Palaeogeography, Palaeoclimatology, Palaeoecology xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Late Miocene ground sloth footprints and their paleoenvironment: *Megatherichnum oportoi* revisited

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ARTICLE INFO

Article history:
Received 19 June 2014
Received in revised form 17 October 2014
Accepted 4 February 2015
Available online xxxx

Keywords:
Ground sloth
Quadrupedal trackway
Tidal flat
Coastal dunes
Megatheriinae
Pyramiodontherium

ABSTRACT

Fossil footprints of ground sloths are mostly restricted to the late Miocene to Pleistocene of South America. This study is focused on the oldest known ground sloth trackways, *Megatherichnum oportoi* Casamiquela, 1974 from the late Miocene Río Negro Formation of northern Patagonia. The section logged at the study site, near Carmen de Patagones (Buenos Aires province), includes the uppermost part of the middle member (marine) and the upper member (aeolian) of the Río Negro Formation. Identified sedimentary facies can be grouped into four facies associations: tidal flat, aeolian dune, dry/damp interdune and wet interdune (shallow lacustrine). *M. oportoi* trackways are preserved in an upper intertidal mixed flat. Associated trace fossils belong to a wet aeolian system developed close to the sea coast and were mostly preserved in interdune facies. These include Poaceae root and stem traces and *Nagtuichnus meuleni* (Chlamyphorinae burrow) in dry interdune facies, indeterminate tetrapod footprints in damp interdune facies, *Lockeia siliquaria* and chevron-like trace fossils (bivalve resting and horizontal locomotion traces) in wet interdune facies (shallow lakes), and *Palaeophycus tubularis* in aeolian dune facies. The most likely trackmaker of *M. oportoi* is *Pyramiodontherium* sp. (Megatheriinae), recorded from the same stratigraphic unit at Chubut province, with a body mass ranging from 2.5 to 3.6 t. *M. oportoi* is interpreted as a quadrupedal trackway of a late Miocene ground sloth without overlap of the pes on the manus. The previously proposed bipedal interpretation for the trackway requires angles of gait in excess of those permitted for such a large and heavy animal. Pleistocene ground sloth trackways are distinctive because of the much smaller size of the fore footprint. For the latter examples, a quadrupedal locomotion with overlap of the pes on the manus may be applied.

1. Introduction

The track record of ground sloths mostly includes trackways interpreted as bipedal and rarer quadrupedal trackways and is essentially restricted to South America. Remarkable Pleistocene examples are those of the Carson City state prison (Nevada, USA) that were attributed to mylodontids (Marsh, 1883) and the Pehuen-Có trackways (Buenos Aires province, Argentina) assigned to megatherids (Aramayo and Manera de Bianco, 1987). In these examples, the trackways include essentially large pes tracks with occasional preservation of associated manus tracks (Aramayo and Manera de Bianco, 1987, 1996, 2009; McDonald, 2007). Late Miocene to Pliocene ground sloth tracks are known from three formations of Argentina: the late Miocene–Pliocene Toro Negro Formation of La Rioja province (Frenguelli, 1950; Bonaparte, 1965; Krapovickas et al., 2009), the late Miocene–Pliocene Río Negro Formation of Patagonia (Casamiquela, 1974; Aramayo, 2007) and the Pliocene Monte Hermoso Formation of Buenos Aires province (Aramayo and Manera de Bianco, 1996). Except for *Venatoripes riojanus* Frenguelli, 1950 (from the Toro Negro Formation), these late Miocene–Pliocene trackways lack manus footprints and were thus interpreted as bipedal. The longest and best preserved late Miocene ground sloth trackways are those of the Río Negro Formation near Carmen de Patagones (Buenos Aires province). They were used by Casamiquela (1974) to erect *Megatherichnum oportoi*, an ichnotaxon attributed to bipedal locomotion by Megatheriinae. Analyses of the superbly exposed Pleistocene trackways from Pehuen-Có and of skeletal material of *Megatherium* either were not conclusive about the preferred bipedal or quadrupedal gait of *Megatherium* (Casinos, 1996) or suggested a rough bipedal locomotion for the producer (Aramayo and Manera de Bianco, 1987; Blanco and Czerwonogora, 2003).

McDonald (2007) recently argued, following early observations by Marsh (1883), that the reason for the scarcity of manus tracks in the Carson City and Pehuen-Có examples is that the pes commonly overprints the manus, except when the animal changed direction. Fossil sloths exhibited a wide variety of locomotory modes, including bipedality, quadrupedality, arboreality or semiarboreality, climbing, and an aquatic or semi-aquatic lifestyle in saltwater (Pujos et al., 2012). The osteological evidence for fossil ground sloths is not conclusive about

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http://dx.doi.org/10.1016/j.palaeo.2015.02.010
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Please cite this article as: Melchor, R.N., et al., Late Miocene ground sloth footprints and their paleoenvironment: *Megatherichnum oportoi* revisited, Palaeogeogr. Palaeoclimatol. Palaeoecol. (2015), http://dx.doi.org/10.1016/j.palaeo.2015.02.010

the purported bipedal locomotion, and most large ground sloths are considered quadrupedal. The presence of pedolateral rotation in the hind foot of sloths, in addition to a stout and anteriorly compressed femur has been used to infer the ability to adopt an erect or semi-erect posture, for defense or feeding (e.g., Coombs, 1983; De Iuliis, 1996; McDonald, 2007). These inferences are mostly made on the basis of Pleistocene to Holocene ground sloths. However, some late Miocene to Pliocene megatherines, in particular *Pyramiodontherium bergi*, lack the falciform in the foot, which is considered a poor adaptation to bipedalism (Cabrera, 1929; Brandoni et al., 2004).

In this context, the purposes of this contribution are threefold: 1) to interpret the paleoenvironmental setting of the late Miocene–Pliocene Río Negro Formation at the type locality of *Megatherichnum oportoi* Casamiquela, 1974, and describe the associated trace fossils; 2) to provide a revised description of the type material of *Megatherichnum oportoi* Casamiquela, 1974; and 3) to assess the likely producer and its mode of locomotion.

2. Geological setting

The Neogene Río Negro Formation crops out roughly between the valleys of the Colorado and Negro rivers, from the Andean foothills to the Atlantic Ocean in northern Patagonia (Andreis, 1965; Folguera and Zárate, 2009) (Fig. 1A). The unit is part of the fill of the aulacogenic Colorado basin, where it overlies the Barranca Final Formation (late middle Miocene) and is covered by the “Rodados Patagónicos” (Pliocene–Holocene) (Fryklund et al., 1996; Gerster et al., 2011). The Río Negro Formation has a maximum thickness of 65 m and can be divided into three informal members named lower (continental), middle (marine) and upper (continental) (Angulo and Casamiquela, 1982; Zavala and Freije, 2001) (Fig. 2). This stratigraphic division is fully observed in sea cliffs of the San Matías Gulf (Río Negro province). The middle marine member represents the late Miocene (Tortonian) “Entrerriense” transgression in the Colorado Basin (del Río and Martínez, 1998). Continental members are composed of dominant aeolian facies (including dune and interdune deposits) and subordinate fluvial facies and paleosols (Zavala and Freije, 2001; Perez et al., 2013). The age of the formation is currently assigned to the interval late Miocene–early Pliocene on the basis of radiometric dates and fossil mammal remains (Zinsmeister et al., 1981; Aramayo, 1987; Alberdi et al., 1997). Zinsmeister et al. (1981) obtained three K–Ar ages ranging from 9.56 ± 0.3 Ma to 9.11 ± 0.1 Ma for a tuff layer from the top of the Puerto Madryn Formation at Punta Cracker (42° 56′ 10″ S, 64° 20′ 00″ W, Chubut province). The Puerto Madryn Formation is correlated with the middle marine member of the Río Negro Formation (Del Río, 2000). In addition, the deposition of the Puerto Madryn Formation was estimated at 10.0 ± 0.03 Ma (middle Tortonian) on the basis of ^{87}Sr/^{86}Sr ages from fossil bivalves (Scasso et al., 2001). The younger date for the uppermost interval of the upper member of the Río Negro Formation is a fission track age of 4.41 ± 0.5 Ma obtained on rhyolitic glass (Alberdi et al., 1997). The studied sedimentary succession containing *Megatherichnum* is located close to Carmen de Patagones city, Buenos Aires province, on the left margin of the Negro river, approximately 7 km upstream of the mouth, close to Cabaña San José (Fig. 1B, C).

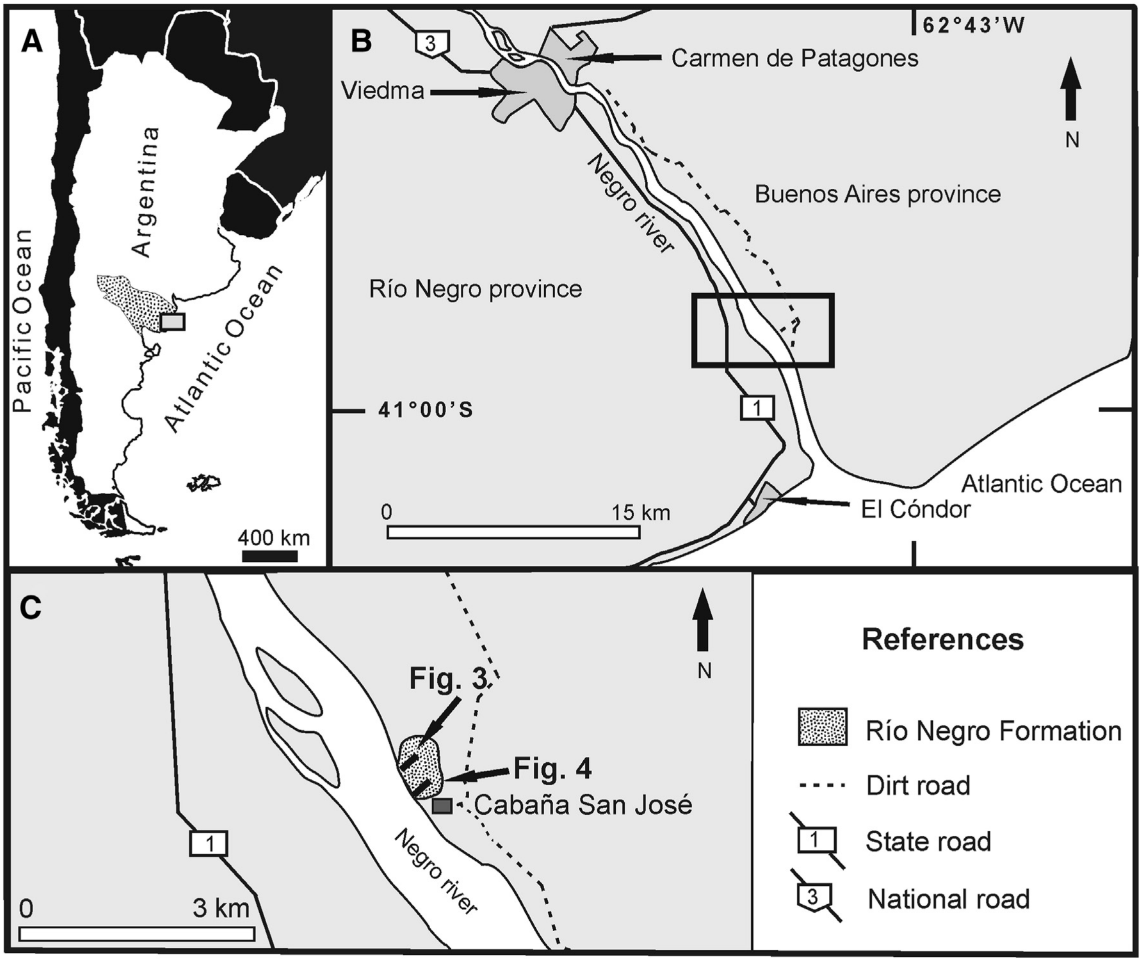

Fig. 1. Location map of the study area. (A) Distribution of the Río Negro Formation (after Folguera and Zárate, 2009) and location of panel B (rectangle). (B) Map of the area between Carmen de Patagones and Viedma cities and the mouth of the Negro river. The rectangle corresponds to panel C. (C) Studied outcrops of the Río Negro Formation near Cabaña San José. Note also location for Figs. 3 and 4.

