Journal Pre-proof

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MIDDLE MIOCENE
VINCHINA FORMATION
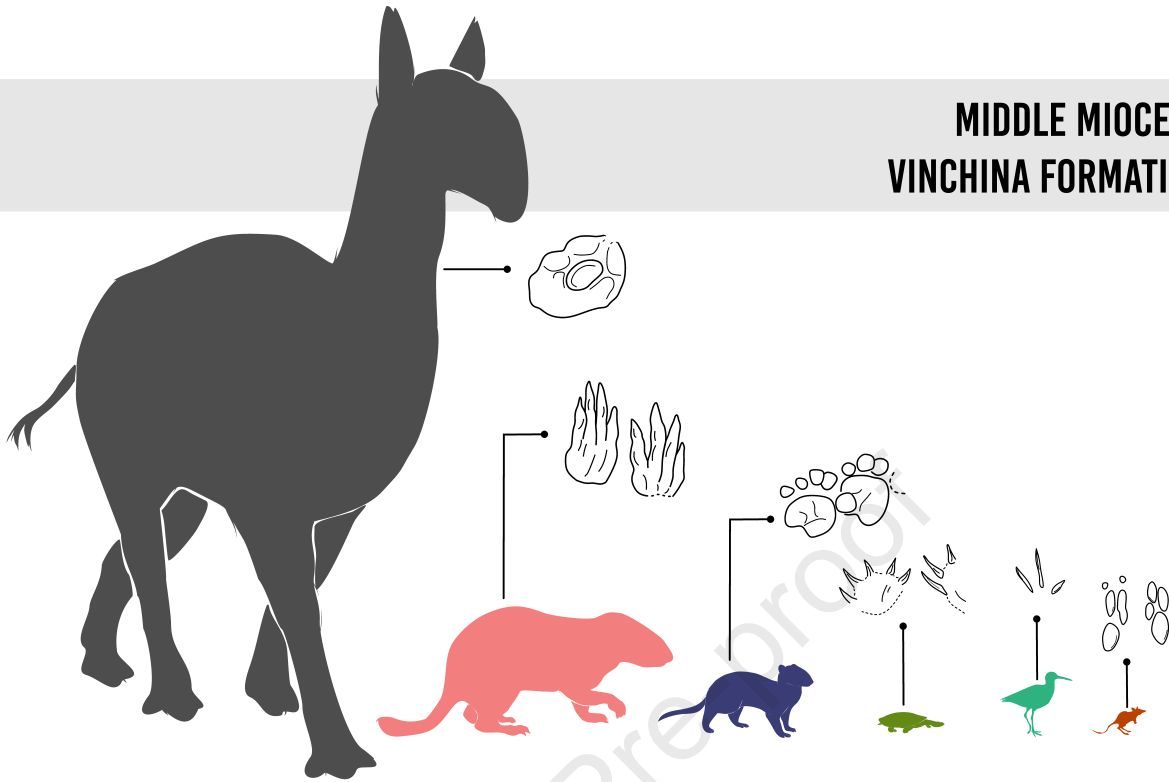
● **Indeterminate ungulate footprints**
≈ 62 — 200 kg

● *Tacheria troyana*
16 kg

● *Carnivoripeda sudamericana*
0.7 kg

● cf. *Chelonipus torquatus*
0.34 kg

● *Aviadactyla vialovi*
0.043 kg

● **Argyrolagid footprints**
0.26 kg

A new vertebrate ichnological association sheds light into the small metatherian record of the Middle Miocene in South America

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Abstract

Vertebrate ichnological associations recorded in Middle Miocene successions were unknown in South America. During that time, South America was isolated from other continents and had a unique endemic fauna and flora. The lower Vinchina succession occurred between 15.6 – 12.7 Ma and records the footprints of highly specialized mammals, reptiles, and birds for the first time. To identify all footprint's producers, we focused on anatomical traits of the

appendicular skeleton represented on the footprints together with body size estimations of the producers as body mass and the apparent trunk length (GAD). *Carnivoripeda sudamericana* nov. isp. reveals a weasel-like producer of ~1 kg and a trunk length of 19 – 26 cm most likely attributed to metatherian carnivores (Sparassodonta). They represent the oldest carnivore footprints in South America. Small bipedal rodent-like mammals of ~ 280 g using a jumping gait (Morphotype A) are interpreted as produced by highly specialized South American marsupials, argyrolagids, whose footprints were unknown until now. Other mammalian footprints recorded are *Tacheria troyana* most likely produced by dinomyid caviomorph rodents. They represent animals of ~16 kg and a trunk length of 48 – 55 cm, like living dinomyids. Subcircular to oval structures (Morphotype B) seems to be produced by medium-sized ungulates, while stepping in cohesive and plastic soupy sediments. cf. *Chelonipus torquatus* suggests small freshwater turtles (Chelidae or Podocnemididae), of ~ 400 g consistent with a trackmaker of carapace size of ~ 9 cm. *Aviadactyla vialovi* was most likely produced by a small shorebird (Scopolacidae) of ~ 40 g. All footprints are preserved on crevasse splay deposits of anastomosing fluvial systems together with meniscate feeding (*Taenidium barretti*) and simple dwelling trace fossils (*Palaeophycus tubularis*) produced by insects and are an example of the *Scoyenia* Ichnofacies.

1. Introduction

The Vinchina Basin of La Rioja Province at Northwestern Argentina (Fig. 1), is a thick continental succession deposited under a wide variety of depositional systems (i.e., fluvial, lacustrine, and eolian) that bears diverse and exceptionally well-preserved trace-fossil assemblages. Within the Vinchina Basin, the Vinchina (Early to Late Miocene) and Toro Negro (Late Miocene – Pleistocene) formations preserve the most remarkable ichnological assemblages (e.g., Krapovickas et al., 2009, 2017; Krapovickas and Nasif, 2011; Farina et al., 2019; Vera and Krapovickas, 2022). Footprints are abundant, easily found, and exceptionally well-preserved, and document the existence of mammals, birds, and reptiles most of which have no representatives alive within extant faunas. The Vinchina succession cropping out at Quebrada de la Troya and Quebrada del Yeso are the most accessible and frequently explored. The Quebrada de la Troya is crossed by route 76 that leads to the Pircas Negras international pass. Even though the Quebrada del Yeso is more difficult to cross than the Quebrada de la Troya, it is a wide creek, and it is possible to access by 4WD vehicle. Recently, we made an exploratory expedition to a northern creek, Quebrada Pedregal Negro, looking for a fallen block with mammalian and avian track found by Dr. Limarino and his team in 2013 (see Krapovickas et al., 2017). We walked through the Quebrada de Pedregal Negro to its highest point, where we were unable to continue exploring. Fortunately, we not only found the countermold of the fallen block, but a wider ichnological assemblage.

The ichnological assemblage is recorded in the lower member of the Vinchina Formation and occurred between 15.6 – 12.7 Ma, during the Middle Miocene. During that time, South America was isolated from other continents and had a unique endemic fauna and flora (Simpson, 1980; Goin et al., 2012). The Great American Biotic Interchange (GABI) is mostly agreed to start right after, during the Late Miocene, when the first North American migrants were recovered (Stehli and Webb, 1985; Reguero and Candela, 2011, Cione et al.

2016). It is one of the largest episodes of biological migration between previously disconnected landmasses, North and South America (Wallace, 1876; Simpson, 1980; Webb, 1991). The first widely accepted skeletal remains recovered in South America are procyonids, the evolutionary lineage of modern coati and raccoon, at about 7.2 – 5.9 Ma (Reguero and Candela, 2011; Prevosti et al., 2021).

During our expedition we found a diverse ichnological association that includes footprints very delicately impressed showing great anatomical details. Among them, footprint morphologies of small-sized animals that has not been recorded until now. The aims of this contribution are (1) to describe the fossil footprints found at Quebrada Pedregal Negro; (2) to identify all footprint's producers by combining the analysis of anatomical traits of the appendicular skeleton represented on the fossil footprints together with body size estimations of the producers as body mass and the apparent trunk length; (3) document and discuss the paleoenvironmental, paleoecological, and stratigraphic implications of the Vinchina footprint.

2. Geological Setting

The Vinchina Formation is a non-marine stratigraphic unit (Turner, 1964), deposited within the Vinchina Basin, a Neogene broken foreland basin (Marenssi et al., 2015). The basin is located near the town of San José de Vinchina in the Sierra de Los Colorados at La Rioja Province, Northwestern Argentina (Fig. 1). At Sierra de los Colorados the Vinchina Formation is cut by seven paralel creeks (i.e from North to South mencionarlas todas). The National route 76 is placed across Quebrada de la Troya and together with the Quebrada del Yeso, are the most explored areas so far. The footprints presented herein are recorded at the Quebrada Pedregal Negro, north of Quebrada de la Troya (Fig. 1).

REFERENCES

National Road	—76—
Town	🟡
Study area	⭐
Permanent river	•••••••••
Ephemeral creek	• • • •
Mountain range	🔺

Fig. 1. Location map of the study area at the Sierra de los Colorados, northwestern Argentina where the Vinchina Formation crops out.

1.5-column fitting image.

The Vinchina Formation comprise red sandstones, mudstones, and conglomerates mostly accumulated by fluvial and lacustrine processes and minor intercalations of eolian deposition, during arid to semi-arid climatic conditions, (Tripaldi et al., 2001; Ciccioli et al., 2013; Marenssi et al., 2015). The unit is divided into two informal members separated by a low angle erosive surface (Ramos, 1970). At Pedregal Negro, the Vinchina succession is 1,996 m thick, mostly composed by reddish sandstone, mudstone, and scarce conglomerate with abundant desiccation cracks, mainly deposited in fluvial systems and fluvio-aeolian interactions. It contacts at its base with the Vallecito Formation and to the top with the Toro Negro Formation, however most of the upper member of the Vinchina Formation was estimated via satellite images, as it is not reachable by foot (Schencman, 2016). As such, most of the explorable outcrops correspond to the lower member of the Vinchina Formation which is dominated by fluvial sandstones and mudstones with high development of interchannel areas.

The fossil footprints presented herein are preserved in fluvial systems composed by medium-grained sandstones, mudstones and conglomerates (Facies 5 according to Schencman, 2016). The sandstones are mostly massive, planar laminated, and planar cross-bedded, deposited in tabular beds, with flat or slightly irregular bases. The mudstones are red to brown, massive to laminated, and deposited in beds of 1 to 5 cm, however they can be stacked in banks up to 10 m thick.

Conglomerates are scarce and mostly composed of intraformational mudstones preserved at the base of fining-upward mudstone-sandstone succession. They are interpreted

by Schencman (2016) as a multichannel fluvial system with good development of interchannel áreas. This anastomosing system is mostly composed of low sinuosity channels with limited lateral migration and floodplain deposits with abundante crevasse splays. The tetrapod footprint association is preserved in the interchannel area at the top of fine-grained sandstones of crevasse splays. But it is also casted at the base of interchannel sandstones. Feeding and dwelling invertebrate traces such *Palaeophycus tubularis*, *Taenidium barretti* are preserved on mudstones levels with multiple sized mudcracks (Fig. 2).

At Pedregal Negro two of the four stages of paleoenvironmental evolution of the Vinchina Formation are exposed (Schencman et al., 2018). The first is in the lower part of the Lower Member, where sediment was transported by braided streams of an ephemeral fluvial system. Here we can see aeolian reworking (aeolian-fluvial interaction). The second stage of paleoenvironmental evolution is observed in the rest of the lower Member, where fluvial transport dominates (anastomosed systems) and large developed terminal lobes are observed.

The other two stages are developed in the upper member. In the lower third, the third stage is observed, which consists of gravelly-sandy braided streams (north), sandy-gravelly braided and meandriform streams (central region) and anastomosed with eolian-fluvial interaction (south). The fourth stage develops in the remainder of the upper member and consists of meandering systems in the Middle sector that provide fine sediment to ephemeral lake systems at the southern.

