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Pehuen Co: Updated taxonomic review of a late Pleistocene ichnological site in Argentina

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ABSTRACT

The paleoichnological site of Pehuen Co, located on the southern coast of Buenos Aires province, Argentina, was discovered in 1986 and the first paper was published in 1987. New discoveries made in the following years have revealed well-preserved Pleistocene mammal and bird footprints of high diversity. Investigations at this site have continued to the present. The most important aim of this paper is to revise the previous ichnotaxonomic assignations, and to present some new discoveries. The described tracks include eleven mammal (*Neomegatherichnum pehuencoensis*, *Mylodontidichnum rosalensis*, *Glyptodontichnus pehuencoensis* nov. igen. and isp., *Eumacrauchenichnus patachonicus*, *Proboscipeda australis* nov. comb., *Dolichotichnus marae* nov. igen. and isp., *Ursichnus sudamericanus* nov. isp., *Hippipeda* isp., *Lamaichnum guanicoe*, *Lamaichnum tulipensis* nov.comb, *Pecoripeda commune* nov. comb.) and four bird icnotaxa (*Phoenicopterichnum pehuencoensis*, *Charadriipeda* isp., *Gruipeda* isp., and *Aramayoichnus rheae* nov. igen. and isp.). The second goal of this paper is to emphasize the world-wide significance of the Pehuen Co site relative to other Pleistocene vertebrate tracksites. Pehuen Co site is unique because of the quality of preservation, and the abundance and diversity of the footprints.
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1. Introduction

The discovery of Pehuen Co paleoichnological site, located on the south coast of Buenos Aires province, Argentina (Fig. 1), occurred in October 1986. The high quality, abundance and diversity of mammal and bird footprints were soon noticed; they merited a first communication during the IV Congreso Latinoamericano de Paleontología, held at Santa Cruz de la Sierra, Bolivia, on July 1987 (Aramayo and Manera de Bianco, 1987a,b). Pehuen Co is a coastal site and is continuously subject to erosion by waves during high tides and storms. These factors, along with harmful human activities, continuously exposed new tracked surfaces and destroyed or covered many others with sand. For this reason, the visits to the site to document and rescue important ichnological material have continued for almost 30 years (Aramayo and Manera de Bianco, 1990, 1994, 1996, 1998; Aramayo, 2001; Aramayo et al., 2003; Manera de Bianco and Aramayo, 2004; Manera de Bianco et al., 2005a, 2010; Manera and Aramayo, 2013).

Conservation of the ichnological record of the site was greatly aided by the Rolex Award for Enterprise, which was given in 2004 to one of us (T. M. de B.). The prize allowed us to make silicon rubber casts of the main ichnotaxa; these are today deposited at the Carlos Darwin Museum, in Punta Alta city, Buenos Aires province, Argentina. The repository collection includes original footprints and casts of trackways. Most of the trackways depicted in Aramayo and Manera de Bianco (1987a,b), including the holotypes, remained in situ and some of them disappeared due to sea erosion. In 2005 the area was designated a reserve area (Reserva Geológica, Paleontológica y Arqueológica Provincial Pehuen Co — Monte Hermoso), and is now protected by provincial law nr. 13394.

The main purpose of the present paper is to provide an updated ichnotaxonomic descriptions and diagnoses, including new footprint discoveries made in the recent years. We also discuss Pehuen Co's world significance, emphasizing its uniqueness among Pleistocene vertebrate tracksites, the quality of preservation, abundance and diversity of fossil footprints.

2. Geological setting

The paleoichnological site is located about 1.5 km east of Pehuen Co village, on the southern coast of Buenos Aires province, Argentina (extending from 39° 00′ 13″ S, 61° 32′ 30″ W to 38° 59′23″ S, 61° 27′ 30″ W) (Fig. 1). Footprint-bearing beds are siltstone, sandstone and claystone, forming modern abrasion platforms outcropping along the beach for at least 10 km; the surface of the whole area is about 1.5 km^2. The exposed sedimentary section is 1.20 m thick (Fig. 2) and is formed by fine-grained sediments deposited in

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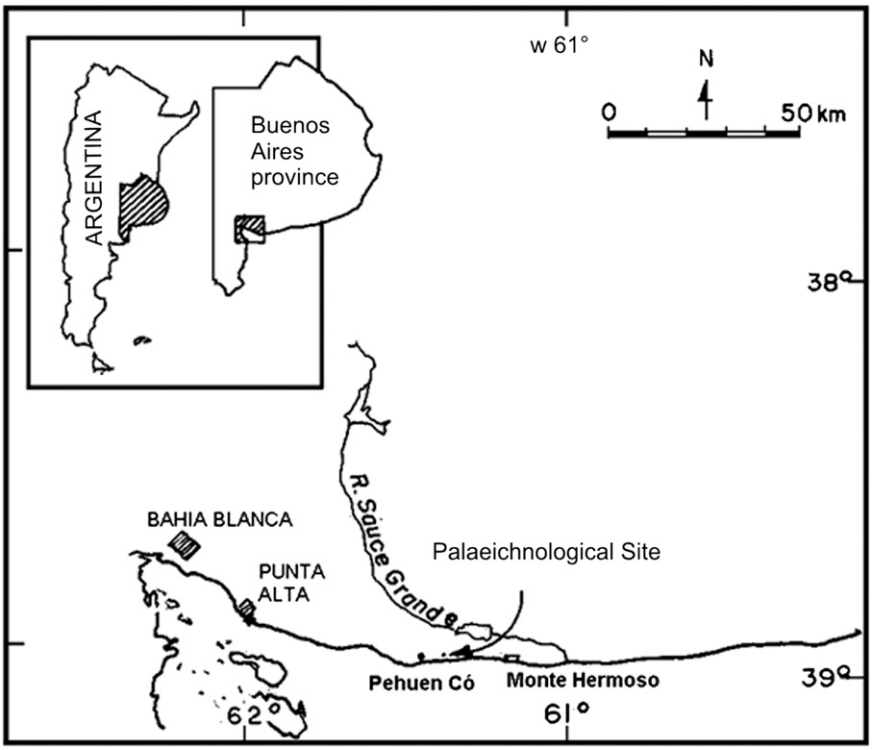


Fig. 1. Map of part of the Buenos Aires province showing the location of the Pehuen Co site.

temporary shallow ponds after flooding events of fluvial origin (Zavala and Quattrocchio, 2001). This outcrop is found in the inter- and supratidal zones of the beach, and is reached and eroded by high tides. Because of this location, the outcrop is covered and uncovered with sand in a random way, which sometimes makes observation of the footprints difficult. The age of this site according to AMS (Accelerator Mass Spectrometry) radiocarbon dating is 12,000 y B.P. ± 100 (New Zealand Rafter Lab) (Aramayo and Manera de Bianco, 1996).

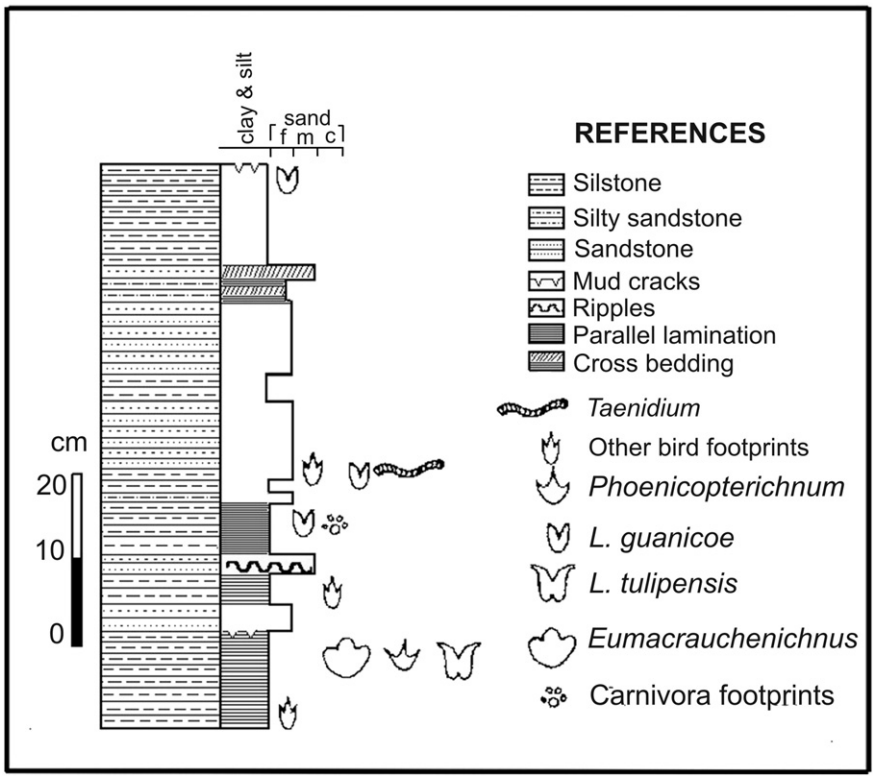


Fig. 2. Sedimentary log of the middle part of the section.
Taken from Manera and Aramayo (2013).

3. Material and methods

As the outcrops are constantly changing due to the dynamics of the beach, fieldwork was carried out during several distinct opportunities after heavy storms with prevailing winds from the S and SE. These onshore winds produce greater erosion by sweeping the beach sand and exposing the layers with fossil tracks. During the fieldwork photos were taken, footprints and trackways were located with a GPS device, and the strike directions of the trackways were taken with a Brunton compass. The measurements were taken following the criteria and using the ichnological terms proposed by Leonardi (1987).

The most significant footprints and trackways were casted using silicon rubber and/or traced using transparent plastic sheets. Blocks of sediment with footprints, detached by marine erosion, were also collected. In the laboratory, some replicas were made from the casts, and the material obtained in the field was analyzed in detail. Neotype material was used in the revision and redescription of some ichnotaxa because the holotype material left in situ was destroyed by marine erosion.

A collection of silicon rubber casts (MD-YPI), plaster casts (MPA/MD-YPI) and original samples (MD/MD-YPI) of the footprints as holotypes, neotypes and paratypes is deposited at the Carlos Darwin Museum (MD) Punta Alta, Buenos Aires province, Argentina and is curated by one of us (T. M. de B.).

Institutional abbreviations includes: MD: "Museo Carlos Darwin"; MPA "Museo Punta Alta" (former name of MD, used for casts and samples taken before 1990), and YPI: "Yacimiento paleoicnológico": paleoichnological site in Spanish.

4. Systematic ichnology

4.1. ***Ichnogenus*** *Neomegatherichnum Aramayo and Manera de Bianco, 1987a*

4.1.1. Type and only known ichnospecies

Neomegatherichnum pehuencoensis Aramayo and Manera de Bianco, 1987a.

4.1.2. Emended diagnosis

Large plantigrade footprints preserved as concave epirelief. Manus footprints circular to subcircular, commonly longer than wide, footprint length about 40% of the associated pes, placed anterior-medially to the pes footprint, large inwardly directed claw mark. Pes footprints subelliptical, up to 1 m long, wider anteriorly, long axis parallel to the trackway midline, most display a ridge located adjacent to the anterior and lateral margins of the footprint, occasional large claw mark at the medial-anterior corner of the footprint that is directed inward or backward. Pace angulation in a straight trackway is 85°–115° (modified from Aramayo and Manera de Bianco, 1996).

4.1.3. ***Ichnospecies*** *Neomegatherichnum pehuencoensis Aramayo and Manera de Bianco, 1987a*

Fig. 3A–D.

4.1.4. Neotype

A trackway of 8 footprints (4 tracks and 4 undertracks). MD-YPI-05-14 is the silicone rubber cast of 3 tracks (Fig. 3A and C, Additional material Table 1A).

4.1.5. Additional material

1) Trackway of 7 footprints in situ (Table 1C). MD-YPI-15-04 is the silicone rubber cast of this trackway. 2) Trackway of 11 footprints in situ (Fig. 3C; Table 1B). 3) A siltstone bed with 6 ground sloth trackways and bird footprints in situ (Fig. 3D). MD-YPI-06-11 is the silicone rubber cast of part of the 6 trackways (48 footprints) and 72 bird footprints (including *Gruipeda* and *Charadriipeda*).

4.1.6. Description

Detailed information on three selected trackways is summarized in Table 1 (supplementary material). Trackway breadth ranges from 1.2 to 1.6 m. Manus footprints occur only in some trackways and average measurements are 0.33 m long and 0.27 m wide, some display a large claw mark that can reach 0.17 m long. Average pes footprint length is 0.85 m (range 0.74–1.00 m) and width is 0.49 m (range 0.30 m–0.71 m). The triangular claw mark of digit III is up to 0.15 m long and forms an angle of 50–90° with the pes footprint axis.

4.1.7. Comments

Neomegatherichnum pehuencoensis footprints are very common at the site. About 80 trackways were registered, each of them comprising at least five footprints. Because of their shape and size, the footprints were undoubtedly imprinted by megatheres (Xenarthra, Tardigrada, Megatheriidae), showing mostly a bipedal locomotion (Aramayo and Manera de Bianco, 1996). Blanco and Czerwonogora (2003) used biomechanical studies on bones and analysis of the holotype trackway of *N. pehuencoensis* to conclude that *Megatherium* locomotion was bipedal. Nevertheless, quadrupedal trackways may be also observed: manus prints are quite circular in shape, and commonly a few manus footprints are associated with pes footprints in several trackways (Aramayo and Manera de Bianco, 1996). In a single case (Fig. 3B, Table 1B), fully quadrupedal locomotion was documented with manus and pes footprints lacking claw impressions. Occasionally, the pes footprint overprints the manus impression and thus a semicircular outline is observed on the anterior part of the pes footprints. In others, manus and pes footprints are clearly distinguished; manus imprints placed in front of pes footprints (Fig. 1B, Table 1C) (see also Aramayo and Manera de Bianco, 2009).

The late Pleistocene *Neomegatherichnum pehuencoensis* differs from the late Miocene to Pliocene *Megatherichnum oportoi* Casamiquela, 1974 in several aspects (see also Melchor et al., 2015–in this volume): 1) the former is larger (including trackway breadth, footprint length and width), 2) pace angulation in *N. pehuencoensis* (85°–115°) is smaller than in *M. oportoi* (110–147°), and 3) size difference between manus and pes is marked in *N. pehuencoensis* (about 2.5:1), whereas in *M. oportoi* it is slight.