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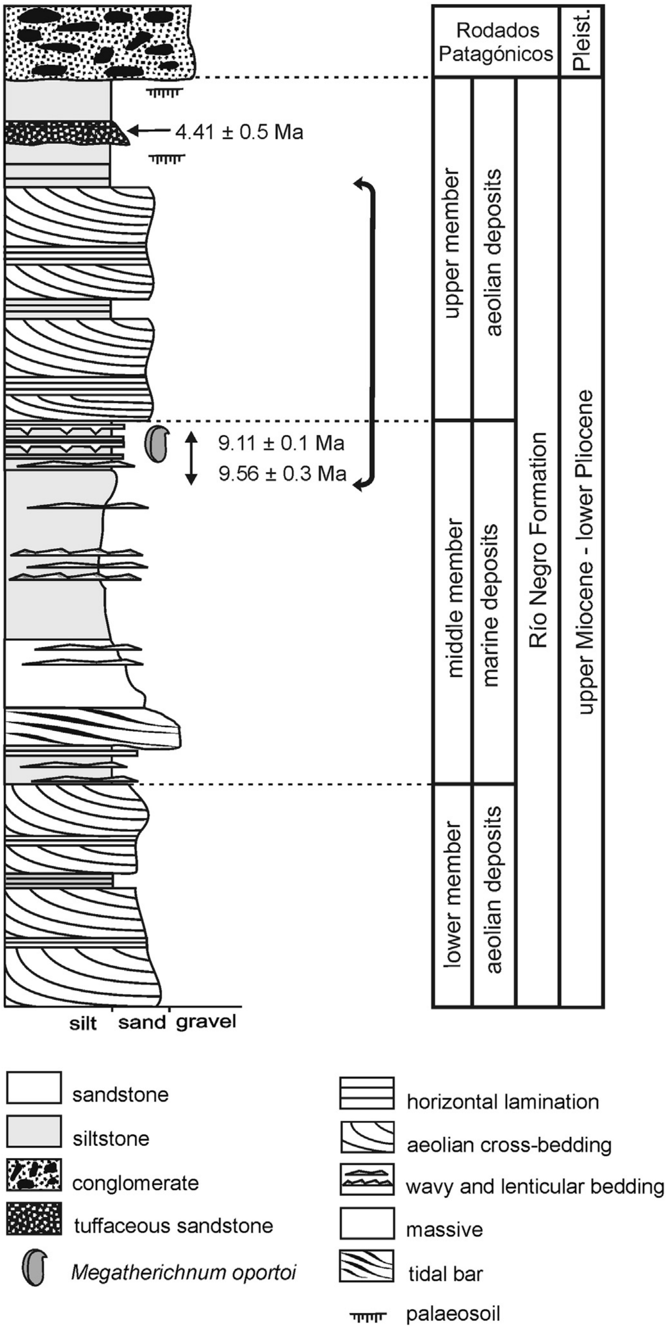

Fig. 2. Schematic stratigraphic section of the Río Negro Formation showing the main sedimentary paleoenvironments, the studied section (bracket), the radiometric dates and the position of *Megatherichnum oportoi* trackways. Modified from Zavala and Freije (2001) and Carmona et al. (2012). Radiometric dates from Zinsmeister et al. (1981) and Alberdi et al. (1997).

3. Material and methods

Sedimentologic logs were measured with standard techniques. Trackway and footprint measurements follow the guidelines by Leonardi (1987). Resin casts of selected footprints are housed at the paleontology collection of the Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Argentina (GHUNLPam). A photomosaic of the largest trackway was obtained by assembling individual photographs using the program Autostitch®. Acronyms used in this work are: MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MAS, Museo de Ciencias Naturales y Antropológicas Profesor Antonio Serrano, Paraná, Entre Ríos, Argentina; MLP, Museo de La Plata, La Plata, Buenos Aires, Argentina; MRVU, Museo Regional de Villa Urquiza, Villa Urquiza, Entre Ríos, Argentina; MPEF Ic, Museo Paleontológico 'Egidio Feruglio', Colección de Paleontología de Vertebrados, Chubut, Argentina; PVL, Instituto Miguel Lillo, Colección Paleontología de Vertebrados, San Miguel de Tucumán, Argentina; MNHNM, Museo Nacional de Historia Natural de Madrid, Spain.

4. Sedimentary facies and facies associations

In the study area the Río Negro Formation is exposed at two nearby hills, which exhibit a similar sedimentary succession. The section of Fig. 3 was measured on the northern hill, whereas the photomosaic of Fig. 4 belongs to the southern hill. The exposed succession ranges in thickness between 13.5 and 15 m. The lower 1.3 m of the succession belongs to the middle member, and the remaining represents the upper member of the Río Negro Formation. The middle member mostly consists of an alternation of fine-grained sandstone and siltstone with heterolithic lamination and minor fine-grained sandstone with horizontal lamination. The upper member is dominated by fine-grained sandstone, in which an alternation of beds with planar–tabular cross-bedding and horizontal lamination is common.

Nine sedimentary facies were defined using lithology, grain size, sedimentary structures and fossil content (Table 1). These can be grouped in four facies associations (FA): tidal flat (FA1), aeolian dune (FA2), dry/damp interdune (FA3), and wet interdune (shallow lake, FA4). Stratigraphic position of each sedimentary facies and facies association can be observed in Fig. 3.

4.1. Tidal flat (FA1)

4.1.1. Description

This facies association is found in the lower 1.3 m of the measured section (Figs. 3, 5A). It is mainly composed of fine-grained sandstone and mudstone forming beds with heterolithic lamination including flaser, wavy and lenticular bedding (facies Hf, Hw and Hl respectively; Figs. 3, 5A–B). The lowermost 0.15 m is a fine-grained sandstone bed with horizontal lamination (facies Sh), which gives an overall fining-upward succession. This facies association contains root traces and bivalve remains, as well as indeterminate plant remains and gastropods. *Megatherichnum oportoi* trackways are preserved on facies Hf, at the top of this facies association (Fig. 5B), and are capped by aeolian dune deposits. Similar sedimentary facies have been described, for the top of the middle member of the Río Negro Formation, in several sections located at sea cliffs near El Cóndor town by Carmona et al. (2012).

4.1.2. Interpretation

The dominance of heterolithic facies, and comparison with well-exposed sections in correlative stratigraphic position described by Carmona et al. (2012), suggests a tidal flat setting. Tidal flats are characterized by the alternation of periods of tractive currents and calm (Reineck and Singh, 1980). The general fining-upward succession and recorded sedimentary and biogenic features suggest an upper intertidal flat setting. In particular, deposition occurred in a mixed-flat to mudflat (Weimer et al., 1982). Although sparse root traces has been identified, the deposits lack the pervasive bioturbation typical of supratidal marshes and are instead overlain by aeolian dune deposits.

4.2. Aeolian dune (FA2)

4.2.1. Description

FA2 is constituted by well-sorted fine-grained sandstones with tabular–planar cross-bedding showing direct and reverse grading of laminae and maximum foreset dip angles of 29° (facies Sp; Figs. 3, 4) and trough cross-bedding (facies St). This FA overlies the tidal flat deposits (FA1) and is interbedded with interdune sediments (FA3 and FA4). Cross-bedded sandstones are arranged in 0.3 to 2.5 m thick sets

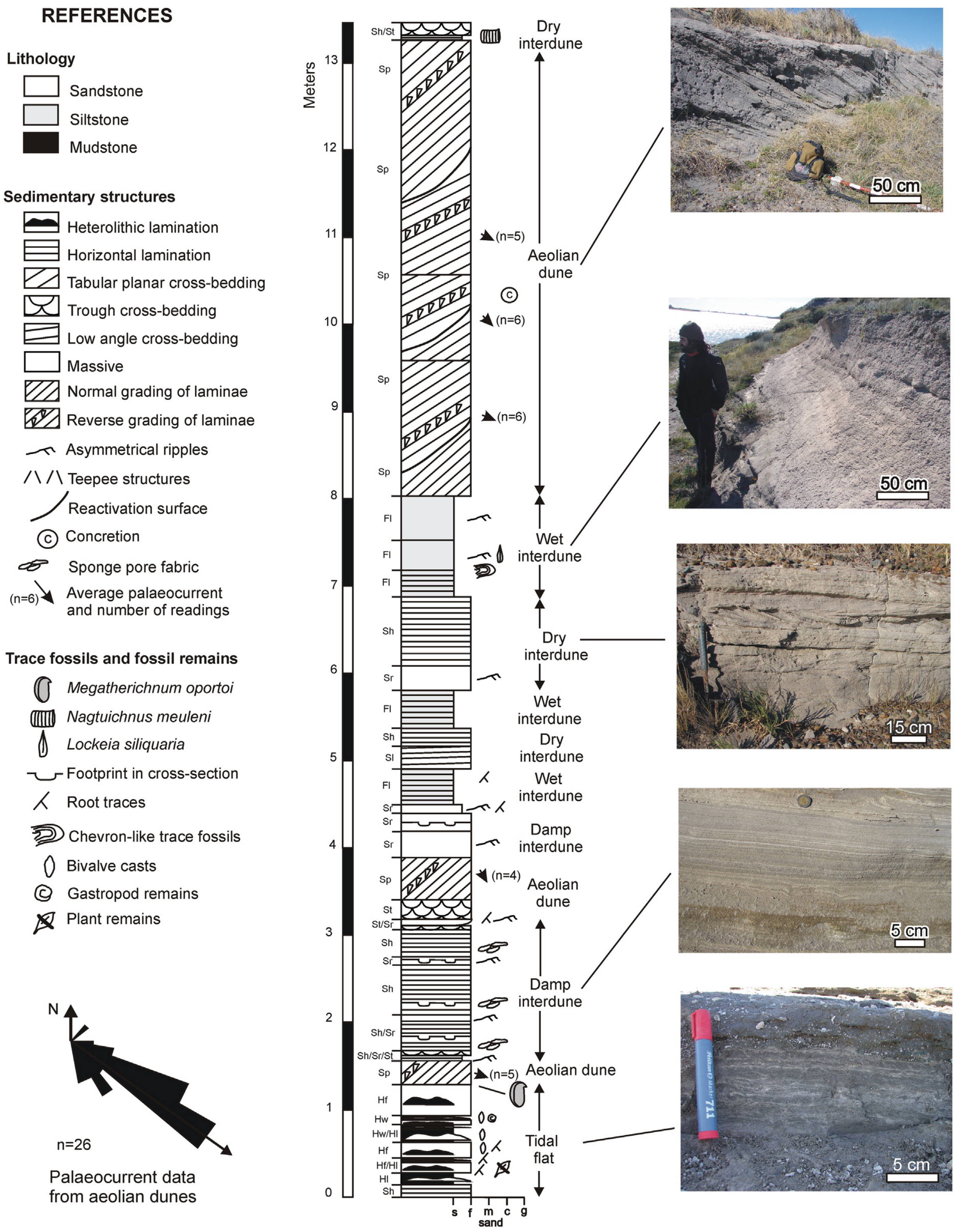

Fig. 3. Detailed sedimentary section measured at Cabaña San José showing sedimentary facies (see Table 1) and facies associations. Location in Fig. 1C. Rose diagram of paleocurrent data for aeolian dune facies association.

which, internally, show concave-upward surfaces (reactivation surfaces after Brookfield, 1977). The sets can be stacked forming cosets up to 5 m thick. Measured paleocurrent data suggest a unimodal orientation toward the southeast (Fig. 3). *Palaeophycus tubularis* burrows arranged parallel to foreset laminae were occasionally identified.