The Vinchina Formation age is based on high-precision CA-TIMS U-Pb dating on volcanic zircons that estimate a span roughly of 15.6 – 9.2 Ma (Ciccioli et al., 2014). More recent U–Pb detrital and volcanic zircon ages from the overlying Toro Negro Formation show that its deposition spans roughly 6.9 – 2.3 Ma (Amidon et al., 2016). Later, Collo et al. (2017) reported a LA-ICP-MS U–Pb zircon dating of 12.62 ± 0.4 Ma for a conspicuous tuff level at the top of the lower member of the Vinchina Formation observable in all localities

including the Pedregal Negro sussession. The Pedregal Negro ichnoassociation is stratigraphicaly below the tuff level, so the ichnoassociation occurred between 15.6 – 12.7 Ma.
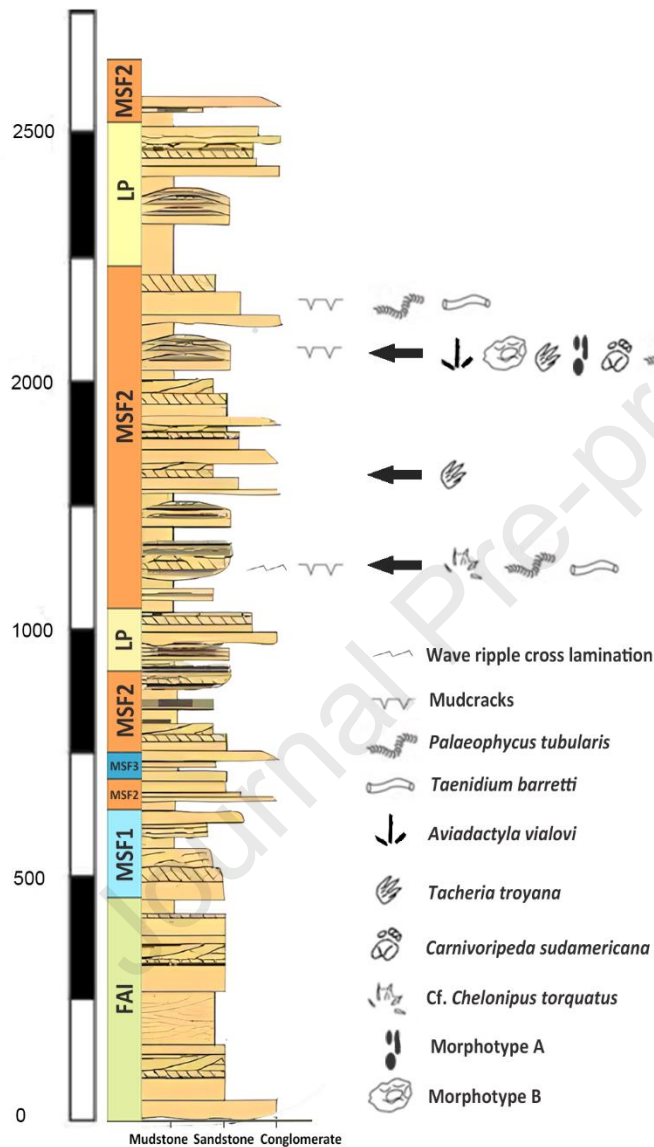
Fig. 2. Lithostratigraphic section of the Vinchina Formation at Quebrada de Pedregal Negro. Modified from Schencman et al. (2016). FAI: fluvial-aeolian interaction. MSF1: Multichannel fluvial system with low developed sandy floodplains. MSF2: Multichannel fluvial system with well-developed sandy-muddy floodplains. MSF3: Multichannel fluvial system with moderate developed sandy-muddy floodplains. LP: Progradation lobes. Single column fitting image.

3. Materials and Methods

The studied material comprises a total of 71 footprints preserved as negative epirelief. All the material remains in situ and most of the material was replicated through silicone casts in the field and is housed at (CPBA-V 14323 and CPBA-V 14324) Colección de Paleovertebrados del Repositorio de Colecciones Paleontológicas FCEN-UBA.

Non-metric parameters were taken to distinguish the track general morphology (outline, digital pad, and metapodial and tarsal pad shape). Then, quantitative parameters to describe mammalian, reptile and morphotypes footprints were used based on Leonardi (1987): number of digit impressions (DN◦), footprint length (FL), footprint width (FW), digit length (LI-V), digit width (WI-V), and additionally we measured the footprint area (A), metapodial pad length (LMp), metapodial pad width (WMp), tarsal pad length (LTp), and tarsal pad width (WTp). The parameters used to describe trackways also follow Leonardi (1987): trackway length (TwL), trackway width (TwW), manus-pes distance (m–p), stride (S), pace (P), and pace angulation (Pα). For avian measurements we followed McCrea and Sarjeant (2001): footprint length (FL), footprint width (FW), ratio length/width (FL/FW), digit length I, II, III and IV (LI, LII, LIII and LIV), digit divarication angle (DivTotal), angle between digits II and III (II-III), angle between digits III and IV (III-IV). Trackway terminology used is based on Leonardi (1987): stride (S), pace (P), and pace angulation (Pα). Tracks and trackways parameters were measured from photographs, using the public domain, open-source software ImageJ (version 1.52.a).

Three-dimensional reconstructions of selected specimens were performed through photogrammetry. Sets of photographs were taken using a Canon PowerShot G16 digital camera at different angles to the track's surface. Photogrammetric models were generated

using Agisoft Metashape Professional version 1.5.2, following the standard methodology

indicated by Mallison and Wings (2014). Scales and depth-colour maps were created with the

open-source software Paraview 5.5.2 (www.paraview.org).

Body size was estimated in terms of body mass and body length. The estimated

mammalian and avian body mass (M) is based on footprint area (A). For mammalian

footprint producers we used the equation proposed by Vera and Krapovickas (2022):

$$M = (A / 2.0797) \char`^ \sfrac{3}{4}$$

For the avian producers we used the equation proposed in Tanaka (2015):

$$\log (M) = 1.15 \times \log (A) - 0.63$$

For the reptile producers we used the equation proposed by Kubo (2010):

$$\log (M) = 0.0625 + 1.36 \times \log (A)$$

To estimate the body length as a linear distance we used the gleno-acetabular distance

(GAD) as proposed by (Leonardi, 1987). The GAD measurements depend on the interpreted

gait and how they are observed in trackways. An excellent explanatory scheme can be found

in Lallensack et al. (2018). Leonardi (1987) proposed three formulas for estimating GAD.

For the walking trot:

$$GAD\ 1 = S/2 + m\text{-}p$$

where S is the stride, and m-p is the manus-pes distance. In the lateral sequence single foot

walk gait:

$$GAD\ 2 = \tfrac{3}{4}\ S + m\text{-}p$$

For the pace gait:

$$GAD\ 3 = S + m\text{-}p$$

The ratio between the average stride and footprint length (S/FL) is a good and simple

indicator of the limb length of the trackmaker in relation to the body length. It is used as a

complementary index to evaluate body proportions. The index is obtained with average

values. Herein it is used as proposed by Krapovickas et al. (2015). Although we inverted the ratio (S/FL vs FL/S) to clearer represent how many footprints the stride represents.

To identify footprint's producers, we combined the study of the appendicular anatomy as represented on footprints and footprint sequences with the obtained body mass and body length estimations.

4. Results

4.1. Systematic Ichnology
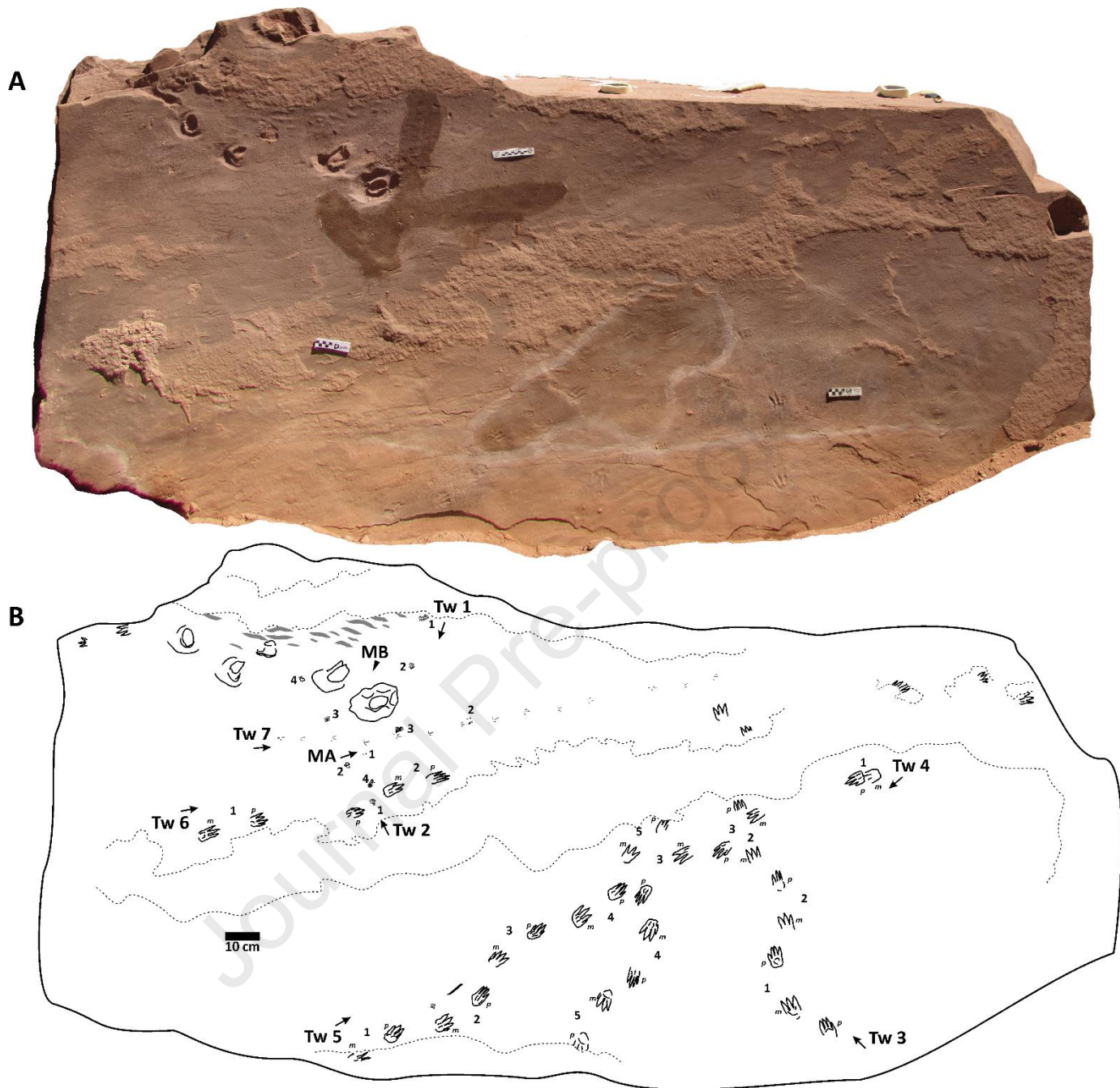
Fig. 3. The track-bearing surface recorded on a multichannel fluvial system with sandy-muddy floodplains. A: Photogrammetric orthophoto showing a fallen block in the field. B: Mapped surface. Tw1-Tw2 correspond to *Carnivoripeda sudamericana* trackways. Tw3-Tw6 correspond to *Tacheria troyana* trackways. Tw7 is the *Aviadactyla vialovi* trackway. MA = Morphotype A. MB = Morphotype B. The manus-pes sets are indicated with numbers. m = manus, p = pes.

2-column fitting image.

4.1.1. Mammalian tracks

Carnivoripeda Kordos 1985

Carnivoripeda sudamericana isp. nov.

Figures 3; 4; Table S1

Material—Two trackways preserved in the field and as silicone cast CPBA-V 14324. Trackways 1 (Tw1) and 2 (Tw2), both composed of four manus-pes sets. Trackways were recovered as 3D digital reconstructions through photogrammetry. One depth-colour map was created for Tw1.

Geographic and Stratigraphic Location—Preserved at the top of the lower member of the Vinchina Formation at Quebrada Pedregal Negro, near San Jose de Vinchina, La Rioja Province, Argentina.

Holotype—Tw1 CPBA-V 14324, trackway preserved as silicone cast, 3D digital reconstructions, and *in situ*.

Paratype—Tw2 CPBA-V 14324, trackway preserved as silicone cast, 3D digital reconstructions, and *in situ*.

Etymology—Refers to the South American continent where the footprints are recorded.

Diagnosis—Tetradactyl to pentadactyl homopod footprints with oval digital pad impressions separated from the metapodial pad. The metapodial pad is rounded with a bilobed posterior margin. The footprints generally lack claw marks and are very small tracks of approximately 2 cm long. Manus and pes are closely placed and are frequently superimposed. Trackways are very narrow, the stride and pace are very long with respect to the footprint length, with a S/FL between 17-20.

Description—Trackways of a quadrupedal and homopod mammal with tetradactyl to pentadactyl, plantigrade, and paraxonic footprints. The manus and pes footprints are subequal in size with an average length of 15.6 mm and an average width of 12.9 mm. The impression of the digital pads is oval in shape and separated from the metacarpal/tarsal pad impression. The digital pad impressions are pointed forward, forming an arc in front of and around the metapodial pad impression. Digital pad impressions are similar in length and width in both manus and pes. Digital impressions range from 6.2 mm to 3.5 mm in length long, and 1.4 to 2.5 mm in width. Metapodial pads are bigger than the digital pads and are subcircular to trapezoidal with a bilobed posterior margin. The metapodial pad is composed at least by three fused interdigital pads. On average, the metapodial pad measures 10.3 mm in length and 9.8 mm in width.

