequiel Ramos Mexia from the Río Negro side area, are virtually unknown. New contributions are expected from all these areas, in order to increase our understanding and add new insights to the palaeobiological reconstructions.

MANUSCRITO ACEPTADO

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MANUSCRITO ACEPTADO

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Figure captions.

Figure 1. Location map. Track-bearing sites in the Río Negro province, Argentina. (1) Tscherig, (2) Vera and (3) Yancaqueo localities, in the Los Menucos area; (4) Puesto Prado and (5) Perdomo sites, in the Arroyo de la Ventana area; (6) Cerro Policía, (7) La Buitrera, (8) “Novas place” and (9) Salas localities, in the Ezequiel Ramos Mexía area; (10) Paso Córdoba área; (11) Montonilo and (12) María Luisa sites, and (13) Bajo Colorado place, IngenieroJacobacci area; and (14) different localities in the Río Negro shoreline area.

Figure 2. Vertebrate tracks from the Los Menucos area (Los Menucos Group). *Dicynodontipus* and *Dicynodontipus*-like: a) MJG, no collection number; b) MPA 76-609-I-E; c) MPA 76-614-I-E. *Pentasauropus*:d) MPCA 27029-16; e) MPCA 27029-33; f) MMLM 075-1 (ex MRPV 1987P.V.06 *in* Domnanovich et al. 2008). The succession outcropping in the Los Menucos area at Puesto Vera (g) and Puesto Tscherig (h). Scale bars: 5 cm (a-f), 1 m (g) and 10 m (h).

Figure 3. Vertebrate tracks from the Arroyo de la Ventana area (Marifil Volcanic Complex). a) undetermined tridactyl track MRPV427/P/13 (Puesto Perdomo site); b) outline drawing of a *in situ* tridactyl track (Puesto Prado site). Vertebrate tracks from the Ezequiel Ramos-Mexia dam area, in the shoreline of the Río Negro side (Candeleros Formation). c) tridactyl track (Sala site); d) track-bearing level (Sala site); e) track bearing level (Sala site); f) sauropod manus-pes set (south of the Villa El Chocón town). Scale bar: 5 cm (a-c). Photographs in c, d and e by S. Apesteguía. Photograph in f by F. E. Novas.

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Figure 4. Vertebrate tracks from the Paso Córdoba area (Anacleto and Allen formations). a) Trampling surface (Cañadon del Desvío locality); b)tracks in cross-section in the same surface that a; c) quadrupedal vertebrate tracks; d) avian footprints; e) avian footprints (exact locality unknown, near the Valle de la Luna Amarillo). Scale bar: 50 cm (b), 8 cm (c, e) and 5 cm (d).

Figure 5. Vertebrate tracks from Ingeniero Jacobacci area (Angostura Colorada and Río Negro formations). a) General view of the succession outcropping the María Luisa site (arrow indicates the outcrop); b) detail of the fossiliferous level indicated in a; c) avian track-bearing slab CICRN 15-IV-78-1 (Montonilo place). Pv: *Patagonichnornis venetiorum*, Ti_p and Ti_m *Tridigitichnus inopinatus* pes and manus. d, e) avian track-bearing slabs (from María Luis site, in the Ingeniero Jacobacci pavement); f) avian track-bearing slab MJG 263 (Bajo Colorado place); g) putative natural cast of a “Rheidae” MJG 304 (Bajo Colorado place). Scale bars: 1 m (b), 5 cm (f, g), 8 cm (e) and 10 cm (c, d).

Figure 6. Vertebrate tracks from the shoreline of the Río Negro province (Río Negro Formation). a) phorusrhacid track; b, f) collapsed rocks, with track-bearing surfaces, from the cliffs; c, e) avian tracks; d) trackway related with cornivorous marsupial. Scale bar: 5 cm (c, e) and 10 cm (a, d).