4.2.2. Interpretation

The presence of well-sorted sandstones with moderately thick tabular–planar cross-bedding showing direct and reverse grading of laminae and moderately high dip foreset angles indicates the migration of two-dimensional aeolian dunes by processes of grain fall and grain flow

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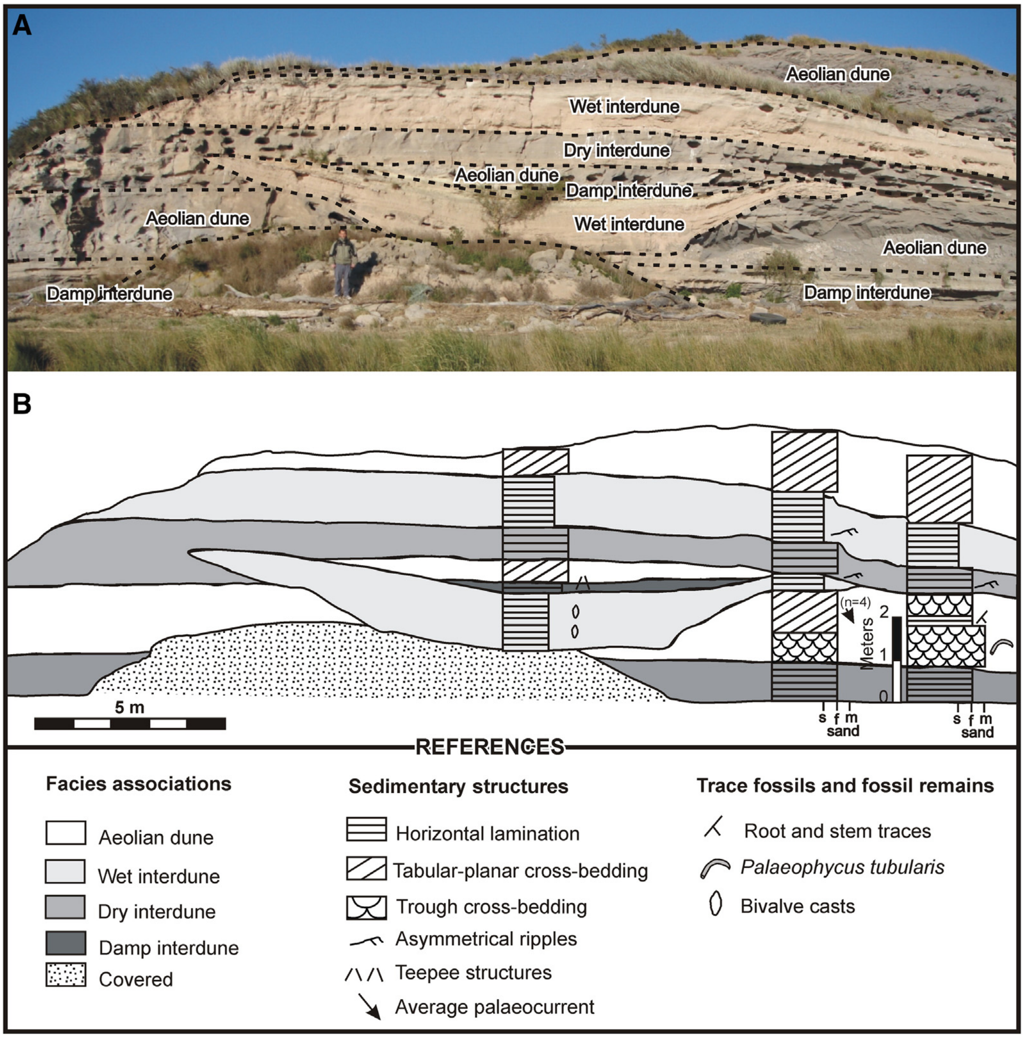

Fig. 4. Geometry of the facies associations of the upper member of the Río Negro Formation (see location in Fig. 1C). (A) Photographic mosaic. (B) Interpretative drawing. Note that the lower occurrence of the wet interdune facies association is flanked by the aeolian dune facies association.

(Mountney, 2006). Reactivation surfaces suggest changes in wind velocity and/or direction. Sandstones with trough cross-bedding may indicate migration of scour pits or of three-dimensional bed forms. The unimodal pattern of paleocurrent data suggests deposition on transverse dunes.

4.3. Damp/dry interdune (FA3)

4.3.1. Description

Damp/dry interdune deposits are interbedded with aeolian dune deposits (FA2) and mainly constituted by medium to very fine-grained well-sorted sandstones with horizontal lamination (facies Sh) and subordinate fine-grained sandstones with ripples, trough cross-bedding and low angle cross-bedding (facies Sr, St and Sl, respectively; Figs. 3, 4). Within facies Sh we can distinguish some beds with vertebrate footprints in cross section, sponge pore fabric (Noffke et al., 2001) (Fig. 5C), gas-escape structures (Fig. 5E, F) and millimeter-thick cemented laminae. These beds occur in an up to 1.5 m thick bedset from the lower part of the section (Fig. 3) and in a 0.3 m thick lenticular intercalation overlying shallow lacustrine deposits of the wet interdune facies (Fig. 4). In the latter, bowed-up carbonate crusts in the form of an inverted "V" as seen in cross section, were also observed (Fig. 5D). These are considered as tepee structures (Kendall and Warren, 1987). In the remaining occurrences of this facies association, facies Sh lacks the mentioned features and instead contains the meniscate burrow *Nagtuichnus meuleni* in addition to root and stem traces.

4.3.2. Interpretation

The interval with sponge pore fabric, cemented laminae, gas escape structures and footprints is interpreted as damp interdune deposits. Sponge pore fabric reflects the trapping of intrasedimentary gases due to sealing of sediment surface by microbial mats (Noffke et al., 2001). Gas escape structures may be related to a similar phenomenon. Microbial mats require, at least, a film of water to develop. This is in agreement with footprint preservation, which is favored by moist to wet substrates and can be enhanced by microbial mats (e.g., Genise et al., 2009; Marty et al., 2009; Carmona et al., 2012). The vertical transition from tidal flat facies association to thin cross-bedded aeolian sandstones and then to horizontally laminated sandstones with sponge pore fabrics and footprints (Fig. 3) suggests that the lowermost occurrence of damp interdune may be influenced by marine or brackish water. The bed of this facies association that overlies shallow lacustrine deposits of the wet interdune facies association (Fig. 4) and contains tepee structures is related to a freshwater lake. The tepee structures can be considered as lacustrine tepees, commonly regarded as result of groundwater resurgence (Kendall and Warren, 1987). Horizontally laminated sandstones with *Nagtuichnus meuleni* and root and stem traces are interpreted as belonging to dry interdune facies.

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Table 1
Description and interpretation of sedimentary facies. See also Fig. 3.

Facies code	Description			Interpretation
	Lithology and texture	Sedimentary structure	Fossil content	
Sp	Fine-grained sandstone	Tabular planar cross-bedding with direct or inverse grading of laminae	*Palaeophycus tubularis*	Migration of two-dimensional aeolian dunes by grain fall and grain flow processes
Sh	Fine- to very fine-grained sandstone	Horizontal lamination, sometimes deformed or poorly defined. Millimeter-thick cemented laminae, occasional teepee structures and gas-escape structures	Footprints in cross-section, *Nagtuichnus meuleni*, Poaceae root and stem traces	Sub-aerial migration of plane beds, development of microbial mats, shallow water table
St	Well-sorted medium to fine-grained sandstone	Trough cross-bedding	–	Migration of three-dimensional aeolian bed forms
Sl	Well-sorted, fine-grained sandstone	Low angle cross-bedding	–	Migration of aeolian ripples
Fl	Siltstone to mudstone	Poorly defined parallel lamination, sometimes massive	*Lockeia siliquaria* and chevron-like trace fossils	Sub-aqueous setting of fine-grained suspended sediments, and locally biological disruption
Sr	Fine- to very fine-grained sandstone, minor siltstone	Asymmetrical ripples with occasional climbing	*Lockeia siliquaria*.	Sub-aqueous migration of asymmetrical ripples
Hf	Fine-grained sandstone, subordinate siltstone	Flaser bedding	Bivalve casts and *Megatherichnum oportoi* trackways. Root traces	Sand deposition from tractive currents and scarce settling of fine-grained suspended sediment, intermittent sub-aerial exposure
Hw	Fine-grained sandstone and siltstone in similar proportions	Wavy bedding	Bivalve casts and gastropod remains	Similar occurrence of sand deposition from tractive currents and settling of fine-grained suspended sediments
Hl	Siltstone and subordinate fine-grained sandstone	Lenticular bedding	Plant remains, millimeter thick root traces	Settling of fine-grained sediments and scarce sand deposition from tractive currents, intermittent sub-aerial exposure

4.4. Wet interdune (shallow lake, FA4)

4.4.1. Description

Pale red laminated and structureless siltstone and mudstone (facies Fl) interbedded with isolated lenses of rippled fine-grained sandstone (facies Sr) compose this facies association (Figs. 3, 4). Some intervals display a highly bioturbated ichnofabric with *Lockeia siliquaria* plus displacement bivalve trace fossils. Massive or laminated mudstone contains external molds of unionid bivalves and gastropods. Measured thickness of this facies association ranges from 0.4 to 1.75 m. At least two intervals belonging to FA4 are recognized, the lower one displays a plane top and concave upward bottom, whereas the upper one is sheet-like (Fig. 4). The lower interval is flanked by aeolian dune deposits (FA2).

4.4.2. Interpretation

The dominance of fine-grained sediments with horizontal lamination and the presence of freshwater clam remains suggest a subaqueous origin for this facies association. These sediments are envisaged as deposited in small ponds between active dunes (lower interval) or larger lakes in interdune areas (upper interval).

5. Systematic ichnology

5.1. Ichnogenus *Megatherichnum*: Casamiquela, 1974

1982 *Megatherichnum*: Angulo and Casamiquela p. 49–50, plate I.
1994 *Megatherichnum*: Leonardi, p. 34, plate XX, Figs. 1–3.
1996 *Megatherichnum*: Casinos p. 88.
2007 *Megatherichnum*: Aramayo p. 574–576, Figs. 3A–B.
2008 *Megatherichnum*: Aramayo p. 14.
2013 *Megatherichnum*: Melchor, Perez, Umazano p. 41–44, Figs. 5, 6A–B.

Type and only known ichnospecies. *Megatherichnum oportoi* Casamiquela, 1974.

5.1.1. Emended diagnosis

Quadrupedal trackway composed of large subelliptical footprints, footprint long axis parallel to trackway midline, moderate pace angulation, breadth between footprints about one third of trackway width. Manus and pes footprints of similar size, at least 0.5 m long, lacking digit impressions, footprint width about half its length, flanked by a clear marginal ridge. Manus footprint of broadly falciform outline, large inwardly directed claw mark, rear of footprint slightly wider than anterior part. Pes footprint kidney-shaped, distinct but smaller claw mark. *Megatherichnum* pes footprint outline similar to *Neomegatherichnum* but of smaller size. Manus print of similar size to pes print in *Megatherichnum* and about one third the length of the associated pes print with a marked claw mark in *Neomegatherichnum*.

5.1.2. Remarks

In the original description, the ichnogenus was based on a trackway composed of 29 moderately preserved tracks. Casamiquela (1974) considered that an additional poorly preserved trackway located close to the former (22 tracks) probably was part of the same trackway. As the trackways are exposed at the coast of the Negro river close to its mouth, they are inundated twice a day during high tides and subject to erosion by waves and desiccation during exposure. In the 40 years since the work by Casamiquela (1974), the footprints were subject to erosion as suggested by comparing the original illustrations (Casamiquela, 1974; plates I to III) with the current state of the footprints (Fig. 6A–D). This erosion resulted essentially in removal of the host rock, and probably also loss of morphological detail of the footprints. As a consequence of this erosion, the footprints are preserved as pedestals composed of compacted and more resistant material (Figs. 5B, 6A). During fieldwork in 2012, we recorded two trackways (that may be a part of a single larger trackway) composed by 59 moderately preserved footprints (Figs. 6A–D, 7A–C) and 14 poorly preserved footprints, respectively. The larger number of footprints in comparison with those described by Casamiquela (1974) suggests that recent erosion also exposed several additional footprints.

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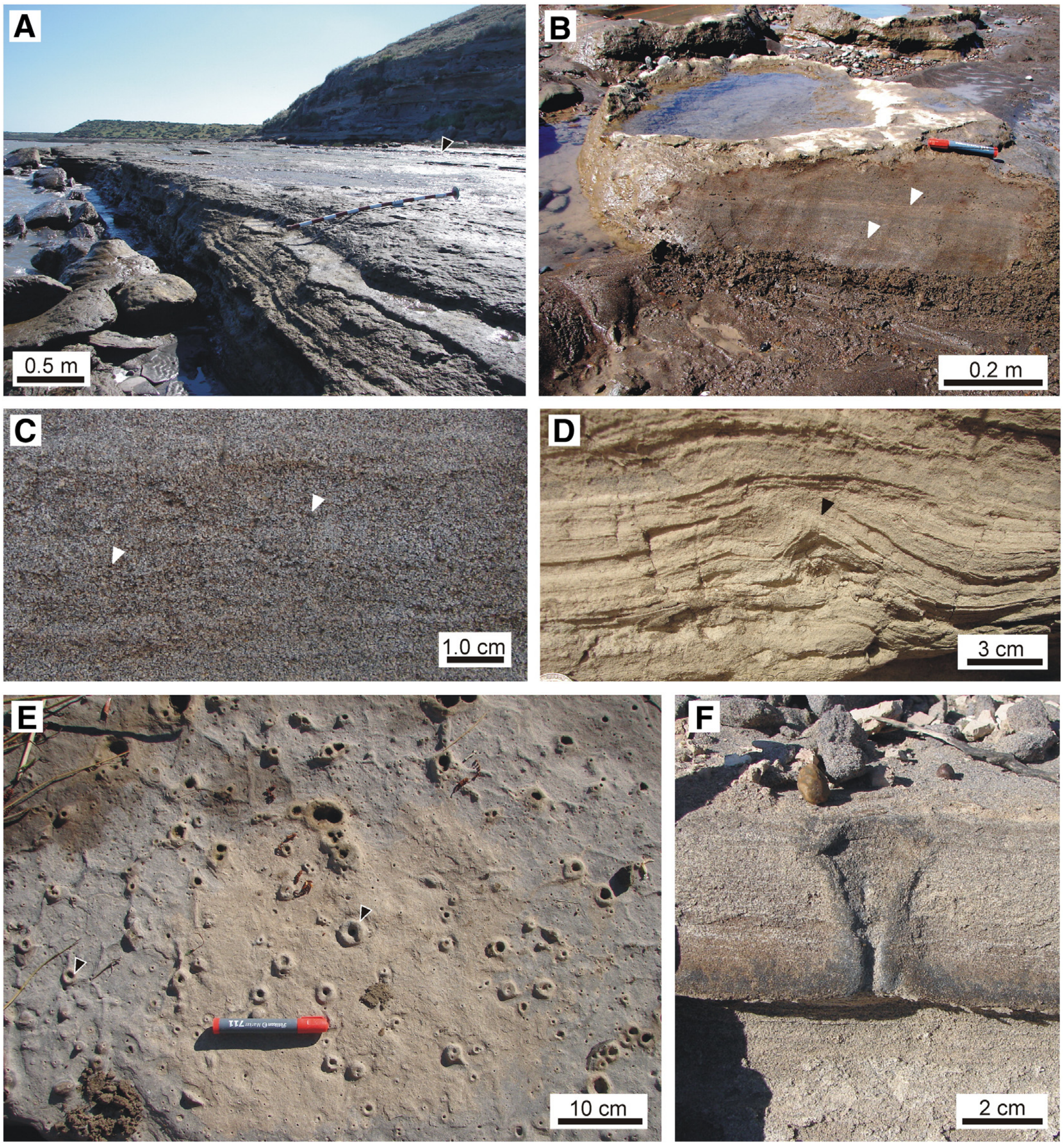