The trackway pattern is characterized by an alternate arrangement of superimposed manus-pes sets. Most frequently, the pes imprint partially overlaps the manus imprint, it is placed behind the manus imprint and more lateral to the midline. In some cases, the manus only show three digital impressions due to the lateral overlap of the imprints. Trackways are very narrow, being the maximum width of 25 mm. The stride and pace are very long with respect to the footprint length (between 17-20 times of the footprint length), on average, the stride is 292.3 mm, the pace is 143 mm, and the pace angulation is 170°. Footprints are preserved as concave epirelief.
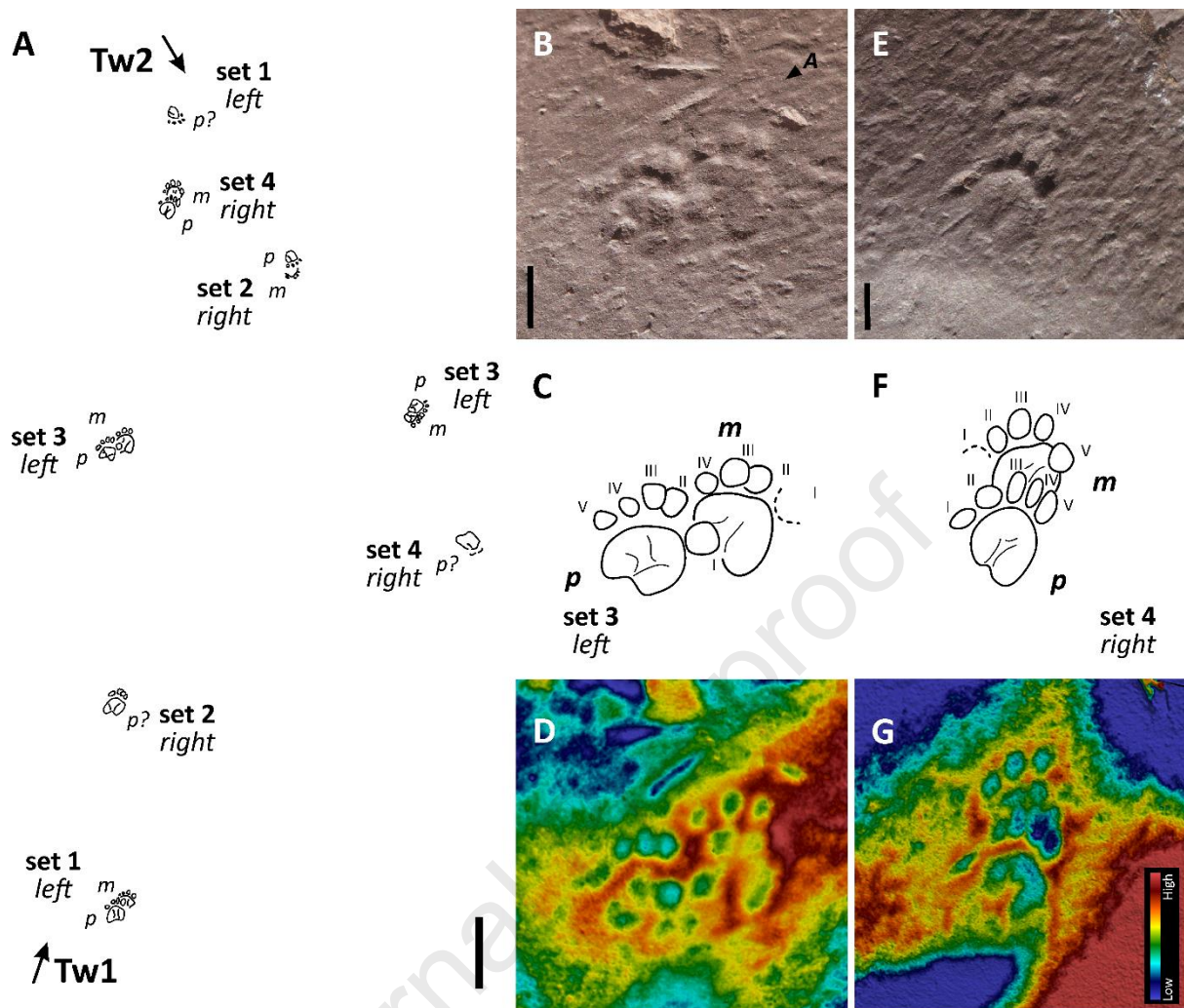
Fig. 4. *Carnivoripeda sudamericana* preserved on a fallen block. A: Outline drawing and interpretation of two trackways (Tw1 and Tw2). B: Close up of set 3 of Tw1. Note *Aviadactyla vialovi* (A). C: Outline drawing and interpretation of set 3. D: Depth-colour map created for set 3. E: Close up of set 4 of Tw1. F: Outline drawing and interpretation of set 4. G: Depth-colour map done for set 4. The deepest areas are shown in blue and the highest in red. The scale bar is 5 cm in A, and 1 cm in B-E.

2-column fitting image.

Comments—The Vinchina footprints are clearly different from other known pentadactyl ichnotaxa proposed to describe carnivore tracks (Fig. 5, A).

Bestiopeda is an ichnogenus firstly described for digitigrade or subdigitigrade tetradactyl

carnivore footprints but has often been used to report both tetradactyl and pentadactyl for all

pawprints of predators (e.g., Buynevich, 2015; Herrero et al., 2022) following dissimilar

criteria from the original description of Vialov (1965, 1966). In the same way, *Canipeda,*

Felipeda, Chelipus and *Tetrastoibopus* were proposed for homopod or slightly heteropod

tetradactyl carnivore footprints (Panin and Avram, 1962) (Fig. 5, A3-4). Among pentadactyl

carnivore footprints, *Phacelopus* was particularly proposed to describe mustelid fossil tracks

(Sarjeant and Langston, 1994). *Phacelopus* consist of heteropod footprints with impressions

of multiple phalangeal pads on manual imprints, elongated and clawed digital pads

impressions, features that are not comparable with our material (Fig. 5, A5). *Platykopus*

(Kordos, 1985) was attributed to a large bear-like animal: footprints with oval digital

imprints, where digit I impression is displaced into medial position and frequently most

deeply impressed, and claw imprints are only slightly visible (Fig. 5, A6). Although the

general configuration of Vinchina tracks coincides with *Platykopus*, they differ in that

Vinchina tracks feature digital pads that are disconnected from the metapodial pad, and they

do not display any impressed claw marks. *Mustelidichnum* has been erected by Aramayo and

Manera de Bianco (1987) for Pleistocene footprints of Argentina (*Mustelidichnum*

enigmaticum) and later emended by Remeika (2001) by describing new material

(*Mustelidichnum vallecitoensis*) (Fig. 5, A7) from the Vallecito-Fish Creek Basin (Late

Pliocene) of California, USA. It is considered plantigrade to digitigrade pentadactyl footprint,

produced by a quadruped, with digital pads elongated and crowded, aligned in a conspicuous

1-3-1 spacing, with outer digits I and V separated slightly from central digits. "This

asymmetric placement of digits and the presence of a chevron-shaped interdigital pad are

diagnostic characteristics of the carnivorian family Mustelidae" (Remeika, 2001 p.61). The

Vinchina footprints are very similar to this material, however they are smaller, on other of

magnitude, and the ichnospecies is erected based on one left pes footprint, that difficult further comparisons. In addition, a previously erected ichnogenus it is also in accordance with the Vinchina footprints. *Carnivoripeda* (Kordos 1985), a monospecific ichnotaxa until now, was described for homopod and pentadacyl carnivoran-like footprints. The original diagnosis for *C. nogradensis* is "Five-toed carnivore footprint. Sole print that is laterally wider than longitudinally, being distally impressed. Toe prints elongated, droplet-shaped, ending in an apex. The imprint of the tip of each claw is quite distinct." (Fig. 5, A8). Vinchina footprints are consistent with the overall features of *Carnivoripeda*, but they differ in terms of the shape of the digital impressions, which are oval, and the absence of claws marks.
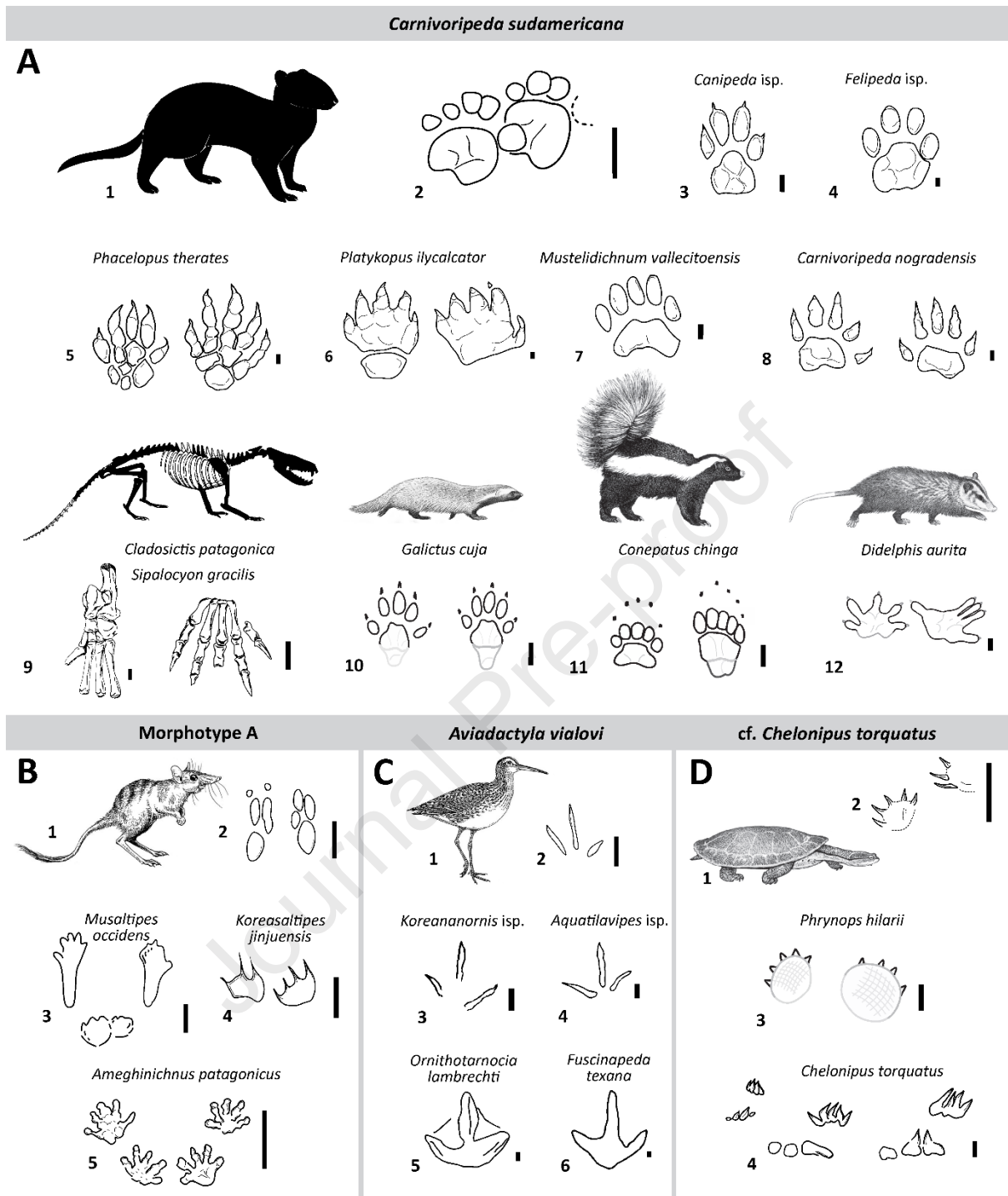
Fig. 5. Comparisons of fossil footprints found at Quebrada Pedregal Negro with other fossil tracks and footprints of living animals. A: *Carnivoripeda sudamericana*. A1: Body proportions of the *C. sudamericana* trackmaker inferred from trackways parameters, the calculated GAD, and the estimated body mass. A2: A manus-pes set of a *C. sudamericana* trackway from Quebrada Pedregal Negro. A3: *Canipeda isp.*, modified from Bjork (2002).