Figure 7. Synoptic scheme showing the vertebrate record of the Río Negro province. a) Los Menucos area; b) Arroyo de la Ventana area; c) Ezequiel Ramos Mexía lake area; d) Ingeniero Jacobacci area; e) Paso Córdoba area; f) Shoreline of the Río Negro province. For radiometric datings see references in the text.

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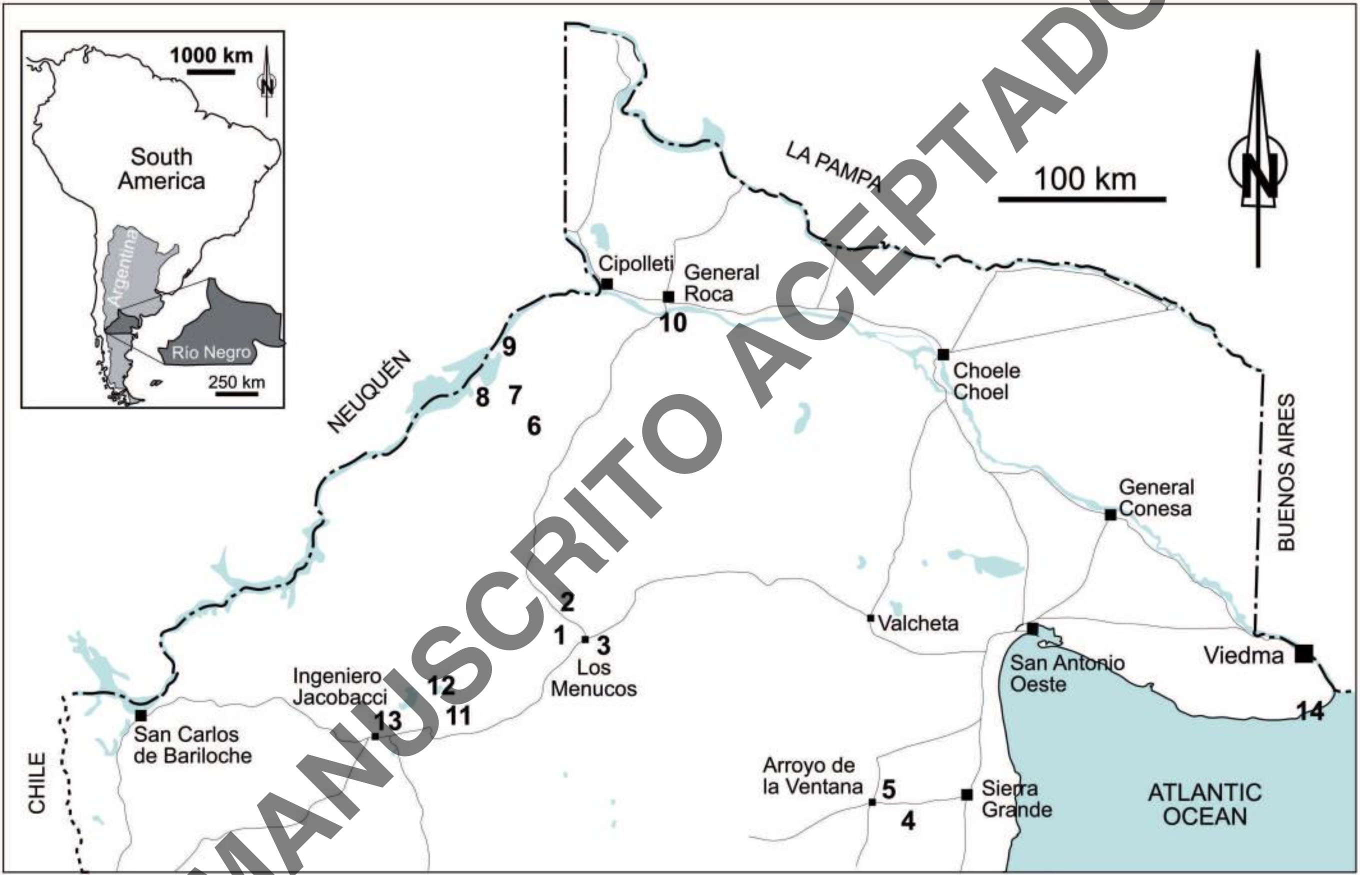

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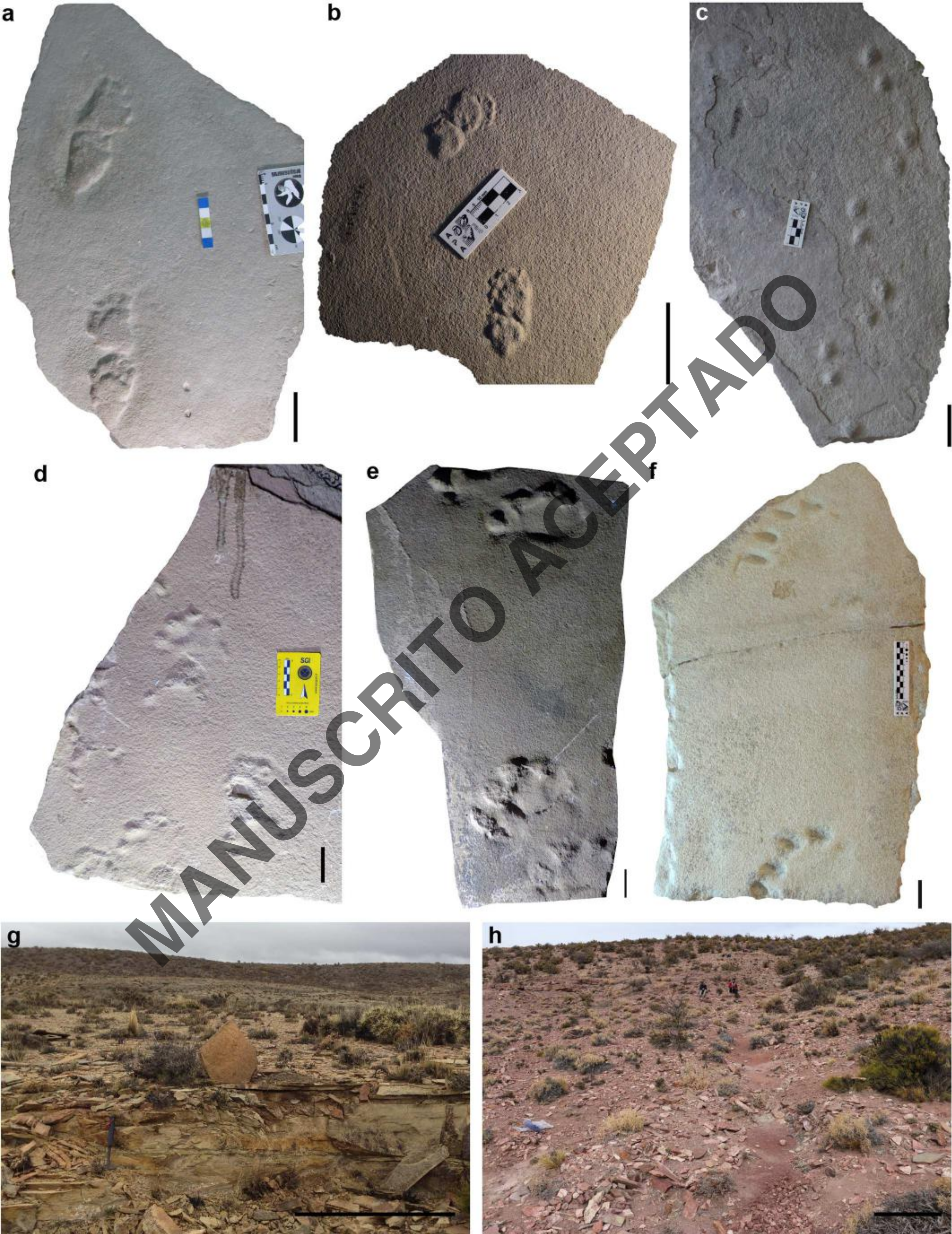

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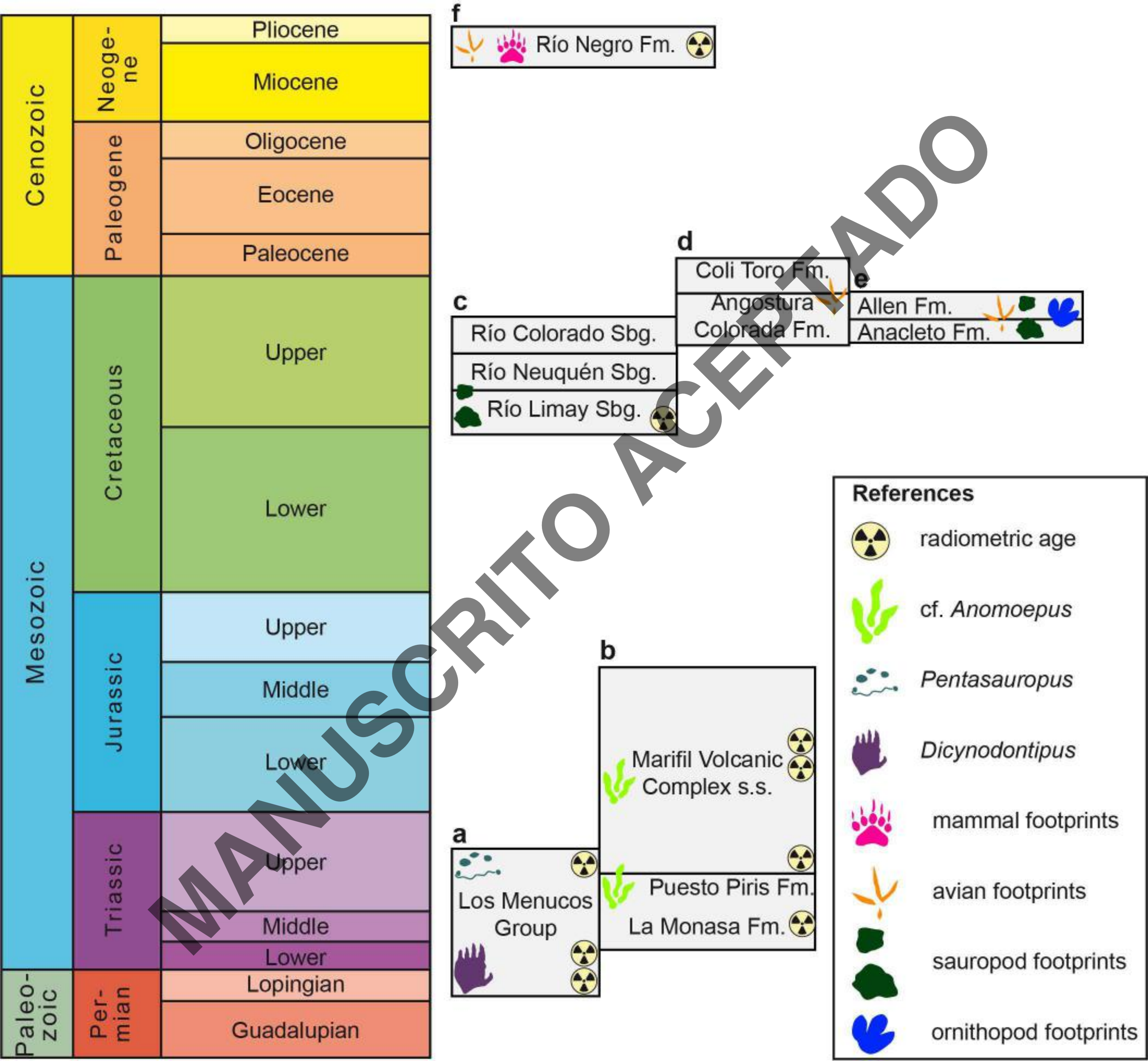

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