Fig. 5. Sedimentary features of the Río Negro Formation at Cabaña San José area. (A) Exposures of the unit at low tide. Note tidal flat facies association in the foreground and the upper member exposed in the hill of the background. Black arrow indicates the approximate horizon with *M. oportoi*. (B) Detail of the erosive pedestal of a *M. oportoi* track showing the sedimentary structures of the hosting rock (arrows point to sandstone laminae). (C) Sponge pore fabric. Arrows point to small voids typical of this structure. (D) Tepee structure (arrow). (E, F) Gas-escape structures. (E) Plan view with several structures, some arrowed. (F) Cross-section. Panels C to F are from the damp interdune facies association.

The ichnogenus *Neomegatherichnum* Aramayo and Manera de Bianco, 1987 from the Pleistocene of Pehuen-Có (Buenos Aires province) displays a similar morphology to *Megatherichnum* Casamiquela, 1974, although there are some relevant differences. *Neomegatherichnum* hind footprints are larger than those of *Megatherichnum*, and the type trackway includes fore footprints that are considerably smaller than the hind footprints (Aramayo and Manera de Bianco, 1987, 2009). Casamiquela (1983) erected the ichnogenus *Iribarnichnum* on the basis of an isolated subelliptical footprint from the Pleistocene of Monte Hermoso (Buenos Aires province), which is similar to *Neomegatherichnum*.

5.2. Ichnospecies *Megatherichnum oportoi* Casamiquela, 1974

Figs. 5B, 6A–D, 7A–C, 8A–J.

5.2.1. Diagnosis

Only known ichnospecies, same as for the ichnogenus.

5.2.2. Lectotype

The lectotype is in the field (trackway A). Resin casts of two well-preserved footprints from trackway A are GHUNLPam 29052, pes footprint # 51 (Fig. 8B) and GHUNLPam 29053, manus footprint # 37 (Fig. 8E).

5.2.3. Examined material

Two trackways composed of 59 (trackway A) and 14 footprints (trackway B), respectively.

5.2.4. Description

Trackway A is 58.8 m long and composed of three nearly straight segments with slight changes in orientation (Figs. 6B, 7A–B). The average azimuth is N335° in the first segment (footprints 1 to 23, 18.3 m), then changes to N343° in the second segment (footprints 24 to 47, 30 m), and is N320° in the last segment (footprints 48 to 59, 10.5 m). Trackway B is 9.7 m long and located a few meters apart from the former trackway. Its average orientation is N341°. Individual footprints in trackway B are

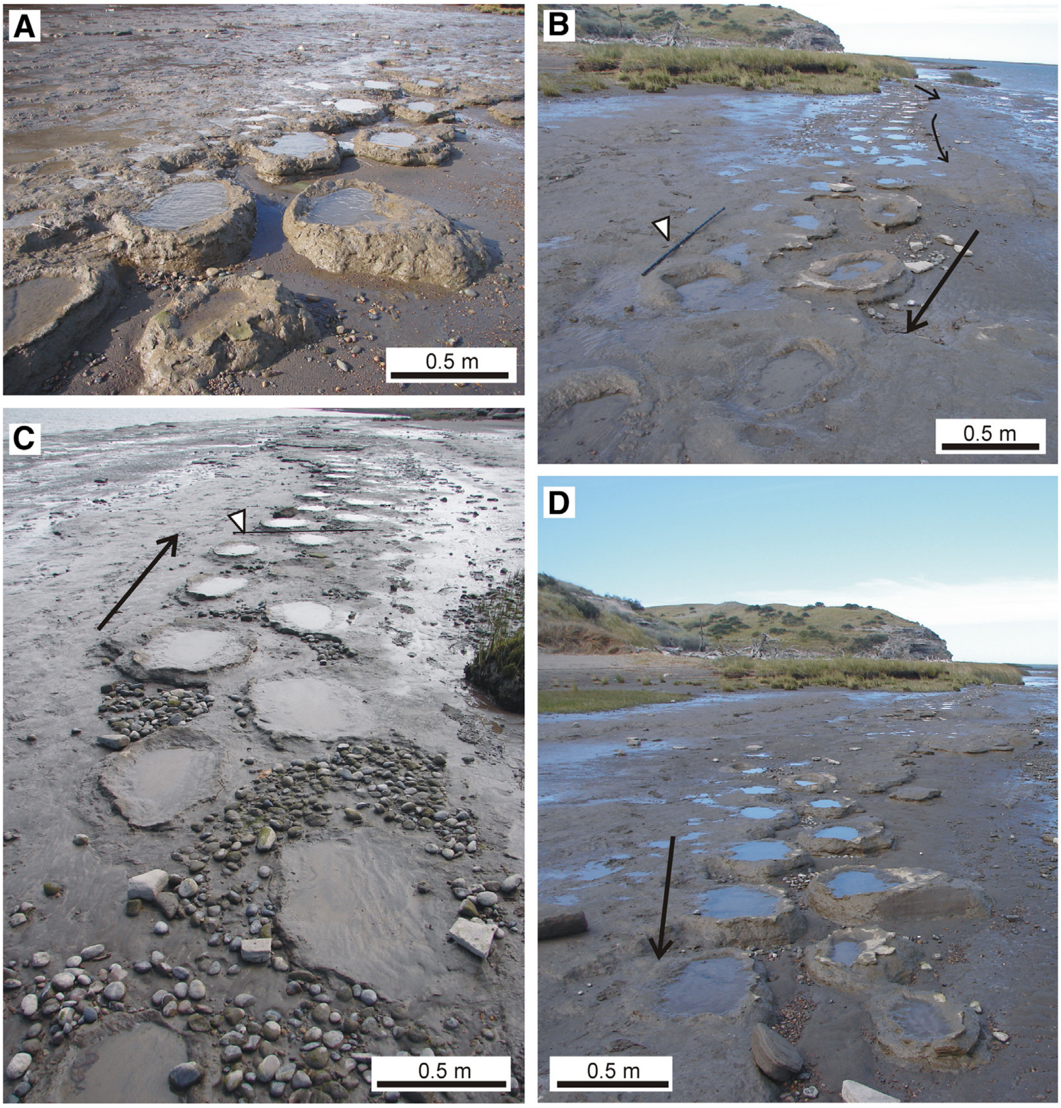

Fig. 6. Views of the trackway A of *M. oportoi*. (A) Pedestals produced by differential erosion of hosting rock and preservation of compacted sediments under and around the footprints. (B–D) General oblique views of trackway A of *M. oportoi*. Individual footprints are highlighted by ponded water. Note breadth between tracks and slight changes in direction. Large black arrows indicate the inferred direction of movement and white arrows point to 1.6 m staff.

poorly preserved. The description is mostly based on trackway A (Fig. 7A–C), which is better preserved and is considered the representative trackway. Footprints long axis is parallel or displays a slight inward rotation (7–14°) with respect to the midline. Average external trackway width is 1.00 m (range: 0.97–1.07 m, n = 8) and the average breadth between footprints is 0.29 m (range: 0.20–0.36 m, n = 8). Average footprint length is 0.66 m (range: 0.52–0.74 m, n = 53), average footprint width is 0.32 m (range: 0.24–0.37 m, n = 45), and mean footprint length/width ratio is 2.1 (range: 1.4–2.7, n = 45). Mean pace length is 0.92 m (range: 0.67–1.10 m, n = 18), mean stride length is 3.11 m (range: 2.88–3.36 m, n = 40), and mean pace angulation is 133° (range: 110–147°, n = 23) (Table 2). Manus and pes are of similar size although they exhibit a different morphology that is best exemplified by the footprints # 37 (manus) and 51 (pes). The best preserved pes footprints are broadly kidney-shaped with an inner straight margin and a convex outward external margin (Fig. 8A–C, G, I, J). A poorly defined claw mark can be identified in most pes footprints (Fig. 8A). The best preserved manus footprint exhibits a falciform outline (Fig. 8D, E) and is composed of a posterior wider portion and a marked triangular, inward pointing claw mark (92 mm wide, 135 mm long) in the anterior part of the footprint (Fig. 8F). A prominent marginal ridge is present, especially in the outer side of manus and pes footprints and gradually reduces its height toward the extremes of the footprint (Fig. 8C, G, J). Some footprints contain a low and poorly-defined internal ridge oriented transverse to the footprint axis that defines two depressions; however the marginal ridge appears continuous (Fig. 8H). Weathered tracks from the middle part of trackway A are composed of two shallow depressions and lack the marginal ridge. Maximum average depth of footprints is 80 mm (range: 30–110 mm, n = 10). Analysis of the better preserved intervals of trackway A suggest that, even if the pace and stride are fairly uniform, it is possible to distinguish sets of four tracks that are separated by longer pace lengths (Fig. 7C). At least, five footprint sets (footprints # 7–10, 11–14, 15–18, 51–54 and 55–58) were distinguished. The sets are composed by two manus and two pes footprints and are distinguished because these footprints are closer than the adjacent footprints in the trackway (Fig. 7C). Average measurements for the distance along the midline of the first track in the set and the last track of the preceding set or the first track of the