Other potentially similar ichnotaxa are *Acugnaichnus dorregoensis* Casamiquela, 1983, *Mylodontidichnum rosalensis* Aramayo and Manera de Bianco, 1987a, and *Iribarichnum megamericanum* Casamiquela, 1983. *A. dorregoensis* is smaller and the posterior end of the footprints is proportionally narrower than in *Neomegatherichnum pehuencoensis*. *Mylodontidichnum rosalensis* has smaller and narrower footprints, the pace angulation can reach greater values (89°–132°), and the pes footprint can show more than a digit impression. Finally, *I. megamericanum* is similar to *Neomegatherichnum*, but this is based on a single poorly preserved footprint, and it is best considered a nomen nudum.

Regarding the locomotion of ground sloths, McDonald (2007) studied the morphology of the pes of *Paramylodon harlani* together with biomechanical information from its footprints, and he concluded that the locomotion of extinct ground sloths was quadrupedal. After a re-examination of the purported bipedal trackway *Megaterichnum oportoi*, Melchor et al. (2015-in this volume) concluded that the most likely interpretation for this Late Miocene–Pliocene ground sloth trackway is quadrupedal locomotion, but a bipedal interpretation remains likely for the late Pleistocene *Neomegatherichnum pehuencoensis*.

4.2. ***Ichnogenus*** *Mylodontidichnum Aramayo and Manera de Bianco, 1987a*

4.2.1. Type ichnospecis

Mylodontidichnum rosalensis Aramayo and Manera de Bianco, 1987a.

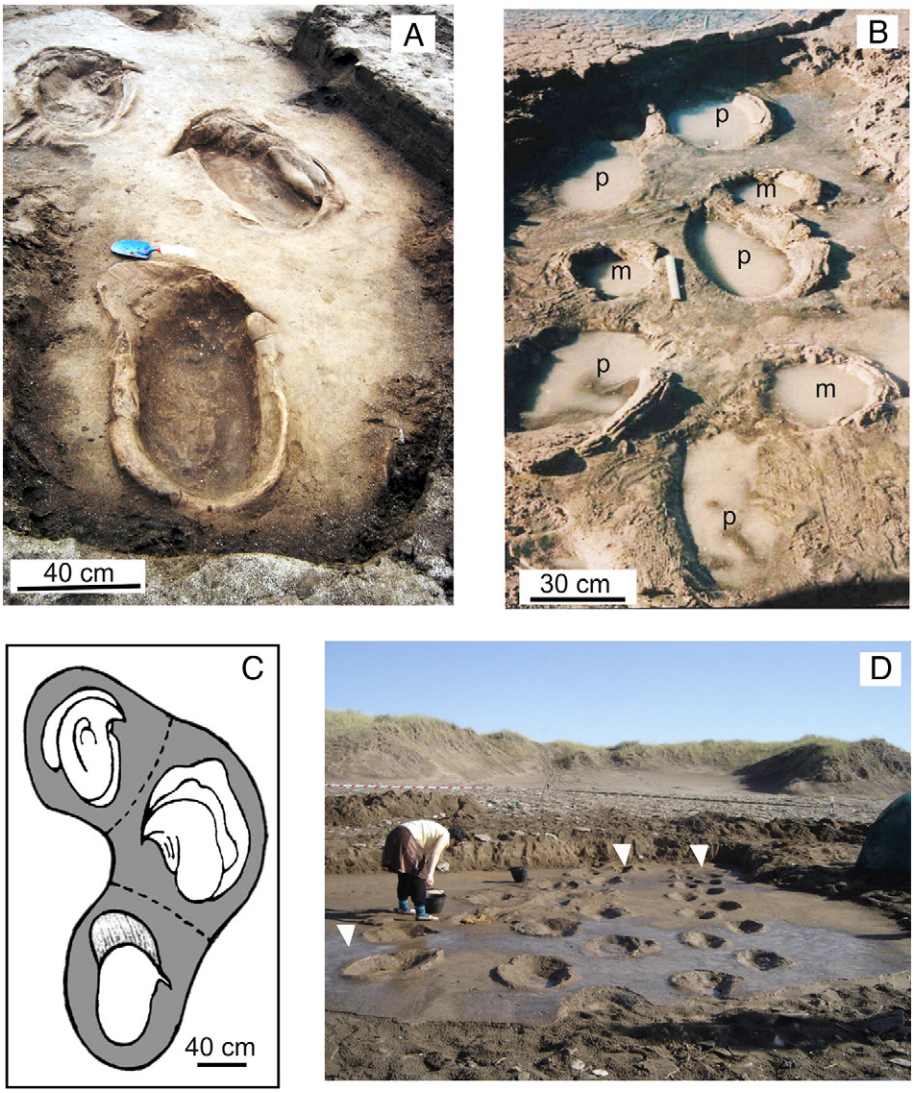


Fig. 3. *Neomegatherichnum pehuencoensis*. (A) Three footprints of the neotype bipedal trackway. (B) Quadrupedal trackway. (C) Sketch of the silicon rubber cast MD-YPI-05-14 taken in the surface illustrated in A. (D) Three trackways on a siltstone level with 6 ground sloth trackways and bird footprints. m: manus, p: pes.

4.2.2. Emmended diagnosis

Quadrupedal trackway composed of medium to large-sized, plantigrade footprints; pes sub-elliptical, manus sub-circular. Pes footprint larger than 0.5 m (average footprint length/width ratio greater than 2), typically with an arched outline and narrower posterior part, pes footprint axis parallel to the trackway midline or slightly inwardly directed, moderate pace angulation. Pes footprint with a marginal ridge in the lateral and anterior margin, up to three broad and blunt digit imprints, related to three short, diverging and laterally oriented claw marks. Manus footprint rarely preserved, subcircular, slightly longer than wide, manus footprint length about half of pes footprint length, manus footprint imprinted anteriorly and/or laterally to the pes footprint.

4.2.3. Ichnospecies

Mylodontidichnum rosalensis Aramayo and Manera de Bianco, 1987a. Fig. 4.

4.2.4. Type material

The holotype proposed by Aramayo and Manera de Bianco (1987a) is a trackway composed for 23 footprints (Fig. 4A, Table 2A, Supplementary Material) that is currently destroyed by erosion. Neotype: A trackway composed of 9 pes and 4 manus footprints (Fig. 4B–D, Table 2B). MD-YPI-05-12 is the silicon rubber cast of the neotype.

4.2.5. Diagnosis

Same as for the ichnogenus, only known ichnospecies.

4.2.6. Description

The holotype was a trackway composed of 23 footprints, including 7 undertracks (#1 to #7) showing a double marginal ridge, originally interpreted as indication of overlap of the pes on the manus (Aramayo and Manera de Bianco, 1987a). However, this double ridge may be the result of differential erosion of the hosting laminated siltstone (Fig. 4A). Measurements on the holotype (excluding undertracks) suggest that average pes footprint length is 0.60 m (range = 0.50–0.72 m, n = 16), average pes footprint width is 0.29 m (range = 0.15–0.40 m, n = 16), and average pes footprint length/width ratio is 2.17 (range = 1.30–3.33, n = 16). Trackway parameters of the holotype (only pes were identified) are: average pace length is 0.568 m (range = 0.40–0.72 m, n = 23), average stride length is 1.15 m (range = 0.88–1.32 m, n = 23), average pace angulation is 108° (range = 89–132°, n = 23), and average divarication from the midline is −6° (range = 0 to −23°, n = 23). The neotype includes 9 pes footprints and 4 manus

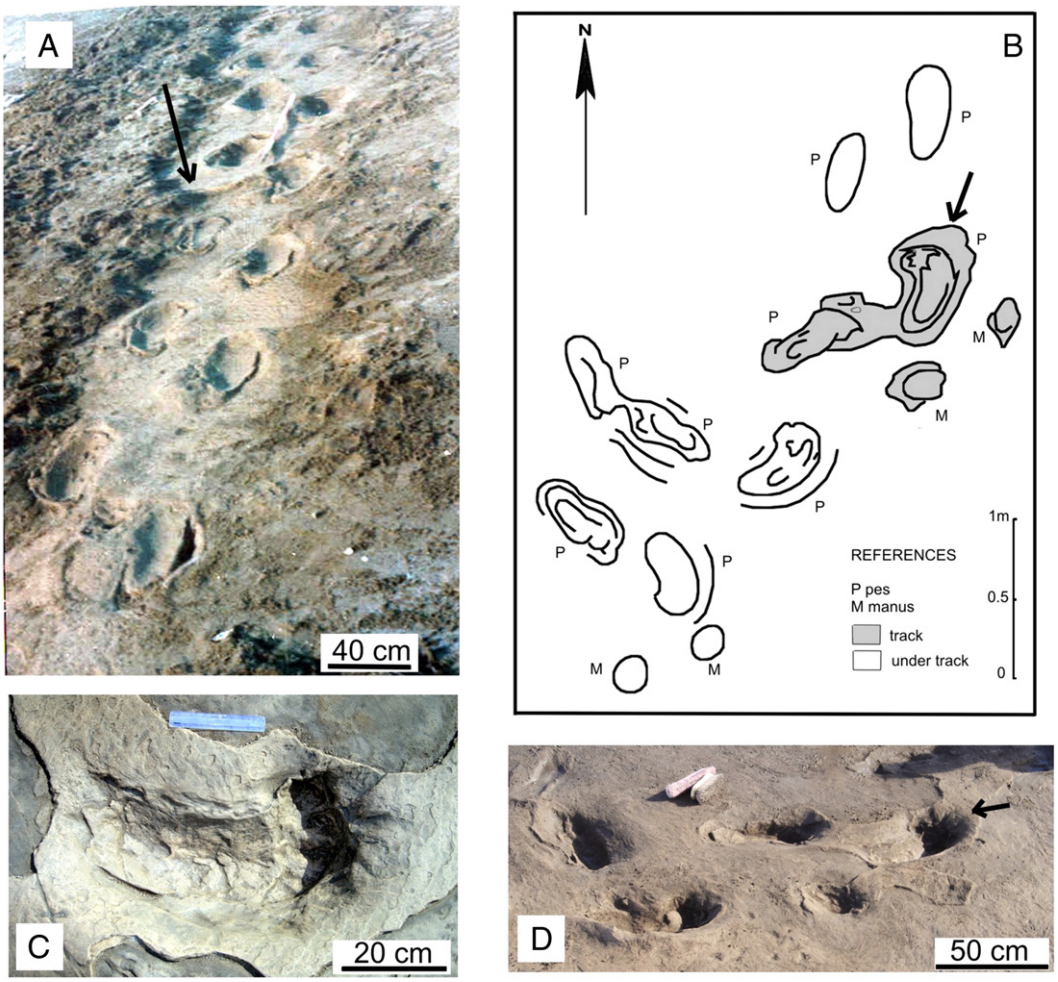


Fig. 4. *Mylodontidichnum rosalensis.* (A) Holotype trackway (currenly missing). The arrow separates the first impressions (lower mid part of photo) that are undertracks from the remaining footprints that are true tracks. (B) Sketch of the neotype trackway. The arrow points to the position of pes footprint of "C". Drawn from the silicon rubber cast MD-YPI-05-12. (C) Detail of the left pes footprint showing 3 digit and claw imprints. (D) Partial view of the neotype. The arrow points to the pes in C. m: manus, p: pes.

footprints composing a curved trackway (with a change in strike of nearly 180°) whose pace length and pace angulation is difficult to measure (Fig. 4B–D). However, the size and shape of footprints are similar to the holotype trackway. The neotype trackway shows associated manus footprints and a single right pes footprint (#8), tracks exhibit a broad sole impression with three digit imprints (I–III) and the corresponding claw marks, which are up to 8 cm long (Fig. 4B–D). Footprint measurements on the neotype trackway are: average pes footprint length is 0.53 m (range = 0.50–0.60 m, n = 9), average pes footprint width is 0.27 m (range = 0.13–0.35 m, n = 9), average pes footprint length/width ratio is 2.1 (range = 1.66–3.84, n = 9), average manus footprint length is 0.23 m (range = 0.22–0.25 m, n = 4), average manus footprint width is 0.19 m (range = 0.15–0.20 m, n = 4), and average manus footprint length/width ratio is 1.24 (range = 1.1–1.46, n = 4).

4.2.7. Remarks

This ichnospecies refers to trackways printed by mylodontids (Xenarthra, Tardigrada, Mylodontidae), showing either bipedal or quadrupedal locomotion. *Mylodontidichnum rosalensis* is smaller than *Neomegatherichnum pehuencoensis*; in some trackways each pes footprint has a kidney-like shape, with the concave part towards the midline. *M. rosalensis* and *Megatherichnum oportoi* (Casamiquela, 1974) display a similar pes footprint size and pace angulation, although the former is slightly smaller on average (Melchor et al., 2015-in this volume). *M. rosalensis* and *M. oportoi* differ in the shape of the manus footprint and by the presence of three clawed digit imprints in the pes footprint of the former.

The referred neotype material can be interpreted in two alternative ways (Fig. 4B–D). One of the interpretations is that, after a short bipedal locomotion, the mylodontid put both manus on the ground probably for drinking water (inferred by the presence of ripple marks) later goes upright, turns left and walks away with a bipedal gait (Fig. 4B). If we assume a quadrupedal locomotion, as proposed by McDonald (2007) for fossil ground sloths, the manus prints were left when the mylodontid was drinking and while it was turning but finally when it resumed its straight path, the manus tracks were overlapped by those of the pes.

4.3. ***Ichnogenus*** *Glyptodontichnus nov. igen.*

4.3.1. Type ichnospecies

Glyptodontichnus pehuencoensis nov. isp.

4.3.2. Derivation of name

After *Glyptodon* Owen, 1838 (Xenartha, Cingulata, Glyptodontia) the inferred producer and "*ichnus*" for trace.

4.3.3. Diagnosis

Large plantigrade padded footprints with pentadactyl, sub-circular to fan-shaped pes footprint somewhat larger than the subelliptical, tridactyl manus footprint. Pes imprint with short, wide and blunt digits; divarication of lateral digits (I–II and IV–V) is wider (40–50°) than in the

central digits (5–10°). Manus footprint with almost parallel, wide digits (II to IV) ending in a short tip directed forward; digit IV is slightly divergent from digits II and III (angle between III and IV: 20°), clear sub-circular metapodial palm imprint.

4.3.4. Glyptodontichnus pehuencoensis nov. isp.
Fig. 5.

4.3.5. Derivation of name
After Pehuen Co, geographic name of the site.

4.3.6. Holotype
An isolated left pes footprint (MD 93-5, Fig. 5A). Paratype: two footprints, right manus and pes (Fig. 5B) left at the field. MD-YPI-04-04 is a plaster cast of the holotype.