A4: *Felipeda isp*., modified from Sarjeant et al. (2002). A5: Right manus-pes set of *Phacelopus therates*, modified from Sarjeant and Langston (1994). A6: Right manus-pes set of *Platycopus ilycalcator*, modified from Sarjeant et al. (2002). A7: Left pes impression of *Mustelidichnum vallecitoensis*, schematized on a photo of Remeika (2001). A8: On the left a manus imprint, and on the right a pes imprint of *C. nogradensis*, modified from Botfalvai et al. (2022). A9: Skeletal restoration of one of the smallest South American Miocene borhyaenoids (Sparassodonta). Above, a complete skeletal restoration of *Cladosictis patagonica*; and below a scheme of a pes and a right manus of *Sipalocyon gracilis* taken and modified from Argot (2003). A10: Above, *Galictis cuja*, a modern Mustelidae of small size, below a scheme of its manus-pes set modified from De Angelo et al. (2017). A11: Above, *Conepatus chinga*, living member of the family Mephitidae, below a scheme of its manus-pes set modified from De Angelo et al. (2017). A12: Above, *Didelphis aurita*, living Didelphoidea, below a scheme of its manus-pes set modified from De Angelo et al. (2017).

B: Morphotype A. B1: Argyrolagid-like mammal as possible trackmaker of Morphotype A. B2: The tracks preserved at Quebrada Pedregal Negro. B3: Pairs of manus and pedes of *Musaltipes occidens*, modified from Lockley and Milner (2014). B4: *Koreasaltipes jinjuensis*, modified from Kim et al. (2017). B5*: Ameghinichnus patagonicus*, modified from Rainforth and Lockley (1996). C: *Aviadactyla vialovi*. C1: A member of the family Scopolacidae as putative trackmaker of *A. vialovi*. C2: Detail of one footprint found at Quebrada Pedregal Negro. C3: *Koreanaornis*, modified from Anfinson et al. (2009). C4: *Aquatilavipes*, modified from Anfinson et al. (2009). C5: *Ornithotarnocia lambrechti*, modified from Kordos, 1985). C6: *Fuscinapeda texana*, modified from Sarjeant and Langston (1994). D: cf. *Chelonipus torquatus*. D1: Pleurodiran-like freshwater turtle as proposed trackmaker. D2: manus-pes set of *C. torquatus* found at Quebrada Pedregal Negro. D3: Scheme of the manus-pes set of *Phrynops hilarii*, a modern member of the family Chelidae

(De Angelo et al., 2017). D4: Some examples of tracks of *C. torquatus* (Avanzini et al., 2005). All scale bars are 1 cm.

2-column fitting image.

Tacheria troyana Krapovickas and Nasif 2011

Figures 3; 6; Table S2

Material—Four trackways are preserved in the field. One silicone cast CPBA-V 14323 recorded two parts of Tw4 and Tw5. Trackway 3 (Tw3) composed of 6 manus-pes sets, Trackway 4 (Tw4) composed of 5 manus- pes sets, Trackway 5 (Tw5) composed of 5 manus-pes sets. All the trackways were recovered as 3D digital reconstructions through photogrammetry. One depth-colour map was created for Tw5.

Description—Trackways of a quadrupedal and heteropod mammal with tetradactyl manus and pes impressions of sub-equal size, with long and robust digits with elongated claws mark. The global average length of the imprints is 58 mm, and the average width is 34 mm. The manus and pes impressions differ in the length and width of the digit impressions and the degree of ground contact of the metacarpal/tarsal pads. The manus footprints are asymmetrical and more robust that the pes impressions, being at least 4 mm wider than the pes. In the manus, digit III impression is the longest (30 mm on average), while digits II and IV impressions are sub-equal and following in size (about 27 mm on average), and finally digit V is the shortest (not more than 20 mm) and at times does not print. The impression of metacarpal pads is absent suggesting a digitigrade foot structure. The pes impression is symmetric, with the lateral digits (II–V) shorter than central digits (III–IV), that are around 20 mm and 30 mm respectively. The pes impression records four metatarsal pads, one behind each digital impression. It could occasionally imprint two heel pads. Trackways are narrow

with footprint impressions near to the midline, and pes impressions are placed in front of, and more lateral to the midline, than the manus impressions. On average, the stride is 502 mm, the pace is 258 mm, and the pace angulation is 140°. Preserved as concave epirelief.

Comments—A partial mold of the material included herein was described in Krapovickas et al. (2017). Herein we describe the complete original tracking surface. We also based our interpretation on both the original surface and the previously found mold.

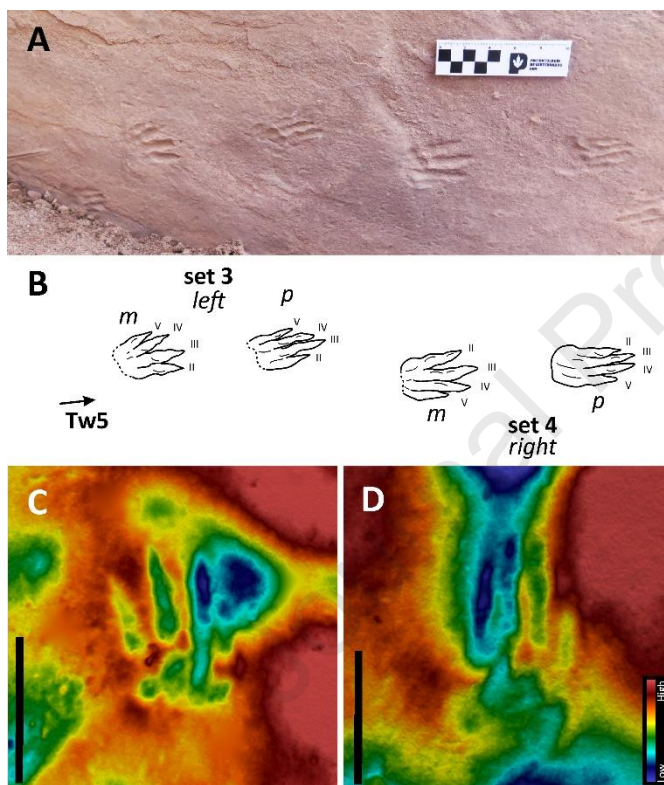Fig. 6. *Tacheria troyana* preserved on the fallen block at Quebrada Pedregal Negro. A: Detail of the trackway Tw5 showing two manus-pes sets. B: Outline drawing and its interpretation. C: Depth-colour map created for the right manus of set 4. D: Depth-colour map created for the right pes of set 4. The deepest areas are shown in blue and the highest in red. The scale bar is 5 cm in C-D.

Single column fitting image.

Morphotype A

Figures 3; 7; Table S3

Material—Three footprints (MA) preserved in the field. Material was recovered as silicone cast CPBA-V 14324. Footprints were recovered as a 3D model through photogrammetry. One depth-colour map was created.

Description—Didactyl footprints corresponding to a small rodent-like mammal with elongated autopodia, claw marks and apparently lacking manus impressions. The length-to-width ratio is approximately 4/1. The footprints are arranged parallel to each other conforming a pair of pedal imprints that suggest a bipedal hopping gait. Individually, each track shows the impression of two subequal elongated digital pads, and a less marked impression that is located posteriorly. The digital impressions are arranged near the anterior margin of an oval-shaped tarsal pad, arranged as separate entities anteriorly directed. The average length of the digital pad III impression is 5.8 mm, and the digital pad IV impression is 5.8 mm. The average width of the digital pad III impression is 1.8 mm, and the digital IV is 2 mm. The tarsal impression is 6.9 mm long and 3.6 mm wide on average. The distance measured in the posterior tips of the heels is 1.7 mm. One isolated footprint allows measuring the stride, that is 323 mm. Footprints are preserved as concave epirelief.

Comments—Currently, no ichnogenera of jumping rodents with similar morphology are known. Lockley and Milner (2014) proposed two ichnogenera that could be compared: *Musaltipes* and *Ranipes*. *Musaltipes* are symmetric footprints of a heteropod jumping animal (Fig. 5, B3). The hind imprints are triangular and exhibit five digital impressions. The footprints analyzed in this study only show the autopodia of the hindlimb, which is elongated and either didactyl or tridactyl. *Ranipes* trackway was assigned to a hopping tetrapod with symmetrical and tetradactyl limbs, and a slight outward rotation in the hind footprint. In

contrast, the Morphotype A is didactyl or tridactyl, exhibits highly asymmetrical footprints at least in the hind limb, which is oriented parallel to the inferred midline.

It has been suggested that *Koreasaltipes* has also been produced by a jumping mammal, possibly a small rodent (Kim et al, 2017; Stanford et al., 2018). The footprint is tetradactyl with the digits joined to the tarsal pad, and the shape is slightly wider than it is long, in comparison to Morphotype A that have no more than three digits and are elongated along the medial axis (Fig. 5, B4). Finally, *Ameghinichnus* has also been attributed to a small homopod and pentadactyl rodent-like animal with jumping behavior (Fig. 5, B5). Morphologically, *Ameghinichnus* is completely distinct from Morphotype A, displaying long and slender digital impressions equidistantly attached to the sole, and with metacarpal and metatarsal imprints.
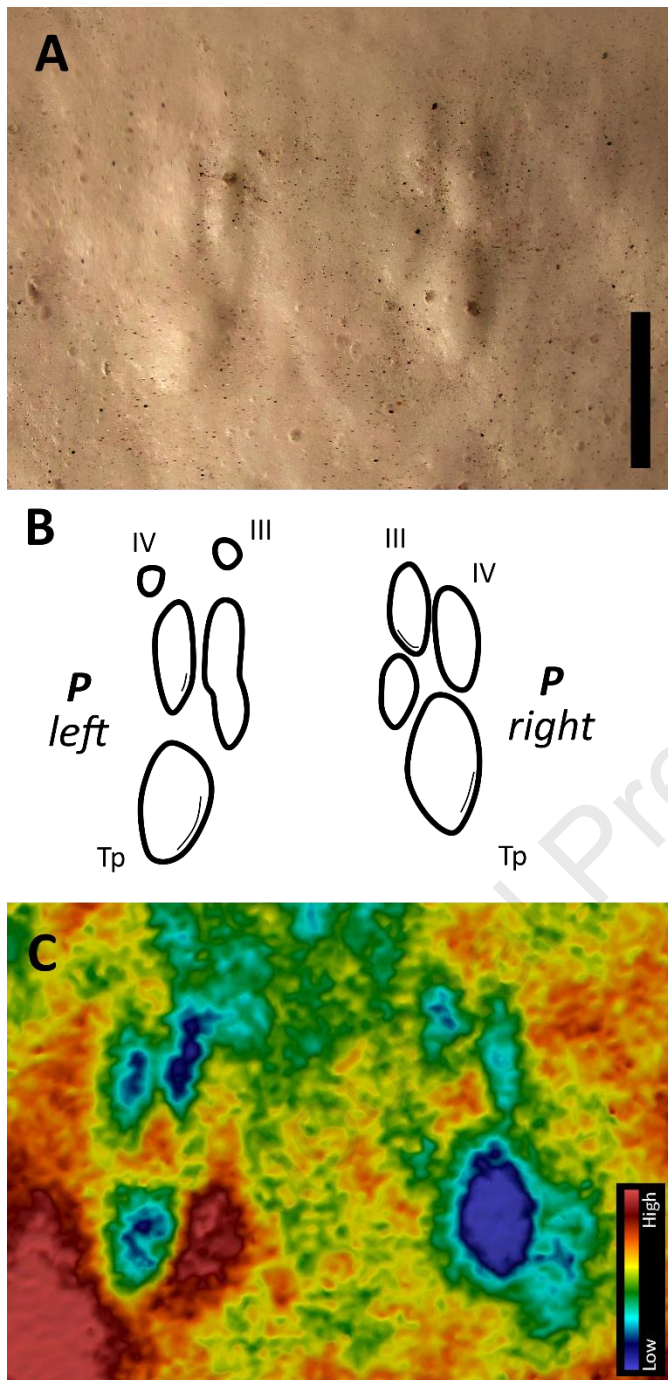
Fig. 7. Morphotype A preserved on the fallen block. A: Detail of the footprints taken from the silicone cast CPBA-V 14324. B: Outline drawing and its interpretation. C: Depth-colour map, where the deepest areas are shown in blue and the highest in red. Scale bar is 1 cm. Single column fitting image.

4.1.2. Avian and reptilian tracks

Aviadactyla vialovi Kordos and Prakfalvi 1990

Figures 3; 8; Table S4

Material—One trackway (Tw7) preserved in the field with eleven tracks. Seven tracks were recovered as silicone cast CPBA-V 14324. The trackway was recovered as 3D digital reconstructions using photogrammetry, and one depth-colour map was created.