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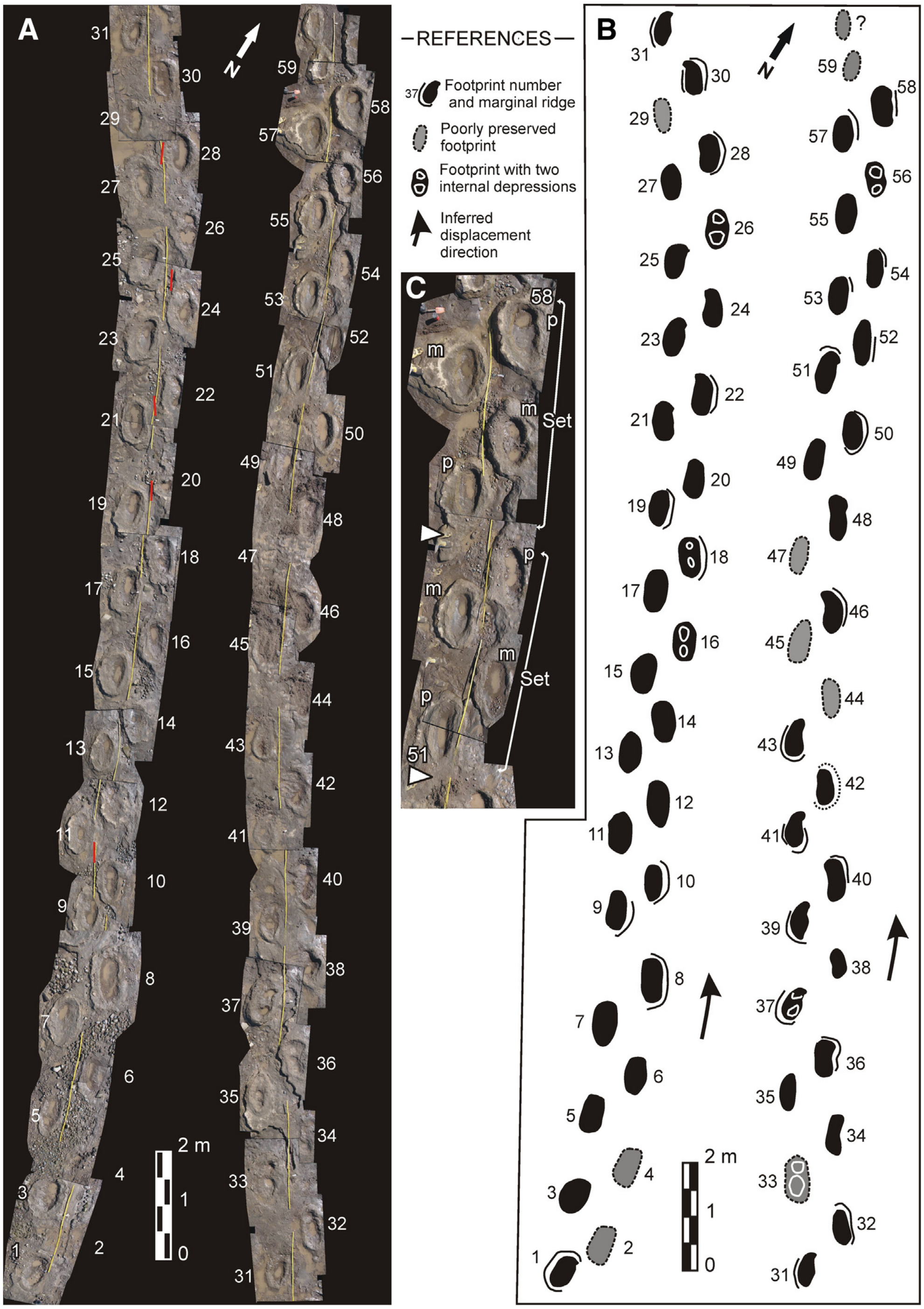

Fig. 7. Trackway A of *M. oportoi*. (A) Photomosaic of the entire trackway. (B) Interpretative drawing of trackway A. (C) Detail of two sets of four tracks (see text for explanation). m: manus, p: pes.

succeeding set is 1.01 m, whereas the average distance between footprints within the set is 0.72 m. The average length for the first and fourth track in the set (pes footprint) is 674 mm, whereas for the second and third track in the set (manus footprint) is 638 mm (Fig. 7C).

5.2.5. Remarks

The triangular imprint seen in many footprints (Fig. 8A, B, D–F) was originally interpreted by Casamiquela (1974) as corresponding to the heel (probably the calcaneum). This imprint has been re-interpreted as corresponding to the claw impression of digit III for *Neomegatherichnum pehuencohensis* Aramayo and Manera de Bianco, 1987 and also for *M. oportoi* (Aramayo and Manera de Bianco, 1987, 2009). As the claw marks are placed anteriorly, their identification allows inferring the direction of displacement of the producer (Fig. 7B).

6. Associated trace fossils

Associated trace fossils are found in different facies associations. Root and stem traces and *Nagtuichnus meuleni* were recorded in dry interdune, indeterminate tetrapod footprints in damp interdune, *Lockeia siliquaria* plus chevron-like trace fossils in wet interdune and *Palaeophycus tubularis* in aeolian dune facies associations.

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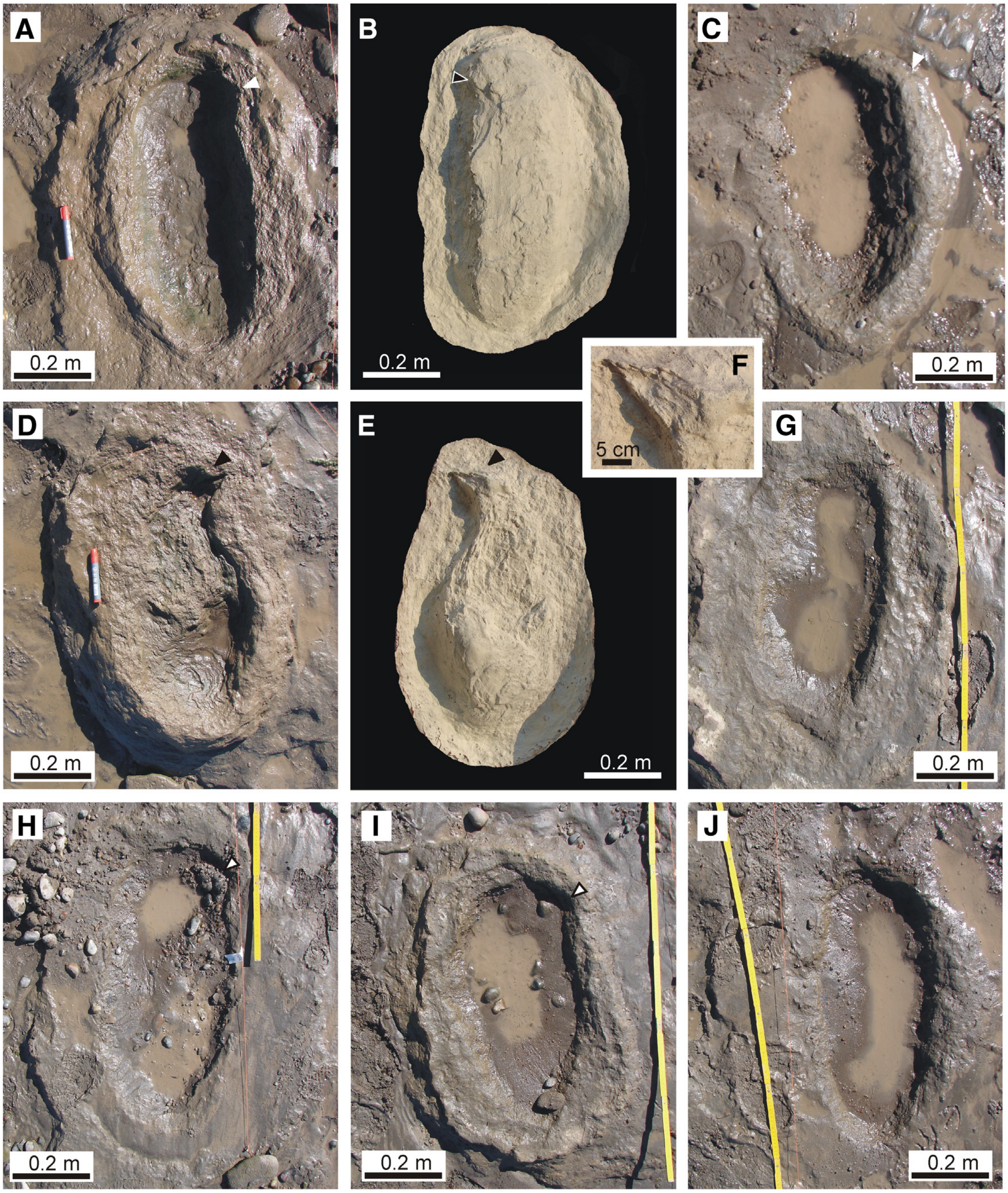

Fig. 8. Detail of individual footprints of *M. oportoi* from trackway A. (A) Left pes footprint # 51, arrows point to claw mark. (B) GHUNLPam 29052. Resin cast of pes footprint # 51. Arrow points to claw mark (digit III). (C) Right pes footprint # 50. Note prominent marginal ridge (arrowed). (D) Left manus footprint # 37, arrow points to claw mark. (E, F) GHUNLPam 29053. Resin cast of manus footprint # 37. (E) General view. (F) Detail of the claw mark of digit III. (G) Right manus footprint # 18. Note marginal ridge. (H) Left manus footprint # 25. Arrow points to claw mark. (I) Left manus footprint # 21; arrow indicates the claw mark. (J) Right manus footprint # 28; note marginal ridge.

6.1. *Lockeia siliquaria* and chevron-like trace fossils

Bivalve trace fossils are common in some intervals of laminated siltstones of shallow lacustrine origin (wet interdune facies association). In these levels, an ichnofabric with a high bioturbation index was observed. Discrete trace fossils are *Lockeia siliquaria* and associated chevron-like trace fossils (Fig. 9B–D). *L. siliquaria* is commonly preserved as negative epirelief and displays an almond- or teardrop-shaped outline, either with a clear acute and an arcuate end or with both acute ends. The average length is 22.9 mm (range: 7.6–33.8 mm, n = 22), average width is 11.1 mm (range: 3.9–22 mm, n = 22) and the mean length/width ratio is 2.1 (range: 1.5–2.9 mm, n = 22). A cross-plot of length against width of *L. siliquaria* suggests a marked positive correlation. The size range of *L. siliquaria* matches that of associated unionid bivalve remains.

L. siliquaria is commonly connected with lateral *spreiten* structures (chevron-like trace fossils). They appear as a straight or slightly curved row of nested chevrons (Fig. 9C–D). Each chevron is similar to the outline of the associated *L. siliquaria*. The chevrons can be either connected to the acute or arcuate end of *L. siliquaria*. On average, the row of lateral

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Table 2
Measurements on *M. oportoi* trackway A.

Track #	FW (cm)	FL (cm)	FD (cm)	FL/FW	PL (cm)	SL (cm)	PA (°)	BPL (cm)	Remarks
1 (m)	35	70	–	2.0	–	–	–	–	
2 (p)	–	–	–	–	–	–	–	–	
3 (p)	33	63	–	1.9	–	–	–	–	
4 (m)	–	–	–	–	–	–	–	–	
5 (m)	30	65	–	2.2	–	–	–	82	
6 (p)	–	60	–	–	110	–	–	110	
7 (p)	37	72	–	1.9	–	336	–	–	
8 (m)	28	62	–	2.2	90	332	–	90	
9 (m)	30	60	–	2.0	–	302	144	67	[a]
10 (p)	34	64	–	1.9	85	316	–	85	
11 (p)	–	58	–	–	–	315	123	60	
12 (m)	36	52	–	1.4	85	316	–	85	
13 (m)	34	65	–	1.9	–	321	143	66	
14 (p)	33	65	–	2.0	100	327	–	100	
15 (p)	30	66	9	2.2	–	317	140	60	
16 (m)	31	69	–	2.2	94	310	–	94	
17 (m)	35	70	–	2.0	–	320	133	70	
18 (p)	30	70	–	2.3	94	312	–	94	
19 (p)	32	66	9	2.1	–	331	136	–	
20 (m)	–	65	–	–	–	–	–	–	
21 (m)	35	63	–	1.8	–	309	125	–	
22 (p)	–	62	–	–	–	314	–	–	
23 (p)	32	68	10	2.1	–	302	137	–	SC
24 (m)	–	–	–	–	–	311	–	–	[b]
25 (m)	36	73	11	2.0	–	282	132	70	
26 (p)	35	66	–	1.9	85	291	–	85	
27 (p)	34	70	–	2.1	–	288	127	64	
28 (m)	35	70	7	2.0	–	293	–	–	
29 (m)	34	54	–	1.6	–	314	110	–	[b]
30 (p)	26	65	–	2.5	90	–	–	90	
31 (p)	29	59	–	2.0	–	299	147	80	
32 (m)	24	65	–	2.7	93	308	–	93	[a]
33 (m)	25	60	–	2.4	–	310	129	–	[a]
34 (p)	–	–	–	–	–	–	–	–	
35 (p)	24	62	–	2.6	–	304	114	–	
36 (m)	26	66	–	2.5	95	323	–	95	[a]
37 (m)	30	65	8	2.2	–	316	142	76	
38 (p)	30	65	–	2.2	92	–	–	92	
39 (p)	32	69	5	2.2	–	330	134	72	
40 (m)	30	74	–	2.5	88	–	–	88	
41 (m)	35	68	3	1.9	–	–	127	78	
42 (p)	–	70	–	–	–	319	–	–	
43 (p)	–	69	–	–	–	–	141	–	
44 (m)	–	71	–	–	–	298	–	–	
45 (m)	–	69	–	–	–	–	136	–	
46 (p)	34	68	–	2.0	–	301	–	–	
47 (p)	–	–	–	–	–	–	–	–	SC[b]
48 (m)	32	69	–	2.2	–	332	–	–	
49 (m)	33	70	–	2.1	–	321	135	70	
50 (p)	35	70	8.5	2.0	100	316	–	100	
51 (p)	30	70	10.5	2.3	–	300	138	68	
52 (m)	33	68	–	2.1	90	316	–	90	
53 (m)	30	62	8	2.1	–	314	139	60	
54 (p)	28	70	–	2.5	110	312	–	110	
55 (p)	33	67	10	2.0	–	288	138	68	
56 (m)	30	67	–	2.2	90	–	–	90	
57 (m)	28	63	–	2.3	–	–	–	46	
58 (p)	34	65	–	1.9	67	–	–	67	
59 (p)	–	–	–		–		–	–	[b]
average	31.6	65.9	8.0	2.1	92.1	311.6	133	80.4	
range	24–37	52–74	3–11	1.4–2.7	67–110	288–336	110–147	46–110	
N	45	53	10	45	18	40	23	35	

FW: footprint width, FL: footprint length, FD: footprint depth, PL: pace length, SL: stride length, PA: pace angulation, BPL: pace length assuming a bipedal trackway, SC: strike change.