4.3.7. Diagnosis
Same as for the ichnogenus, only known ichnospecies.

4.3.8. Description
The holotype is a pes imprint in a siltstone block, about 0.185 m long and wide, showing a rough sole with crevices and a shallow heel impression in the back of the footprint. A remarkable rough and anterior marginal rim is observed. The paratype is a manus–pes pair preserved in a sandy siltstone left in situ. The pentadactyl pes footprint shows less detail than the holotype and overlaps slightly on digit IV of the manus footprint. The manus is 0.17 m long and 0.10 m wide and displays the impressions of digits II, III and partially IV (Fig. 5 B, C and D).

4.3.9. Comments
The morphology of these tracks is so peculiar that it was not possible to find fossil footprints with similar features in previous studies. Among the other ichnotaxa present at the site, *Eumacrauchenichnus patachonicus* shows a similar size and sub-circular outline to *Glyptodontichnus pehuencoensis* pes, but they are easily distinguishable because of the number (three) and shape of the digits of *E. patachonicus*. Although *G. pehuencoensis* manus print is tridactyl, like those of *E. patachonicus*, its shape, size and presence of a palm print distinguish it from the latter.

The morphological features and size of these footprints allow us to infer that the trackmarker could have been a species of the genus *Glyptodon*. This genus had 5 digits in the pes, while other Pleistocene glyptodonts had a reduced number of digits (Pascual et al., 1966). Although the hand of glyptodonts had four digits (II to V), it is likely that digit V was not recorded because it was divergent and smaller. A comparison of the paratype footprints with a skeletal reconstruction of the manus and pes of *Glyptodon* sp. (at 70% of their original size), suggests a remarkable match, except for some variation in the angles between the digits of the pes (Fig. 5B–D).

Aramayo and Manera de Bianco (1996) reported the holotype specimen, which was already considered as produced by *Glyptodon* sp. The later finding of a manus–pes couple confirms this interpretation. Apparently, these are the only glyptodont tracks that have been published until now. The only other mention of probable glyptodont footprints is a tetradactyl manus–pes couple from the Tertiary of Mogna, San Juan, Argentina (Leonardi, 1994, plate XIX, fig. 11), which differs from *Glyptododontichnus* in the number of digits, the absence of sole imprint and the presence of long digit imprints. The absence of records of glyptodont footprints in other sites and its rare occurrence at Pehuen Co are quite remarkable when we consider that the presumed producer is very common in the skeletal record. This rarity is quite significant for the Pehuen Co site, which contains many tracks of most of the species of mammals that lived in the Pampean region during the late Pleistocene. On the basis of biomechanical studies, Fariña et al. (2013) stated that glyptodonts may have avoided walking on muddy substrates, like those of the study site, where these animals were at risk of getting trapped.

*4.4. **Ichnogenus** Eumacrauchenichnus Aramayo and Manera de Bianco, 1987a*

4.4.1. Type ichnospecies
Eumacrauchenichnus patachonicus Aramayo and Manera de Bianco, 1987a.

4.4.2. Emended diagnosis
Quadrupedal trackway composed of large equidimensional trydactyl footprints with manus and pes of similar size and shape. Pace length/footprint length ratio about 5, high pace angulation (125–150°). Manus and pes footprints sub-circular in outline, anterior edge with three broad undulations corresponding to short and stout digits, digit III is wider and longer, smooth sole/palm surface. The posterior part of the footprints shows a characteristic medial concavity of the footprint edge.

*4.4.3. **Ichnospecies** Eumacrauchenichnus patachonicus Aramayo and Manera de Bianco, 1987a*
Fig. 6.

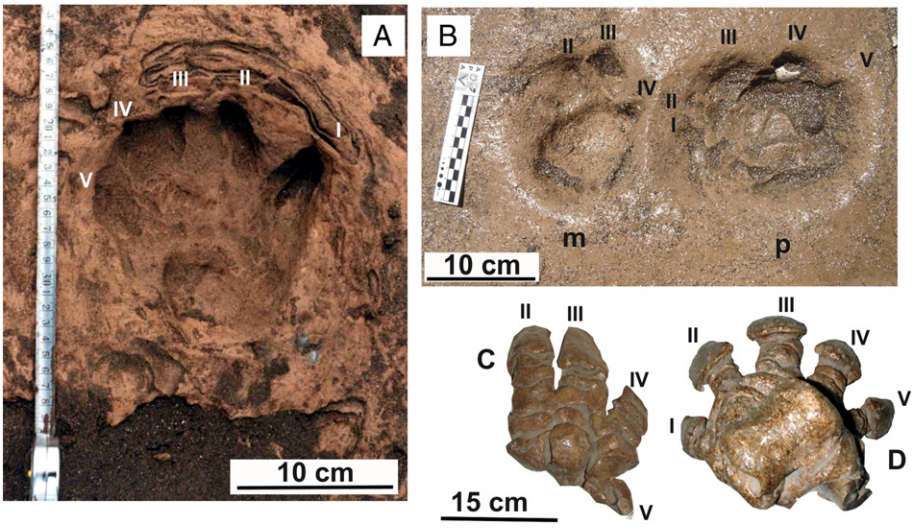


Fig. 5. *Glyptodontichnus pehuencoensis*. (A) Holotype specimen (left pes footprint) MD 93-5. (B) Paratype specimen, right manus–pes couple (in situ). The pes partially overlaps the digit IV of the manus. (C, D) Replicas of the right manus and pes skeleton of *Glyptodon* sp. m: manus, p: pes. I to V: digits.

4.4.4. Holotype

A trackway of at least 10 clear footprints (Fig. 6A, Table 3A, supplementary material) (Aramayo and Manera de Bianco, 1987a). The holotype is currently missing due to marine erosion.

4.4.5. Additional material

1) Trackway of 4 footprints in situ. MD-YPI-05-11 is a silicone rubber cast of 3 footprints of the former trackway (Table 3B). 2) Several footprints printed by two or more individuals of the same species in situ (Fig. 6B). MPA-87-55-I-E-a and MPA-87-55-I-E-b are plaster casts of 2 footprints of the former (Fig. 6C). 3) Trackway of 9 footprints in situ. MD-YPI-06-08 is a silicon rubber cast of this trackway. 4) A trackway of 6 footprints in situ (Table 3C).

4.4.6. Description

The general shape of the footprints, including the larger digit III impression and the posterior concavity is common to all specimens. The footprint size exhibits a large range, for example footprint length is from 0.13 to 0.24 m. The footprint length/width ratio is also variable, between 0.94 and 1.21. This size range can be related to the presence of adults and juveniles, as observed in some trampled surfaces, although this inference requires further study. The pace length ranges from 1.05 to 1.40 m and the trackway breadth between 0.41 and 0.87 m.

4.4.7. Comments

The morphology of the footprints and the high pace angulation value of the trackways suggest that the most likely producer was *Macrauchenia patachonica* Owen, 1838 (Litopterna, Macraucheniidae). Measurements of the fossil bones of the limbs of the mentioned species match the size of the footprints.

4.5. ***Ichnogenus*** *Proboscipeda Panin and Avram, 1962*

4.5.1. Type ichnospecies

Proboscipeda enigmatica Panin and Avram, 1962.

4.5.2. Emended diagnosis

Large oval to subcircular footprints, large and flat sole/palm surface either ornamented or smooth, three to five short and blunt digit impressions pointing anteriorly, deep footprints with a noticeable marginal ridge.

4.5.3. Remarks

The emended diagnosis is modified from the redaction proposed by McNeil et al. (2007) and Lucas et al. (2007) using an English translation of the original Romanian description provided by Nicolae Panin (written communication, 2015). McNeil et al. (2007) suggested that a pockmarked sole surface is diagnostic of the ichnogenus, but the original description indicated that the sole is smooth. Panin and Avram (1962) recognized that this feature depends upon the grain-size of the hosting sedimentary rock. Lucas et al. (2007) indicated that the overstepping of pes on manus is diagnostic, but this feature is not always present. An additional feature of the type material is that the footprints occur in large number in a small surface area, which was used by Panin and Avram (1962) to suggest likely herding behavior. Coincidentally, spectacular late Miocene surfaces from the United Arab Emirates showing hundreds of proboscidean tracks have been used to infer a complex social structure for this group (Bibi et al., 2012). However, we believe that this feature should not be included in the diagnosis to allow for the identification of isolated or poorly exposed tracks.

4.5.4. ***Ichnospecies*** *Proboscipeda australis nov. comb.*

Fig. 7A–D.

1987a *Stegomastodonichnum australis*: Aramayo and Manera de Bianco, p. 21–522, fig. 7.

4.5.5. Holotype

An in situ trackway of 7 footprints (Fig. 7A–B). MPA.87-56-I-E is a plaster cast of a footprint of the holotype (Fig. 7C).

4.5.6. Additional material

A partial in situ trackway of 3 footprints (Fig. 7D–E).

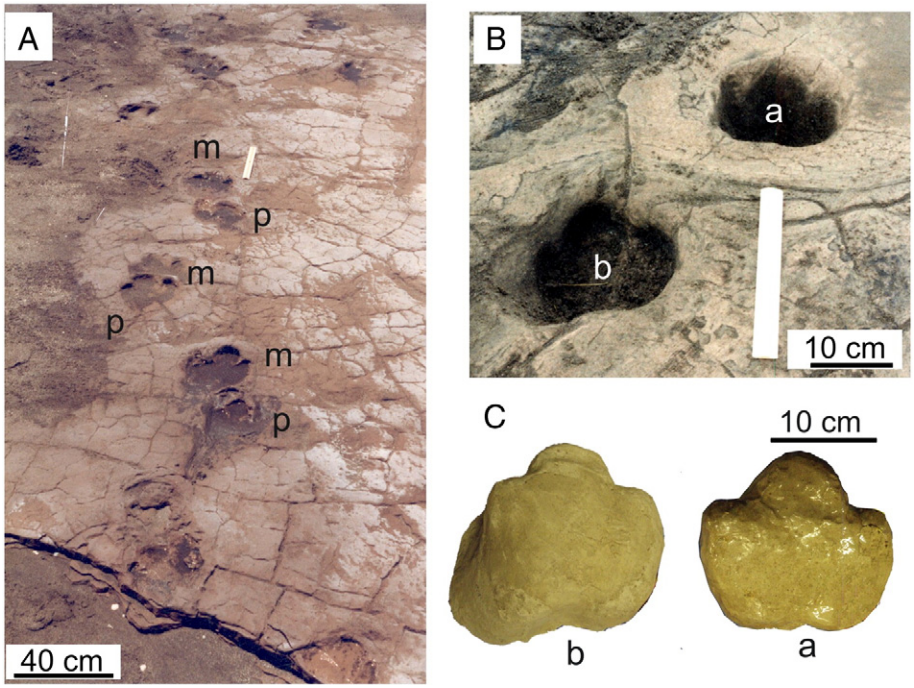


Fig. 6. *Eumacrauchenichnus patachonicus.* (A) Holotype trackway originally described by Aramayo and Manera de Bianco (1987a) and currently missing due to marine erosion. (B) Detail of two footprints that may belong to more than one individual. (C) Plaster of Paris casts of the previous footprints (MPA-87-55-I-E-a and MPA-87-55-I-E-b). The images have been horizontally flipped to facilitate comparison with "B". m: manus, p: pes.

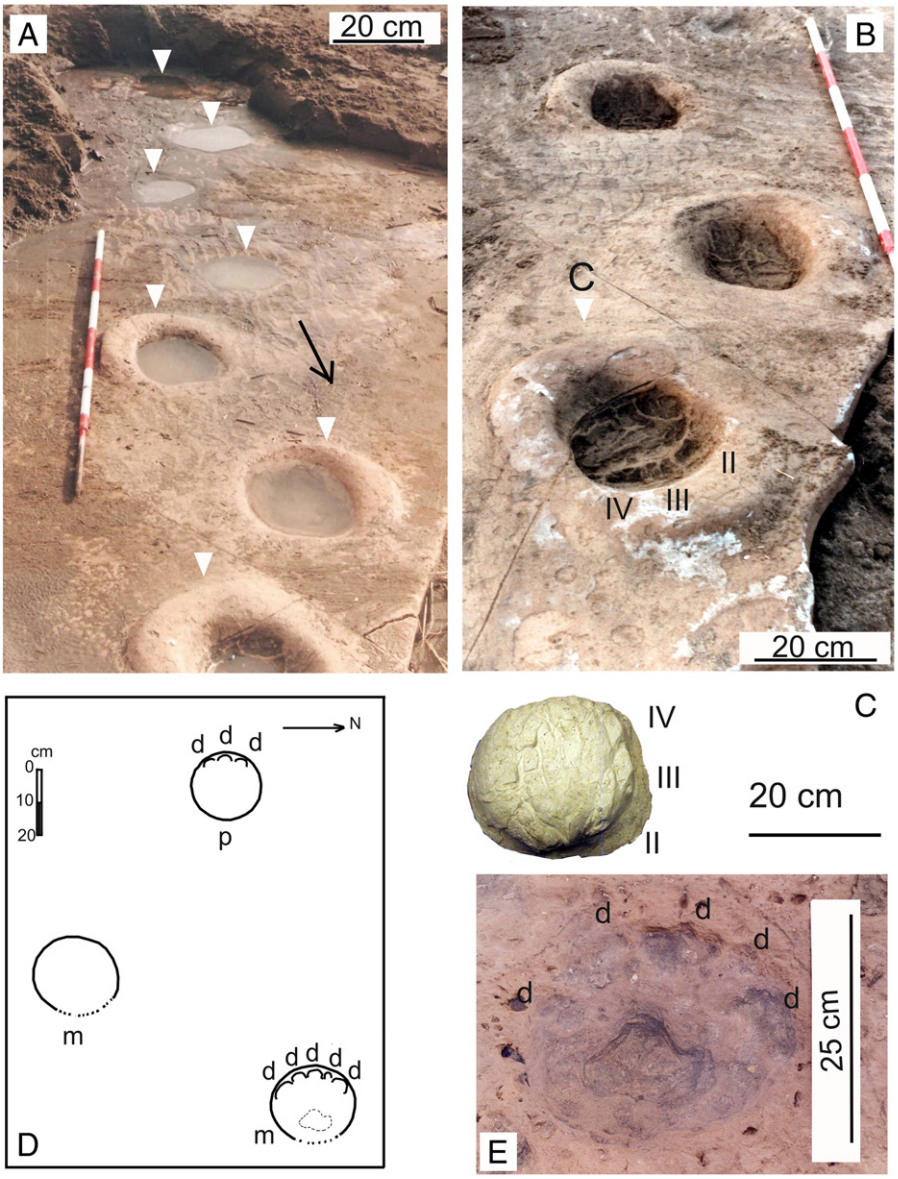


Fig. 7. *Proboscipeda australis.* (A) Holotype trackway of 7 footprints (arrowed). (B) Three footprints of the holotype trackway, "C" pes from which a plaster cast was taken. (C) Plaster cast (MPA 87-56-I-E) of a pes imprint of the holotype. (D) Diagram of a partial trackway of 3 footprints. (E) Pes footprint of the trackway D. d: undifferentiated digit, m: manus, p: pes, II to IV: digit imprints.