Description—Avian tridactyl and unwebbed footprints, with occasional presence of a hallux. The average length is 20 mm, and the average width is 21 mm. Digits are directed forward without a union between them. The digits are slender and tubular-shaped with no clear claw marks. The digit III is 25% longer than the lateral digit. The average interdigital angle II-III is 44° and III-IV is 37° and III-IV is 37°. The average interdigital angle II-IV is typically less than 90° with an average of 81°.Total divarication is on average of 90°. The stride average is 195 mm and the disparity ranges from 147 mm to 312 mm. The pace angulation average is 175° and does not have great disparity (min 167°, max 179°). The pace average is 103.3 mm with a range from 72 mm and 218 mm. The tracks are arranged in an only trackway with a total length 1280 mm. The footprints are preserved as concave epirelief

Comments—Along the trackway, the pace and stride are not regular. It is observed that it widens at the beginning and at the end. This may be due to a change in speed. At the same time, the trackway is not perfectly straight, but curves coincide with speed changes. *Aviadactyla* morphologically resemble *Koreanaornis*, *Aquatilavipes, Ornithotarnocia*, *Fuscinapeda*, *Uvaichnes,* and *Barrosupus* (Fig. 5, C). However, *Koreanaornis* is up to 30% larger in both length and width (Fig. 5, C3). The interdigital angles are much larger between II-III, although smaller between III-IV. The total divarication is up to 40% wider. The average pace and stride are higher in *Aviadactyla* in comparison with *Koreanaornis* (Kim 1969; Xing et al,. 2018*).* In *Aquatilavipes* the digits are joined proximally (Fig. 5, C4). In

addition, the width is greater than the length, in contrast to what we observed in *Aviadactyla* (Currie 1981). In *Aviadactyla* the digits II and IV are subequal, while in *Aquatilavipes* the digit IV is longer than the digit II. *Ornithotarnocia* differs from *Aviadactyla* in size, total divarication, the relationship between digits II and IV and the proximal union between digits (Fig. 5, C5) (Kordos 1985). *Fuscinapeda*, which has a proximal interdigital union and shows a prominent heel, which is not present in *Aviadactyla* (Fig. 5, C6) (Sarjeant & Langston 1994). *Uvaichnes* has a distinctive metatarsal pad that is not observed in *Aviadactyla*. Both *Fuscinapeda* and *Uvaichnites* have been reported in the Miocene of the Iberian Peninsula (Diaz-Martínez et al., 2012; Herrero et al., 2023). *Barrosupus* is a non-avian dinosaur ichnogenus similar to *Aviadactyla*. One of the diagnostic features is the impression of digit II separated from the impressions of digits III and IV (Coria et al., 2002), which is absent in *Aviadactyla*. The Pedregal Negro footprints exhibit remarkable similarities to *Aviadactyla media* described for the northwest of Iran (Kazemi and Abbassi 2023). The Iranian footprints are larger in size, differing on the ichnospecific assignation.
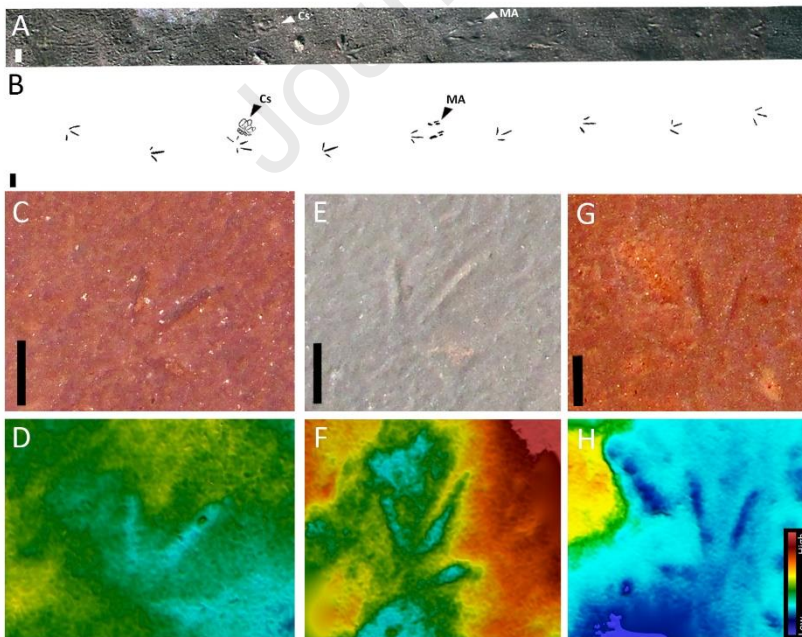

Fig. 8. *Aviadactyla vialovi* preserved on the fallen block. A: Complete trackway. B: Outline drawing and its interpretation. C-E-G: Detail of the footprints taken from fallen block. D-F-

H. Depth-colour map, where the deepest areas are shown in blue and the highest in red. Cs =

Carnivoripeda sudamericana. MA=Morphotype A. Scale bar is 1 cm.

single column fitting image.

cf. *Chelonipus torquatus* Rühle von Liliestern, 1939

Figure 9; Table S5

Material—One trackway (Tw8) with nine footprints, preserved in situ, and recovered as 3D

digital reconstructions through photogrammetry technique.

Description—The footprints correspond to a quadrupedal heteropod animal. Forefoot is

pentadactyl and hindfoot is tridactyl, generally digitigrade. The footprints average about 14

mm in length and 10 mm in width. Manus imprints are tridactyl to pentadactyl with sub-equal

digits, and pedes imprints are mostly tridactyl with relatively longer digits than in the manus.

Sole/palm imprints are rounded when preserved. The digital impressions are sub-equal in

shape and size, are slender and acuminate, they average about 5.2 mm in length and 1.5 mm

in width. Three central digits are parallel to the direction of movement. Digit I is oriented at

an approximately right angle, while digit V is slightly externally deviated from the axis of

movement. Digit and claw marks are spaced, forming an arc around the palm, and

occasionally connected by arched structures. The trackway pattern is characterized by the

arrangement of sets in two parallel rows. Footprints are oriented forward, but manus prints

are medially recurved in most cases. On average, the stride is 95 mm (about seven times the

imprint length), the pace is 61 mm, and the pace angulation is 68°. The total preserved

trackway length is 4287 mm, and the maximum width is 54 mm. Footprints are preserved as

concave epirelief.

Comments—Along the trackway, preservational differences between tracks are observed. Generally, only three digital impressions are preserved, and solely two manual imprints are complete at the left side of the midline. The absence of surrounding rims and deeply claw marks suggest that the sediment was firm but soft enough for feet to leave an impression. A possible explanation is that the sediment had lateral variations in water content or there was a slight slope through which the animal had to traverse perpendicularly.

The vinchina footprints are assigned to chelonians (see Discussion below); other similar footprints and valid ichnogenera attributed chelonians are: *Chelonipus*, *Australochelichnus*, *Marinerichnus* and *Emydhipus*. We consider *Chelonichnium* to be a synonym of *Emydhipus* following Avanzini et al. (2005). *Australochelichnus* and *Marinerichnus* are trackways attributed to hatchling sea turtles that exhibit traces of the ventral plastron and wing-like front limb (Lockley et al., 2019). Due to the distinct morphological characteristics, they are not included in the comparison.

Emydhipus presents an anterior autopodium with four long and parallel ungual marks (Fuentes Vidarte, 2003), in comparison to the Vinchina footprints which are pentadactyl and only the three central digits are parallel. In our sample, complete posterior autopodia are not preserved, but a rounded plantar area with digits oriented parallel to the direction of movement, like *Emydhipus*, can be inferred. However, the absence of a complete hind-limb track limits our ability to determine the number of digits present and therefore to make more accurate comparisons.

Chelonipus exhibits three or five digits, all bearing claws, and an interdigital membrane (Avanzini et al., 2005) like the newly found specimens (Fig. 5, D). The orientation of the medial (inward) and lateral (outward) digits shows a configuration consistent with the footprints of Vinchina. The central digits are oriented in the direction of movement as in *Chelonipus* (Avanzini et al.,2005) The absence of a complete hindfoot impression precludes

us from making more in-depth comparisons. We consider that *Chelonipus* exhibits great

similarity with the footprints of Vinchina.
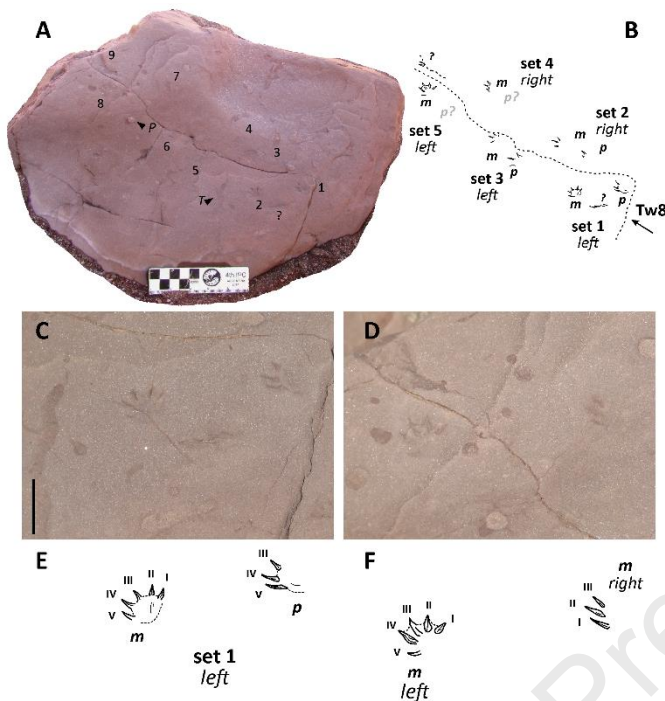
Fig. 9. cf. *Chelonipus torquatus* preserved on a small fallen block at Quebrada Pedregal

Negro. A: Photogrammetric orthophoto of the block, where all the footprints are indicated

numerically. Note *Paleophycus* (P) and *Taenidium* (T). B: Outline drawing and the

interpretation of the trackway. C: Detail of the left set 1. D: Detail of the right manus of the

inferred set 4, and the left manus of the inferred set 5. E-F: Outline drawings and

interpretation. Scale bar is 2 cm.

1.5 column fitting image.

4.1.3. Non identified footprints

Morphotype B

Figures 3; 10; Table S6

Material—Four aligned footprints (MB), preserved *in situ*, and recovered as 3D digital

reconstructions through photogrammetry technique, and one depth-colour map.

Description—Series of tracks of inconsistent oval shape. The external outline is roughly sub-circular to slightly oval, with an average length of 116 mm and width 95 mm. In the central section, footprints have an inner high and narrow rim forming an oval outline, with an average length of 58 mm and width 35 mm. Digital impressions are not clearly defined. Preserved as concave epirelief.

Comments—Focusing on the preservational conditions, the studied fossil footprints are comparable, in shape but not size, with the sauropod tracks mentioned by Carvalho (2004), and Carvalho and Leonardi (2021) (see Fig. 2A on the last paper cited). The authors explain that the origin of this kind of structures can be attributed to the superimposition of two successive footprints or to the mud suction during the lifting off the pes from the substrate. Despite the difference in the morphology and the identity of the trackmakers, the printing process seems to be the equivalent due to similar substrate conditions.
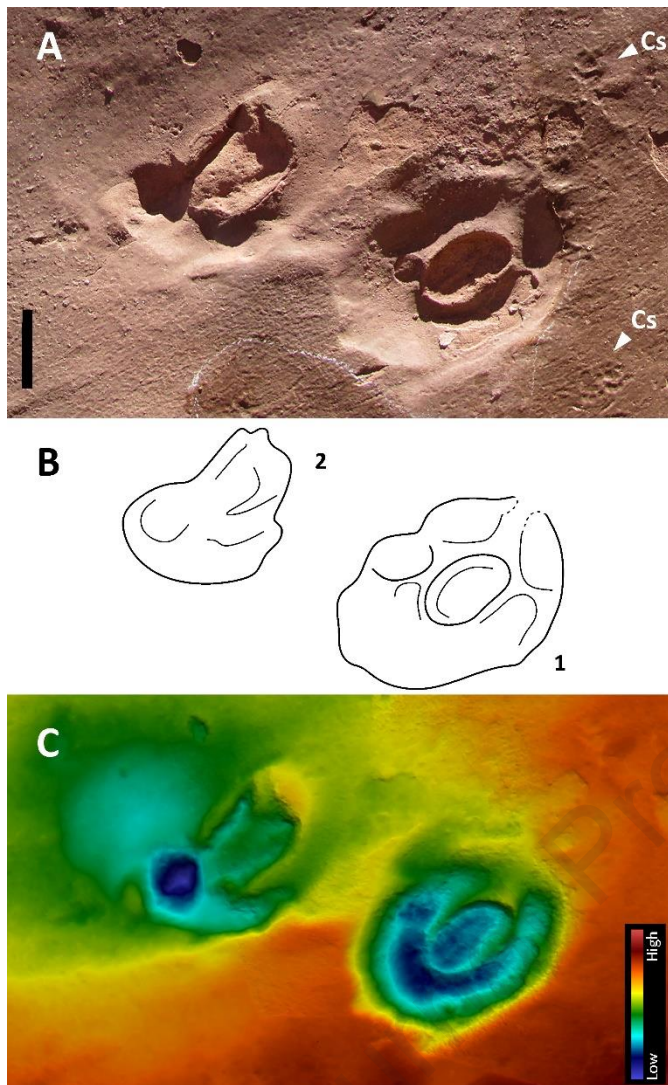
Fig. 10. Detail of subcircular structures preserved on the fallen block. A: Close up the best completed footprints. B: Outline drawing. C: Depth-colour map, where the deepest areas are shown in blue and the highest in red. Cs = *Carnivoripeda sudamericana*. Scale bar is 5 cm. single column fitting image.