[a] Two internal depressions.

[b] Poorly preserved.

spreiten is 38.9 mm long (range: 28.5–54.0 mm, n = 5) and 14.9 mm wide (range: 12.8–17.7 mm, n = 5), and the number of chevrons by row is between 5 and 10 (average spacing is one chevron every 6.5 mm). The width of the row of chevrons is up to 50% wider than the associated *L. siliquaria*. Isolated or groups of chevrons not connected to *L. siliquaria* are also common (Fig. 9C–D). Similar locomotion, resting and escape structures produced by bivalves were recently mentioned at other locations of the Río Negro Formation (Carmona et al., 2013a, 2013b).

Lockeia is commonly interpreted as a bivalve resting trace fossil (Seilacher and Seilacher, 1994) and, in our study, associated unionid bivalves are the best candidates due to a similar size to the trace fossils.

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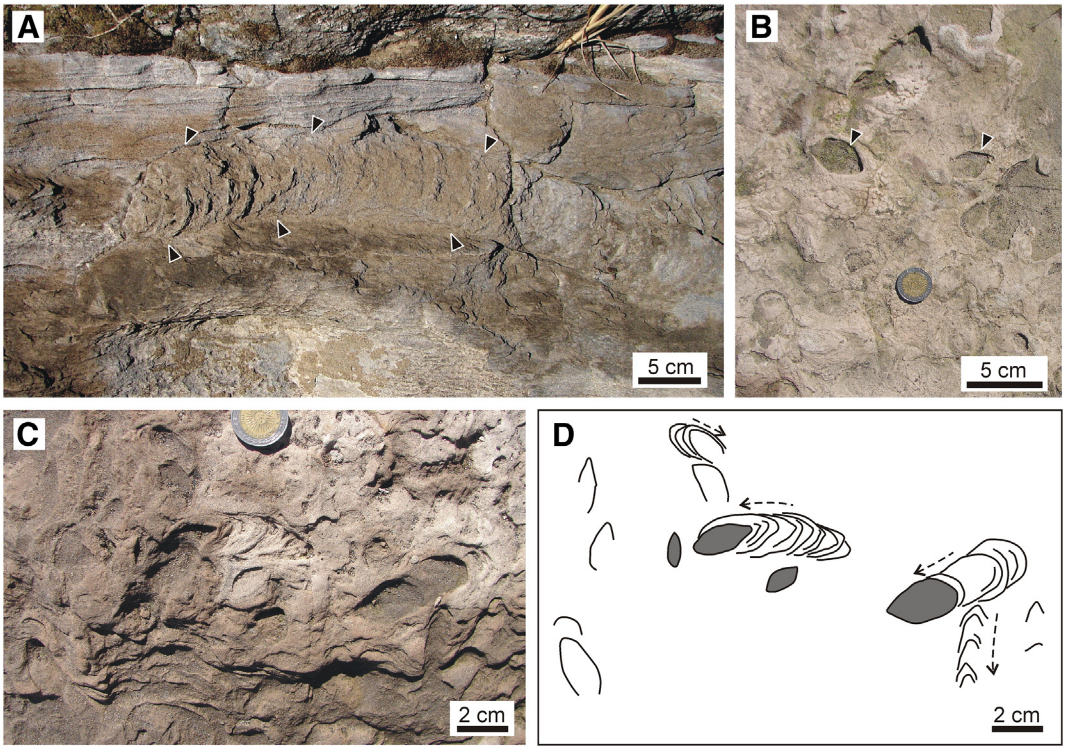

Fig. 9. Associated trace fossils. (A) *N. meuleni* (arrowed). (B) *Lockeia siliquaria* (arrows). (C, D) *L. siliquaria* and chevron-like trace fossils. (C) Field photograph. (D) Drawing of panel C. Arrows indicate the inferred direction of movement.

The chevron-like trace fossil is interpreted as reflecting horizontal movements of unionid bivalves, and represents a new ichnotaxon, which will be described elsewhere. Horizontal displacement by unionid bivalves is accomplished by repetition of digging cycles (Trueman, 1968).

6.2. *Nagtuichnus meuleni*

Short (up to 0.5 m long), straight or slightly curved, subhorizontal cylindrical burrows with a meniscate filling (Fig. 9A). Average diameter is 65 mm (range: 56–70 mm, n = 5) and average meniscus thickness is 14.7 mm (range: 12–18 mm, n = 4). These specimens are similar to those described from the same member of the Río Negro Formation at La Lobería locality (Melchor et al., 2012).

Nagtuichnus meuleni is found essentially in late Miocene to Holocene damp to dry interdune facies (Melchor et al., 2012). For distinction of *N. meuleni* from other potentially similar ichnotaxa, see discussion in Melchor et al. (2012). Its producer, probably a relative of the pink fairy armadillo (*Chlamyphorus truncatus*), preferred dry sandy substrates.

6.3. *Palaeophycus tubularis*

Up to 100 mm-long, slightly curved cylindrical burrows with massive sandstone fill, ranging in diameter from 6 to 7 mm. Shorter (up to 40 mm long) burrows with a slightly meandering path are also included under this ichnospecies (Fig. 10C). *Palaeophycus tubularis* occurs as positive hyporelief in foreset laminae.

Palaeophycus tubularis is a facies-crossing trace fossil that has been recorded in a wide variety of environments (e.g., Buatois and Mángano, 2011). This simple burrow is difficult to assign to a definite producer and behavioral type.

6.4. Root and stem traces

This structure starts on the top of aeolian dunes (facies St), continues upward into the lower part of overlying dry interdune facies (facies Sh), and is truncated by an upper erosive surface. It is composed of groups of up to 6 stem traces originating from a common point and composing the outline of an inverted triangle (Fig. 10A–B). The base (70–185 mm) and height (70–155 mm) of that triangle is similar in each of the three recognized specimens. Stem traces are 0.5 to 4.0 mm wide and form a maximum angle of 56 to 68°. Adventitious root traces (about 0.5 mm wide, up to 35 mm long) arise from the lower fifth of the structure forming an angle with the horizontal ranging from 0 to 45°.

Root and stem traces are assigned to monocotyledonous plants due to their homorhizy character, in particular there is a strong resemblance with Poaceae root systems. The root system resembles those of Type VII by Cannon (1949), which are typical of mesophytic to hygrophytic plants.

6.5. Indeterminate tetrapod footprints

These structures are composed of a set of deformed laminae that defines a concave upward U-shaped shaft, which is draped by undeformed laminated sandstone that fill the shaft (Fig. 10D–E). The shaft can be symmetric or asymmetric. These structures are 30–90 mm deep and 60–330 mm wide. Tens of specimens were observed in the field, dominantly in exposures transverse to bedding in laminated sandstone of the damp interdune facies association. Partial trackways (up to four footprints in negative epirelief) are preserved on bedding plane exposure of the same facies association. Individual footprints may display a subcircular outline (150 mm long by 139 mm wide) or have a rounded posterior part and a quasi-triangular anterior end (about 92 mm long by 75 mm wide). The latter morphology resembles *Macrauchenichnus* Angulo and Casamiquela, 1982 (Fig. 10F).

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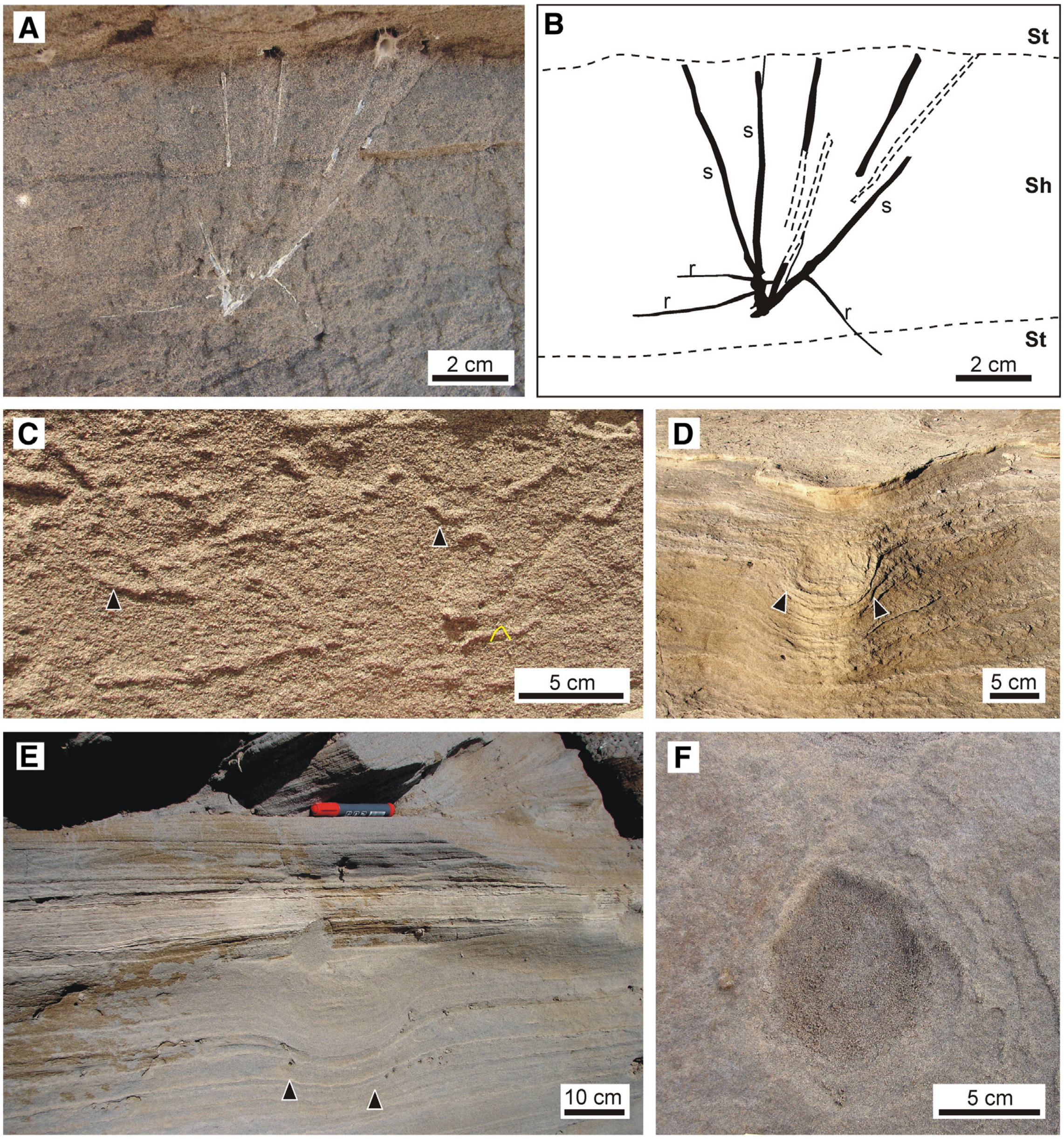

Fig. 10. Associated trace fossils. (A, B) Poaceae root and stem trace fossils. (A) Field photography. (B) Interpretative diagram. r: adventitious root trace, s: stem trace, St: trough cross-bedded sandstone, Sh: horizontally laminated sandstone. (C) Bottom of foreset laminae (trough cross-bedding) of aeolian dune facies association with abundant *P. tubularis* (some arrowed). (D) Indeterminate footprint in cross section (arrows point to lower part of structure). (E) Horizontally laminated sandstones of damp interdune facies association with a footprint in cross-section (arrowed) overlain by cross-bedded sandstone of aeolian dune facies (above marker). (F) Plan view of poorly preserved tetrapod footprint resembling *Macrauchenichnus* from damp interdune facies association.