4.5.7. Diagnosis

Large circular to slightly oval footprints (length: 0.23–0.27 m, width: 0.23–0.30 m), manus similar to the pes and slightly larger, oval footprints can be wider than long or longer than wide. Commonly 3 to 5 digit imprints in the anterior margin of the sole or palm, sometimes appearing as slight undulations on the anterior margin with a roughly rectangular shape, with their long axis tangential to the margin of the footprint. Sole/palm surface irregular, cracked and wrinkled.

4.5.8. Description

The holotype is a trackway of 7 footprints left in situ (Fig. 7A–B), which is 4.40 m long, 0.59 m wide, and the average footprint width and length is 0.23 m (Aramayo and Manera de Bianco, 1987a). The plaster cast of one pes footprint (MPA.87-56-I-E, Fig. 7C) is 0.27 m long, 0.25 m wide, and 0.08 m deep. The sole surface texture suggests the presence of a thick pad. The holotype trackway was preserved in a clayey siltstone bed. The first five footprints occur near ripple marks and lack a marginal rim, whereas the last three footprints are on a flat surface and exhibit a marginal rim that is gradually wider (maximum 0.12 m) towards the trackway end (Fig. 7A). Despite the frequent field studies carried out at the site over the last 30 years, this trackway has not been observed again since its first description. It may be eroded or covered by modern beach sand. The remaining partial trackway was identified in 2003 on a trampled surface preserved in a diamictite. In this partial trackway, the first footprint is slightly ovoid with five digit imprints (length: 0.24 m, width: 0.28 m) and displays an eroded posterior margin, the second footprint is ovoid, more irregular than the first and lacks digit imprints (length: 0.24 m, width: 0.30 m), and the third footprint is subcircular in outline (length and width: 0.24 m) and displays three digit imprints (Fig. 7C). The first and second footprints of this partial trackway have a clear anterior margin and a less defined posterior margin.

4.5.9. Comments

Research on living elephants have shown that the African elephant (*Loxodonta africana* Blumenbach, 1797) usually has four digits on the

manus and three digits on the pes, and the Asian elephant (*Elephas maximus* Linnæus, 1758) has five digits on the manus and four on the pes (Benz, 2005). In modern proboscideans, the manus imprint is not overstepped by the rear foot, and, during normal walking, both tracks are clearly visible (Benz, 2005; McNeil et al., 2007). These premises allow interpretation of the partial trackway discovered in 2003. The five digit marks of the first footprint, its larger size and ovoid shape, suggest that it may be the impression of a fore foot (Fig. 7D–E). The second footprint lacks digit imprints, although its shape and size are similar to the former, suggesting that it is a manus imprint. The third footprint is smaller, subcircular and exhibits three digit marks and can be interpreted as a hind footprint (Fig. 7D). Proboscidean trackways from the late Pleistocene of Jeju Island, South Korea (Kim et al., 2009, 2010), also showed manus imprints larger than those of the pes.

We follow the recommendation of Lucas et al. (2007), who proposed to apply *Proboscipeda* to all Neogene proboscidean fossil footprints. This is the oldest proposed ichnogenus for proboscidean tracks that was erected to name footprints from the Miocene of Romania (Lucas et al., 2007). Therefore, we consider *Stegomsatodonichnum* Aramayo and Manera de Bianco, 1987a, a junior synonym of *Proboscipeda* Panin and Avram, 1962 (as already proposed by Lucas et al., 2007).

The footprints described herein are broadly similar to *P. enigmatica* and *P. panfamilia* McNeil et al., 2007 but differ in the following features: 1) The footprints of *P. panfamilia* are always wider than long, *P. enigmatica* are longer than wide, and in *P. australis* the largest dimension can be either the width or the length of the footprint. 2) The palm/sole surface in *P. enigmatica* and *P. panfamilia* is relatively featureless (Panin and Avram, 1962; McNeil et al., 2007) and in *P. australis* is rough and cracked. 3) *P. australis* is smaller than the remaining ichnospecies and manus and pes can be distinguished considering the relative size and number of digit imprints.

Proboscipeda footprints with a larger antero-posterior axis could be interpreted as two tracks that are partially overlapped or adjacent, producing a single relatively long or ovoid shape (Lucas et al., 2007; Neto de Carvalho, 2011). *Proboscipeda australis* does not show any indication of overlapping footprints and manus and pes can be distinguished.

The only two known *Proboscipeda* trackways from Pehuen Co display a very similar footprint size and suggest a small-sized producer. This is consistent with the findings of proboscidean skeletal remains of late Pleistocene age from the area near the footprint site. On the basis of remains found in Playa del Barco (3 km to the west of Pehuen Co site), Cabrera (1929) created the genus *Notiomastodon*, with the type species *Notiomastodon ornatus*. This author noted that, judging from the few remains that were found at that moment, *N. ornatus* was a mastodon of small size compared to the other species of South American mastodons. This taxon was later synonymized under *Stegomastodon platensis* Ameghino, 1888 by Alberdi and Prado (1995). A bivariate analysis on *S. platensis* remains from late Pleistocene sites of the Buenos Aires province, including two sites located 10 km to the east of Pehuen Co site, suggested that the remains from these nearby localities are among the smallest *S. platensis* remains found in Argentina. Recently, taxonomic and phylogenetic studies pointed out that South Americam forms described as *Stegomastodon* Pohlig, 1912 are not closely related to the North American *Stegomastodon*, and thus do not belong to this genus (Ferretti, 2010; Fariña et al., 2013). Lucas (2013) and Mothé et al. (2013) by means of modern studies on taxonomy, age dating and phylogenetic relationships identified only two valid genera of the South American Quaternary gomphotheres, *Cuvieronius* and *Notiomastodon* (= "*Haplomastodon*", = "*Stegomastodon*" from South America). Therefore, although Aramayo and Manera de Bianco, 1987a inferred that the track maker of the Pehuen Co footprints was a *Stegomastodon* (Proboscidea, Gomphotheriidae), it is now more appropriate to say that it was probably a *Notiomastodon*.

4.6. ***Ichnogenus*** *Dolichotichnus nov. igen.*

4.6.1. Type ichnospecies

Dolichotichnus marae nov. isp.

4.6.2. Derivation of name

After the generic name of the inferred producer: *Dolichotis patagonum* Zimmermann, 1780 (Rodentia, Cavidae, Dolichotinae) and "*ichnus*" for trace.

4.6.3. Diagnosis

Semi-plantigrade footprints of moderate size. Manus footprints of sub-circular shape, with four divergent digits (II–V) of similar size ending in sharp claw marks, and a kidney-shaped padded palm. Pes footprints longer than the manus imprint, circular palm pad and three parallel digits with claws, central digit (III) longer than the lateral ones (II–IV) and having a deep claw mark. The pes oversteps the manus and is rotated inward with respect to the midline.

4.6.4. ***Ichnospecies*** *Dolichotichnus marae nov. isp.*

Fig. 8A–B.

2009 "small heteropod footprint": Krapovickas et al., p. 143–144, figs. 8D–8H, 11.

4.6.5. Derivation of name

After the Spanish "mara", the common name of *Dolichotis patagonum*.

4.6.6. Holotype

A manus–pes couple preserved in situ (Fig. 8A, B). MD-97-14 is a plaster cast of the holotype.

4.6.7. Diagnosis

Same as for the ichnogenus, only known ichnospecies.

4.6.8. Description

Pes length 7.4 cm; width 3.2 cm, length of central digit: 3.2 cm; manus: length 4.8 cm, width: 5.0 cm; divarication of digits: II–III: 30°, III–IV: 25°, IV–V 30°; II–V: 85° (Fig. 8A–B).

4.6.9. Comments

The tracks of *Dolichotichnus marae* are quite similar to the "small heteropod footprints" (tetradactyl manus and tridactyl pes) from Miocene deposits of the Toro Negro Formation, La Rioja province, Argentina (Krapovickas et al., 2009). The likely producers of these footprints were two separate groups: hegetotherid notoungulates and caviomorph rodents (most likely dolichotine caviids) (Krapovickas et al., 2009).

Dolichotichnus marae from Pehuen Co can be distinguished from other ichnotaxa interpreted as produced by caviomorph rodents, including *Porcellusignum conculcator* Angulo and Casamiquela, 1982 and *Tacheria troyana* Krapovickas and Nasif, 2011. *Porcellusignum conculcator*, from the Río Negro Formation (late Miocene–early Pliocene, Río Negro province, Argentina), are digitigrade footprints, functionally tridactyl, occasionally tetradacyl, manus and pes nearly equal and the presumed trackmaker are hydrochoerids (Angulo and Casamiquela, 1982; Aramayo, 2007). *Tacheria troyana* from the Vinchina Formation (early Miocene, La Rioja Province, Argentina), are digitigrade, tetradactyl, of subequal size, with long and robust digits. The morphological analysis of *T. troyana* suggests that they were produced by a dinomyd caviomorph rodent or a close relative (Krapovickas and Nasif, 2011).

McDonald et al. (2007) compiled a worldwide bibliographic database of Cenozoic tracks and trackways, and listed the taxa given in each reference to the lowest taxonomic category mentioned. This database included two ichnospecies referred to rodents: *Ptyariopus aichmanticheirus* Sarjeant and Langston, 1994 and *Trycorinopus*

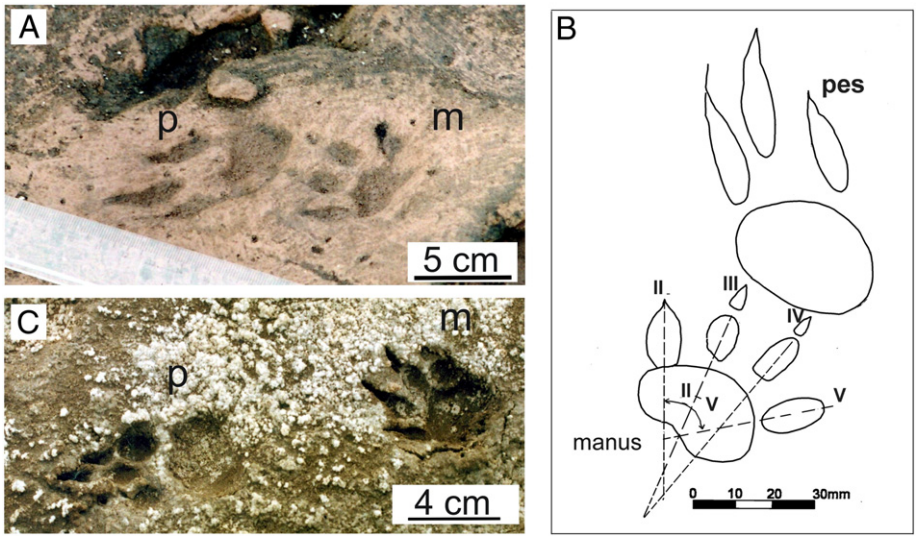


Fig. 8. *Dolichotichnus marae* (A) Holotype specimen (manus–pes set). (B) Sketch of the holotype. (C) Manus and pes footprints of extant mara (*Dolichotis patagonum*) imprinted on a salt encrusted substrate from La Pampa province (Argentina). m: manus, p: pes.

elaphrus Sarjeant and Langston, 1994 from the late Eocene of Texas, both of which are not comparable to *Dolichotichnus marae*. The former are plantigrade, pentadactyl footprints of moderate size, with pes somewhat larger than the manus, slender digits with the pollex reduced, greatly thickened and sigmoidally curved inward. This ichnospecies has been attributed to a member of the Family Ischyromidae (Sciurognathi) (Sarjeant and Langston, 1994). *Trycorinopus elaphrus* are very small tridactyl footprints, all digits narrow proximally, more expanded distally; and manus and pes of almost equal size. Sarjeant and Langston (1994) considered that the producer of these footprints was a Sciurognathi of an undetermined family. Therefore, according to the Index to Cenozoic Vertebrate Ichnotaxa (McDonald et al., 2007), *D. marae* would be the first described Pleistocene Rodentia ichnotaxon.

Only one set of well-preserved footprints has been found to date. On the basis of the morphology and size of these footprints, we can infer that the trackmaker was similar to the extant "mara" (Fig. 8C). This is a cursorial rodent that only inhabits Argentina and which is distributed from 28°S to 50°S; skeletal material is known since the late Pleistocene (Campos et al., 2001). Mara is a hare-like rodent, which nowadays prefers open brushy areas, commonly with sandy soil and which is quite common in the arid grasslands of Patagonia. Its general form is modified for cursorial life: hind limbs are longer and more muscular than forelimbs, with reduction in the number of digits, manus have four digits and pes three digits (Campos et al., 2001). It is remarkable that in the holotype the manus print is placed behind the pes footprint, suggesting a running gait, comparable to a galloping mode in Lagomorpha (Leonardi, 1987).

4.7. ***Ichnogenus*** *Ursichnus Diedrich, 2011*

4.7.1. Type ichnospecies

Ursichnus europaeus Diedrich, 2011.

4.7.2. Diagnosis

Quadrupedal trackway composed of plantigrade, pentadactyl manus and pes imprints of different morphologies, manus nearly circular and pes of ellipsoidal shape, and manus/pes length ratio of about 1:1.25. In normal gait, the manus is placed close and in front of the pes footprint. The heel of the manus footprint is absent and the palm is ovoid to kidney-shaped and small, while the large sole of the pes footprint is roughly triangular and shows a well-developed heel. Manus and pes footprints with short, oval to rounded digit imprints with clear claw marks. Digit imprints not connected with heel impression.

4.7.3. Remarks

Diedrich (2011) did not provide an ichnogeneric diagnosis as the only known ichnospecies was *Ursichnus europaeus*. A diagnosis for the ichnogenus is proposed herein on the basis of both known ichnospecies.

4.7.4. ***Ichnospecies*** *Ursichnus sudamericanus isp. nov.*

Fig. 9.

2009 "Ursidae footprints": Aramayo and Manera de Bianco, p. 29.

4.7.5. Holotype

Four consecutive footprints in situ (Fig. 9A–B). MD-97-14 is a silicone rubber cast of a manus–pes couple of the holotype (Fig. 9A).

4.7.6. Additional material

A manus–pes couple and four consecutive footprints associated with bird footprints, all left in situ (Fig. 9C–E). MD-YPI-06-07 is a silicone rubber cast including the mentioned manus–pes couple, the incomplete trackway of four footprints, plus 5 footprints of a webbed bird and a trampled zone with other bird footprints. MD YPI-07-01 is a clayey siltstone block containing a left manus footprint. MD-YPI-07-02 is a compact claystone block with well-preserved right manus and possible plant impressions.

4.7.7. Derivation of name

After South America, which is the provenance of all species of *Arcthoterium* Burmeister, 1879 (Ursidae, Tremarctine), the presumed producer of these tracks.

4.7.8. Diagnosis

Quadrupedal trackway with plantigrade, pentadactyl footprints showing marked heteropody. The manus footprint (11.5 to 15 cm long, 10 to 19 cm wide) with oval digit imprints showing parallel orientation and inward rotation with respect to the midline. Palm impression well defined and separated from the digital pad impressions by a ridge, clear claw marks, manus heel impression absent. Pes footprint narrower than manus footprint (20 to 23 cm long, 10.5 to 13 cm wide) with a broad sole separated from the heel impression by a notch, digit imprints not connected with the sole, digit III imprint longer.

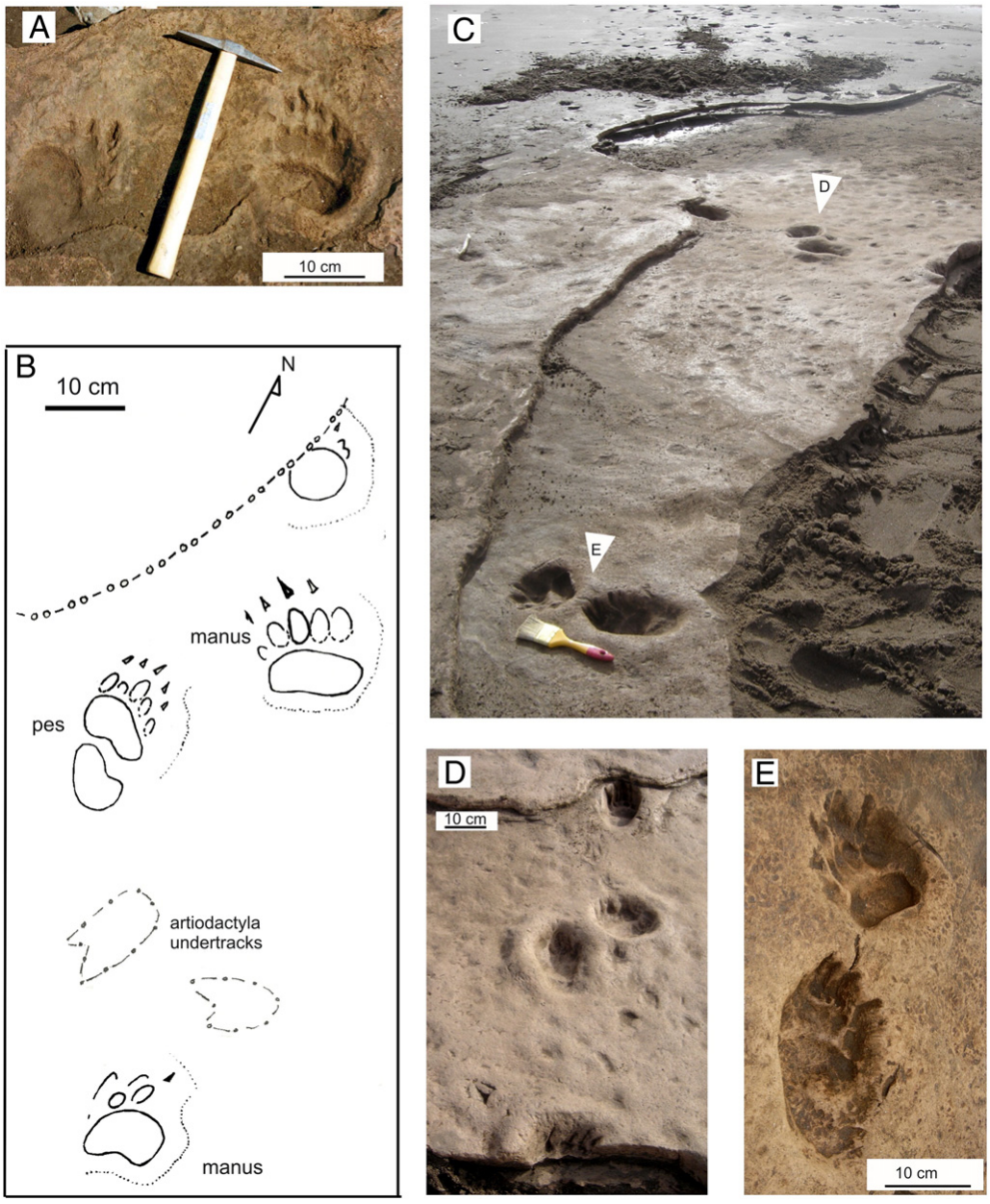


Fig. 9. *Ursichnus sudamericanus*. (A) Manus–pes couple of the holotype. (B) Diagram of the holotype trackway. (C, D, E) Siltstone bedding plane trampled by birds with the holotype trackway (D) and an isolated manus–pes couple (E) of *U. sudamericanus*.

4.7.9. Description

The holotype is a 1.07 m long incomplete trackway composed of a central (right) manus–(left) pes couple and the immediately posterior left manus and anterior right pes (Fig. 9B). Trackway breadth is 0.37 m, manus and pes show an inward rotation of 10°, and the azimuth of the incomplete trackway is N350°. The second in situ incomplete trackway is 1.2 m long and 0.37 m wide. This second incomplete trackway allowed estimation of the pace length, which is 0.65 m for the manus and pes. The distance between manus and pes is between 0.14 m and 0.16 m (n = 2). Size measurement on complete footprints from all available material suggest that manus displays an average footprint length of 0.138 m (range = 0.125–0.150 m, n = 6), average footprint width of 0.132 m (range = 0.095–0.140 m, n = 6), and mean footprint length/width ratio of 1.08 (range = 0.79–1.31, n = 6). Mean measurements for the pes are: footprint length: 0.220 m (range = 0.200–0.230 m, n = 4), footprint width: 0.118 m (range = 0.105–0.130 m, n = 4), and footprint length/width ratio: 1.86 (range = 1.68–1.92, n = 4).

4.7.10. Remarks

The described footprints display a strong resemblance to the ichnogenus *Ursichnus*, proposed by Diedrich (2011) for isolated manus and pes footprints of cave bears from the late Pleistocene Urşilor Cave (Romania). The size of footprints of *Ursichnus sudamericanus* lies within the range of *Ursichnus europaeus*. *Ursichnus sudamericanus* is distinguished from *U. europaeus* by the absence of a heel impression in the manus, and for having the digit III imprint longer than the remaining digits (in *U. europaeus* the three central digits are longer than the lateral digits).

Sarjeant et al. (2002) created the ichnospecies *Platycopus ilycalcator* for footprints referred to bears of the Miocene of Nevada. The distinction between *Ursichnus* and *Platycopus* was already discussed by Diedrich (2011). The described tracks are not comparable with that ichnotaxon because, in contrast to *P. ilycalcator*, the digit imprints are separated from the palm/sole pad.

Ursichnus sudamericanus is very similar to the footprints of the South American extant spectacled bear *Tremarctos ornatus* Cuvier,

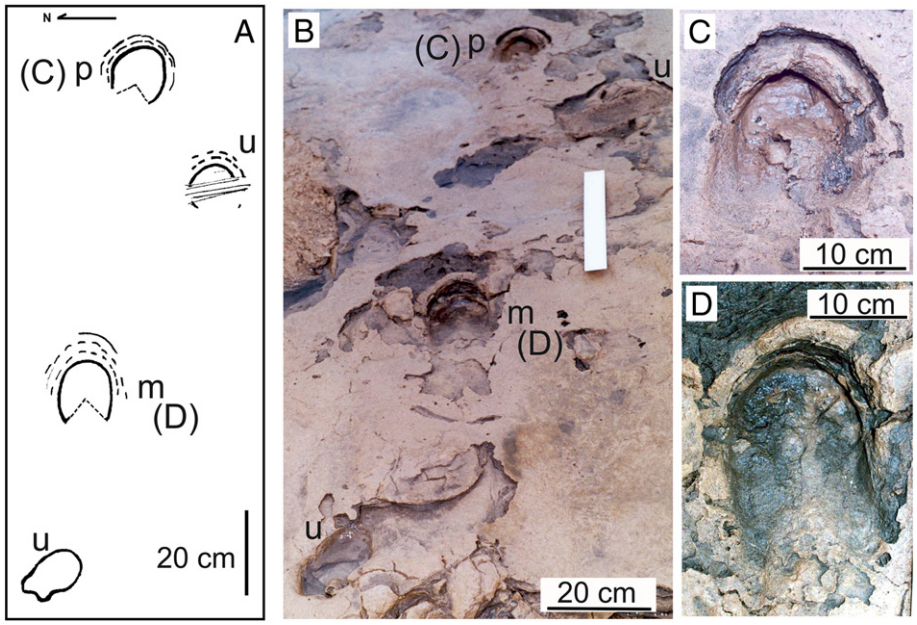


Fig. 10. *Hippipeda* isp. (A) Sketch of the trackway in B. (B) Trackway. (C) Pes footprint. (D) Manus footprint. m: manus, p: pes, u: undertrack.

1825 (Torres, 2011). The morphology of the footprints allows us to identify the potential trackmaker as a carnivore of the Ursidae family (subfamily Tremarctinae), an immigrant group that reached South America by the end of the Pleistocene. The subfamily Tremarctinae is distributed exclusively in America and comprises four genera: two fossil genera (*Plionarctos* Frick, 1926 and *Arctodus* Leidy, 1854) from North America; one fossil genus *Arctotherium* Burmeister, 1879 from South America; and *Tremarctos* Gervais, 1855 with one fossil species in North America and a living one in South America (Soibelzon, 2004; Soibelzon and Tarantini, 2009). *Arctotherium* has five valid Pleistocene species showing different size and geographic distribution: *Arctotherium angustidens* Gervais and Ameghino, 1880, *Arctotherium bonariensis* Gervais, 1852, *Arctotherium tarijense* Ameghino, 1902, *Arctotherium vetustum* Ameghino, 1885 and *Arctotherium wingei* Ameghino, 1902 (Soibelzon and Tarantini, 2009; Fariña et al., 2013). Estimates of the body mass of these five species permitted grouping them into three categories; small- to medium-sized (*A. wingei* 51–150 kg, *A. vetustum* 102–300 kg), medium- to large-sized (*A. tarijense* 135–400 kg, *A. bonariense* 171–500 kg) and large- to giant-sized (*A. angustidens* 412–1200 kg) (Soibelzon and Tarantini, 2009). In Argentina, the most complete record of *Arctotherium* comes from the Buenos Aires province, where all known species (except for *A. wingei*) have been recorded, but *A. tarijense* is the only species from the late Pleistocene (Soibelzon et al., 2005). The weight of the living South American bear *Tremarctos ornatus* varies from 60 kg (female) to 150/175 kg (male) and the average size of a male footprint is: manus length and width 0.10 m, pes length 0.20 m, pes width 0.10 m (Soibelzon and Tarantini, 2009; Torres, 2011). The size of the described footprints and their stratigraphic and geographic provenance suggest that the trackmaker of the Pehuen Co *U. sudamericanus* was an *A. tarijense* specimen with a body mass similar to an extant male *T. ornatus*.

4.8. ***Ichnogenus*** *Hippipeda (Vyalov, 1966)*

4.8.1. *Hippipeda isp.*

Fig. 10.

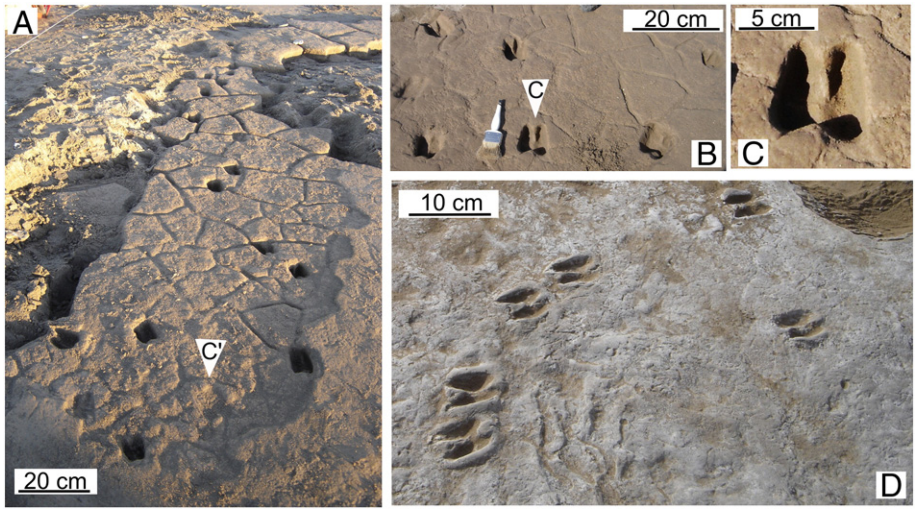


Fig. 11. *Lamaichnum guanicoe.* (A) Mudcracked siltstone bedding surface with 21 footprints (neotype), partially covered with sand. C′ points the location of C. (B) Detail of the anterior surface after cleaning the loose sand. (C) Close-up of a single footprint (location in A). (D) Several *L. guanicoe* footprints from a large bedding surface trampled by other mammals and birds (the cast MD-YPI-15-01 was obtained in this place).

4.8.2. Material

A trackway with four footprints including two true tracks and two undertracks (Fig. 10). MD-YPI-05-02 is one footprint in a fine-grained diamictite slab. MD-YPI-05-08 is one footprint in a clayey siltstone. MD-YPI-05-10 is a silicon rubber cast of 2 equid and 2 bird footprints.

4.8.3. Description

Footprints with a hemi-ellipsoidal shape, the anterior part is remarkably deep and shows a marginal rim. At the back, a frog is easily distinguished. The trackway has two footprints clearly preserved (Fig. 10C–D), and two undertracks ("u" in Fig. 10A–B). The trackway length is 1.40 m and the width is 0.35 m. One of the well-preserved footprints is a manus (length 15 cm, width 12 cm) and the other one is a pes (length 13 cm, width 10 cm). The manus footprint is slightly larger and more elongated than the pes footprint. Length/width ratio is: 1.25 for the manus and 1.30 for the pes.

4.8.4. Comments

In 2003, we recorded the first evidence of equid footprints at the site. The footprints were assigned to *Hippipeda* Vyalov, 1966 as emended by Sarjeant and Reynolds (1999) (Manera de Bianco and Aramayo, 2003). Sarjeant and Reynolds (1999) characterized *Hippipeda* as footprints of a monodactyl ungulate mammal with a hemi-ellipsoidal hoof, and with or without a frog.

Regarding the potential producer of these footprints, there are at least two equid genera and three species recorded for the late Pleistocene of the study area. From Playa del Barco (3 km west of the ichnological site) fossils of both *Equus* (*Amerhippus*) sp. (Aramayo and Manera de Bianco, 1989) and *Equus* (*Amerhippus*) *neogeus* (Tomassini et al., 2010) were recorded. The later species was also recorded from Monte Hermoso City, about 3 km east of the end of Pehuen Co site (Alberdi and Prado, 1995). The finding of a phalanx of *E.* (*Amerhippus*) *neogeus* from the Pehuen Co site reported by Rodriguez Brizuela (2005) is of dubious provenance. Prado et al. (2012) also described further late Pleistocene species of equids from the area between Pehuen Co and Monte Hermoso: *Hippidion principale* Lund, 1846 and *Hippidion devillei* Gervais, 1855. In consequence, the most likely producers are representatives of *Equus* or *Hippidion*.

4.9. ***Ichnogenus*** *Lamaichnum Aramayo and Manera de Bianco, 1987a*

4.9.1. Type ichnospecies

Lamaichnum guanicoe Aramayo and Manera de Bianco, 1987a.

4.9.2. Diagnosis

We follow the revised diagnosis proposed by Lucas and Hunt (2007).

4.9.3. Lamaichnum guanicoe Aramayo and Manera de Bianco, 1987a

Fig. 11.

See synonymy list in Lucas and Hunt (2007).

4.9.4. Diagnosis

Lamaichnum with footprint length ranging from 40 to 120 mm.

4.9.5. Neotype

Twenty-one in situ footprints preserved in a siltstone bedding surface with mudcracks (Fig. 11A–B and Table 3, supplementary material). MD-YPI-05-15 is a silicone rubber cast of the neotype.

4.9.6. Additional material

A trampled area with mammal and bird footprints, and plant impressions (Fig. 11D). MD-YPI-15-01 is a silicone rubber cast of part of this area.

4.9.7. Description

The neotype consists of, at least, three intersecting trackways (Fig. 11A–B). The footprints are of a digitigrade, quadrupedal mammal of medium size (average length 9.49 cm, width 7.18 cm, Table 3) that are deeply imprinted (average depth 6.7 cm). Manus and pes are of similar shape and size and show two digit imprints with pads separated by a median ridge (Fig. 11C). Lateral and medial borders of each footprint are slightly curved. Each footprint has a cleft pointing forwards and another pointing backward. Digit imprints are pointed anteriorly and rounded at the posterior part.

4.9.8. Comments

Aramayo and Manera de Bianco (1987b) suggested that the producer is the living camelid species *Lama guanicoe* (Artiodactyla, Tylopoda, Camelidae).

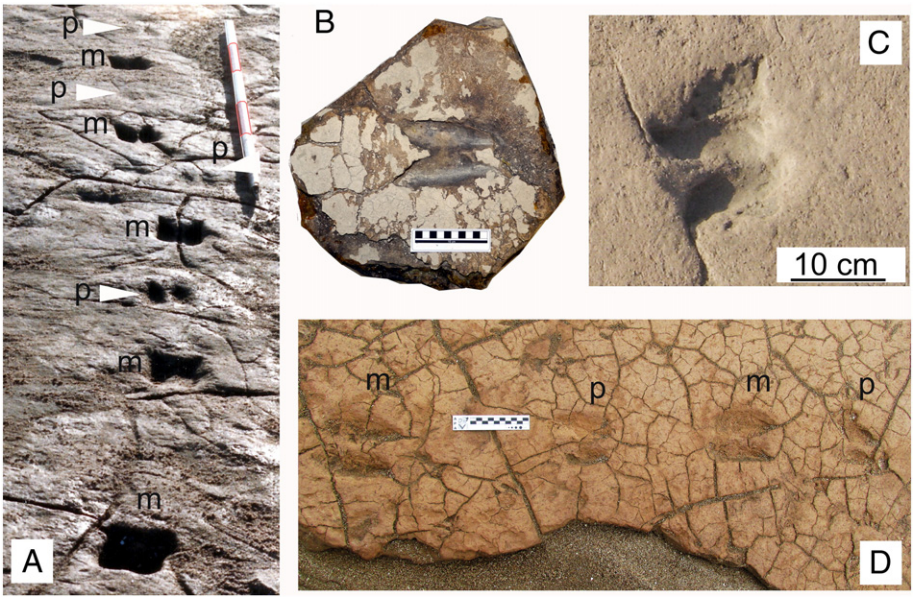


Fig. 12. *Lamaichnum tulipensis.* (A) Holotype trackway in situ (Aramayo and Manera de Bianco, 1987b) showing differences in shape, size and depth between manus (m) and pes (p). (B) Isolated footprint, probably a manus (paratype MD-YPI-06-04). (C) Detail of a manus footprint from a silicone ruber cast (MD-YPI-06-10) of a trackway of 13 footprints. (D) View of the neotype trackway in situ. m: manus, p: pes.

4.10. Lamaichnum tulipensis nov. comb.

Fig. 12.

1987b *Megalamaichnum tulipensis*: Aramayo and Manera de Bianco, p. 536–537, fig. 6.

1996 *Megalamaichnum tulipensis*: Aramayo and Manera de Bianco, p. 50, 52, plate II, figs. 1–2, fig. 4a.

part 2007 *Lamaichnum guanicoe*: Lucas and Hunt, p. 159.

4.10.1. Emended diagnosis

Quadrupedal trackway composed of medium- to large-sized bidactyl and digitigrade footprints with each digit represented by a single pad, manus and pes of roughly similar shape, posterior end biconvex and anterior pointed. Manus is slightly larger and deeper imprinted than the pes. Manus footprints consist of two elongated concavities with a pointed anterior end facing outwards, the central ridge between both concavities is short and widens anteriorly. Pes footprints consist of two elongated depressions with parallel anterior ends. The size of the footprints is greater than those observed in *Lamaichnum guanicoe* (modified after Aramayo and Manera de Bianco, 1996).

4.10.2. Neotype

A trackway of 4 footprints in situ (Fig. 12D, Table 4A, supplementary material). Paratype: MD-YPI-06-04, one collected footprint on a sedimentary block (Fig. 12B).

4.10.3. Additional material

1) A trackway of 13 footprints in situ. MD-YPI-06-10 is a silicon rubber cast of that trackway (Table 4B, supplementary material). 2) A trackway of 45 footprints in situ (the latter described by Aramayo and Manera de Bianco, 1996).

4.10.4. Description

One of the distinguishing features of *L. tulipensis* is a manus footprint with digits slightly diverging anteriorly and forming a cleft (Fig. 12C).

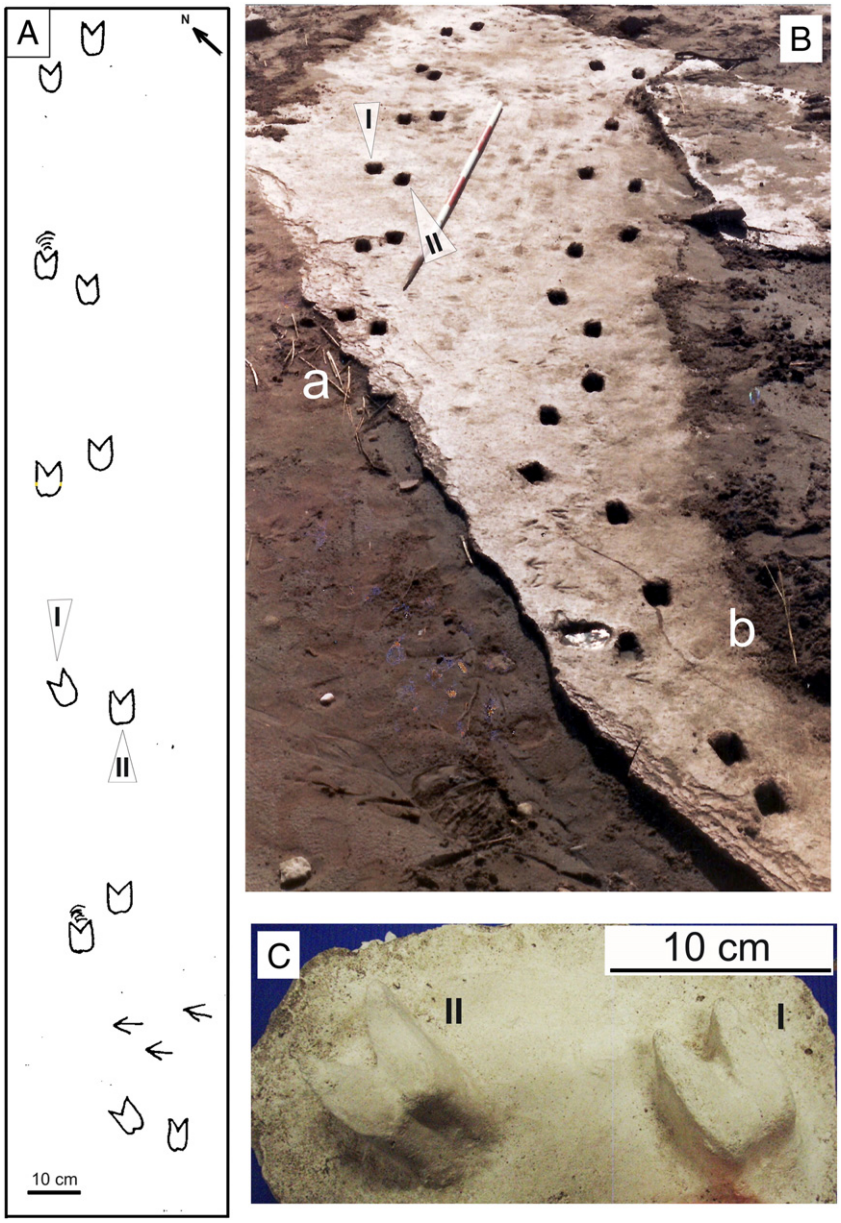


Fig. 13. *Pecoripeda commune* nov. comb. (A) Sketch of the holotype trackway composed by12 footprins (taken from Aramayo and Manera de Bianco, 1987b). I and II point to the footprints of the plaster cast of C. (B) Two in situ trackways of *P. commune* ("a" and "b", the former is the holoype) on a bedding surface also showing bird footprints. I and II also point to the footprints of C. (C) Plaster cast of two footprints (MPA-87-54-I-E).

MD-YPI-06-04: footprint length 15 cm, width: 10 cm; MD-YPI-06-10: footprint (average) length 11.2 cm, width 10.1 cm, depth 3.5 cm (Table 4, supplementary material). The pes footprints are similar to *L. guanicoe* and show parallel digital pads pointing forwards, separated by a low sediment ridge.

4.10.5. Remarks

Lucas and Hunt (2007) revised the ichnotaxonomy of camel footprints and proposed assignment of all of them to the ichnogenus *Lamaichnum*, a suggestion that is followed herein. On the basis of a compilation of camel footprints from two Miocene units of USA, these authors conclude that the range of footprint length for *Lamaichnum guanicoe* is from 40 to 150 mm. As this range encompasses the known record of *Megalamaichnum tulipensis*, Lucas and Hunt (2007) proposed to synonymize that ichnospecies under *L. guanicoe*. In this work, we maintain the ichnospecies *tulipensis* because of two distinctive features: shape of the manus footprints, and the size difference between manus and pes. Aramayo and Manera de Bianco (1987b) did not point out the difference between manus and pes of the holotype footprints, even though these features were evident in the accompanying illustration (fig. 6a). Aramayo and Manera de Bianco (1996) described a trackway of this ichnospecies formed by 45 footprints, and remarked the size difference between manus and pes (manus: 12 cm long and 8 cm wide, pes: 9 cm long and 8 cm wide) and the presence of more deeply imprinted manus with digit tips pointing laterally. All these characteristics can be observed in the proposed neotype and in a trackway of 13 footprints in situ.

The likely trackmaker is *Hemiauchenia* Gervais and Ameghino, 1880 (Artiodactyla, Tylopoda, Camelidae), a camelid of large size that lived in the Buenos Aires province during the late Pleistocene (Scherer et al., 2007).

4.11. ***Ichnogenus*** *Pecoripeda Vyalov, 1965*

Type ichnospecies: *Pecoripeda gazella* Vyalov, 1965.

4.11.1. Pecoripeda commune nov. comb.

Fig. 13.

1987b *Odocoileinichnum commune*: Aramayo and Manera de Bianco, p. 537–538, fig. 7.

4.11.2. Holotype

Trackway of 12 footprints (Fig. 13A–B) that was originally proposed by Aramayo and Manera de Bianco (1987b). MPA-87-54-I-E is a plaster cast of 2 footprints of the holotype (Fig. 13C). MPA-87-53-I-E is a plaster cast of 2 footprints of the holotype and 2 bird footprints.

4.11.3. Diagnosis

Quadrupedal trackway composed of small- to medium-sized (50–120 mm long), hoofed didactyl footprints, digit imprints with flat or slightly concave surface; separation between digits are commonly absent or poorly developed. The anterior border is acutely marked by both hooves; lateral sides are straight while the posterior border is slightly convex.

4.11.4. Description

MPA-87-54-I-E: footprint length 7 cm, width 5 cm.