4.2. Body size estimations

We approached body size through two estimators: body mass and body length. The direct relationship between body mass and foot contact area, has allowed researchers to estimate the body mass of dinosaurs, pterosaurs, birds, and mammals based on their fossil footprints (e.g., Kubo, 2010; Schanz et al., 2013; Tanaka, 2015; Michilsens et al., 2009; Vera

and Krapovickas, 2022; Melchor et al., 2019). Herein we estimated the body mass of three mammals (*Carnivoripeda sudamericana* nov. isp*., Tacheria troyana*, and Morphotype A), one bird (*Aviadactyla vialovi*), and one reptile (cf. *Chelonipus torquatus*) based on a series of formulae described at the Material and Methods section.

The estimated body mass of all the producers is resumed on Table 1. The producer of *T. troyana* is the largest with an average body mass of 15.76 kg (it ranges from 8.7 – 22.35 kg), the trackmaker of *C. sudamericana* is a small mammal with a body mass of, in average, 0.75 kg and ranging from 0.17 kg to 1.82 kg. The smallest mammal represented is Morphotype A with an estimated body mass of 0.26 kg. The trackmaker of *A. vialovi*, has an estimated body mass of in average 0.043 kg, with a range of 0.025 kg to 0.067 kg. Lastly, the trackmaker of cf. *C. torquatus* has an estimated body mass of 0.39 kg, ranging from 0.35-0.43 kg, according to our calculations.

In terms of linear dimensions, the gleno-acetabular distance (GAD) is a good body size indicator that can be measured from trackways (e.g., Leonardi, 1987; Lallensack et al., 2018). Different GAD estimators are used depending on the interpreted gait on the trackway. The walking trot is most frequently used by amphibians and reptiles, it almost lacks a period of suspension and implies a contralateral limb pair (e.g., left hind limb and right forelimb) moving forward at the time the other pair (e.g., right hind limb and left forelimb) is in stance phase touching the ground (Biknevicius and Reilly, 2006). The glenoid fossa mostly corresponds with the midpoint between two left and right manus impressions at the time the acetabulum corresponds with the midpoint between the left and right pes impressions (GAD 1)

In the lateral-sequence single-foot walk (LSSF), at a certain point during the step cycle both hind limbs and one forelimb are in stance phase touching the ground while one forelimb moves forwards and is frequently seen among mammals (Biknevicius and Reilly,

2006). When an animal is using this gait, the GAD can be measured from trackways as the midpoint of the pes pace and the most advanced point of one manus. The relationship can be resumed as ¾ of the stride plus the parallele manus-pes distance (GAD 2) (Leonardi, 1987).

The walking pace occurs when the ipsilateral fore- and hind limb moves forwards while the contralateral fore- and hind limb are in contact with the ground in stand phase (Biknevicius and Reilly, 2006). When that gait is present the GAD between the manus and pes footprints of the same step cycle. It has been proposed as equivalent to the stride plus the manual pedal distance (GAD 3) (Leonardi, 1987).

As we do not know the gait used by the trackmakers, we chose the GAD measurement linked to the gaits used in body mechanics studies for closely related taxa as mentioned in Biknevicius and Reilly (2006) (i.e., quadrupedal anuran, lizard, crocodilian, mammal). *T. troyana* and *C.* are interpreted as quadrupedal mammals, and we choose to use the LSSF GAD measurement (see GAD2 in Table 2). For cf. *Chelonipus*, interpreted as a reptile, chose the walking trot approach (see GAD1 in Table 2). The pace is a singular gait not frequently found among tetrapods, and is mostly known as used by camelids, certain horses, and dogs (Van der Sluijs et al., 2010, Biknevicius and Reilly, 2006). We have no evidence to interpret any Pedregal Negro trackmaker has using a pace gait. Finally, the S/FL ratio was used as a complementary measurement to comprehend body proportions wile interpreting possible producers of the footprints.

5. Discussion

5.1. Animals represented at the Pedregal Negro ichnoassociation

5.1.1. Carnivoran-like footprints

Carnivoripeda sudamericana trackway configuration suggests a small, short-limbed and long-torsoed mammalian producer due to its large stride relative to the footprint length

(17.8 – 19.8 mm), the long-estimated GAD (19.6 – 26.4 cm), the small size of the footprints (< 2 cm), and the proximity of the manus-pes sets to the midline of the trackway (Fig. 4, 5A1, Table S1, Table 2). The footprints point towards a mammal with a homopod, pentadactyl, and digitigrade autopodia with retractable or semi-retractable claws, or simply straight claws that did not leave impressions on the substrate, evidenced by the lack of claw marks, either as anterior circular impressions or claw drag marks. The metapodial pad impressions have a unique configuration, with a pad of bilobed posterior margin, that allows discerning between taxa with living representatives′ descendants, as they are very conservative within Families (Elbroch, 2003). Considering these traits, the pentadactyl to tetradactyl homopod autopodia with small and oval digital pad impression, bilobated metapodial pad impression, the small size range of the footprints, the estimated body mass of less than 1 kg and the estimated trunk length of approximate 20 – 26 cm , it is highly probable that they were produced by a carnivoran-like mammal of small size (< 1 kg).

South American marsupials such as didelphoids, are pentadactyl and inhabited in the continent since the Late Miocene (e.g., Abello et al., 2015). Some Late Miocene species as *Thylophorops perplanus* (~ 1.5 kg) and *Hyperdidelphys pattersoni* (~ 1.16 kg) had a body size comparable to *C. sudamericana* (Zimics, 2014), however, their feet configuration is unknown. All living didelphoids have elongated digit impressions and a divergent to highly divergent digit I impressions on the pes (e.g., Szalay, 1994; Canevari and Vaccaro, 2007) strongly differing from *C. sudamericana* (Fig. 5,A12).

Among metatherian carnivoran mammals that inhabited South America during the Miocene, Sparassodonta presents several features comparable with *C. sudamericana* of Vinchina. Sparassodonta is a clade of mammalian predators that evolved in South America from the early Paleocene or early Eocene to the middle Pliocene (~ 3 Ma). (Prevosti and Forasiepi, 2018). The clade reached its diversity peak during the late Early Miocene, when

most of the small sized examples (below 7 kg) are recorded and declined since the Late Miocene until the last record of sparassodont on the middle Pliocene (Prevosti et al., 2013). Their manus are pentadactyl, with elongated digits II-IV, digit V follows in length and digit I is the shortest (Szalay, 1994). The pollex (digit I) was interpreted as pseudo-opposable in some taxa as *Sipalocyon*, *Cladosictis* (Fig. 5, A9) and *Lycopsis* allowing them to skillfully manipulate prey (Argot, 2004). Digits have elongated and sharp claws. Pes are also pentadactyl (Szalay, 1994). A reduction of the hallux (digit I) is variable within sparassodonts. It is present in certain dasyuromorphs and borhyaenoids while normally developed in closely related taxa, as in *Sipalocyon* and *Lycopsis* (Argot, 2004). In terms of body proportions and from a functional-adaptive perspective, small sized borhyaenoids have been compared with living mustelids (Argot, 2003, 2004). And are the only known up to date sparassodonts that could be considered among the putative producers of *Carnivoripeda*. The body plan and the ecology of *Pseudonotictis pusillus* (with a body mass of 1,17 kg) was assumed as not far from an extant weasel (Argot, 2003, 2004; Ercoli and Prevosti, 2011). *Sipalocyon gracilis* (2,11 kg) is suggested as having climbing capabilities while *Cladosictis patagonica* (6,6 kg) interpreted as a short-legged predatory terrestrial forms (Fig. 5, A9), comparable to the living South American mustelid tayra (*Eira barbara*) (Argot, 2003, 2004; Ercoli and Prevosti, 2011).

The producer of *C. sudamericana* is coincident in terms of in body plan as short legged and long-torsoed forms, the general aspect of the appendicular skeletal anatomy as homopod and pentadactyl mammals, and their size, with the small sized sparassodonts of the Santa Cruz formation as *Pseudonotictis* (~ 1 kg). Another small sparassondont, *Australogale* (~840 g), is known from the late Middle Miocene Locality of Quebrada Honda, Bolivia. It is coincident with the *C. sudamericana* producer in terms of body mass and approximate paleogeographic and stratigraphic occurrence, however its postcranium is unknown

(Engelman et al., 2018). We interpret the producer of *C. sudamericana* as a small sized

sparassodonts, however, it is not the only mammalian example that could be interpreted as a

possible trackmaker.

The clade Carnivora is recorded in South America from Late Miocene to Recent times

by representatives of the families Felidae, Canidae, Ursidae, and Musteloidea (Soibelzon and

Prevosti, 2007). Carnivores arrived in South America from North America during the "Great

American Biotic Interchange" (GABI). The oldest records are represented by procyonids in

the Late Miocene (6 –7 Ma), followed by mustelids and canids in the Late Pliocene (~2.5

Ma), and since the Early Pleistocene (~1.8 Ma) most families, genera, and species are

recorded (Prevosti et al., 2012; Prevosti and Forasiepi, 2018).

Felid and canid footprints are tetradactyl, digitigrade to subdigitigrade, paraxonic and

typically homopodial, although fore prints tend to be larger than the hind prints (Melchor et

al., 2019). This set of characteristics allow us to precisely rule out canids and felids as

possible producers of Vinchina tracks. In addition, the so far known temporal lifespan of

felids and canids do not overlap with the Vinchina Carnivoripeda. The oldest records of felids

in South America corresponds to *"Felis" vorohuensis* and *"Felis"* sp. from the Ensenadan

(Late Pliocene to early middle Pleistocene, sensu Cione and Tonni, 1999), and *"Herpailurus*

yagouaroundi" from the "Ensenadan" of Bolivia (Hoffstetter, 1963; Deschamps and

Borromei, 1992; Berman, 1994).

Among ursids, the only known fossil footprints in South America is *Ursichnus*

sudamericanus a large-sized plantigrade, pentadactyl footprints with marked heteropody, and

claw marks (Aramayo et al., 2015; Krapovickas and Vizcaíno, 2016), like that of modern

ursids. The small Vinchina tracks are characterized by being tetra to pentadactyl with the lack

of claw marks and highly homopod, due to these difference ursids can be discarded as

trackmakers. In addition, Tremarctinae ursids are endemic to America and recorded since the

Late Miocene of North America. South American species have been recorded since the

Ensenadan (Early – Middle Pleistocene) (Soibelzon et al., 2005), so the lifespan of the South

American species does not overlap with *C. sudamericana*. Moreover, their body mass

estimations using allometric equations from cranial, dental, and postcranial measurements

result in values much higher than our estimates, at least three orders of magnitude, from

hundreds of kilograms up to one tone compared to the one kilogram of *C. sudamericana* (see

Soibelzon and Tarantini, 2009).

Musteloidea is a Carnivora superfamily that emerged 32.4 – 40.9 Ma ago in Asia,

including the families Ailuridae, Mephitidae, Mustelidae and Procyonidae (Sato et al., 2012).

In general, the autopodium morphology and the body proportions of the weasel-like

Musteloidea superfamily overlaps with the Vinchina *C. sudamericana* footprints. They have

pentadactyl feet with oval-shaped digit pads, not connected to and placed around the

metapodial pad, which has an arcing pattern and a bilobed posterior margin, as in *C.

sudamericana* (Fig. 5, A10-11). Digit I is the smallest, is located on the inside on track and

does not reliably print. The heel pad and claw marks may print or not depending on the

family and species (De Angelo et al., 2008; Elbroch, 2003). Some of these features slightly

vary between families. Red pandas (Ailuridae) are only recorded from Europe and North

America (Salesa et al., 2022), so it is not considered herein.

Skunks and stink badgers (Mephitidae) have the general musteloid footprint with the

particularity that claws are large and long, and reliably register, and the heel may register or

not (Elbroch, 2003) (Fig. 5, A11). The oldest Mephitidae recognized to date is *Miomephitis

pilgrimi* from the early Miocene of Germany, around 17.6 – 20.3 Ma. In the Americas, the

oldest known species was found in early Pliocene beds in central Mexico, *Conepatus

sanmiguelensis* (Wang and Carranza-Castañeda, 2008). Putative Mephitidae fossil footprints

(corresponding to an isolated manus and a partially preserved manus-pes set) are reported

from the lower Pleistocene of Virginia, United States (Weems, 2021). The footprints are partially preserved and lack morphological detail, somewhat reassembling *C. sudamericana* on the pentadactyl and metapodial pad configuration.