7. Discussion

7.1. Paleoenvironmental setting and associated trace fossils

The section logged at the study locality represents the transition from an upper intertidal mixed flat to a wet aeolian system. The whole succession is envisaged as located close to the sea coast. The lower 7 m of the succession (Fig. 3) was deposited in a lowland area that included the upper intertidal flat (FA1), where the producer of *M. oportoi* traveled, and a sandy interdune zone with sparse low-relief aeolian sand dunes (FA2). This interdune zone included large sandy flat areas (FA3) and small freshwater ponds (FA4), which may have occupied depressions between dunes. The flat areas close to the ponds were sites for development of microbial mats that enhanced the preservation of tetrapod tracks. The shallow ponds were stable enough to support a bivalve and gastropod community. Raised flat areas were preferred foraging zones for the producer of *N. meuleni*, probably a small armadillo, and also supported low, herb-like vegetation as suggested by traces produced by the roots and stems of grasses. The upper 6 m of the succession reflects the development of a dune field largely composed of transverse dunes with large freshwater lakes in the interdune areas (Fig. 3).

Unionid bivalve activity was recorded in the bottom of these large freshwater lakes in the form of an intensely bioturbated ichnofabric. The aeolian dunes probably composed a coastal dune field, with dune crests parallel to the shoreline. Assuming a dominant inland transport direction (in our case toward the southeast), then the megatherine that produced *M. oportoi* was heading seaward (toward the northwest). Other stratigraphic sections from the upper member of the Río Negro Formation located more than 35 km toward the southwest (Zavala and Freije, 2001), also display two lacustrine intervals (FA4) in similar positions to those described here. In consequence, the occurrence of wet interdune facies (shallow lacustrine deposits) may be related to extrinsic factors like sea level changes. The aeolian system is characterized as wet according to Kocurek and Havholm (1993), given that it can be inferred that the water table or its capillary fringe was at or near the depositional surface during accumulation.

7.2. Producer of *Megatherichnum oportoi*

The large size and broad oval outline of the footprints, along with the presence of a marked marginal ridge, and reduction of digit imprints (Fig. 8A–J) is in agreement with a pedolaterally rotated foot as found in large ground sloths, especially Mylodontidae and Megatheriidae. The record of late Miocene to Pliocene Mylodontidae from Argentina is diverse, and mostly consisting of isolated teeth or partial skulls of medium- to large-sized animals. For this interval, the Mylodontinae are scarce in the Pampean region and Patagonia, whereas Scelidotheriinae are more abundant in both of these areas (Scillato-Yané, 1981; Scillato-Yané et al., 1995). Although hind limb bones are scarce for late Miocene–Pliocene genera, the pes of the scelidothere *Scelidotherium leptocephalum* Owen, 1839 from the Pleistocene of Buenos Aires province is about the size of *M. oportoi* footprints (547 mm long by 240 mm wide after plate 10.1 of Miño-Boilini, 2012). However, late Miocene to Pliocene Mylodontidae are commonly smaller than Pleistocene representatives of the clade (e.g., Pascual et al., 1966), and it is thus unlikely that any known late Miocene to Pliocene mylodontid produced footprints of the size of *M. oportoi*. This is in agreement with the presence in the Río Negro Formation of mylodontid footprints that are about half the size of *M. oportoi* (Aramayo, 2007; Melchor et al., 2013). From northern Argentina, there are some moderately large late Miocene–Pliocene Mylodontinae, including *Pleurolestodon* Rovereto, 1914, *Megabradys* Scillato-Yané, 1981 and *Ranculcus* Ameghino, 1891 (Oliva and Brandoni, 2012), but no postcranial skeletal elements are known. Although large for the clade, these mylodontines are still too small to be potential producers of *M. oportoi*.

The remaining group of large ground sloths that are potential candidates for producing *M. oportoi*, are the late Miocene to Pliocene Megatheriinae from Argentina. Although there are many recognized species (Brandoni et al., 2012), and most of them have been recently revised, postcranial remains are scarce and it is not common to find both cranial and postcranial remains for the same species. Comparison of relative size of known taxa is possible, using linear measurements like maxillary tooth row length (MTRL) and astragalus length (Table 3). Middle Miocene Megatheriinae from Patagonia, including *Megathericulus* and most *Eomegatherium* species are excluded from this analysis because they are small (Brandoni and De Iuliis, 2007) and older than the Río Negro Formation. Among the valid late Miocene–Pliocene species from Argentina (Brandoni and De Iuliis, 2007; Brandoni et al., 2012); *Eomegatherium nanum* (Burmeister, 1891), *Promegatherium smaltatum* Ameghino, 1883 and *Pliomegatherium lelongi* Kraglievich, 1930 from the Ituzaingó Formation (Entre Ríos province); *Anisodontherium halmyronomum* (Cabrera, 1928) from the Chasicó Formation (Buenos Aires province) and *Anisodontherium* sp. from the Saladillo Formation (Tucumán province) are small- to medium-sized (Table 3) and are thus not likely candidates. The remains of megatherines from the Río Negro Formation or correlative lithostratigraphic units are scarce and include two specimens referred to *Megatheridium annectens* Cabrera, 1928 from Río Negro province (Brandoni et al., 2012) and a single specimen assigned to *Pyramiodontherium* sp. from Chubut province (Guillaume, 2005; Guillaume et al., 2005). The MTRL value for *M. annectens* (Table 3) suggests a medium-sized megatherine, whereas astragalus length and other postcranial dimensions of *Pyramiodontherium* sp. from Chubut province (no cranial material was recovered) suggest a fairly large megatherine (Table 3). The specimen of *Pyramiodontherium* sp. from Chubut province includes forelimb and hind limb bones. Long bones of the forelimb and hind limb of *Pyramiodontherium* sp. from Chubut are of subequal length (Table 3). This specimen from Chubut is also unique among late Miocene–Pliocene megatherines because it preserves the complete manus and pes. The reconstruction of the pes by A. Guillaume (2014, electronic communication) suggest that it is 630 mm long by 300 mm wide (length/width ratio = 2.1), a size and outline that match that of *M. oportoi* footprints (allowing for soft tissues, compare with data in Table 2 herein). The manus of the same specimen (Guillaume, 2005; Fig. 21) is almost as large as the pes, although slightly wider (595 mm long by 370 mm wide). In consequence, *Pyramiodontherium* sp. from Chubut province, is a very good candidate for producing *M. oportoi* because of a similar manus and pes size that match the size of the footprints and occurrence in the same sedimentary unit. The body mass of *Pyramiodontherium* sp. from Chubut is unknown. However, it can be approximated by comparison with body mass estimates for the Pleistocene–Holocene *Megatherium americanum*, which displays a similar limb length to *Pyramiodontherium* sp. from Chubut, and with those of the late Miocene–Pliocene *P. scillatoyanei* De Iuliis et al., 2004, which exhibits a much smaller astragalus length (Table 3). The estimates for different specimens of *M. americanum* range from 3.61 to 3.95 t (Casinos, 1996; Fariña et al., 1998; Vizcaíno et al., 2006), whereas *P. scillatoyanei* was about 2.5 t (De Iuliis et al., 2004). In consequence, until a more precise estimate for the body mass of *Pyramiodontherium* sp. from Chubut is available, a body mass ranging from 2.5 to 3.6 t is likely.

The remaining late Miocene–Pliocene megatherines are medium- to large-sized and belong to *Megatheriops rectidens* (Rovereto, 1914) from Mendoza province and several species of *Pyramiodontherium* Rovereto, 1914 from northern Argentina (Table 3). In particular, *Pyramiodontherium bergi* (Moreno and Mercerat, 1891) from the "Araucanense" sensu lato of the Catamarca province is represented by cranial and postcranial remains, including a complete pes, femur and tibia (Brandoni et al., 2004). The pes, as reconstructed by Brandoni et al. (2004) is about 545 mm long by 235 mm wide. Allowing for the soft tissues, this size is slightly smaller than the average measurements for *M. oportoi* footprints (660 by 310 mm, Table 2) and the length/width ratio of the *P. bergi* pes (2.2) is similar to the comparable measurement from the footprints (Table 3). In consequence, the best known candidate for the producer of *M. oportoi* was similar to *Pyramiodontherium* and its size approached that of the specimen from Chubut described by Guillaume (2005). The information on the postcranial skeleton of *P. bergi* (Brandoni et al., 2004) and *Pyramiodontherium* sp. from Chubut (Guillaume, 2005) is useful for biomechanical inferences and comparison with *M. oportoi*.

7.3. Quadrupedal or bipedal?

In this section we will consider three alternative interpretations for *M. oportoi*: 1) a quadrupedal trackway without overlapping footprints, 2) a quadrupedal trackway with overlap of the pes on the manus, and 3) a bipedal trackway.

Quadrupedal trackway without overlapping footprints. The sets of four tracks described for trackway A (Fig. 7C) and the contrasting footprint morphology inferred for the manus and pes (Fig. 8A, B, D, E) is suggestive of a quadrupedal gait. The best candidate for producing *M. oportoi*, *Pyramiodontherium* sp. from Chubut, has manus and pes of roughly similar size and limbs of comparable length, which is also suggestive of a quadrupedal posture. The large size of the presumed producer would allow only for a slow walking gait, in consequence, an alternate placement of manus and pes is expected. Considering this constraint and the slight size difference of the tracks within the set (in average, about 30 mm, see Systematic Ichnology), it may be inferred that the first and fourth tracks in the set represent the pes and the remaining correspond to manus tracks (Fig. 7C). Geometric estimation of the gleno-acetabular distance (Leonardi, 1987) using the five sets of four tracks from trackway A, produced values ranging from 1580 to 1980 mm (average 1720 mm, n = 5).

Quadrupedal trackway with overlap of the pes on the manus. McDonald (2007) argued that both *M. oportoi* and *N. pehuencoensis* represent quadrupedal megatherine trackways, where the pes overprinted

Table 3
Late Miocene–Pliocene Megatheriinae from Argentina, including age, provenance and selected postcranial and cranial features.

Species	Age/provenance	Astragalus length (mm)	Other postcranial material (mm)	MTRL	Specimen	Source/comments
Eomegatherium nanum (Burmeister, 1891)	Late Miocene–Pliocene, Ituzaingó Fm., Entre Ríos province	130			MACN Pv-4992	Brandoni and Carlini (2009)
Anisodontherium halmyronomum (Cabrera, 1928)	Late Miocene, Arroyo Chasicó Fm., Buenos Aires province			114[a]	MLP-30-XII-10-21	Cabrera (1928), Brandoni and De Iuliis (2007), Brandoni et al. (2012)
Anisodontherium halmyronomum (Cabrera, 1928)	Late Miocene, Arroyo Chasicó Fm., Buenos Aires province	120 (incomplete, from Fig. 4A)			MLP 28-X-11-81	Brandoni and De Iuliis (2007)
Anisodontherium sp.	Late Miocene, Saladillo Fm., Tucumán province		Manus digit III claw: 90 long, 64 wide	93[a]	PVL 6425	Brandoni et al. (2012)
Promegatherium smaltatum Ameghino, 1883	Late Miocene–Pliocene, Ituzaingó Fm., Entre Ríos province			Isolated teeth and fragmentary mandible	MACN-A 1582, MLP M-52/53, MACN-A 11560	Brandoni and Scillato-Yané (2007)
Pliomegatherium lelongi Kraglievich, 1930	Late Miocene–Pliocene, Ituzaingó Fm., Entre Rıos province			135	MACN Pv-13213	Brandoni (2006), Brandoni et al. (2012)
Pliomegatherium lelongi Kraglievich, 1930	Late Miocene–Pliocene, Ituzaingó Fm., Entre Rıos province			145	MACN Pv 5269	Brandoni (2006)
?*Pliomegatherium lelongi* Kraglievich, 1930	Late Miocene–Pliocene, Ituzaingó Fm., Entre Rıos province	148			MLP 99-XI-1-1	Brandoni (2006)
Megatheridium annectens Cabrera, 1928	Late Miocene–Pliocene, Río Negro Fm., Río Negro province			Incomplete maxilla	MLP 2-69	Cabrera (1928)
Megatheridium annectens Cabrera, 1928	Late Miocene–Pliocene, Río Negro Fm.?, Río Negro province			146	MACN Pv-2833	Kraglievich (1930), Brandoni et al. (2012) Probably not an adult specimen after de Iuliis (1996)
Megatheriops rectidens (Rovereto, 1914)	Late Miocene, Huayquerias Fm., Mendoza province		Humerus length: 482, 475 (right, left)	168	MACN Pv-2818	Rovereto (1914), Brandoni and Carlini (2009), Brandoni et al. (2012)
Pyramiodontherium bergi (Moreno and Mercerat, 1891)	Late Miocene–Pliocene, "Araucanense", Catamarca province	162	Femur length: 514, Tibia length: 499, Complete pes length: 542, Crural index: 97.7 Extrapolated ungueal: 78 long by 75 wide (Fig. 6I). Calcaneus length: 329	195	MLP 2-66	Cabrera (1928), Carlini et al. (2002), Brandoni et al. (2004), de Iuliis et al. (2004)
Pyramiodontherium brevirostrum Carlini et al., 2002	Late Miocene–Pliocene, "Araucanense", Catamarca province		Femur length: 590, tibia incomplete	188	MLP 31-XI-12-25	Carlini et al. (2002). Larger than *P. bergi*
Pyramiodontherium scillatoyanei De Iuliis et al., 2004	Late Miocene–Pliocene, Toro Negro Fm., La Rioja province	147	Humerus length: 591, femur length: 485, tibia length: 472, calcaneus length: 264, scapula, clavicle. CI: 98.1.	No cranial material	MLP 68-111-14-1	De Iuliis et al. (2004). Body mass: 2.5 t
Pyramiodontherium sp.	Late Miocene–Pliocene, Ituzaingó Fm., Entre Ríos	167	Partial humerus length: 580, partial radius, metacarpal, partial femur		MRVU 107 (humerus) MAS 1392 (astragalus)	Brandoni and Carlini (2009)
Pyramiodontherium sp.	Late Miocene–Pliocene, Ituzaingó Fm., Entre Rıos province			166	MLP 31-XI-12-26	Brandoni and Carlini (2009). Brandoni et al. (2012)
Pyramiodontherium sp.	Late Miocene?–Pliocene, Río Negro Fm., Chubut province	259 (after Fig. 29B)	Humerus length: 729 (incomplete), ulna length: 625, manus length: 595, manus width: 370 (Fig. 21), femur length: 677, tibia length: 540 (Fig. 28), pes: 630 mm by 300 mm		MPEF-Pv 1144	Guillaume (2005), Guillaume et al. (2005)

MTRL: maxillary tooth row length, CI: crural index.