4.11.5. Discussion

The characteristics of *Odocoileichnum* Aramayo and Manera de Bianco, 1987b match those of the ichnogenus *Pecoripeda* Vyalov, 1965. Vyalov (1965) proposed *Pecoripeda* for tracks of several families of Pecora, including Cervidae (Lucas, 2007). Vyalov (1965) described six *Pecoripeda* ichnospecies (Lucas, 2007): *Pecoripeda* (*Gazellipeda*) *gazella*, *Pecoripeda* (*Gazellipeda*) *amalphaea*, *Pecoripeda* (*Ovipeda*) *satyri*, *Pecoripeda* (*Ovipeda*) *diaboli*, *Pecoripeda* (*Ovipeda*) *djali*, and *Pecoripeda* (*Cervipeda*) *dicroceroides*. Although these ichnospecies are in need of a revision, none of them match the features of *Pecoripeda commune*. *Pecoripeda* (*Cervipeda*) *dicroceroides* is easily distinguished because of its tetradactyl character. The remaining ichnospecies are essentially smaller than *P. commune* (commonly smaller than 45 mm long); only *P.* (*Ovipeda*) *satyri* partially overlaps in size with the former, but it is distinguished by its oval shape and outer convexity of digits. *P. commune* lacks the posterior widening of digits typical of *P.* (*Gazellipeda*) *gazella* and *P.* (*Gazellipeda*) *amalphaea*. The latter is also distinguished by its heart-shaped posterior part. *Pecoripeda* (*Ovipeda*) *diaboli* is distinguished by wide and short footprints with the anterior tip of digits pointing inward. Finally, *P.* (*Ovipeda*) *djali* can be differentiated from *P. commune* by its oval shape. In consequence, we propose to recognize a new ichnospecies of *Pecoripeda* by combining that ichnogenus with the specific name *commune*.

The presumed producers are the odocoileini (Artiodactyla, Ruminantia, Cervidae), which are deer that reached South America, migrating from the north, and are common as fossils in the Buenos Aires province (Pinder and Grosse, 1991; Grubb, 2000; Deschamps, 2005). A more precise assignation is not possible with the available evidence.

4.12. ***Ichnogenus*** *Aramayoichnus igen. nov.*

4.12.1. Type ichnospecies

Aramayoichnus rheae isp. nov.

non 1965 Rheiformes ichnites: Bonaparte, p. 11, fig. 2.

?1970 Rheiformes ichnites: Ramos, p. 369, photo 1 and 2.

non 1982 Morphotype I: Covacevich and Rich, p. 245–249, fig. 27.2.

1996 "trackway comparable to *Rhea americana*": Aramayo and Manera de Bianco, p. 52, plate II (fig. 4), fig. 4.

2007 *Anchisauripus* isp.: Melchor et al., p. 54.

2009 Rheidae footprints: Aramayo and Manera de Bianco, p. 29.

2009 South American rhea footprint: Aramayo, fig. 5.

2009 Large incumbent footprint: Krapovickas et al., p.139–140, fig. 7.

2013 bird ichnites: Bayón and Politis, fig. 5A, B.

4.12.2. Derivation of name

After "*Aramayo*" in honor to the ichnology contributions of late Silvia Aramayo and "*ichnus*" for trace.

4.12.3. Diagnosis

Bipedal trackway of high pace angulation with mesaxonic tridactyl footprints of moderate size (footprint length usually greater than 10 cm), footprint length/width ratio less than 2, footprints with small positive rotation with the midline. Footprints with three thick digits directed forward showing clear phalangeal pad impressions and claw marks. At least half of the length of digit III impression projecting forward of the imaginary line formed by the tip of lateral digits, digit IV impression longer than that of digit II. Divarication of digits II–IV is commonly smaller than 80°. Digits proximally separated from or joined to a deep, circular metatarsal–phalangeal pad impression. Interdigital web trace absent. Differs from *Anchisauripus* by the presence of a metatarsal–phalangeal pad impression, greater digit divarication and a lower footprint length/width ratio.

4.12.4. Remarks

The parameters measured on *Aramayoichnus* and related modern footprints are summarized in Fig. 14A (see Table 5, supplementary material). The footprints described by Bonaparte (1965) as those of Rheiformes from the Miocene Toro Negro Formation of northwest Argentina (see also Leonardi, 1994; plate XIX, fig. 1), display features that distinguish them from *Aramayoichnus* and from modern Rheidae footprints. These features include a footprint length/width ratio near 1, absence of a separated metatarsal–phalangeal pad impression (connected with digit III), and thin digit imprints. The Toro Negro Formation

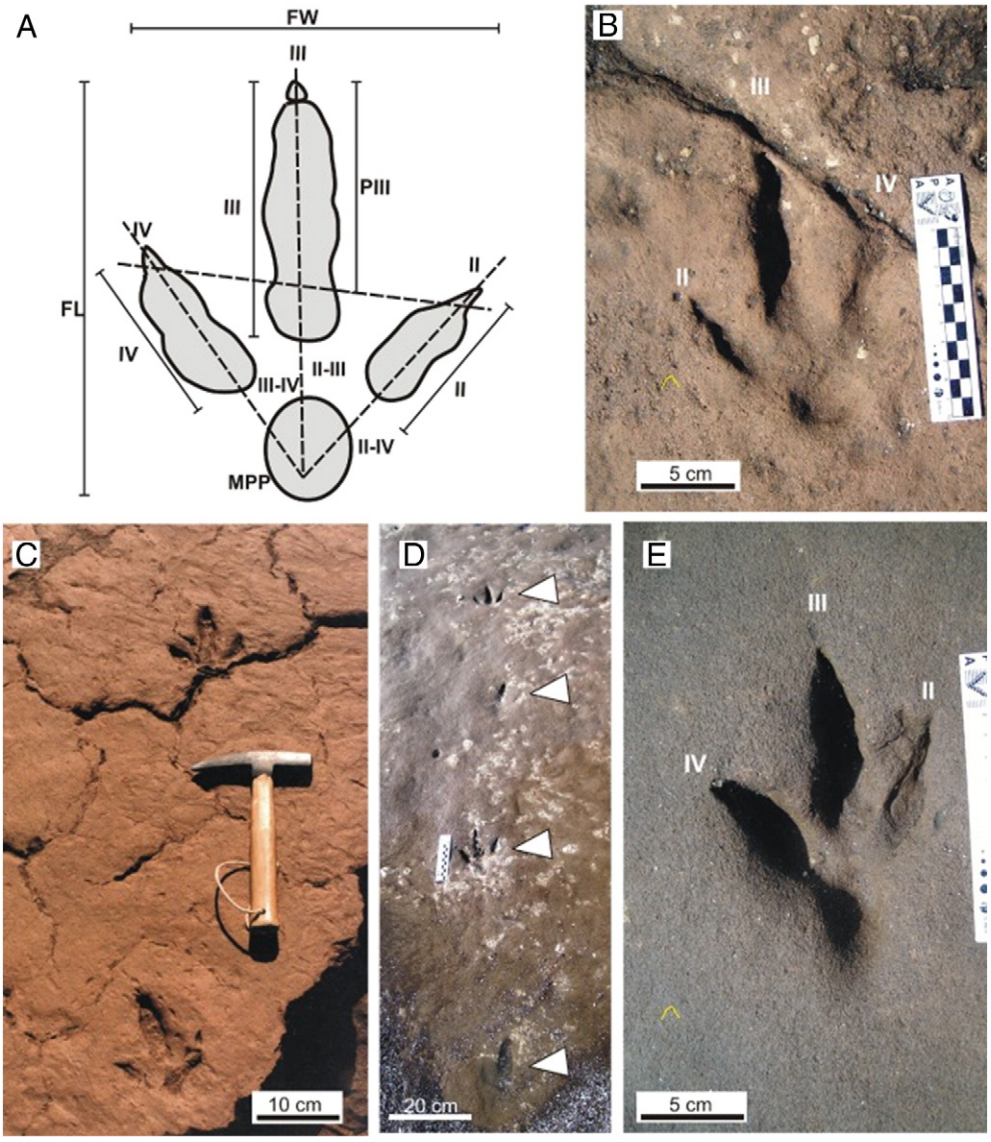


Fig. 14. *Aramayoichnus rheae* nov. igen. and isp. (A) Measurements on *A. rheae* and related modern footprints. FW: footprint width; FL: footprint length; II–III–IV: length of digit imprints II, III and IV; II–III, III–IV, II–IV: divarication of digits; PIII: projection of digit III; MPP: metatarsal–phalangeal pad impression. (B) Right footprint from the type trackway. (C) Two consecutive footprints from the other described trackway. (D) Part of the type trackway (arrows point to individual footprints). (E) Left footprint (# 6) from the type trackway.

also has yielded a single, poorly preserved "large incumbent footprint" (Krapovickas et al., 2009) that is comparable with *Aramayoichnus*. The footprints from the Oligocene–Miocene Vinchina Formation of northwest Argentina described as Rheiformes ichnites by Ramos (1970) are undertracks that may be compared with doubts with *Aramayoichnus*. Covacevich and Rich (1982) identified possible Ratites or phororacoid footprints (undertracks) from the Eocene of King George Island, Antarctica. These tracks differ from *Aramayoichnus* in having a footprint length/width ratio near 1 and a divarication of digits II–IV of about 80°; in consequence their affinity to Rheiformes is doubtful. *Aramayoichnus* has an overall resemblance and similar size to the Mesozoic ichnogenus *Anchisauripus* Lull, 1904 as modified by Olsen et al. (1998). *Aramayoichnus* differs from *Anchisauripus* because of the presence of a metatarsal–phalangeal pad (not recorded in *Anchisauripus*), greater digit II–IV divarication (20–35° in *Anchisauripus and* 54–78° for *Aramayoichnus*), and less elongated footprint (footprint length/width ratio about 2 in *Anchisauripus*). The ichnogenus *Rivavipes* was erected for tridactyl footprints of a large Eocene bird from USA (Mustoe et al., 2012). *Rivavipes* is distinguished from *Aramayoichnus* by a broader metatarsal–phalangeal pad impression, digit III impression projecting less than 50% of its length and indistinct digit terminations.

4.12.5. ***Ichnospecies*** *Aramayoichnus rheae isp. nov.*

Fig. 14 B–E.

4.12.6. Holotype

A trackway of 10 footprints left in situ (Fig. 14D). MD-YPI-15-2 is a silicone rubber cast of the holotype.

4.12.7. Additional material

Another in situ trackway of 5 footprints, described by Aramayo and Manera de Bianco (1996). MD-93-6 is a slab containing an isolated footprint from the former.

4.12.8. Derivation of name

After the living greater rhea, *Rhea americana* Linnæus, 1758, and the lesser rhea, *Rhea* (*Pterocnemia*) *pennata* D'Orbigny, 1834, which are the extant relatives of the presumed producers of the trace fossils.

4.12.9. Diagnosis

Same as for the ichnogenus, only known ichnospecies.

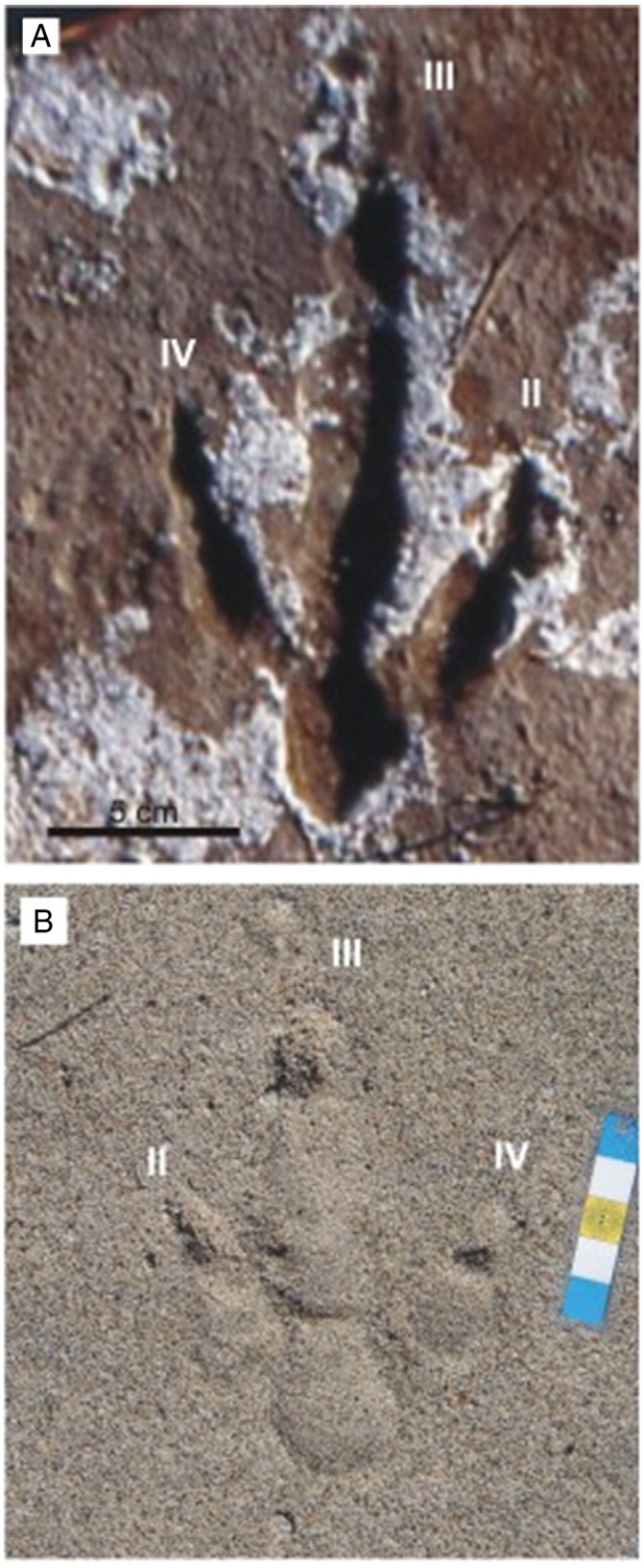


Fig. 15. Modern rhea footprints from Argentina. (A) *Rhea americana* footprint in mud from western La Pampa province. (B) *Rhea* (*Pterocnemia*) *pennata* in sand from north western Santa Cruz province.

4.12.10. Description

The holotype is a 4.84 m long trackway composed of 10 consecutive footprints preserved as natural casts. The pace angulation averages 173° (range = 170–180°, n = 6), the trackway breadth is 0.20 m, and the footprints display an outward rotation with respect to the midline (average: 10°, range = 0–15°, n = 6). Average pace length is 0.46 m (range = 0.47–0.50 m, n = 9) and stride length is 0.94 m (range = 0.96–1.13 m, n = 8).

The second in situ trackway is 2.20 m long, 0.15 m wide and is composed of 5 footprints. Footprint measurements of both trackways indicates an average footprint length of 0.137 m (range = 0.126–0.153 m, n = 8), and a mean footprint length/width ratio of 1.24 (range = 1.1–1.35; n = 8). Digit length is III > IV > II. Digit III projects markedly forward, on average, 65% of the digit III length is located beyond a line joining the tips of digits II and IV (Fig. 14B, C, E). Digits are thick (the thickness of digit III averages 28% of digit III length) and display marked phalangeal pads. Divarication of digits II–IV averages 65° (range = 54–78°, n = 8), and that of digits II–III and III–IV are subequal, although usually the latter is larger. The proximal part of the digit impressions is close, although usually not connected, with a deep and well-defined metatarsal–phalangeal pad. This pad is subcircular to oval, usually its longest axis is oriented parallel to the footprint axis, and about 0.03 m in diameter (Fig. 14B).

4.12.11. Remarks

The shape and size of *Aramayoichnus rheae* are very similar to the extant South American rheas including the greater rhea or "ñandú" (*Rhea americana*) and the lesser rhea or "choique" (*Rhea pennata*) (Aves, Palaeognatha, Rheiformes) (Fig. 15A, B). The new ichnospecies also shows a similar shape to the Australian emu (*Dromaius novaehollandiae* de Vis, 1892) footprints, although these are considerably larger (Milàn, 2006). The footprints of other extant ratites differ from those of the rhea and emu in being bidactyl in ostriches, *Struthio camelus* Linnæus, 1758 (e.g., Fowler, 1991), or having a very long claw mark in digit II for southern cassowaries, *Casuarius casuarius* Linnæus, 1758 (e.g., Moore, 2003). The footprint of the extinct New Zealand moa exhibits at least three morphotypes (Lockley et al., 2007). Moa footprints can be distinguished from *A. rheae* by: 1) larger size (usually longer than 15 cm), 2) commonly isometric or wider than long footprints, 3) showing broad massive digit imprints connected to an ample metatarsal–phalangeal pad, and 4) relatively short pace length.

Measurements on modern rhea footprints suggest that the lesser rhea footprints are smaller, have a lower footprint length/width ratio and a lower divarication angle than footprints of the greater rhea (Fig. 15A, B). However, when considering both datasets together, modern rhea footprints and *Aramayoichnus rheae* display similar average footprint length (13.9 cm and 13.7 cm, respectively), mean divarication of digits II–IV (64° and 65°, respectively), mean projection of digit III (68% and 64%, respectively), and average width/length ratio of digit III (0.28 and 0.24, respectively).

The oldest Rheiformes were recorded from the Paleocene of Brazil and Argentina (Tambussi and Noriega, 1996) and the early Miocene representatives of the group are very similar to the extant Rheidae (Tambussi, 1995). The late Pleistocene to Holocene record of Rheidae from the Buenos Aires province includes representatives of both *Rhea* and *Pterocnemia* (Tambussi and Tonni, 1985; Tambussi and Acosta Hospitaleche, 2002; Picasso et al., 2011). In consequence, the Pehuen Co footprints can be attributed to relatives of both genera of Rheiformes.

4.13. ***Ichnogenus*** *Phoenicopterichnum Aramayo and Manera de Bianco, 1987a*

4.13.1. Type ichnospecies

Phoenicopterichnum pehuencoensis Aramayo and Manera de Bianco, 1987a.

4.13.2. Diagnosis

We follow the emended diagnosis proposed by Melchor et al. (2012).



Fig. 16. *Phoenicopterichnum pehuencoensis*. (A) Original trackway of the silicon rubber cast MD-YPI-05-10. (B) Four footprints in situ. (C) Detail of the footprint "x" in B.

4.13.3. ***Ichnospecies*** *Phoenicopterichnum pehuencoensis Aramayo and Manera de Bianco, 1987a*

Fig. 16.

4.13.4. Neotype

MD YPI 05-09: A siltstone boulder with two footprints. Additional material: A trackway of 18 footprints (Fig. 16A). MD YPI 05-10 is a silicon rubber of the former. 4 footprints in situ (Fig. 16B–C).

4.13.5. Remarks

See Aramayo and Manera de Bianco (1987b) for further details.

4.14. ***Ichnogenus*** *Charadriipeda (Panin and Avram, 1962)*

4.14.1. Charadriipeda isp.

Fig. 17.

4.14.2. Material

MD-YPI-04-16, a silicon rubber cast composed of 16 footprints.

4.14.3. Description

Footprint (average) length: 0.044 m, width 0.046 m. Divarication of digits II–III: 55°, III–IV: 55, II–IV: 110°. Tridactyl webbed avian footprints of medium to large size, left by short-legged birds (Aves, Anseriformes).



Fig. 17. *Charadriipeda* isp. trackway. From here a silicon rubber cast MD-YPI-04-16 was taken.

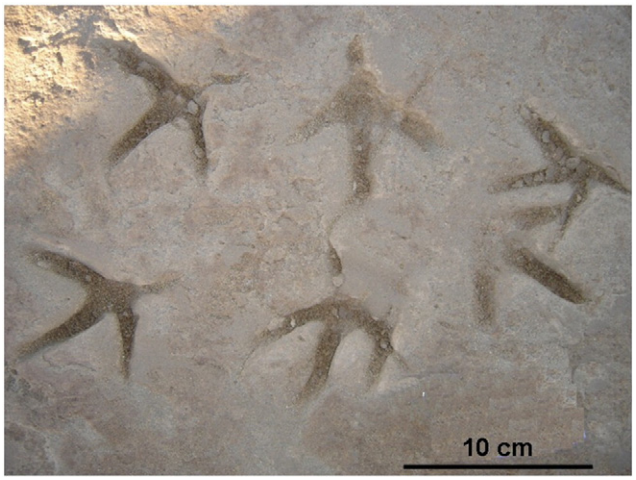


Fig. 18. *Gruipeda* isp. footprints. From here the silicon rubber cast MD-YPI-06-11 was taken.

4.14.4. Remarks

We follow the emended diagnosis by Sarjeant and Langston (1994).

4.15. ***Ichnogenus*** *Gruipeda (Panin and Avram, 1962)*

4.15.1. Gruipeda isp.

Fig. 18.

4.15.2. Material

MD-YPI-06-11: silicon rubber cast (including ground sloth and bird footprints).

4.15.3. Description

Tetradactyl anisodactyl tracks that are as long (including hallux) as wide. Two trackways of 33 and 24 footprints were recorded. A few tracks are tridactyl, most of them (90%) are tetradactyl. Digits II to IV are large and directed forward and digit I (hallux), directed backward. Trackway: length 6.70 m (33 footprints) and width 0.14 m. Footprint (average) length (hallux included) 0.10 m and width 0.10 m. Digits length (average): I: 0.026 m, II and IV: 0.03 m, and III: 0.050 m. Divarication of digits: I–II: 120° and II–IV: 140°.

4.15.4. Comments

We follow the emended diagnosis by Sarjeant and Langston (1994) and de Valais and Melchor (2008). The features and the size of these footprints, allow us to infer that its trackmaker could be the extant "chajá" (*Chauna torquata* Oken, 1816 Anseriformes, Anhimidae). This bird lives in ponds and wet sites in the Pampean region along with other waterfowl.

5. Discussion

The high ichnodiversity of mammal and bird tracks (11 mammal and 4 bird ichnospecies) at Pehuen Co site is a reflection of a high vertebrate biodiversity during the late Pleistocene in southern South America, that paleocommunity lived in an environment where there were temporary fresh water lakes and ponds. According to Zavala and Quattrocchio (2001), during the late Pleistocene in the region, the climate was cold and dry, and during rains, ephemeral streams transported sediments of nearby areas and deposited them in the lowlands. The sediments that were transported farther away formed layers of fine-grained sandstone and claystone with mud cracks, which contain the vertebrate footprints. The footprint-bearing strata overlie a succession of sandstone, silty-sandstone, diamictite and conglomerates that were dated at 16,440 ± 320 y BP (Aramayo, 1997). This older succession has yielded a large amount of remains of mammals of the orders Xenarthra, Notoungulata, Litopterna, Rodentia, Carnivora, Perissodactyla, Proboscidea and Artiodactyla (Ameghino, 1908; Frenguelli, 1928; Cabrera, 1929; Kraglievich, 1946; Aramayo and Manera de Bianco, 1989; Prado and Alberdi, 1994; Alberdi and Prado, 1995; Tomassini et al., 2010; Prado et al., 2012). Many of these are the likely producers of the footprints described in this contribution.

Until now, more than 100 trackways, hundreds of isolated ichnites and trampled areas have been registered, all of which belong to approximately 22 different ichnospecies of mammals and birds, including those described herein. The latter include: *Neomegatherichnum pehuencoensis*, *Mylodontidichnum rosalensis*, *Glyptodontichnus pehuencoensis*, *Eumacrauchenichnus patachonicus*, *Proboscipeda australis*, *Dolichotichnus marae*,*Ursichnus sudamericanus*,*Hippipeda* isp., *Lamaichnum guanicoe*, *Lamaichnum tulipensis*, *Pecoripeda commune*, *Aramayoichnus rheae*, *Phoenicopterichnum pehuencoensis*, *Charadriipeda* isp. and *Gruipeda* isp. In addition to the vertebrate ichnospecies discussed in this paper, we have registered and taken numerous photographs of other footprint types present in the site that will be the focus of future studies. Among them, we can highlight those made by different species of Carnivora (Felidae and Canidae) and birds. For example: 1) footprints of a digitígrade (?) mammal of medium size that were described as *Pumaeichnum biancoi* Aramayo and Manera de Bianco, 1987b, whose morphology and size match those of the living puma *Felis* (*Puma*) *concolor*. 2) *Pehuencoichnum gracilis* Aramayo and Manera de Bianco, 1987b are footprints attributed to a fissipede carnivore of small size; and 3) *Mustelidichnum enigmaticum* Aramayo and Manera de Bianco, 1987a are footprints of a plantígrade animal of small to medium size, which was questionably attributed to a species of the family Mustelidae.

In addition, in 2005, a finding was made of footprints that suggest the presence of humans on the shores of the temporary ponds (Manera de Bianco et al., 2005b; Aramayo and Manera de Bianco, 2009). Until now, two traces of human presence have been identified. One of them consists of two isolated footprints found on big blocks of claystone which had been removed by the tide. On each of them, there is a human footprint; both belonging to the left foot. The other evidence, found at the medium levels of the stratigraphic section, is a trackway of 13 consecutive footprints where right and left pes impressions alternate. They are interpreted as left by a walking human (Bayón et al., 2011).

Our studies have also revealed that this site, Pehuen Co, is unique, because of the number of tracks, the quality of their preservation and the vertebrate paleocommunity that they represent. Among these tracks, undoubtedly, those printed by the huge ground sloth *Megatherium* (*Neomegatherichnum pehuencoensis*) are the most remarkable, due to its number, size and peculiar aspect.

Although, there are Pleistocene vertebrate track sites in all continents (McDonald et al., 2007); Cenozoic mammal footprints have been little studied until recently (Lucas, 2007). In addition, there are few known sites of late Pleistocene age showing high ichnodiversity of birds and mammals.

To highlight the importance of Pehuen Co, we can advance that there are only two other Pleistocene paleoichnological sites in North and South America that share similar characteristics, such as enhanced mammal and bird footprint diversity and presence of ground sloth tracks. These are the Nevada State Prison (USA) and Guaminí, Buenos Aires province (Argentina).

The only known tracks of a ground sloth in North America are from the Nevada State Prison, near Carson City (McDonald, 2007). They were discovered during stone quarry works and were preserved on sandstone. Blake, in, 1884, reported that the tracks had been left by different animals including mammoth, elk, buffalo, horse, carnivorous mammals,

a giant sloth, and birds. Unfortunately, the construction of the prison covered every footprint left in situ and no detailed study has been conducted on the footprints. Only a few original slabs remain unharmed at Keck Earth Science and Mineral Engineering Museum, University of Nevada; and copies of four footprints are still preserved at the George Page Museum, in Rancho La Brea, Los Angeles, USA (McDonald, 2007). Such an association of footprints reflects the faunistic composition of North America at the end of Pleistocene, with the integration of living and extinct species. Although this association coincided with the paleoichnological site of Pehuen Co, they are different due to their location — one in North America and the other in South America — where mammal communities were differently composed at the end of the Pleistocene (e.g., *Macrauchenia* is a species exclusively found in South America).

Recently, Oliva et al. (2013) reported the discovery of a new paleoichnological site in Guaminí, about 100 km north of Pehuen Co. After a prolonged drought which resulted in lake-level drawdown of the Laguna del Monte, Pleistocene siltstones with vertebrate tracks became exposed. These footprints are mainly of mammals and some of birds. Most of the ichnospecies present are similar to those found at Pehuen Co, although no detailed ichnological study has been published to date and the preservation quality seems to be lower than for Pehuen Co. There is no more information on this site available, since its chances of study are heavily dependent on weather conditions.

In consequence, the Pehuen Co paleoichnological site stands out from the few known Pleistocene sites with ground sloth footprints. Regarding the high ichnodiversity of mammals and birds, we can argue that the Pehuen Co is one of the most interesting and promising Pleistocene vertebrate tracksites on Earth.

6. Conclusions

This review confirms that the Pehuen Co ichnofauna shows a high ichnodiversity of mammal and bird footprints. The newly described specimens of the mammal ichnotaxa *Neomegatherichnum pehuencoensis*, *Mylodontidichnum rosalensis*, *Eumacrauchenichnus patachonicus*, *Hippipeda* isp. and *Lamaichnum guanicoe*, help to improve the existing descriptions and diagnoses.

A revision of the previously erected mammal ichnoespecies *Stegomastodonichnum australis*, *Megalamaichnum tulipensis* and *Odocoileichnum commune* suggest that they should be transferred to *Proboscipeda australis* nov. comb., *Lamaichnum tulipensis* nov. comb. and *Pecoripeda commune* nov. comb., respectively.

Three new mammal ichnospecies are proposed: *Glyptodonichus pehuencoensis* nov. igen. and isp., *Dolichotichnus marae* nov. igen. and isp.and *Ursichnus sudamericanus* nov. isp. *Glyptodonichus pehuencoensis* is the only glyptodont track known to date. New materials corresponding to the bird icnotaxa *Phoenicopterichnum pehuencoensis*, *Charadriipeda* isp. and *Gruipeda* isp. were described and a further new bird ichnospecies is proposed, *Aramayoichnus rheae* nov. igen. and isp., to distinguish Rheidae footprints. The Paleoichnological Site of Pehuen Co is one of the most important and promising Pleistocene vertebrate tracksites on Earth. Further studies are needed to complete the ichnotaxinomical, paleoecological and tapohonomical characterization of the site.

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