In raccoons and coati (Procyonidae) digital pads tend to connect with the metapodial pads, the pes heel most frequently prints and, in some species, claws are semi-retractable and do not imprint (De Angelo et al., 2008). Procyonidae were the first generally agreed northern placental carnivorans that reached the Neotropics, at 7.24–5.95 Ma (Reguero and Candela, 2011; Prevosti and Forasiepi, 2018; Prevosti et al., 2021). In South America, they are represented by two extinct genera: *Cyonasua* and *Chapalmalania* (Late Miocene – Early Pleistocene), found in Argentina (Reguero and Candela, 2011), Uruguay (Soibelzon et al., 2019), Bolivia (Soibelzon et al., 2020), Venezuela, Colombia (Forasiepi et al., 2014), and Perú (Tarquini et al., 2020). Morpho-functional analysis based on autopodial elements indicate that the autopodium of *Cyonasua* had a short robust manus compared to other forelimb elements and to extant South American procyonids, and plantigrade stance (Tarquini et al., 2019). Estimate body masses for *Cyonasua* range between 12.63 and 28.45 kg (Tarquini et al., 2017), while *Chapalmalania* is about 88 kg (Prevosti and Forasiepi, 2018). The so far known procyonids are much larger than the *C. sudamericana* producer and autopodium morphology does not match with the footprints.

In weasels, ferrets, otters, martens, badgers, and relatives (Mustelidae) the general Musteloidea foot morphology is present. There is generally a separation between digital and metapodial pads, digit I may print or not as well as the heel depending on the species (De Angelo et al., 2008; Elbroch, 2003) (Fig. 5, A10). Despite the divergent morphology of Mustelidae, their general body plan and size range also overlap that of the Vinchina *C. sudamericana*. The calculated body mass of the *C. sudamericana*. trackmaker ranges from 1.1 – 0.27 kg (Table 1), the estimated trunk length (GAD) ranges from 264 mm to 196 mm

(Table 2). Most modern weasels and ferrets vary in length from 173 to 217 mm, and their weight ranges between 0.55 – 1.31 kg (The Mammal Society, 2017; Horner and Biknevicius, 2007). They have long and slender bodies, have a highly flexible spinal column; the limbs are comparatively short, ending in feet with five digits, and they walk either digitigrade or plantigrade (Horner and Biknevicius, 2010). The claws are not (or only partly) retractable (Kollias and Fernández-Morán, 2015). All these characteristics are observable in *C. sudamericana,* with the particularity that all recorded footprints lack heel impressions and claw marks.

The most accurate records about the arrival of Musteloidea in South America indicate that the first occurrence of mustelids and most other carnivorans dispersed to South America at about 2.9–2.6 Ma, and procyonids at about 7.2–5.9 Ma (Cione et al., 2007; Reguero et. al., 2007; Prevosti and Soibelzon, 2012, Prevosti and Forasiepi, 2018; Prevosti et al., 2021), while the age of the lower Vinchina succession is much older, spanning from 15.6 – 12.7 Ma (Middle Miocene).

Despite this, when considering the all-morphological traits expressed in tracks and trackways, they are in accordance with a weasel-like producer. Moreover, the ancestral form of the family Mustelidae has been associated with terrestrial weasel-like forms (Gambaryan,1974), but also, the one of the smallest Miocene sparassodont known so far (*Pseudonotictis*), is associated with a weasel-like form (Argot, 2003, 2004). Despite the strong resemblance of *C. sudamericana* to modern mustelid footprints, we cannot assure it, and more evidence is needed to deepen into this hypothesis. If they were produced by a small Carnivora, it implies their arrival to South America between 8 to 5 Ma before it was previously known at 7.2 – 5.9 Ma by procyonids (Reguero and Candela, 2011; Prevosti et al., 2021). This could imply that the first wave of North American immigration started much earlier than it was previously thought at approximately 15 – 12 Ma.

Sparassodont digital and metapodial pads are unknown, as well as any footprint. If *C. sudamericana* was produced by a small metatherian carnivore, they represented the first footprint evidence of sparassodonts ever found. The occurrence of *C. sudamericana* it agrees with the record of sparassodonts in South America (early Eocene - middle Pliocene) and occurred after the highest diversity of the clade (late Early Miocene).

5.1.2. Other mammalian footprints

The trackmakers of *Tacheria troyana* were deeply discussed by Krapovickas and Nasif (2011) by inquiring among both living and extinct South American rodents and rodent-like mammals of medium to large size with tetradactyl feet. Analyzing the morphology of the tracks, the authors discard notoungulates (e.g., miocene hegetotheriids and mesotheriids) as possible producers. Among South American rodents, the Hystricognathi (caviomorphs) are the most likely producer candidates of *T. troyana*. Several families were ruled out, but species of Dinomyidae, one of the largest livings caviomorph rodents, can be related to the Vinchina footprints. Neoepiblemidae is another family of caviomorph that include large-sized species in accord with the inferred body proportions from trackways. Nevertheless, their distal appendicular skeleton is unknown because the fossil remains are generally isolated teeth and small pieces of mandibles (Rinderknecht and Blanco, 2008).

T. troyana was redefined by Krapovickas et al. (2017), and additionally authors offered an interpretation of gait patterns expressed in trackways. The *T. troyana* producer seems to be compatible with an overstep walk gait, with plantigrade pes impress in front of the more digitigrade manus. The footprints herein described denote a producer of relatively short limbs in relation to the trunk length, large stride relative to the footprint length (8.3 – 9.0), a long trunk length (GAD 373.5 – 420 cm), and a body mass ranging from 8.7 kg to 22.35 kg with an average of 16 kg (Tables 1, 2). Rinderknecht and Blanco (2008) reported a

body mass of *Dinomys branickii* of 12 kg. Engelman (2022) estimated body masses between 6.5 kg and 14 kg from cranial measurements, being the known weight, the specimen studied of 9.5 kg. The producer of the Pedregal Negro *T. troyana* is comparable in size to the only dinomyids living species (*D. branickii*), while the *T. troyana* recorded at the upper Member of the Vinchina Formation at Quebrada de La Troya are almost twice as big as those produced by *D. branickii*, denoting a much bigger trackmaker (Krapovickas and Nasif, 2011).

The morphology of the imprints of Morphotype A indicates that they were produced by a small mammal with thin and elongated hind limbs with two elongated digits and claw marks. Due to the apparent absence of manual impressions, and the parallel position between the right and left pedal impressions, we infer that the animal was moving with a hopping-bipedal gait, probably like jerboas do today (family Dipodidae), but gerbils are unknown in the entire American continent.

Verzi and Montalvo (2008) proposed that cricetid rodents, procyonids, and mustelids arrived in South America during a single early dispersal event in the late Middle Miocene. These rodents exhibit various locomotor types, including quadrupedal saltation, where the hind and forelimbs strike the ground simultaneously (Carrizo et al., 2021). However, this behavior is observed only under specific conditions and habitats (Taraborelli et al., 2003). Additionally, their track pattern is distinct, characterized by complete metapodial pads and pentadactyl distinguishable digits (see Fig. 3 in Taraborelli et al., 2003). These features are quite different from the didactyl Morphotype A, excluding them as potential trackmakers.

On the other hand, argyrolagids (Argyrolagidae), one of the most notably specialized South American marsupials, have been proposed to exhibit a bipedal saltatory gait. This inference was suggested based on their overall morphological similarity to noted bipedal rodents (Simpson, 1970; Straccia, 1999) and more recently supported by morphofunctional analysis (Abello and Candela, 2020). Simpson (1970) pointed out that argyrolagids exhibit

strong morphological similarities with bipedal desert rodents as jerboas (Dipodidae) and kangaroo rats (Heteromyidae), representing a striking example of evolutionary convergence. Argyrolagoids (Argyrolagidae + proposed basal argyrolagoids) diversified during the Paleogene in response to climatic and environmental change (greenhouse to icehouse) that occurred at the Eocene – Oligocene boundary (Goin et al., 2010, 2016). Argilolagids first appear occurred during the late Oligocene (Sanchez-Villagra and Kay, 1997). Their distribution in Argentina is well known for the Miocene – Pliocene (see Abello and Candela, 2020) with documented records in the region at Quebrada Honda, Bolivia (Middle Miocene, Sánchez-Villagra et al., 2000) and northwestern Argentina (?Late Miocene, García-López and Babot, 2015). Paleobiological studies on argyrolagids, using living marsupials as a reference, suggest that *Hondalagus altiplanensis* body weight was approximately 100 grams (Sánchez-Villagra et al., 2000), which is approximately in line with our calculation for Morphotype A (~0.26 kg). Argylolagids have elongated metatarsal III and IV, and sharp ungual phalanges (Simpson, 1970; Babot and García-López, 2016) in agreement with the two-digit impressions observed on Morphotype A. Hence, we attribute the trackmaker of Morphotype A to argyrolagids (Fig. 5, B1).

5.1.3. Avian footprints

The *Aviadactyla* consist of a small tridactyl footprint, without a proximal digital union (Fig. 8). These are considered among the typical foot traits of some shorebirds (Weidmann and Reichel, 1979). Sarjeant and Reynolds (2001) agreed on this and proposed sandpipers (Scolopacidae), as potential trackmakers of *Aviadactyla.* On the other hand, many members of the family Scolopacidae have a semi-membrane between digits III and IV, which is not observable in the Vinchina *Aviadactyla*. The presence of a membrane between the digits III-

IV is a trait also observed within Charadriformes, a broader taxonomic group that included sandpipers and can be considered also as possible trackmakers.

Exploring other possible producers of similar tracks, some passerines and even columbiformes can be considered as potential trackmaker. Even though they are tetradactyl and inhabit woody lowlands and ponds, distinct from the arid fluvial environment of the lower Vinchina succession. Tridactyl impressions can occur from tetradactyl foots by imprinting in well-consolidated substrate where the weight of the birds did not print the entire foot, due to track morphology varying with substrate consistency (Falk et al., 2017). The experimental work of Davis et al. (2007) on arthropods, also showed that firm ground causes tracks to become shorter and narrower. We noted that the Vinchina *Aviadactyla* are narrow and have well-preserved details. The absence of the metatarsal pad and the putative loss of digit I impression could be related to well-consolidated substrate where the weight of the birds did not imprint the entire foot.

Elbroch and Marks (2001) point out that in the Mourning Dove (*Zenaida macroura*) and other doves the metatarsal pad may be absent. We observe the same morphology in quails whose metatarsal pad and digit I are not observed when the animal is running. However, where the pedal morphology is so similar, we must consider the stride. Doves are short legged with strides of 25 – 32 mm and stride/footprint length (S/FL) ratio of 3.43, much smaller than the observed on *Aviadactyla* (194 mm - S/FL of 9.75) suggesting a larger-legged bird and excluding doves as a possible trackmaker. The same occurs in quails that are short legged and have a running stride of 205 to 305 mm. Even though the stride length is similar to that of *Aviadactyla*, the footprint of quails and doves are much larger in width and length than that of *Aviadactyla*, and in quails the foot impression records individual phalangeal pads. As such, the relation of stride length to footprint length, implies further body proportions and results very helpful to differentiate between possible trackmakers of similar foot morphology.

Falk (2014), on the other hand, pointed out that birds living in water margin environments tend to have thin, non-fleshy pads. The reason for the relatively low number of pad impressions preserved in fossil bird tracks is due to the inestability of the substrate and the advantage of having small pads.

The *Aviadactyla* body mass (43 g) is in line with the expected for a Scopolacidae trackmaker recorded within the genus *Caladris* of ~40 g (Fiora, 1933; Salvador, 2014). Even though a wide range of birds could be considered as potential trackmaker, it is more likely that the producers were shorebirds rather than birds from wooded lowlands and ponds. Although, in this case we have no strong morphological evidence to distinguish between a shorebird and a passerine, and they inhabit similar environments. However, we prefer to be conservative and maintain the previous conclusions of the Scolopacidae trackmakers, which are the most reliable given the current evidence.

5.1.4. Chelonian footprints

The footprints cf. *Chelonipus torquatus* suggests a five-toed producer with symmetric forelimb, short, subequal and clawed digits, and a hind limb with at least three digits. The trackway denotes an animal with broad gauge, putative heteropody when walking, and a possible "high walk" due to the lack of structures attributed to body dragging or belly dragging, and the lack of tail drag traces (Fig. 9). All these traits relate the Vinchina footprints at least to a small sauropsid trackmaker. Affinities with other animals with pentadactyl and clawed autopodia, as small rodentiforms, are discarded because the trackway does not denote neither their non-cursorial posture, with foot impression near the midline, nor their metapodial pads usually one behind each digit. Among sauropsids, the clades Lepidosauria and Testudinata generally fit with the trackmaker identity.

Firstly, fossil remains of sphenodontians are frequent and well known for the Mesozoic era but were driven to extinction towards the early Tertiary in South America (Apesteguía and Novas, 2003). Therefore, they certainly can be removed from discussion.