[a] Average value.

Please cite this article as: Melchor, R.N., et al., Late Miocene ground sloth footprints and their paleoenvironment: *Megatherichnum oportoi* revisited, Palaeogeogr. Palaeoclimatol. Palaeoecol. (2015), http://dx.doi.org/10.1016/j.palaeo.2015.02.010

the manus except when the animal changed direction. A similar interpretation was proposed by Stock (1925) for the Carson City (Nevada, USA) mylodont trackways and by De Iuliis (1996) for the mentioned Argentine megatherine trackways. No distinctive smaller footprints related to the trackway (probable manus imprints) were identified by Casamiquela (1974) or during this study for *M. oportoi*, although trackway A exhibits only slight changes in direction (Fig. 7A–B). Some *M. oportoi* footprints have two internal depressions, but the curved marginal ridge lacks discontinuities or sharp bends that can result from partial overprinting of the pes over the manus (Fig. 8G–H). The two internal depressions on these footprints are considered a reflection of the walking dynamics of the producer. The intermediate portion of trackway A exhibits weathered footprints composed of two nearby depressions with no marginal ridge (Fig. 7B). These tracks can be confused with manus–pes couples, but they are in fact poorly preserved tracks due to erosion of the upper part of the footprints. In consequence, *M. oportoi* does not exhibit any evidence for overlapping of pes on manus tracks.

However, the hypothesis of a quadrupedal trackway with overlap of the pes on the manus may be valid for the producer of the Pleistocene *N. pehuencoensis*, given that smaller manus footprints have been identified for this ichnospecies. For a quadruped, the relationship between the gleno-acetabular distance over the sum of the length of the limb bones is an indication of the degree of coupling (Peabody, 1959). The coupling value estimated for the purported producer of *N. pehuencoensis*, *Megatherium americanum* Cuvier, 1796 (data from the type specimen MNHNM 6 presented by De Iuliis, 1996) is about 0.64. This is a value that would allow for primary overlap of the pes over the manus according to Peabody (1959, fig. 5). In summary, it is possible that the pes overlapped either partial or totally on the manus print for the Pleistocene *N. pehuencoensis*, but that is unlikely for the late Miocene–Pliocene *M. oportoi*.

Bipedal trackway. It is generally accepted that ground sloths were capable of assuming a bipedal posture for defense and feeding, and thus were not obligatory quadrupeds (e.g., Coombs, 1983; Hirschfeld, 1985). Some of the anatomical adaptations for bipedalism found in megatherines are a well developed odontoid process in the astragalus (McDonald, 2007), an antero-posteriorly compressed and nearly rectangular femur (Casinos, 1996), and the presence of a falciform bone in the pes (Cabrera, 1929). The candidate for producing *M. oportoi*, a representative of the genus *Pyramiodontherium*, exhibits a well-developed odontoid process, a rectangular and flattened femur and the falciform is present only in the specimen from Chubut (Brandoni et al., 2004; De Iuliis et al., 2004; Guillaume, 2005). The absence of a falciform bone in *P. bergi* has been considered as indicative of a poor adaptation to bipedalism (Brandoni et al., 2004). The crural index (lengths of tibia/femur × 100 after Coombs, 1983) for *P. bergi* is similar of that of extant obligatory quadrupeds and suggests greater agility than other megatherines (De Iuliis et al., 2004). The length of the hind limb in *Pyramiodontherium* sp. from Chubut can be inferred by adding the length of the femur + tibia (hind limb length 1217 mm). This estimate of the length of the hind limb along with the measurements of bipedal pace length of trackway A (Table 2), if simplified as a triangle, yield values of angle of gait ranging from 30° to 56° (average about 40°). Comparison of these gait angles with those of extant relatives is difficult because, aside from humans, the only extant bipedal mammals (kangaroos and wallabies) have a hopping gait. Bears can adopt a temporary upright posture but no study documenting their gait angle is known to the authors. For comparison, some estimates of the angle of gait during quadrupedal locomotion in the hind limb of a polar bear is 32° (Renous et al., 1998) and for the elephant is 22° (Demathieu, 1986) or 36°(Muybridge, 1899). These gait angles may be considered as the maximum value if these extant animals adopted an upright posture. Similarly, the maximum value for gait angles used to estimate bipedal dinosaur speeds is about 40° (Demathieu, 1984, 1986). In consequence, the angle of gait inferred for a bipedal posture of the producer of *M. oportoi* is too high for a heavy quadrupedal animal.

The most intriguing question for the bipedal interpretation is why such a heavy quadrupedal animal would walk on two legs in a flat area almost barren of vegetation (upper intertidal flat). There is no indication of the presence of shrubs or trees that could explain an upright posture during browsing, as envisaged for Pleistocene–Holocene megatherines. An alternative explanation is that the producer was walking on two legs in a flooded tidal flat, with part of the body underwater. This hypothesis may be supported by the presence of Miocene–Pliocene sloths from Peru (Megalonychidae, Nothrotheriinae) with an aquatic or semi-aquatic mode of life (De Muizon and McDonald, 1995). Although enough information to test this hypothesis is lacking (body mass of *Pyramiodontherium*, sediment consistency, depth of water), the footprints seems too shallow (up to 11 cm deep) to have been produced underwater. In addition, there is no indication of partial prints or elongated traces as result of buoyancy of the producer (e.g., Whyte and Romano, 2001). Furthermore, no aquatic or semi-aquatic mode of life has been suggested for any megatherine from Argentina. The evidence presented in this study for recognition of manus and pes footprints in *M. oportoi* is also evidence against the bipedal interpretation. However, the very similar size of manus and pes footprints may have led to confusion in the past.

The original bipedal interpretation for *M. oportoi* (Casamiquela, 1974; Angulo and Casamiquela, 1982) was supported by further discoveries in younger rocks. Purported scelidothere footprints from the Pleistocene of Monte Hermoso (Buenos Aires province) led Casamiquela (1983) to confirm the bipedal gait for Megatherioidea. Abundant and spectacularly preserved trackways of giant megatherines were later discovered (Aramayo and Manera de Bianco, 1987, 2009) in the late Pleistocene of Pehuen-Có (Buenos Aires province). Most megatherine trackways from Pehuen-Có are composed of only pes footprints, except for the type trackway of *N. pehuencoensis*, which also contains a few manus prints, thus lending further support for the bipedal interpretation. The manus prints in this case are considerably smaller than the pes prints (about 35%).

In summary, the most likely interpretation for *M. oportoi* is an alternate quadrupedal trackway without overlap of tracks. This interpretation is the most parsimonious and is supported by the identification of manus and pes footprints, the sets of four tracks in trackway A and the similar length of fore- and hindlimbs and subequal size of manus and pes in *Pyramiodontherium* sp. from Chubut, the presumed producer. The hypothesis of a quadrupedal trackway with overlap of the pes on the manus is not supported by any evidence from the footprints. This interpretation is probably adequate for Pleistocene and younger trackways, particularly *N. pehuencoensis* from Pehuen-Có (Buenos Aires province). Pleistocene megatherines exhibited a much smaller manus track in comparison with the foot track. This is probably a reflection of a evolutionary trend in megatherines and is in agreement with biomechanical studies suggesting adaptations to bipedalism by *Megatherium* (Casinos, 1996; Blanco and Czerwonogora, 2003). The bipedal interpretation for *M. oportoi* is not preferred because the angle of gait inferred for a bipedal posture of the producer of *M. oportoi* is too high for a heavy quadrupedal animal, and it is difficult to explain the bipedal walking in a flat area with sparse, low vegetation.

8. Conclusions

- *Megatherichnum oportoi* is reinterpreted as a quadrupedal trackway composed of large (≥0.5 m) footprints of similar size, but showing contrasting morphology. The pes is kidney-shaped and the manus is falciform, both showing a distinct and inwardly directed claw mark.
- *Megatherichnum oportoi* tracks were imprinted in the upper intertidal flat and the producer was walking seaward. This mixed intertidal flat was flanked by a coastal dune field composed by transverse dunes and freshwater ponds and larger lakes in the interdune areas.
- Associated trace fossils that reflect additional components of the biological community where this large ground sloth lived are: 1) Poaceae

root and stem traces and *Nagtuichnus meuleni* (Chlamyphorinae burrow) in the dry interdune facies, 2) indeterminate tetrapod footprints in the damp interdune facies, 3) *Lockeia siliquaria* plus chevron-like trace fossils (bivalve resting and horizontal locomotion traces) in the wet interdune facies (shallow lake deposits with unionid remains), and 4) *Palaeophycus tubularis* in the aeolian dune facies.

- The best candidate for trackmaker of *M. oportoi is Pyramiodontherium* sp. from Chubut (Argentina). This Megatheriinae displays a similar manus and pes size that match the size of the footprints and its bones occur in the same sedimentary unit. Additional features that are common to other ground sloths are the large size (more than 0.5 m long) and broad oval outline of the footprints, the presence of a marked marginal ridge, and the reduction of digit imprints. The approximate body mass of the purported producer ranges between 2.5 and 3.6 t.
- The most parsimonious interpretation for the late Miocene–Pliocene ground sloth trackway *M. oportoi* is that it represents quadrupedal locomotion without overlap of tracks. This interpretation is supported by the similar length of fore- and hindlimbs and subequal size of manus and pes in *Pyramiodontherium* sp. from Chubut (the presumed producer), the presence of sets of four footprints identified in the trackway, the distinct shapes of manus and pes footprints, and the similar size of manus and pes footprints.
- Pleistocene and Holocene ground sloth trackways composed of large hind footprints and much smaller fore footprints (including *N. pehuencoensis*) may represent quadrupedal locomotion with overlap of the pes on the manus or, less likely, bipedal locomotion.

Acknowledgments

Ciro Zavaleta, the owner of Cabaña San José, gave permission to work on his property. Adrián Guillaume kindly provided his unpublished Licenciate thesis and further information on the foot and manus of *Pyramiodontherium* sp. from Chubut. José J. Del Col (Instituto Superior Juan XXIII, Bahía Blanca, Argentina) kindly provided a copy of Casamiquela (1983) publication. Claudia Montalvo read a preliminary version of the manuscript. The comments and suggestions of reviewers Spencer G. Lucas and Greg McDonald, as well as those of guest editor David Loope, improved the initial version of the manuscript. This work was funded by projects 218/CN (Universidad Nacional de La Pampa), PIP CONICET 80100164 and PICT ANPCyT 2013–1129 to RNM.

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Please cite this article as: Melchor, R.N., et al., Late Miocene ground sloth footprints and their paleoenvironment: *Megatherichnum oportoi* revisited, Palaeogeogr. Palaeoclimatol. Palaeoecol. (2015), http://dx.doi.org/10.1016/j.palaeo.2015.02.010

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Please cite this article as: Melchor, R.N., et al., Late Miocene ground sloth footprints and their paleoenvironment: *Megatherichnum oportoi* revisited, Palaeogeogr. Palaeoclimatol. Palaeoecol. (2015), http://dx.doi.org/10.1016/j.palaeo.2015.02.010