On the other hand, among the rest of the lepidosaurs, sprawling-legged squamates are commonly found in Cenozoic South American deposits, but most findings correspond to fragmentary cranial materials or isolated vertebrae, being the varanoiids the most recurring taxa (e.g., Albino et al., 2006; Albino and Brizuela, 2014; Quadros et al., 2018; Albino, 2020a, 2020b). Several squamates share a general autopodia pentadactyl configuration. The typical "lizard" manus possess digit lengths that increase from I through III and IV, which are somehow subequal in length; V is shorter than IV, and the hypex between digits IV and V is proximally deep. The pes is similar, except that digit IV often extends well beyond the end of III (Farlow and Pianka, 2000; Shapiro et al., 2007). In addition, usual "lizard" fossil tracks are registered worldwide and South American Mesozoic deposits (e.g., Buck et al., 2022), and in agreement with Kubo (2010) observations we can determine that the Vinchina trackmaker is not a squamate.

Regarding the clade Testudinata, fully shelled body-fossil records are found in rocks dated from the late Triassic across the world. Since then, there remains are common in the fossil record, however turtle or tortoise footprints are less frequently reported. Known tracks are almost all swim tracks (Lockley et al., 2018), and found in Mesozoic deposits. Examples corresponding to the Cenozoic age are rare, such as *Chelonipus* isp. found in lower Eocene strata at northwest Washington, USA (Mustoe, 2019). Consequently, ichnotaxonomy and interpretation of purported chelonian tracks are still a matter of some debate (Moratalla et al., 1995). Delving into this discussion is out of scope of our work (see Avanzini et al., 2005; de la Fuente et al., 2021; and cited authors).

Testudinatans body plan has remained relatively constant over time, therefore actualistic comparisons are a useful implement to determine trackmaker affinities (e.g., Avanzini et al., 2005). Modern turtles and tortoises display peculiar patterns of trackways given by the functional restrictions implied by the shell presence. General features observed in terrestrial and semi-aquatic testudine tracks and trackways are tetra to pentadactyl digitigrade imprints disposed in parallel rows, which the digits IV and V are the longest; short stride length; contralaterally distant manus-pes sets; and closely spaced ipsilateral manus and pes imprints (Avanzini et al., 2005). Considering this, traits of cf. *C. torquatus* suggest the trackmaker was a small testudine that walked on a slightly inclined surface or with different moisture degrees. In at least two footprints, the digital impressions are connected by an arched structure hinting at the presence of an interdigital web, a morphological element which could determine that the trackmaker was a freshwater turtle (Fig. 5, D).

In northwestern Argentina, outcrops geographically and stratigraphically close to Vinchina record aquatic chelonian body fossil indicating that members of Chelidae (Pleurodira) were present during the Neogene. In the Huayquerías Formation (Late Miocene–Early Pliocene), remains of chelids were found in fluvial channel-fill deposits that represent permanent rivers of small magnitude (de la Fuente et al., 2022). At the same time, in Diamante Strata (Miocene–Pliocene), Southern Mendoza, were recovered small specimens referred to Chelidae (de Broin and de la Fuente, 1993). Further north, outcrops of the El Morterito Formation (Bossi et al., 2000) and the Andalhuala Formation (de la Fuente, 1992), both dated on Late Miocene, bear chelids fossils too. On the other hand, Podocnemididae (Pelomedusoidea, Pleurodira) fossil remains were registered in the Vinchina basin, but in bone beds of earlier ages belonging to the Oligocene Puesto La Fecha Formation (de La Fuente et al., 2003).

Cf. *C. torquatus* body mass (average 0.4 kg, see Table 1) is coincident with the weight of small-sized members of the Chelidae family. An example is *Hydromedusa maximiliani,* with carapace length values lower than 200 mm and body mass lower than 520 g for (Souza and Martins, 2006). For *Pseudemydura umbrina* the carapace does not exceed 155 mm and a weight of 550 g in males, and 133 mm and 408 g in females (Burbidge, 1981). These values are similar to the minimum (358 g) and maximum (432 g) calculated for the ichnogenus cf. *C. torquatus* in this work (Table 1). The carapace measurements of these chelids are in concordance with the calculated trunk length of (GAD 1) of cf. *C. torquatus* (~9 cm) (Table 2). As such, we consider cf. *C. torquatus* was probably produced by small freshwater turtles. Moreover, they clearly overlap the temporal and geographical span of bony-fossil turtles and strongly suggest the Vinchina tracks were produced by chelids or podocnemid pleurodiran.

5.1.5. Subcircular estructures

The producer of Morphotype B needs to be interpreted within a taphonomical and mechanical context. Different factors act together to result in structures with no consistent shape along the trackway. These factors are high water content on the substrate; and the weight and the pressure exerted by the animal on the substrate (see below). Consequently, anatomical features expressed in footprints are poorly defined making the anatomical fidelity to the autopodia very low.

Based on the sizes of the footprints (up to 147 mm long), potential trackmakers that could be related with Morphotype B are animals with medium-sized bodies. Within the known vertebrate fauna of Vinchina, ungulates of variable sizes were previously registered by their fossil footprints. Macraucheniids and toxodontids were abundant walkers that frequented the ancient environments of Vinchina (Vera and Krapovickas, 2022). According

to the authors, the maximum length of their footprints is about 140 mm, being consistent with the dimensions of Morphotype B. The estimated body sizes of macraucheniids and toxodontids suggest that they are the most likely trackmakers of Morphotype B, in function of proportions only.

5.2. Paleoenvironmental and taphonomic considerations

Overbank mudstones deposited within anastomosing fluvial systems of the Vinchina Formation are moderately bioturbated (BI II, Droser and Bottjer, 1986). They are characterized by infaunal invertebrate assemblage of low diversity, dominated by meniscate feeding (*Taenidium barretti*) and simple dwelling structures (*Palaeophycus tubularis*) produced by insects. The overbank mudstones have overcrossing desiccation cracks of multiple sizes ranging from 100 mm to 3 mm, that denote multiple dewatering events.

The top of crevasse splay deposits however is almost devoid of invertebrate trace fossils, with scarce insect dwelling structures (*P. tubularis*), but record a diverse tetrapod ichnofauna. This ichnofauna represents locomotor behavior (repichnia) of a terrestrial epifauna. The stacked crevasse splay deposits in the anastomosed fluvial system overbank prevented the colonization and establishment of a diverse infauna. However, the periodic floodings and the cyclic repetition of muddy, silty, and fine-grained sandy sediments, most likely favors the preservation of the tetrapod footprints due to rapid burial. Most of the footprints in the Vinchina crevasse splay deposits are produced in soft to firm sediments with low standing water conditions. The footprints are shallowly impressed, without rims of displaced sediment and high autopodial definition, with all digit impression and digital pads are well defined (Preservational Mode A, Mancuso et al., 2020).

On the other hand, subcircular to oval structures were produced in cohesive and plastic soupy sediments within high standing water conditions. They are deeply impressed,

with external and internal rims of displaced sediment. The rims of displacement sediment are of variable shape and sizes including an internal positive rim, most likely produced by suction of the plastic sediment after releasing the pressure over the sediment at take-off (Preservational Mode C, Mancuso et al., 2020). Oval structures are overcrossed by symmetric ripples, suggesting they could have formed underwater, or they were flooded after footprint formation. As such, the tracking surface denotes lateral variations in water content evidenced by the varying preservation styles of footprints and the partial record of symmetric ripples. The time span involved for the formation of the tracking surface was short enough such that there is no pedogenic disturbance evidenced and a low diversity and low bioturbation of the infauna. But long enough to allow the dewatering of the sediment via subaerial exposition evidenced by the presence of contrasting footprint preservational modes (A and C) in the same area.

The overbank ichnofauna of both, muddy flood basin and sandy crevasse splays, are an example of the *Scoyenia* Ichnofacies representing a low diversity ichnocoenoses, mainly composed of meniscate trace fossils and tetrapod footprints (Frey et al.,1984). The *Scoyenia* Ichnofacies is intermediate between aquatic and non-aquatic environments and characterizes low energy deposits periodically exposed to air or periodically inundated as observed in the Vinchina over bank deposits. In fluvial systems, this Ichnofacies is commonly placed in over bank deposits and abandoned channels, including a wide variety of sub environments, such as pond, levees, sand bars and crevasse splays (Frey et al., 1984; Frey and Pemberton, 1984, 1987; Buatois and Mángano, 1995, 2002, 2004).

6. Conclusions

The new findings recorded at the Vinchina Formation at Quebrada de Pedregal Negro, enhance the knowledge about the South American continental faunas into the Middle

Miocene. This work describes an ichnoassociation which denotes how diverse and complex the tetrapod faunas were before the Great American Biotic Interchange in north-western Argentina.

The presence of *Carnivoripeda sudamericana* reveals a weasel-like producer, most likely a small sparassodont whose footprints were unknown until now. In association with *C. americana*, tracks and trackways of *Tacheria troyana* provided new data that enriches the previous interpretations to inquire into the ancient dinomyids paleobiology. The trackmaker of *T. troyana* has two different body sizes, the footprints recorded at the lower member Vinchina Formation are almost half the size of those previously recorded at the upper member of the Vinchina Formation. Small rodent-like footprints (Morphotype A) reveal the presence of small bipedal mammals with symmetric jumping gait at the tracksite, most likely produced by one of the highly specialized South American marsupials, argyrolagids, whose footprints were unknown until now. The footprints show detailed autopodial definition, but the scarce number of footprints does not allow us to assign them to any known ichnotaxa or to place them within a new ichnospecies. About the bird footprints, *Aviadactyla vialovi* is herein interpreted as most likely produced by a small shorebird of the family Scopolacidae. They resemble footprints of passerines and even columbiformes, however those interpretations are less likely. The reptilian ichnofauna was unknown at the Vinchina Formation until now. New evidence shows the occurrence of small freshwater turtles, whose size and morphology resemble that of the families Chelidae or Podocnemididae. Subcircular to oval structures (Morphotype B) appear in association with mammalian and avian tracks in a highly bioturbated surface. They were produced before other footprints in cohesive and plastic soupy sediments. Morphotype B are deeply impressed, with external and internal rims of displaced sediment, produced by suction of plastic sediment after releasing the pressure over the sediment at take-off. Based only in the apparent dimensions, these structures

suggest the presence of medium-sized mammals, probably native ungulates. All other mammal and bird footprints are shallowly impressed, without rims of displaced sediment, they have high autopodial definition, and well-defined digital pads. Their crosscutting relationship denote that all footprints were produced after Morphotype B in soft to firm sediments with low standing water conditions. All invertebrates (*P. tubularis* and *T. barretti*) and tetrapod footprints represent unique and diverse Middle Miocene ichnocoenoses and are considered an example of the *Scoyenia* Ichnofacies.

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Table 1. Summary of estimated body mass for three mammals, one bird, and one reptile based on footprint parameters. All values are in kilograms.

	Body mass				
	Tacheria troyana N = 27	*Carnivoripeda sudamericana* N = 14	*Aviadactyla vialovi* N = 5	Cf. *Chelichnus torquatus* N = 2	Morphotype A N = 2
Min	8.70	0.17	0.025	0.35	0.24
Max	22.35	1.82	0.067	0.43	0.28
Av	16	0.7	0.043	0.39	0.26
SD	4	0.6	0.020	0.2	0.03

Table 2. Summary of gleno-acetabular distances (GAD), and the ratio between the average stride and footprint length (S/FL) calculated for two trackways of *Carnivorpeda sudamericana*, four trackways of *Tacheria troyana*, and one trackway of cf. *Chelonipus torquatus.* The results for GAD were obtained by the employment of three methods (see Materials and Methods). All values are in millimeters.

	GAD 1	GAD 2	GAD 3	S/FL
C. sudamericana **Tw1**	108.29	264.10	347.92	19.8
C. sudamericana **Tw2**	133.75	196.13	254	17.8
T. troyana **Tw3**	373.5	485.75	598	8.3
T. troyana **Tw4**	408.5	536	663.5	8.8
T. troyana **Tw5**	383.97	509.55	635.13	8.4
T. troyana **Tw6**	420	556.5	693	9.0
cf. *C. torquatus* **Tw8**	84.87	108.81	132.75	6.6

Highlights

- *C. sudamericana* nov. isp. may represent the first sparassodont footprints ever found.

- *C. sudamericana* nov. isp. are the oldest carnivore footprints in South America.

- First footprints found of highly specialized South American marsupials, argyrolagids

- The lower Vinchina succession records the only well constrained Middle Miocene (15.6 – 12.7 Ma) ichnoassociation in South America.

- The ichnoassociation is dominated by small-sized mammals (sparassodonts and argyrolagids), reptiles (freshwater turtles) and birds (shorebirds), followed by medium sized, dinomyid rodent and ungulates.

Declaration of interests

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

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: