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Pink fairy armadillo meniscate burrows and ichnofabrics from Miocene and Holocene interdune deposits of Argentina: Palaeoenvironmental and palaeoecological significance

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ABSTRACT

The possible producer and environmental setting of large meniscate burrows (*Nagtuichnus meuleni* igen. and isp. nov.) occurring in late Miocene and Holocene aeolian deposits from Argentina are discussed. These are unbranched burrows with an uniform meniscate filling that range in width from 46 to 78 mm. *N. meuleni* distinguishing features are a filling composed of a discontinuous, outer massive layer between a central meniscate core and the excavation boundary, sets of parallel ridges in the external wall, and a particular outline plus the presence of paired pits in the concave surface of menisci (or hollows in the convex surface). The late Miocene lower member of the Río Negro Formation at La Lobería (Río Negro province) is interpreted as aeolian dune, damp interdune and dry interdune deposits. The Holocene sediments from Gran Salitral (southwestern La Pampa province) represent aeolian dune, wet interdune and dry interdune deposits. *N. meuleni* occurs only in damp and dry interdune deposits. The composite ichnofabric produced by *N. meuleni* in the Holocene of the Gran Salitral is composed of two suites of trace fossils. A former *Skolithos* suite includes *Skolithos linearis*, *Taenidium barretti*, *Polykladichnus aragonensis* and root traces developed in lacustrine calcareous mudstone deposits (wet interdune). This suite is overprinted by *N. meuleni*, with subordinate participation of *S. linearis* and root traces, composing the *Nagtuichnus* suite. The later suite is developed in brown silt and sand of dry interdune areas. The *Nagtuichnus* ichnofabric is considered indicative of damp to dry interdune facies of late Miocene to Holocene age. The burrow systems of the likely producers of the Holocene *N. meuleni* structures were studied in the field and in the laboratory. The candidates were selected from the extant local fauna of the Gran Salitral, including southern cavies (*Microcavia australis*, Rodentia), tuco-tucos (*Ctenomys azarae*, Rodentia), and pink fairy armadillos or pichiciegos (*Chlamyphorus truncatus*, Xenarthra). The most likely producer of *N. meuleni* are *pichiciegos* because they have fully subterranean habits and insectivorous diet involving the production of long, unbranched, horizontal burrows excavated in sand, which are mostly backfilled. In contrast to this, tuco-tucos and southern cavies, which are herbivores that forage aboveground, use their more permanent burrows for dwelling and reproduction. As observed in a live, captive-kept *C. truncatus*, the meniscate structure of the fill can be explained by the animal packing the excavated sand with its rump plate. This mechanism also results in a massive layer of sediment in the burrow fill. Other significant bioglyphs that are a sort of fingerprint of *pichiciegos* are the outline of menisci in cross-section (mimicking their rump plate) and pairs of rounded pits in the concave surface of menisci (probably tail traces).

1. Introduction

Invertebrate meniscate burrows in continental settings have been documented or proposed for different taxa, namely insects (Brussaard, 1985; Genise and Hazeldine, 1995; Smith and Hasiotis, 2008; Smith et al., 2008; Counts and Hasiotis, 2009), millipedes (Retallack, 2001), crayfishes (Bedatou et al., 2008; Genise et al., 2008), and earthworms (Bown and Kraus, 1983; Fitzpatrick, 1984; Jégou et al., 1999; Bastardie et al., 2003; Verde et al., 2007; Bedatou et al., 2009). In contrast, records of meniscate burrows attributed to vertebrates are scarce (Angulo and Casamiquela, 1982; Ward, 1988; Smith, 1993; Loope, 2008; Schmeisser et al., 2009). Most of the later cases, except for Smith (1993), have been documented in aeolian settings.

The large meniscate burrows described herein had been previously recorded from the Miocene Río Negro Formation of Río Negro Province, Argentina (Angulo and Casamiquela, 1982; Aramayo, 2008) and

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interpreted as Octodontoidae (Rodentia) burrows, particularly from the South American burrowing rodent tuco-tuco (*Ctenomys*, Ctenomyidae) (Angulo and Casamiquela, 1982). The finding of the same type of meniscate burrows in Holocene aeolian sediments of the Gran Salitral area (great salt lake) in La Pampa province, Argentina allowed an expansion of the existing data with material from another locality. This finding provided an opportunity to study components of the extant fauna inhabiting modern dunes and interdunes at the same locality to search for potential producers of these large meniscate burrows.

Regarding the affinities of the Miocene burrows from the Río Negro Formation, the hypothesis that they had been constructed by *Ctenomys* (Angulo and Casamiquela, 1982) was later contradicted by the record of simpler, mostly inclined, burrows by the ancestral *Actenomys* for Pliocene rocks (Genise, 1989). Still later, by the phylogeny of Octodontoidae that indicates that extensive cladogenesis of *Ctenomys* took place during the Pleistocene (Reig et al., 1990; Lessa et al., 2008; Verzi et al., 2010), whereas the oldest *Ctenomys* specimens come from the Pliocene (Verzi et al., 2010). Data presented here on the morphology of these burrows also argue against *Ctenomys* as possible producers of these trace fossils.

The objectives of this contribution are therefore: (1) to describe and interpret large meniscate burrows occurring in aeolian deposits of the Miocene Río Negro Formation from the Río Negro province and in Holocene aeolian sediments exposed at Gran Salitral in La Pampa province, Argentina by comparing them with burrows of extant mammal fauna from the latter locality, and (2) to infer the palaeoenvironmental meaning of the ichnofabric produced by these large meniscate burrows.

2. Materials and methods

Sedimentologic logs were measured with standard techniques. At the Prospecting Pit site (Gran Salitral) a sedimentary peel was obtained from a vertical surface of the highly bioturbated ichnofabric of large meniscate burrows following the methodology of Voigt and Gittins (1977). Selected modern burrows of *Ctenomys azarae* and *Microcavia australis* (Rodentia) were casted with low density polyurethane foam, obtained by mixing in a jar polyol VO 715 and isocyanate in a proportion of 100:85. The mixture was homogenized, immediately poured into the burrow entrance and the hole plugged to facilitate expansion of the foam into the whole burrow system. After a few minutes, the casts were excavated and any incompletely casted portion of the burrow was completed by pouring plaster of Paris. For the description of burrow systems we adopted the terminology of Hickman (1990).

The surface texture of the external wall of fossil burrows from the Holocene sediments of the Gran Salitral and the Río Negro Formation were molded using plaster of Paris or polyester resin. In the case of the burrows from the Río Negro Formation, the surface was first fixed with nitrocellulose lacquer, let to dry, and sprayed with cooking oil. After complete drying, several layers of polyester resin mixed with catalyst were applied with a brush. The casting was reinforced by applying a linen cloth over uncured resin and then covered with a new layer of resin. The cast was cured overnight and then collected.

The large meniscate burrows on deflated surfaces at the Holocene Gran Salitral sites are best seen after several weeks of drought. Holocene fossil burrows exposed in deflated surfaces were sprayed several times with low viscosity Butvar (in a proportion of 1 part of Butvar with 12 parts of acetone) following the methodology by Stidham and Mason (2009), let to dry for one hour, and then collected. This procedure, which can be applied to poorly consolidated sediments, results in a sort of instant peel.

Collected material, and casts and molds of uncollected material, are housed at the Palaeontology collection, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Santa Rosa, Argentina (institutional abbreviation GHUNLPam).

As the observation of a wild pink fairy armadillo was not possible, a captive-kept individual was filmed with infrared cameras and photographed (Superina, 2011) to obtain reference data on its digging behaviour and its burrow size and shape. Burrow size and meniscus length and width were measured on the photographs by using morphometric measurements of the animal as a reference.

3. Geological setting

This study was conducted in two locations from Argentina where similar large meniscate burrows (*Nagtuichnus meuleni* igen. and isp. nov.) were found: (1) the sea cliffs at La Lobería (LO site) west of El Condor town (Río Negro province) and (2) the margin of the Gran Salitral (GS site) in southwestern La Pampa province (Fig. 1a–d). In the latter locality, additional neoichnologic observations were conducted on selected modern subterranean mammals that were possible candidates for trace makers of *N. meuleni* igen. and isp. nov. An additional isolated specimen was found in Holocene inactive aeolian deposits near Jagüel del Monte (see Umazano et al., 2011). This specimen was found at an unnamed spot close to provincial road 14 (36° 41′ 01″ S, 65° 41′ 35″ W; Fig. 1a) in central La Pampa province. Sedimentological studies were not conducted at this locality.

3.1. Río Negro Formation

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). In the exposures located south of the Negro river mouth (mostly between El Cóndor and La Lobería, Fig. 1d) the unit was divided in a lower and upper member of continental origin and a middle member of marine origin (Angulo and Casamiquela, 1982; Zavala and Freije, 2001). The continental members essentially contain aeolian facies (including dune and interdune facies), and reduced participation of fluvial facies and arid paleosols developed on loess deposits (Zavala and Freije, 2001). These aeolian facies have yielded abundant mammal and bird footprints, including large xenarthran footprints assigned to *Megatherichnum oportoi* and cf. *Mylodontidichnum* isp. (Angulo and Casamiquela, 1982; Aramayo, 2007). The age of the formation is currently assigned to the interval late Miocene–early Pliocene on the basis of radiogenic dates and fossil mammal remains (Zinsmeister et al., 1981; Aramayo, 1987; Alberdi et al., 1997). Zinsmeister et al. (1981) obtained an average K-Ar age of 9.41 Ma for a tuff layer from the top of the middle marine member of the Río Negro Formation. A fission track age of 4.41 ± 0.5 Ma was obtained by Alberdi et al. (1997) for rhyolithic glass from the uppermost interval of the Río Negro Formation. The trace fossils studied here essentially come from the lower member of the unit at La Lobería locality (41° 09′ 19″ S, 63° 07′ 36″ W; Fig. 1d), although they have also been recorded occasionally from the lower few meters of the upper member at El Faro beach site (41° 03′ 31″ S, 62° 50′ 18″ W; Fig. 1d). In consequence, the age of *N. meuleni* igen. and isp. nov. from this unit is probably in the range of late Miocene (Tortorian) to early Pliocene (Zanclean).

3.2. Geology and geomorphology of Gran Salitral

The surface geology of the area bordering the large depression of Gran Salitral (Fig. 1b) is composed of Permo-Triassic to Recent units (Linares et al., 1980; Melchor and Casadío, 2000). Permian-Triassic volcanic rocks (Choique Mahuida Formation) are overlain by early Danian shallow-marine carbonates (Roca Formation), early Eocene lacustrine mudstones and palustrine carbonates (Gran Salitral Formation), and Eocene shallow- to deep-lacustrine mudstones and sandstones (El Fresco Formation). This succession is capped unconformably by Pliocene (?) fluvial sandstones and calcrete included in the El Sauzal

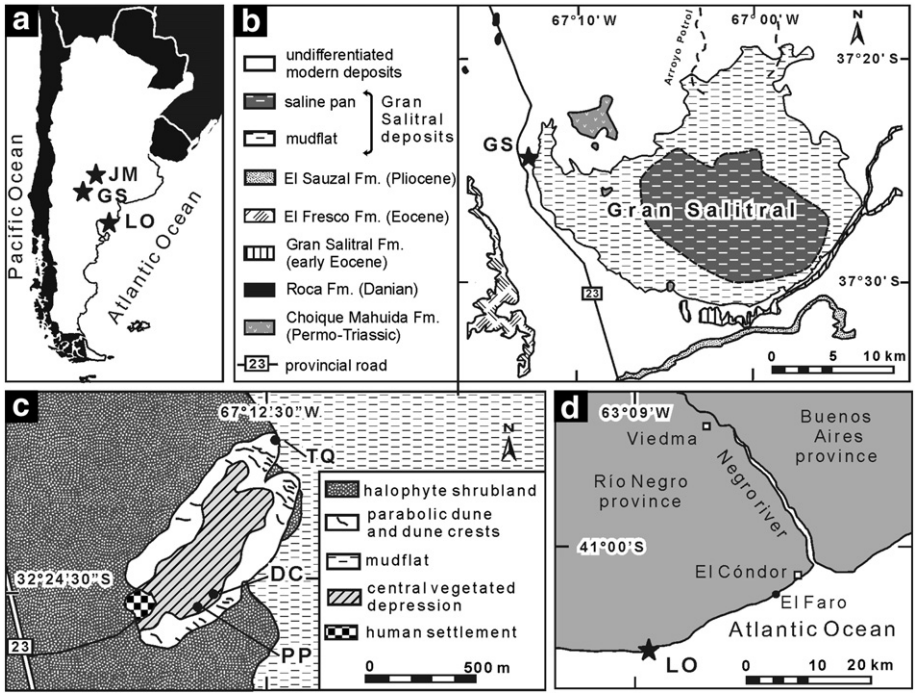

Fig. 1. Location maps. (a) Study localities, GS: Gran Salitral, LO: La Lobería, JM: Jagüel del Monte. (b) Geologic map of the Gran Salitral area, La Pampa Province, Argentina. The star indicates the study locality (GS). (c) Geomorphologic map of the Gran Salitral Holocene locality and sites of observation. PP: Prospecting Pit site, DC: Dead Cows site, TQ: Tuquera site. (d) Map of the localities of the late Miocene–early Pliocene Río Negro Formation, Río Negro Province, Argentina. LO: La Lobería.

Formation, overlain by Holocene aeolian and lacustrine deposits, and modern deposits of lacustrine and aeolian origin (Melchor and Casadío, 2000; Melchor, 2002). Although absolute ages are not available, herein we distinguish more indurated and older sediments as Holocene deposits. These are separated by an erosive surface from overlying friable sands that include the deposits of the active aeolian dune, which are informally named as recent deposits. The sedimentary facies of the Holocene trace fossil bearing section and overlying recent sediments are described in detail in the next section.

The area studied in detail is located immediately to the east of Puesto La Porfia (37° 24′ 31″S, 67° 12′ 54″ W; human settlement in Fig. 1c). It is covered by a parabolic dune (Pye, 1982) that roughly initiates at the settlement and reaches the border of the saline depression (Fig. 1c). The dune is elongated in a southwest-northeast direction after the dominant winds and is 1.1 km long and 0.47 km wide. The downwind margin displays a lobate morphology and the arms and central depression are sparsely vegetated. The trace fossils are exposed in parts of the central depression of the parabolic dune where older stabilized aeolian sands are exposed due to enhanced deflation (at Prospecting Pit site, PP in Fig. 1c). Near the Prospecting Pit site there are metre-scale sand mounds (commonly 1–3 m wide, up to 1.5 m high) surrounding shrubs, which are interpreted as nabkhas or coppice dunes (Cooke and Warren, 1973). Southern cavies (*Microcavia australis*) commonly dig their burrows in these dunes. Nabkhas often display an asymmetric cross-section with a steeper stoss face and a more gently sloping lee side. The longest axis of the nabkhas was approximately N60°E. The burrows in one of these nabkhas were molded and later excavated at Dead Cows site (DC in Fig. 1c). Toward the saline depression, the active sand lobes are fringed by halophyte shrubs growing in a shifting sand deposit with a similar grain-size to that of active dunes. Near the lobate nose of the parabolic dune the halophyte shrubs are less abundant, and a fringing low-relief and sparsely vegetated sand deposit, lacking visible stratification, marks the transition to the dry mudflat environment. Tuco-tuco (*Ctenomys azarae*) burrows are preferentially located in this area and were studied at the Tuquera site (TQ in Fig. 1c). The low-relief sandy deposits are replaced by a dry mudflat with sparse saline vegetation toward the lacustrine basin.

4. Sedimentary facies

4.1. Facies of the Río Negro Formation at La Lobería locality

The outcrop of the lower member of the Río Negro Formation at La Lobería locality is approximately 3.3 m thick (Fig. 2a). The base is not exposed and is overlain by yellowish siltstones with marine fauna of the middle member of the unit.

The recognised lithofacies can be grouped into three facies associations, namely the aeolian dune, damp interdune and dry interdune facies associations (Figs. 2a and 3a). The former facies association (comparable with the dune facies of Zavala and Freije, 2001) is found in the lower part of the section and is represented by sets of fine-grained sandstone with tangential cross-bedding (facies Sta) showing reactivation surfaces and inverse grading in individual laminae and parallel laminated sandstone (facies Sh). This facies association is separated by an erosive surface with a local relief up to 0.3 m from the overlying damp interdune facies association (Fig. 3a, b). The latter is composed of sandstone with horizontal lamination (facies Sh) that may exhibit a wave-rippled top covered by a mud-drape and thin, mud-draped, wedge-shaped sets of planar cross-bedded sandstone (facies Sp). Facies Sh also displays footprints of medium-sized mammals, which deform the underlying laminae. The overlying dry interdune facies association is dominated by fine-grained sandstone with horizontal to low-angle lamination (facies Sh and Sl) and occasional sets of planar cross-bedding (facies Sp). *Nagtuichnus meuleni* igen. and isp. nov. is restricted to horizontal to low-angle, fine-grained sandstone facies (facies Sh, Sl) and only rarely cut across thin cross-bedded sets (Fig. 2a). The mentioned ichnotaxon is commonly found in weathered fallen blocks near the sea cliffs. The trace fossil-bearing facies from the upper member of the Río Negro Formation at El Faro beach are very similar to those described.

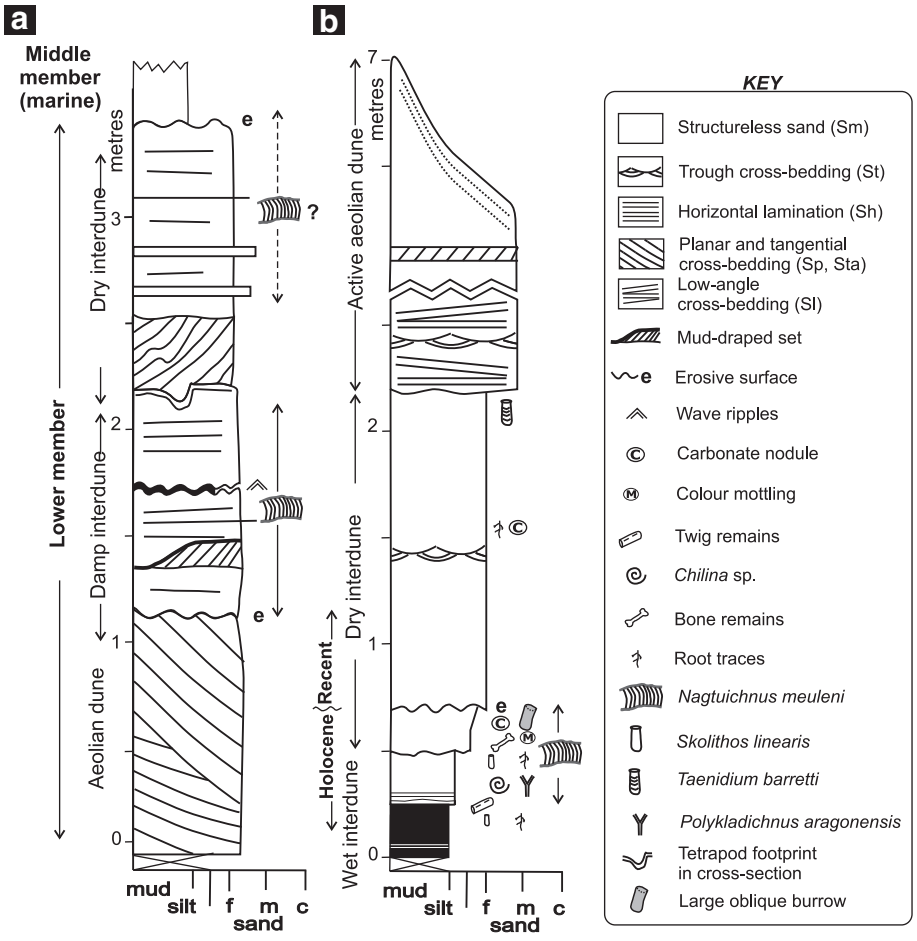

Fig. 2. Measured sedimentary logs. (a) Section of the lower member of the Río Negro Formation at La Lobería. (b) Logged section of Holocene and recent sediments at the Prospecting Pit site (Gran Salitral).

4.2. Sedimentary facies at the Gran Salitral locality

A 7 m thick sedimentary section was measured for this study, including a lower part logged in a pit dug in the Holocene sediments of the central depression of the parabolic dune (the Prospecting Pit) and the adjacent recent active dune (Fig. 2b). The lower part of the section is composed of mudstones and fine-grained sands with sheet-like to hollow geometry, whereas the upper sector is constituted of medium-grained sands. Three facies associations were distinguished:

Wet interdune facies. The lowermost 0.50 m of the succession is composed of greenish yellow to dark olive gray, plane parallel-laminated or structureless, occasionally organic-rich mudstone (facies Mh) with vertical burrows (*Skolithos linearis*) and root traces. Facies Mh is overlain in sharp contact by pale-brown, parallel-laminated calcareous mudstone with millimetre laminae of brown siltstone (Mc). The calcareous mudstone facies contains twig remains, root traces, trace fossils described below (*Nagtuichnus meuleni* igen. and isp. nov., *Skolithos linearis*, *Polykladichnus aragonensis*, *Taenidium barretti*, and root traces), and the freshwater pulmonate gastropod *Chilina* sp. aff. *Chilina lallemanti* Doering, 1884 (S. Miquel, written communication, 2009).

Dry interdune facies. Facies Mh is overlain through an irregular contact by poorly consolidated, yellowish brown, well-sorted, structureless fine-grained sand to coarse silt (facies Sm). The lowermost, 0.2 m thick bed displays a slightly greater consolidation, small carbonate nodules, and colour mottling, and it is separated from the overlying beds by an erosive surface. This bed and the uppermost part of the underlying Mc facies display a highly bioturbated ichnofabric dominated by *Nagtuichnus meuleni* igen. and isp. nov. Intercalations of decimetre-thick sand with trough cross-bedding (facies St) or root traces and carbonate nodules are rare. Facies Sm bears scarce indeterminate vertebrate bones and vertical millimetre-sized *Taenidium barretti*.

Aeolian dune facies. This facies association corresponds to the arms of the modern parabolic dune (Fig. 3c) that is mostly composed of two-dimensional dunes. The uppermost 4.8 m of the succession are mainly composed of unconsolidated, yellowish brown, very well-sorted, structureless, medium-grained sand. Trenching revealed one decimetre-thick intercalations of trough cross-bedded sands (facies St) or low-angle cross-bedding (facies Sl) near the base of this facies association and a single, 0.15 m thick level of sand with planar cross-bedding and inversely graded laminae (facies Sp) near the top of the succession.

5. Systematic ichnology

5.1. Nagtuichnus igen. nov.

Etymology. Derived from the Mapuche language of central and southern Argentina, *Nagtu* meaning what is or exists below (Erize, 1960), and from the Greek *Ikhnos*, meaning trace. Herein, *Nagtu* is related to the inferred subterranean habits of the producer of meniscate backfilled burrows.

Diagnosis. Variably oriented, large, sinuous, unbranched, unlined, cylindrical burrow with a two-zoned backfill composed of a larger

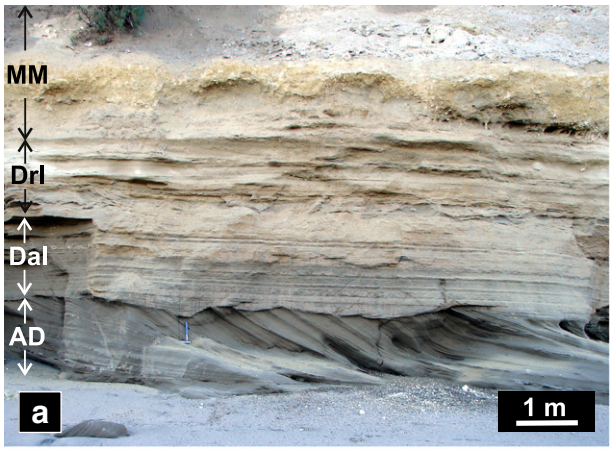

Fig. 3. Views of the sedimentary trace-fossil bearing section from the Río Negro Formation and the modern parabolic dune at the Gran Salitral locality. (a) Measured section of Río Negro Formation at La Lobería, mostly belonging to the lower member (see Fig. 2a). MM: middle member. Facies associations: AD: aeolian dune, DaI: damp interdune, DrI: dry interdune. (b) Detail of the damp interdune facies association from the lower member of the Río Negro Formation showing sandstone with horizontal lamination (facies Sh) and wave-rippled top covered by a mud-drape (arrow). (c) View looking southeast from the central vegetated depression of the parabolic dune at Gran Salitral (foreground) and part of the arm of the parabolic dune (background).

central meniscate core and an outer massive, discontinuous and thinner layer. Moderately arcuate menisci of uniform thickness, averaging one fifth of burrow diameter. External surface of burrow fill with sets of two or three parallel ridges arranged at an oblique angle to the burrow axis. Concave surface of menisci showing groups of paired, rounded pits. In transverse section, outline of menisci composed of a semicircular upper half and a lower half composed of three straight segments, the middle segment is horizontal and the remaining oblique. Burrow fill lithologically similar to the surrounding rock matrix.

Remarks. Nagtuichnus can be distinguished from other meniscate trace fossils by the discontinuous, massive layer between a central meniscate core and the excavation boundary, and the presence of sets of parallel ridges in the external wall (Fig. 4a). The particular outline and the presence of paired pits in the concave surface of *Nagtuichnus* menisci are further key differences.

Nagtuichnus may superficially resemble marine spatangoid trace fossils like those included in the ichnogenus *Bichordites* (e.g., Bromley and Asgaard, 1975; Uchman, 1995). However, the mentioned ichnogenus displays a more complex structure including a central drain that is lacking in *Nagtuichnus*.

Type ichnospecies: *Nagtuichnus meuleni* isp. nov.

5.1.1. Nagtuichnus meuleni isp. nov.

Figs. 4, 5, 6, 7

1982 Galerías de ?Octodontidae *incertae sedis* Angulo and Casamiquela, p. 55

2008 *Taenidium barretti*: Aramayo, p. 12.

Etymology. From the Mapuche language, *meulen*, meaning wind (Erize, 1960), in reference to the preservation of these structures in aeolian sucessions.

Holotype. GHUNLPam 27390, a burrow fill preserved in full relief from the Holocene sediments of Gran Salitral (Figs. 4b, 5a, b).

Paratypes. GHUNLPam 27391 (Fig. 7b), peel obtained from Holocene sediments at Prospecting Pit site (Gran Salitral); GHUNLPam 3144 (Fig. 6a), subhorizontal meniscate burrow fill and hosting sandstone from the lower member of the Río Negro Formation at La Lobería; GHUNLPam 27408 (Fig. 6h), a resin cast of the surface texture from the upper member of the Río Negro Formation at El Faro; GHUNLPam 27399–27400 (Fig. 5c and d, respectively), menisci with bioglyphs from the Holocene Dead Cows site (Gran Salitral).

Examined material. Lower Member of the Río Negro Formation: Two cylindrical burrow fills (GHUNLPam 3145, 3146), four fragments of burrow fill (GHUNLPam 3147–3150), and about 80 specimens examined at the field (La Lobería locality). Upper member of the Río Negro Formation: eight specimens examined at the field (El Faro locality). Holocene aeolian sediments at Gran Salitral: seven cylindrical burrow fills (GHUNLPam 27393–27398, 27409), one cylindrical burrow fill and host sediment (GHUNLPam 27392), seven meniscus fragments (GHUNLPam 27401 to 27407), five instant Butvar peels (GHUNLPam 27412–27416), and about 60 specimens measured at the field. Holocene inactive aeolian sands near Jagüel del Monte locality: a single field specimen (Fig. 4f).

Diagnosis. Only known ichnospecies, same as for the ichnogenus.

Description. Mostly horizontal or inclined cylindrical burrows with a straight or sinuous path, and ranging in width from 46 to 78 mm (mean: 63.7 mm, n = 137). The cross-section is roughly circular with a large diameter/minor diameter ratio ranging from 1.0 to 1.12 (mean: 1.05, n = 27). Crosscuts are common (Fig. 4d), whereas branching or enlargements were not observed. The burrows appear either as relatively short, horizontal or inclined structures, or as an inclined short section connected with a longer horizontal one, or simply as slightly sinuous subhorizontal burrows, up to 2.5 m long at GS locality (Fig. 6c, d, e). The external wall shows paired rounded ridges (rarely three parallel ridges) that are arranged at an oblique angle with the burrow midline (Fig. 4b, g, h). They are more clearly marked on the floor, where a chevron pattern was observed, and on the sides of the burrow (Fig. 6g, h). Longitudinal ridges were also seen roughly along the midline in the floor of the burrow (Fig. 4h). Individual ridges are 2.8 to 5 mm wide (mean: 3.8 mm, n = 24) and up to

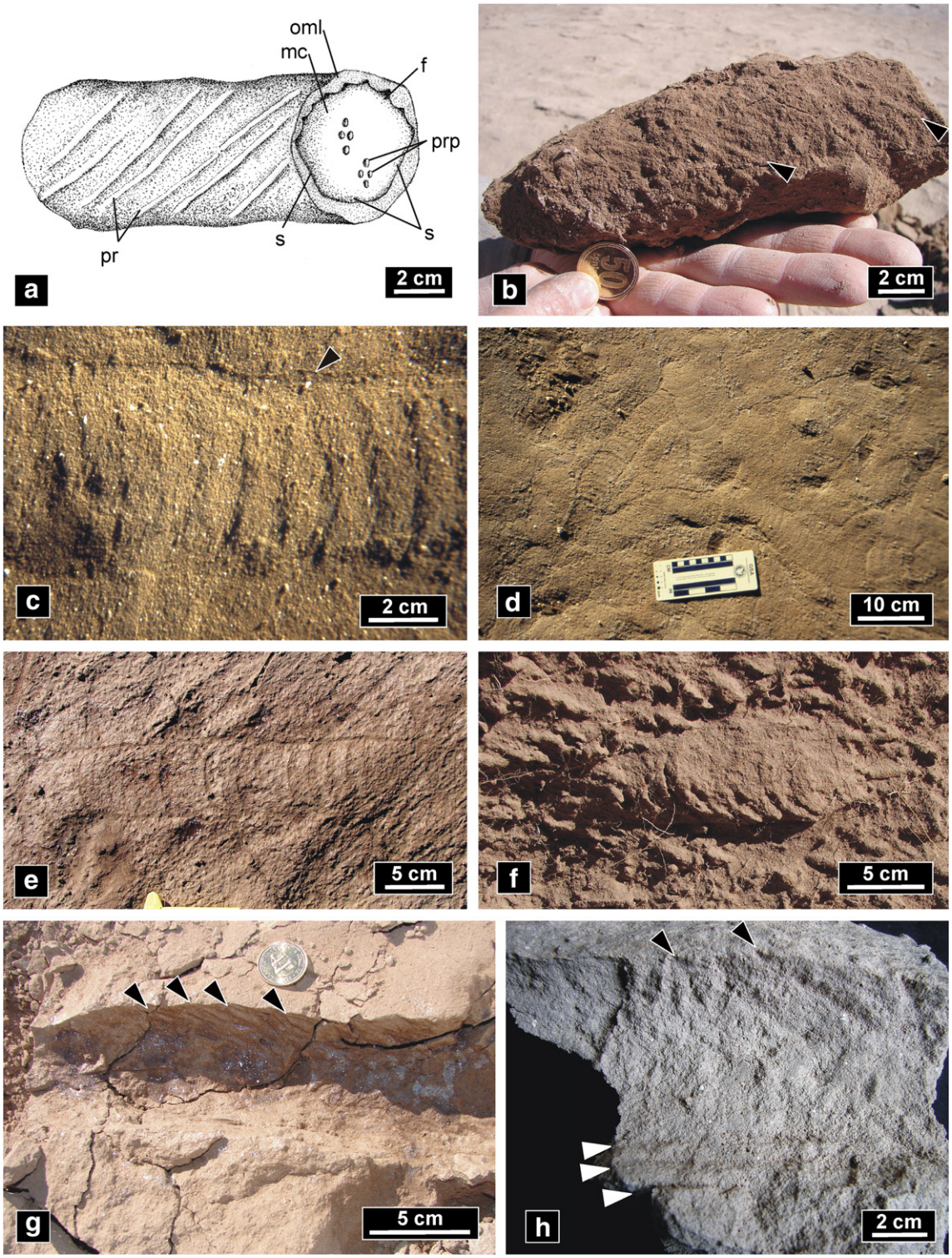

Fig. 4. *Nagtuichnus meuleni* igen. and isp. nov. from Holocene localities. The figures are from the Holocene Dead Cows site (Gran Salitral) except for figure f, which comes from Holocene aeolian sediments of Jagüel del Monte locality. (a) Schematic diagram illustrating the main features of the ichnotaxon, as preserved in full relief. mc: meniscate core, oml: outer massive layer, f: upper festooned outline of meniscus, s: lower segmented outline of meniscus, prp: paired rounded pits, pr: paired ridges. (b) Side view of holotype showing ridges in the external wall of specimen, some of them arrowed (GHUNLPam 27390). (c) Close up view of surface exposure (1997 year) of partially eroded *N. meuleni* showing detail of menisci in cross-section. The arrow points to the outer massive layer. (d) Several subhorizontal cross-cutting *N. meuleni* specimens at a surface exposure (1997). (e) Single subhorizontal *N. meuleni* impregnated with Butvar (2009 exposure). (f) Vertical deflation surface in Holocene aeolian sediments showing a single subhorizontal specimen of *N. meuleni*. (g) Surface texture in the boundary of the fill of subhorizontal *N. meuleni* after extraction of the fill (preserved in the hosting sediment). Arrows indicate grooves arranged oblique to burrow axis. (h) Oblique view of surface texture in a portion of hosting sediment of *N. meuleni* showing grooves oblique (black arrows) and parallel (white arrows) to burrow axis. The fragment is arranged in horizontal position (GHUNLPam 27392).

80 mm long. Distance between ridges in a pair (measured from centre to centre of ridges) ranges from 5 to 11 mm (mean: 8.2 mm, n = 26). Width of the three parallel ridges is from 17 to 20 mm with a similar separation and ridge width than the paired ridges. The chevron pattern observed especially in the floor of the burrows is composed of ridges forming an acute angle that ranges from 28°

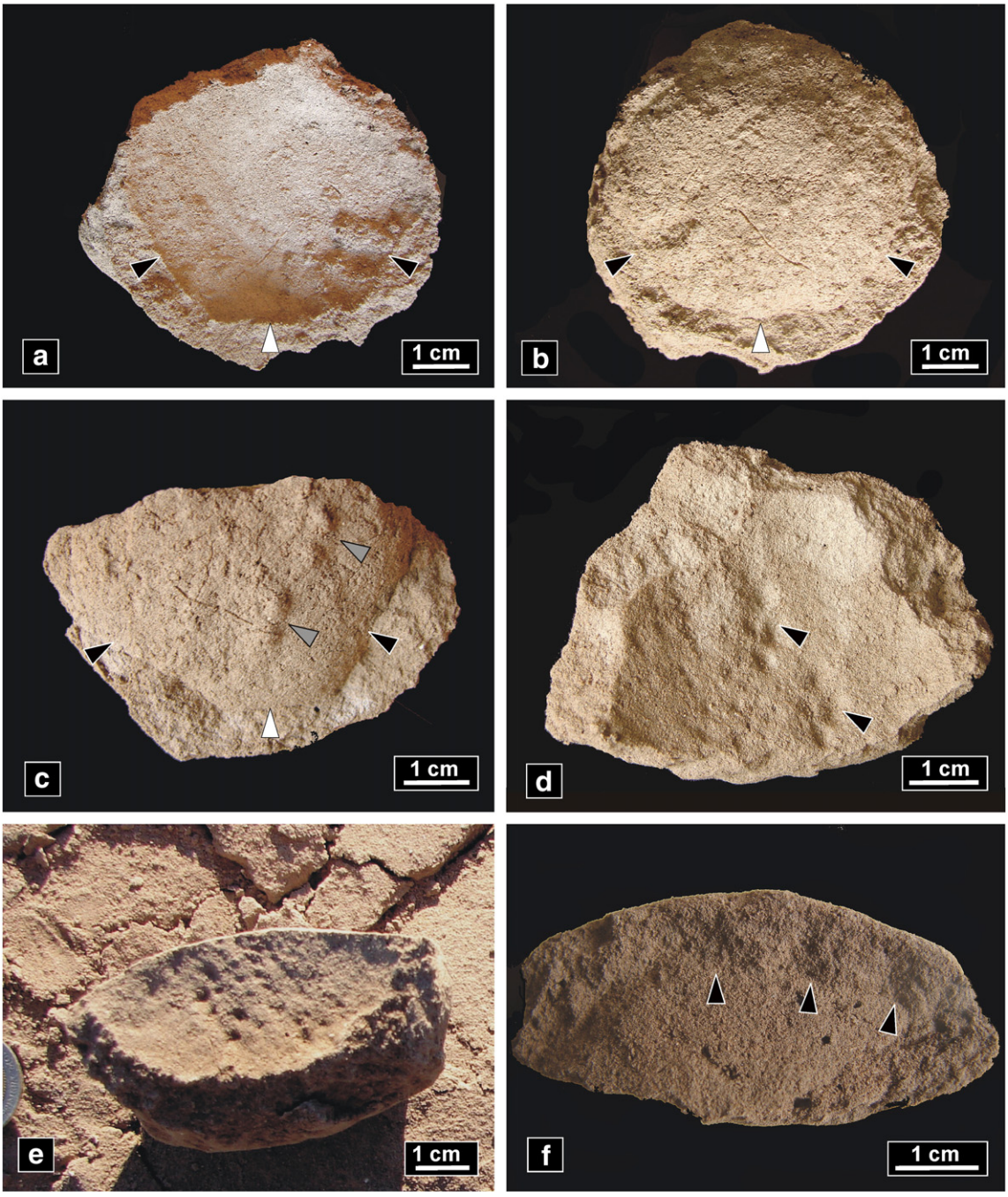

Fig. 5. Bioglyphs in the surface of fresh broken menisci of *Nagtuichnus meuleni* igen. and isp. nov. from the Holocene Gran Salitral locality. (a) Lower segmented outline of concave surface of meniscus. Black arrows point to oblique segments and the white arrow to a horizontal segment. Note also discontinuous outer massive layer (GUNLPam 27390). (b) Lower segmented and upper semicircular outline of convex surface of meniscus. Black arrows point to oblique segments and the white arrow to a horizontal segment (GHUNLPam 27390). (c) Lower half of convex surface of meniscus showing segmented outline and paired rounded protuberances indicated by grey arrows (equivalent to paired rounded pits in Fig. 4a). Black arrows point to oblique segments and the white arrow to a horizontal segment. Note also root traces to the left of protuberances (GUNLPam 27399). (d) Concave surface of fragment of meniscus showing two groups of paired rounded pits with a roughly rhomboidal arrangement (black arrows) (GHUNLPam 27400). (e) Concave surface of a broken meniscus showing many rounded pits, some of them arranged in pairs (GHUNLPam 27401). (f) Fragment of upper semicircular outline of meniscus (convex surface) showing the boundary between meniscate core (below) and outer massive layer (above): Arrows point to subtle festooned outline of meniscus (GHUNLPam 27402).

to 52° (mean: 37°, n = 12), whereas individual ridges form an angle with the midline that is in the range of 14° to 27° (mean: 19°, n = 11). The filling is composed of a meniscate central zone and a thin massive outer layer (Fig. 4a, c, e, f). The outer layer is 2 to 8.8 mm thick (Fig. 5a, b) and commonly accounts for 5% to 30% of the large burrow diameter (mean: 5.6 mm, n = 20). Meniscus thickness is uniform in every specimen (Figs. 4a, d, e, 5a, b, c, f, 6b) and ranges from 7.8 to 22.6 mm (average: 13.2 mm, n = 84). The ratio meniscus thickness/burrow width is in the range of 0.12 to 0.30 (mean: 0.21, n = 84). Horizontal width of menisci, measured transverse to burrow axis in broken specimens preserved in full relief, is in the range of 50.5 to 67.5 mm (n = 12); the largest measured menisci come from the Río Negro Formation. The aspect ratio of an ellipse (semi-minor axis/semi-major axis) fitted in a plan view of selected specimens is in the range of 0.28 to 0.61 (average: 0.46, n = 20). Freshly broken surfaces of menisci display two distinctive features (seen especially in the Gran Salitral specimens):

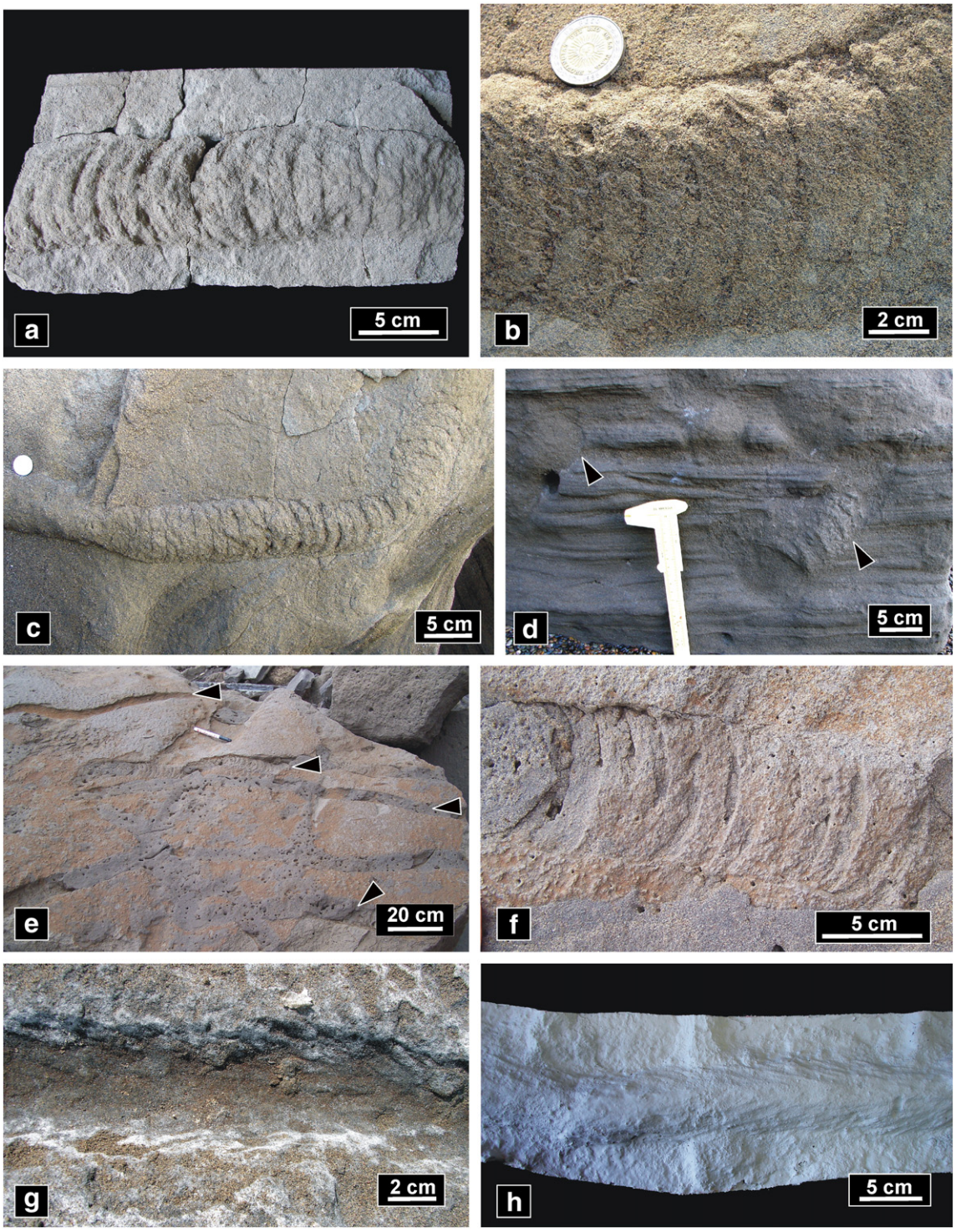

Fig. 6. *Nagtuichnus meuleni* igen. and isp. nov. from the late Miocene–early Pliocene Río Negro Formation. (a) Specimen GHUNLPam 3144 (paratype). (b) Detail of meniscus exposed in a horizontal bedding plane. (c) Subhorizontal surface with *N. meuleni* specimen showing an almost straight track and a curve. (d) Surface of sandstone block with parallel lamination and two specimens of *N. meuleni* (arrows) at an oblique angle with lamination. (e) Top of bedding surface with several subhorizontal *N. meuleni* specimens (some arrowed). In some specimens the fill is completely eroded, exposing the surface texture in the burrow boundary (as in figure g), whereas others exhibit the more common preservation with weathered menisci (as in figure f). (f) Detail of meniscate core in one of the specimens of figure e. (g) Detail of surface texture in form of grooves oblique to burrow axis of a weathered specimen from figure e. (h) Polyester resin cast of the whole specimen pictured in figure g (GHUNLPam 27408). Figures a to d are from the lower member at La Lobería locality. Figures e to h are from the upper member at El Faro locality.

(1) the lower half of the meniscus displays a polygonal outline composed of three segments of similar lengths, the central being horizontal and the lateral ones oblique (Figs. 4a, and 5a, b, c), whereas the upper half is convex upward with several re-entrants spaced about 10 mm apart (Figs. 4a and 5f). (2) Near the centre of the concave surface of the meniscus, there are paired rounded pits connected by a shallow depression (or paired protuberances in the convex surface; Fig. 5c, d, e). The paired rounded pits are 2 to 4.8 mm in diameter (average: 3.7 mm, n = 24) and the total length is in the range of 6 to 11 mm (average: 8.6 mm, n = 12). Occasionally, two nearby paired rounded

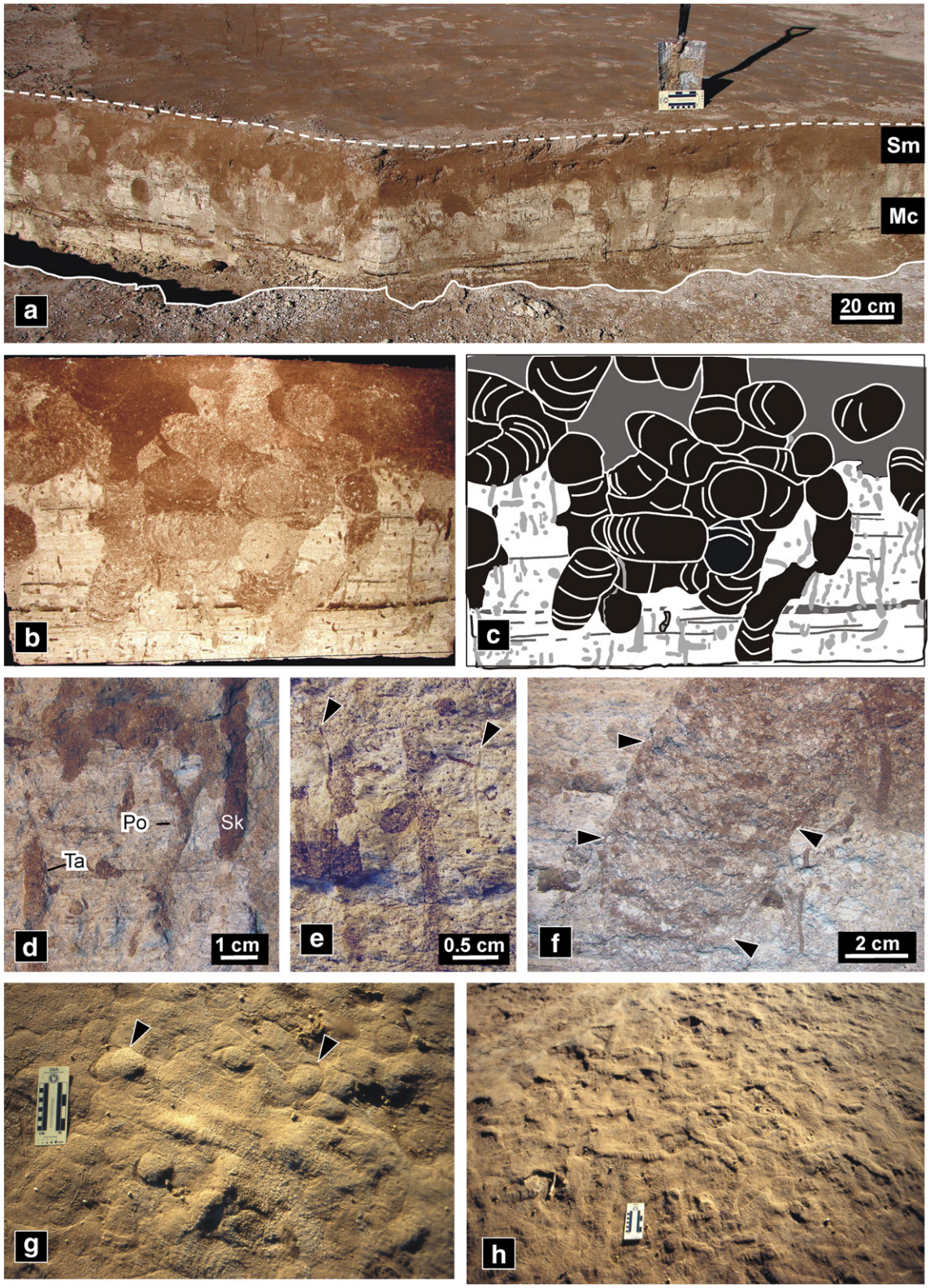

Fig. 7. Nagtuichnus ichnofabric at Holocene Gran Salitral deposits. (a) Overall view of Prospecting Pit site showing the composite ichnofabric exposed in two vertical planes. Solid white line indicates the proximal margin of the trench and the dashed white line marks the distal margin of the trench. Mc: calcareous mudstone facies. Sm: brown siltstone and sandstone. (b) Picture of the sedimentary peel (GHUNLPam 27391) obtained in the left end of the trench of figure a. The whitish lower part exhibits the Skolithos suite of trace fossils in calcareous mudstone facies (Mc), and the upper darker interval belongs to the Nagtuichnus suite of trace fossils in brown siltstone and sandstone (Sm). (c) Interpretative drawing of the ichnofabric of the peel of figure b. White background with light grey burrows: calcareous mudstone facies (Mc) with the Skolithos trace fossil suite. Black: filling of *N. meuleni*, mostly consisting of brecciated calcareous mudstone in a brown siltstone matrix. Medium grey: brown siltstone and sandstone (facies Sm). (d) Detail of *Polykladichnus aragonensis* (Po) *Taenidium barretti* (Ta) and *Skolithos linearis* (Sk) from the peel (GHUNLPam 27391). (e) Vertical submillimetre-sized root traces (arrows) (GHUNLPam 27391). (f) Detail of brecciated fill in *N. meuleni* (GHUNLPam 27391). The arrows point to the margin of the burrow. (g) and (h) Views of a subhorizontal surface exposure of the Nagtuichnus trace fossil suite in brown siltstone and sandstone facies. The arrows in figure g point to burrow at a high angle with bedding (possible entrances). Note almost complete bioturbation in figure h. Figures a to f are from the Prospecting Pit site (2009). Figures g and h are from the Dead Cows site (1997).

pits may describe a rhomboidal outline (Fig. 5d). On weathered surfaces, the concave part of the meniscus appears to be more resistant to weathering (Figs. 4c and 6a, c, f); this is especially clear in the specimens from the Río Negro Formation (La Lobería locality).

6. Holocene *Nagtuichnus* ichnofabric at Gran Salitral

The ichnofabric was observed both in vertical section at the Prospecting Pit site (Fig. 7a) and in plan view at the same place and in the nearby Dead Cows site (Fig. 7g, h). In the last site, the observations were conducted in two different years (1997 and 2009). In vertical section, the ichnofabric develops at the interface between two beds (Fig. 7a, b); the lower part is composed of pale brown, parallel-laminated calcareous mudstone with interbedded brown siltstone (facies Mc), and the upper part is composed of massive brown siltstone to fine grained sandstone (facies Sm). Discrete trace fossils identified in the peel include *Nagtuichnus meuleni*, *Skolithos linearis*, *Taenidium barretti*, *Polykladichnus aragonensis*, and root traces. In addition, a larger (180 mm wide) oblique burrow with a massive sand fill was identified in plan view at the Prospecting Pit site. *Nagtuichnus* displays diverse orientations, from horizontal to oblique and vertical, and is typically filled with a brecciated sediment product of the mixing of angular fragments of the lighter coloured mudstone with brown siltstone (Fig. 7b, f). The orientation of the burrow and the meniscate fill indicate downward, upward and horizontal movement of the producer. *Skolithos linearis* is the second most abundant ichnofossil, which is represented by vertical to oblique burrows that range in thickness from 2 to 6 mm and are up to 50 mm long (Fig. 7d). *S. linearis* displays a massive fill typically composed of brown siltstone and also of lighter coloured sediments. In addition, there are shorter and wider burrows (11–17 mm) with a massive filling of lighter sediments and a dominantly vertical orientation that may be accommodated under *S. linearis*. A few specimens of *Taenidium barretti* are 6 to 8 mm wide and up to 65 mm long, with a vertical to oblique orientation and a filling that either contains brown siltstone or brecciated mudstone (Fig. 7d). *Polykladichnus aragonensis* is represented by a single specimen in the peel and is composed of an upright, Y-shaped unlined burrow, 3.5 mm wide and 45 mm long, that is filled with brown siltstone (Fig. 7d). The angle formed by the arms of the burrow is 55°. Root traces appear as tubular cavities, submillimetre to 2 mm in diameter, and oriented at a high angle to bedding. They can display an incipient cementation in the wall (Fig. 7e). In the peel GHUNLPam 27391 (Fig. 7b, c), 40 % of the area display the original bedding (consisting of 28% of laminated mudstone and 12% of brown siltstone), while the remaining area (60 %) corresponds to the ichnofabric. The latter is mostly represented by *N. meuleni* (56.4%) and has a subordinate participation of the remaining trace fossils (3.6%). Features attributable to pedofabric were not observed.

Two suites of trace fossils can be distinguished: a Skolithos suite, composed of *Skolithos linearis*, *Taenidium barretti*, *Polykladichnus aragonensis* and root traces, that is developed in the calcareous mudstone (facies Mc). This suite is overprinted by *N. meuleni*, with subordinate participation of *S. linearis* and root traces (Nagtuichnus suite), which are developed in brecciated mudstone and brown siltstone (Fig. 7b). Larger oblique burrows with massive sand filling also belong to this suite and cross-cut *N. meuleni*. Root traces are more abundant in the Skolithos suite.

The plan view of the *Nagtuichnus* suite was studied at the Dead Cows site during the 1997 exploration, as it was visible in a better definition than during the 2009 field study (Figs. 4d and 7g, h). This surface exposure roughly coincides with the top of the Prospecting Pit site and the peel of Fig. 7a. At least 4 m^2 of deflated and weathered siltstone to fine-grained sandstone displayed almost a complete bioturbation by *Nagtuichnus* with a dominantly subhorizontal and subordinate subvertical orientation. Cross-cutting of meniscate burrows is very common. Orientation of burrows and displacement of the producer (indicated by the curvature of the meniscus), as seen in plan view at the Dead Cows site (2009), is fairly diverse, although a preferential southeastward and, secondarily, northeast-southwestward movement can be distinguished (Fig. 8).

7. Neoichnological data

Different burrowing mammals are mentioned for the Gran Salitral area (Siegenthaler et al., 2004). Some of them are discarded *a priori* as potential producers of the meniscate burrows because of their larger size, such as hairy armadillos (*Chaetophractus villosus,* Dasypodidae), pichis (*Zaedyus pichiy,* Dasypodidae), gray leaf-eared mice (*Graomys griseoflavus,* Muridae) and Molina's hog-nosed skunks (*Conepatus chinga,* Mustelidae). In contrast, southern cavies (*Microcavia australis*, Cavidae) and tuco-tucos (*Ctenomys azarae*, Ctenomyidae) are medium- to small-sized fossorial rodents whose burrow cross-section is close to the diameter of the fossil meniscate burrows. The burrows of both rodent species, which are very common in the Gran Salitral area, were studied in detail and casted. The pink fairy armadillo or pìchiciego (*Chlamyphorus truncatus*) is another potential producer of the meniscate burrows that was formerly recorded for this region. Field observations of this poorly-known, subterranean armadillo are extremely rare (Superina, 2006; Abba and Superina, 2010), and there are no recent records from the surveyed area of Gran Salitral (Siegenthaler et al., 2004). The discussion for this species is therefore based on the scarce scientific literature (Jakob, 1943; Minoprio, 1945; Rood, 1970; Meritt, 1985) and observations of the digging behaviour of a captive individual briefly reported by Superina (2011). In addition, specimens preserved at the Museo Provincial de Historia Natural of La Pampa (MPHNLP) were used for morphological comparison.

7.1. Southern cavy burrow systems

Cavies dig their burrows in vegetated sand dunes (nabkhas) located in the arms and central vegetated depression of the larger parabolic dune at Gran Salitral, usually below shrubs of *Suaeda divaricata*, *Sarcocornia perennis*, *Atriplex lampa* (Chenopodiaceae), and *Chuquiraga erinacea* (Asteraceae). Burrow entrances are about plane convex in cross section (Fig. 9b). Entrance width and height range from 53 to 124 mm (mean: 86.3 mm, n = 26) and from 53 to 95 mm (mean: 74.2 mm, n = 26), respectively. Active southern cavy burrow systems

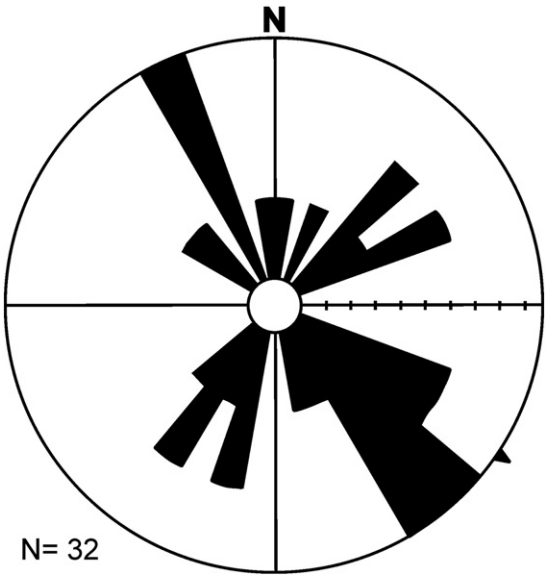

Fig. 8. Rose diagram of the direction of displacement of subhorizontal *N. meuleni* at Dead Cows site (2009), as suggested by the morphology of menisci. The triangle in the outer circle indicates the resultant direction.

located in an isolated nabkha, about 3 m wide and 1.1 m high (Fig. 9a) and accumulated around a *S. divaricata* shrub, were studied in detail at the Dead Cows site (DC in Fig. 1c). This nabkha is a few metres apart from the deflated surfaces where Holocene *N. meuleni* occurs. Five entrances (#2 to #6 in Fig. 10a, b), located near the top of the mound, were externally interconnected by cavy trails. The latter are revealed by trampling, common faecal pellets and urine, and the development of low relief terraces on the surface of the nabkha (Fig. 9b). The sixth entrance was smaller in diameter and located almost at the base of the mound; it was probably in use at the time of observation (#1 in Fig. 10a, b). Accumulated urine produces dark colour and tamped trails. Apart from the connections among these entrances, cavies were observed entering burrows of nearby nabkhas, suggesting that burrows from different dunes were used by the same social group.

The upper five entrances correspond to three burrow systems that are externally connected. The upper system (#5 in Figs. 9b, c, d, 10a, b) was a small blind tunnel, about 0.5 m long, probably connected with the intermediate burrow system (#3–4 in Fig. 10a, b) because the polyurethane foam poured into the latter also casted part of the upper one. Alternatively, the pressure related to the expansion of the foam may have broken a sediment bridge separating two nearby burrows. In any case, entrances of both casted burrows were connected by external trails, revealing that they belonged to the same group (Figs. 9b and 10a). Accumulation of urine and faecal pellets at the entrance of the small uppermost burrow (#5) suggested that, despite its size, it was an occupied dwelling. The intermediate and lower burrow systems have a similar architecture consisting of two entrances connected with an enlarged end or terminal chamber. The intermediate burrow system (#3-4, Figs. 9c, d, h, 10b) is Y-shaped; the near horizontal entrance tunnel (#3) leads to a blind and enlarged end (terminal chamber) with its long axis sloping about 25 degrees, that is also connected with the exterior by a steeper (30°), shorter ramp tunnel (#4). Total length of the intermediate burrow system is 1.05 m. Its cross-section is circular near the entrance (66 mm high and wide) and becomes wider and slightly enlarged toward the chamber (72 mm high and 75 mm wide). The floor is riddled by faecal pellets and bears a central ridge (Fig. 9h) that flattens in the same direction. The chamber is 150 mm long, 101 mm high, and 108 mm wide. Roots up to 23 mm wide (as well as rootlets) are present in the burrow walls and run at a low angle with the burrow axis. The lower burrow system is T-shaped and lies 0.3 m below the former (Figs. 9c, e, 10a, b) but in this case, the longest, almost horizontal, tunnel crossing through the whole nabkha has entrances at both ends (1.5 m long). A shorter, perpendicular sloping branch located near the middle of the tunnel has an enlarged end (0.53 m long). The burrow cross-section displays a bilobate floor and a convex ceiling. From entrance # 6 towards the T-junction, the burrow diminishes in diameter from 75 mm height and 86 mm width, to 64 mm height and 74 mm width. The horizontal tunnel is enlarged or inflated at the T-junction, describing a roughly triangular cavity 180 mm long, 160 mm wide and 103 mm high. The terminal chamber of the lower burrow system is 190 mm long, 125 mm wide and 90 mm high and thus slightly larger than that of the middle system (Fig. 9e). The sixth entrance is followed by a horizontal burrow with an apparently blind end. The burrow casts of the middle and lower burrow systems display abundant, roughly tubular projections ranging from 6 to 13 mm in diameter and up to 30 mm long that may have resulted from the filling of invertebrate burrows opened into the cavy burrow system (Fig. 9f). A few specimens of Trogidae adhered to the burrow cast, further supporting the idea that they had been inside burrows opening into the cavy tunnel. Scratch traces are rare in the burrow casts; they are only recognizable in the burrow chambers or in short rounded to conical projections – herein called knobs – located in the ceiling of the entrance tunnels (Fig. 9f). Scratch traces in the chambers appear as isolated groups of 3–4 parallel ridges or a crisscross pattern on the sides of the chamber (Fig. 9g), forming an angle of approximately 45° (separation between scratches 4–5 mm). The knobs are nearly circular to oval in plan view, with a diameter range of 25 x 26 mm to 30 x 37 mm and a height range of 17 to 30 mm (n = 2). These knobs bear groups of four parallel ridges that run approximately radially from the top of the knob (Fig. 9f). In the cast of the middle burrow system, the groups of ridges from the knobs and chamber range from 9 to 11.3 mm (average: 10.1 mm, n = 5), and the mean separation between ridges increases from one side to the opposite (2.6 mm, 2.7 mm, and 3.4 mm). The lower cast displays sparse scratches but only one group of four ridges, which is wider than the remaining (17.8 mm) and has a larger separation between ridges (3.6–5.3 mm). A possible isolated footprint can be observed in the bilobed floor of the intermediate burrow system (Fig. 9h, inset).

Cavy burrow systems described in the literature from western Argentina have a similar tunnel size range and are preferentially located in mounds of sand and associated with plants of low branches as observed at the Gran Salitral (e.g., Tognelli et al., 1995, 2001; Taraborelli et al., 2009). More complex systems with more burrow entrances and higher densities may occur (Contreras and Roig, 1978). Diverse biotic and abiotic factors (including sun exposure, orientation of prevailing cold winds and predatory pressures) have been identified as the causes for variation of the number of entrances and overall architecture of *M. australis* burrow systems (Taraborelli et al., 2009).

7.2. Tuco-tuco burrow system

At Gran Salitral, *tuqueras* (tuco-tuco burrow systems) were found at the low relief sandy area bordering the parabolic dune and close to the lake mudflat (Figs. 1c and 11a), where the predominant vegetation consisted of *S. divaricata, Salicornia ambigua* (Chenopodiaceae), and *Senna aphylla* (Fabaceae). No superficial signs of tuco-tucos were found in the mudflat and active sand dunes, but one of the branches of the *tuquera* seemed to enter the dune. *Tuquera* entrances are free of faecal pellets, roughly circular in cross-section, with horizontal diameter ranging from 58 to 79 mm (mean: 67 mm, n = 21) and vertical diameter ranging from 56 to 80 mm (mean: 66 n = 21). They are typically plugged with sand and surrounded by a sand mound (Fig. 11b). The whole system is roughly Y-shaped, with at least three visible entrances (A, B, and C in Fig. 12). Following the nomenclature suggested by Hickman (1990), the longest axis of the system was considered the main tunnel.

The main tunnel is 4.95 m long, oriented roughly parallel to the margin of the active dune (N 20°W), and began close to a *S. ambigua* shrub. Its entrance was plugged, and the two arms of the Y were almost perpendicular to the main tunnel (Fig. 12). One lateral tunnel, 1.8 m long and directed towards the active dune, contained a living tuco-tuco that kept on filling the extreme of the uncovered tunnel while being excavated with a shovel. It is possible that this lateral tunnel was partially modified by the rodent during the excavation of the system. Work on this tunnel was not continued to preserve the animal. A second lateral tunnel, oriented toward the mudflat, was 2.2 m long and reached a *S. divaricata* shrub. Its entrance (C in Fig. 12) was also plugged with soil for several centimetres, and this branch also had a perpendicular, short *cul-de-sac* tunnel (CDS in Fig. 12) (Hickman, 1990). Excavation beyond the end of this blind tunnel revealed no occluded excavation or any other particular feature. The main and lateral tunnels display a slightly curved path in plan view. Different segments can be distinguished based on the inclination of the tunnel, ranging from nearly horizontal to 20°, whereas its depth is in the range of 0.20–0.35 m. Changes in inclination of the main tunnel are probably linked to underground (or future aboveground) access to plants. When the main tunnel approaches plants it raises a little up to reach the more proximal parts of the roots, then deepens again to continue roughly at the same depth. The entrance ramps display an inclination ranging from 28° to 35°. The main tunnel exhibits a 0.15 m long entrance ramp (B in Fig. 12) concealed below a mound on mostly bare soil. A possible incipient

short lateral tunnel was detected near this entrance (Fig. 11c, e). A partial cast of this *tuquera* (1 m long) was made by pouring polyurethane foam inside the ramp, which filled it and adjacent sections of the main tunnel (Fig. 11c).

Cross-section of the casted burrow interval is roughly circular with a slightly flattened and smooth floor (Fig. 11f). Tunnel ceiling and sides display sets of up to four parallel ridges, with the two central ones being more deeply imprinted (Fig. 11e). The group of ridges forms an acute angle with the midline averaging 30°, then curves downward to end in the sides of the tunnel with an orientation perpendicular to the midline (Fig. 11d). The orientation of the group of ridges is consistent in the whole cast. Groups of four parallel ridges range in width from 16.1 to 21 mm (average: 18.3 mm, n = 9), with an average separation between ridges of 5.6 mm, 5.0 mm, and 4.8 mm. Groups of three ridges are also present, although the most common are pairs of ridges, up to 3 mm high, that display a comparable separation to those of the central ridges in the groups of four. Other surface features of the burrow cast are shallow steps in the ceiling of the tunnel, spaced between 47 and 67 mm (Fig. 11f).

7.3. Pichiciego burrow morphology and burrowing mechanism

The only contributions dealing with *pichiciego* burrows are those of Jakob (1943), Minoprio (1945), Rood (1970), and Meritt (1985). Of these, only Minoprio (1945) provides a detailed description along with other data on the biology and anatomy of this small armadillo. *C. truncatus* is famous for its reduced size, adaptations to underground life, and, particularly, for the scarcity of field sightings, which may result from the species being naturally rare or from its cryptic, subterranean habits (Jakob, 1943; Minoprio, 1945; Rood, 1970; Superina, 2006). Minoprio (1945) already warned about population declines caused by human activities; several decades later, the situation is far from having improved (Superina, 2006).

The pichiciego's range is restricted to central-western Argentina, roughly between 30°–39°S and 62°–69°W, including southern Catamarca, eastern La Rioja and San Juan, western Córdoba, large parts of Mendoza, San Luis, and La Pampa, southern Buenos Aires, and the northernmost tip of Río Negro province (Minoprio, 1945; Crespo, 1960; Abba and Superina, 2010). Minoprio (1945) stated that this species inhabits aeolian sands (which are easily excavated) and rejects neighboring lower areas with more clay content or hard soils (interdunes). This author did, however, not distinguished between dunes and adjacent low relief sandy zones (the latter also belonging to interdunes).

Direct observations on a captive individual suggest that, similar to other armadillos, *C. truncatus* starts excavating its burrow with the snout (Fig. 13a). It then uses the forelimbs to excavate, and the hindlimbs to thrust the soil backward while digging. The tail is used for support while removing soil with the forelimbs. The vertical rump plate helps avoid that the loose substrate falls back inside the tunnel, but it is also actively used to compact the soil behind the animal (Fig. 14a–f). For this, the animal supports itself on the front legs and extends its body, pushing the soil backwards with its hind feet and rump plate. This movement is repeated at regular intervals and is sometimes accompanied by a lateral vibration of the hind quarters that further compacts the soil. As a result, the soil behind the animal is accumulated in the form of menisci roughly corresponding to the shape of the rump plate. Partially similar observations have been made by Minoprio (1945) and Rood (1970), who noted that the pink fairy armadillo he maintained in captive conditions did not leave a permanent open tunnel while excavating.

Minoprio (1945, p. 51–54) described three types of burrows. All of them were mostly horizontal, no more than 150 mm below ground, and excavated arising from a sloping surface. The first type is very short, empty and probably a temporary refuge, while the other two represent longer burrows with either two entrances (probing burrow) or with many entrances and ending in a chamber (probable nesting burrow). Large portions of the longer burrows are actively filled backwards by the *pichiciego*. According to Minoprio (1945), burrow architecture is random, and even shallow burrows are impossible to follow. Similarly, Rood (1970) recorded that the *pichiciego* moved freely underground while excavating, without leaving a permanent open tunnel. This behaviour is expected, considering that *pichiciegos* mostly feed below ground on insects (mainly ants, but also coleopteran larvae) and other invertebrates (Minoprio, 1945, p. 52; Roig, 1995). A subterranean predator, such as the *pichiciego*, needs to constantly move around belowground in search of food, excavating tunnels only to reach preys, which are never used again.

The ten individuals described by Minoprio (1945) and those deposited at the MPHNLP (three uncataloged specimens) range in length from 111 to 154 mm (mean: 131 mm, n = 13), which is in accordance with the measurements provided by Harlan (1825), Jakob (1943), Rood (1970), and Wetzel (1985). The rump plate ranges from 26.5 to 33 mm height (mean: 29 mm, n = 13) and from 39 to 46.5 mm width (mean: 42.8 mm, n = 13), displaying a height/width ratio in the range of 0.61–0.72 (data from Minoprio [1945] and specimens from MPHNLP). In posterior view, it is roughly fan-shaped and composed of a semicircular upper half rimmed by bristles of hair, while the lower half is represented by two straight segments reaching downward to the area of insertion of the tail (Fig. 13c). The straight segments form an obtuse angle between 115° and 121° (data from Minoprio [1945] and specimens from MPHNLP). The aspect ratio of an ellipse (semi-minor axis/semi-major axis) fitted in a dorsal view of the rump plates of the MPHNLP specimens is in the range of 0.49–0.63 (compare Fig. 13b). The tail is covered by scales and displays rounded protuberances, about 2–2.9 mm wide, on its ventral surface (Fig. 13c). The distance between two adjoining protuberances lies between 6.4 and 8.9 mm (data from MPHNLP specimens). The forelimbs are stronger than the hindlimbs and bear long claws, especially in digits II to V (Fig. 13a, b). For the prepared specimens at MPHNLP, claw width ranges from 2 to 4.7 mm (mean: 3.1 mm, n = 13) and the separation between claws taken from centre to centre ranges from 4.1 to 8.4 mm (mean: 6 mm, n = 7), whereas the width of the forelimb is in the range of 10–17.9 mm.

8. Discussion

8.1. Palaeonvironmental interpretation

The lower member of the Río Negro Formation outcropping at La Lobería locality records the migration of aeolian dunes, as revealed by the presence of well-sorted, fine-grained sandstones composing

Fig. 9. Extant southern cavy burrow systems at Dead Cows site (Gran Salitral). (a) View of the lee side of the vegetated dune (nabkha) where the studied cavy burrows were found. (b) Lateral view of nabkha showing several plane-convex entrances (4 to 6, see also Fig. 10) connected by urine and faeces trails (arrows). The dominant wind direction is also shown. (c) Plan view of the cast of the upper and intermediate burrow system, after partial excavation (entrance numbers are those of Fig. 10). CH: terminal chamber (GHUNLPam 27409). (d) Lateral view of the nabkha (opposite side of that shown in figure b) after casting of the burrow systems and excavation (see also Fig. 10). (e) Plan view of the lower burrow system (GHUNLPam 27410) showing an overall "T" outline with a terminal chamber (CH). Entrance numbers are those of Fig. 10. (f) Two rounded to conical knobs (white arrows) in the ceiling of the upper burrow system (GHUNLPam 27409) with a surface texture in the form of groups of four parallel ridges. Quasi horizontal and discontinuous ridges are probably an artifact of the casting with polyurethane foam. Cylindrical features near the left knob are possible partial casts of insect burrows. (g) Surface texture in the side of the terminal chamber of the lower burrow system (GHUNLPam 27410). (h) View of the floor of the cast of the upper and intermediate burrow systems (GHUNLPam 27409), showing a bilobed floor that is smoothed toward the terminal chamber (CH). The floor is riddled with feacal pellets mainly near the centre of the cast. The inset displays a partially imprinted footprint (white arrow) and a faecal pellet adhered to the casting foam (black arrow). The scale bar in the inset is 1 cm long.

cross-bedded sets (facies Sta) with a minimum thickness of 1.2 m (lowermost part of the measured section, Figs. 2a and 3a). These aeolian dunes were eroded prior to the deposition of the upper part of the section that is dominated by fine-grained sandstone with horizontal to low-angle lamination (facies Sh, Sl), which are interpreted as interdune deposits mostly generated by migration of wind ripples. In this interdune section, where *Nagtuichnus meuleni* occurs, it is possible to distinguish a lower interval with a mud-draped cross-bedded set,

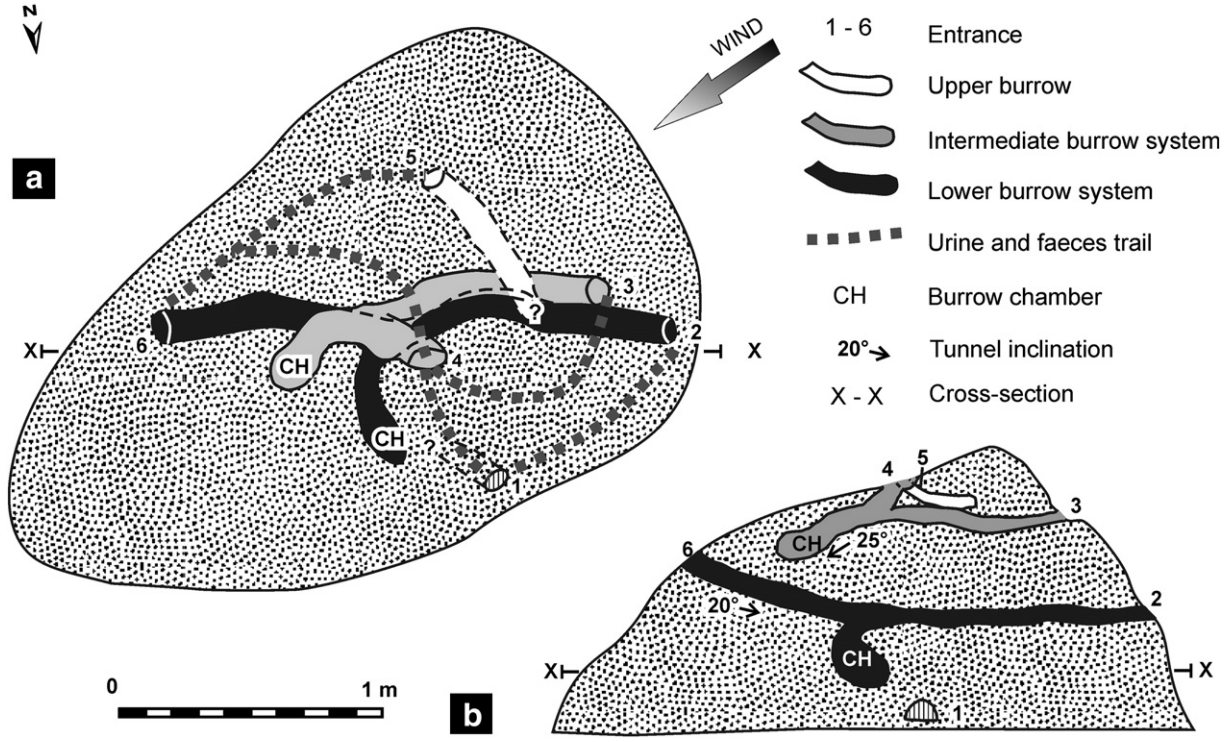

Fig. 10. Schematic diagram of the studied cavy burrow systems and the hosting nabkha from Dead Cows site (Gran Salitral). (a) Plan view displaying the arrangement of the burrow systems and the surface trails connecting the entrances (1–6). X–X indicates the location of the cross-section of figure b. (b) Cross-section of the studied nabkha with the cavy burrow systems (compare with Fig. 9c).

and a wave-rippled bed with a mud-draped top (Fig. 3b). These features suggest the presence of aqueous currents and occasional ponding of flood waters in the interdune area. The preservation of deeply imprinted vertebrate footprints may also suggest a high moisture content of the sediments. This interval is best compared with a damp interdune area (e.g., Kocurek, 1981). The upper interval of the interdune section is dominated by sandstone with horizontal to low-angle lamination (facies Sh and Sl) and a single and laterally discontinuous, 0.4 m thick cross-bedded sandstone set (facies Sta). They are interpreted as reflecting low-relief sandy areas between dunes with intermittent migration of small dunes, suggesting a comparison with dry interdune areas (Kocurek, 1981).

The measured section from the Gran Salitral site (Fig. 2b) starts with Holocene sediments, including olive green mudstone (facies Mh) and pale brown calcareous mudstone (facies Mc) with parallel lamination, and remains of the pulmonate gastropod *Chilina* sp. aff. *Chilina lallemanti*. This gastropod is typical of the cold and temperate regions of South America, mainly of Patagonian lakes and rivers, where it is found at the air-water interface adhered to rocks and logs. It is a freshwater gastropod but can tolerate higher salinities (Castellanos and Gaillard, 1981). The interval composed of facies Mh and Mc is interpreted as lacustrine sediments, including shallow subaqueous deposits (facies Mh) and dry carbonate mudflat deposits (after Hardie et al., 1978) with sparse vegetation (facies Mc). These lacustrine sediments are considered former deposits of the Gran Salitral. The thin intercalations of brown siltstone may suggest occasional transport of windblown sediments over the mudflat. The Skolithos trace fossil suite composed of *S. linearis*, *T. barretti*, *P. aragonensis*, and root traces developed in the calcareous mudstone (facies Mc; Fig. 7b, c) suggests sparse colonization of the dry carbonate mudflats by plants and invertebrates.

The overlaying interval in the section (dry interdune facies association, Fig. 2b) is dominated by structureless fine-grained sand (Sm). The lowermost, 0.2 m thick bed containing the *Nagtuichnus* suite of trace fossils (Holocene deposit, Sm in Fig. 7a) can be distinguished in this interval; it displays a higher induration than overlying friable sands of the modern interdune and parabolic dune. This bed was deposited in low-relief sandy areas bordering the lacustrine mudflat that had been colonized by the producer of *N. meuleni*, and probably bore sparser vegetation (lower abundance of root traces) and fewer invertebrates (*S. linearis*) than the underlying bed. Comparison with similar modern structures found in the Gran Salitral area suggest that the larger oblique burrow with structureless fill occurring in this bed was probably produced by a medium-sized Dasypodidae. The constructor of *N. meuleni* burrowed from the top of the upper siltstone bed (facies Sm) into the probably harder lower calcareous mudstone bed (facies Mc), breaking and mixing both substrates during backfilling of the burrows (Fig. 7b, f). In a few cases, whitish *N. meuleni* burrows in silty darker substrate indicate that the organisms were moving upwards while backward filling the burrow with lighter coloured, finer-grained material (Fig. 7b). These specimens may reveal another deposit that was eroded or, less likely, that material from epigeous soil mounds previously removed from the underlying lacustrine deposit were incorporated into the burrows. The first explanation is in agreement with an upper bounding erosive surface of the hosting bed. The rose diagram with the direction of movement inferred for *Nagtuichnus meuleni* confronted with the present geography suggests that the producer of the meniscate burrows preferentially dug along the margin of the lacustrine deposits and also toward the mudflats (compare Figs. 1c and 8).

The overlying medium-grained, friable sand corresponds to the arms of the modern parabolic dune (Figs. 2b and 3c). In this context, the different stratification styles can be interpreted as the migration of two-dimensional bed-forms with grain-flow events in the lee slopes (facies Sp), three-dimensional bed-forms (facies St), and wind ripples (facies Sl). The pedogenic features (root traces, carbonate nodules, Fig. 2b) are indicative of transient stabilization of the dune by vegetation.

Fig. 11. Tuco-tuco burrow system at Tuquera site (location in Fig. 1c). (a) Setting of the Tuquera site. Tuco-tuco burrows are found in low-relief sparsely vegetated sandy zones of the foreground and are rare in active dunes (right side of the figure). The Gran Salitral mudflat is in the background (arrow). (b) Typical sand mound around a tuco-tuco burrow entrance. (c) Partial cast of tuco-tuco burrow system (GHUNLPam 27411). B stands for entrance "B" in Fig. 12. The arrow indicates an incipient short lateral tunnel. (d) Close-up of part of the ceiling of the tuco-tuco burrow cast (above) and a drawing (below) showing the surface texture in the form of parallel ridges with a chevron-like arrangement (GHUNLPam 27411). (e) Side view of burrow cast showing a group of four curved parallel ridges (black arrows point to the first left ridge in each group) and an incipient lateral tunnel (white arrow) (GHUNLPam 27411). (f) Close-up of part of the tuco-tuco burrow cast (GHUNLPam 27411), showing a flat floor (above) and shallow steps on the ceiling (below) indicated by white arrows.

8.2. Trace makers

8.2.1. The southern cavy hypothesis

Of the three potential producers of *N. meuleni*, southern cavies (*M. australis*) are the less likely ones. Neoichnological observations presented herein suggest that their burrows are located in vegetated sand dunes (nabkhas), but not in interdunes where *N. meuleni* mostly occurs. These rodents construct open burrow systems that will result in a massive filling when abandoned and buried, and their distinctive architecture is composed of two entrances and a terminal chamber (Figs. 9d, e, 10). A massive filling and the presence of a terminal chamber were not recorded in any of the hundreds of *N. meuleni* specimens observed for this study. Cross-section of a cavy burrow typically has a bilobed floor (with urine and faeces) and a convex ceiling (Fig. 9h), with a width/height ratio of 1.2, while the cross-section is circular in *N. meuleni* (Table 1). In addition, the average cavy burrow diameter is about 35% larger than that of *N. meuleni* (86.3 mm and 63.7 mm, respectively). Further distinctive features of cavy burrows are the presence of rounded knobs with radial scratch traces on the ceiling (which were not observed in *N. meuleni*) and smooth burrow walls, except for the sides of chambers (Fig. 9f, g), instead of a fully scratched burrow wall as seen in *N. meuleni* (Figs. 4g, h, 6g, h). All these morphological characters argue against southern cavies as producers of *N. meuleni* (Table 1). In addition, these rodents are

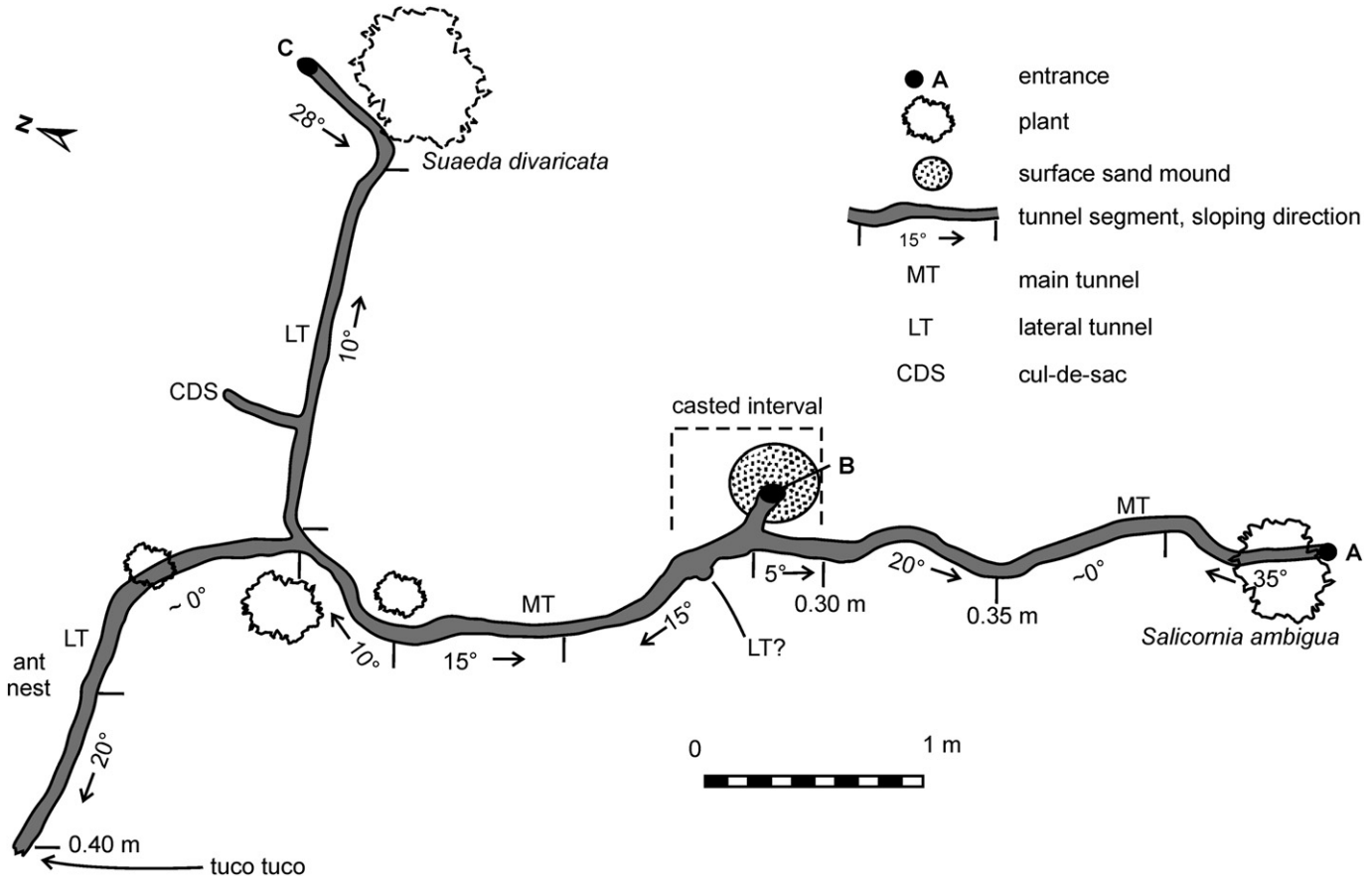

Fig. 12. Diagram of the tuco-tuco burrow system at Tuquera site, drawn after a photographic mosaic. See text for description. Burrow system nomenclature after Hickman (1990).

only partially subterranean and spend most of the day foraging aboveground (Tognelli et al., 2001), while *pichiciegos* and tuco-tucos are almost exclusively subterranean mammals that either forage underground (*pichiciego*; Minoprio, 1945) or both below and above ground (tuco-tucos, Lacey and Wieczorek, 2003).

Most of the features observed in the cavy burrow system of Gran Salitral are indicative of an active burrow that has been in use for a long time (e.g., Laundre, 1989). For instance, the walls have been smoothed by the repeated passage of its occupants, and the surface of the floor has a bilobed appearance due to repeated trampling; both features are probably more common in burrow systems with multiple occupants. A similar bilobed floor has been found in Permian burrow casts attributed to dicynodonts (Stanistreet and Turner, 1979; Smith, 1987) and Triassic burrow casts assigned to cynodonts (Groenewald et al., 2001; Damiani et al., 2003; Sidor et al., 2008). The Triassic burrows were commonly interpreted as reflecting a semi-sprawling posture akin to the upright posture of mammals, although the bilobed floor has not been previously recorded in extant mammal burrows (Voorhies, 1975; Damiani et al., 2003). The plane-convex cross-section of extant burrows of *M. australis* is probably linked to the deposition of airborne material in an open burrow or to sediment failure due to gravity in a sloping tunnel. The presence of insect burrows arising from the cavy burrow wall is also suggestive of an open tunnel that was used by the mentioned invertebrates. Scratched knobs on the ceiling of Miocene burrow casts probably belonging to rodents (Gobetz, 2006) are very similar to those described herein for modern cavy burrow casts.

8.2.2. The tuco-tuco hypothesis

The *tuquera* studied at Gran Salitral matches the general features described for burrow systems of *Ctenomys* spp. (Pearson, 1951, 1959; Contreras and Reig, 1965; Altuna, 1983; Contreras, 1984; Antinuchi and Busch, 1992; Rosi et al., 1996, 2000). It had probably been built by *C. azarae*, as this is the only species of tuco-tuco recorded from this area (Tiranti and Massarini, 1999).

The following features of the Gran Salitral *tuquera* match those of *N. meuleni*: 1) their location in low-relief sandy deposits (interdune area); 2) long, horizontal burrows of circular cross-section and similar diameter; 3) entrances may occur close to each other, which, in addition to the expectable accumulation of soils with time, could be the reason for the high density of entrances recorded at the Dead Cows site (Fig. 7g). Critical morphological characters that argue against tuco-tuco burrow systems as possible modern analogs of *N. meuleni* are, basically, the lack of branching in the latter and the small proportion of backfilled tunnels, either meniscate or structureless, in the *tuquera* studied here and those recorded elsewhere (i.e. Pearson, 1951, 1959; Contreras and Reig, 1965; Altuna, 1983; Contreras, 1984; Antinuchi and Busch, 1992; Rosi et al., 1996, 2000). In the studied *tuquera*, only a few centimetres of the burrow entrances are backfilled (Fig. 11b). According to studies on *C. mendocinus*, only 12% to 16% of the *tuquera* – mainly lateral tunnels – are occluded (Rosi et al., 1996, 2000). These occluded tunnels are filled with loose, unpacked sandy soil to maintain the microclimatic conditions inside the burrow system (Contreras, 1984; Antinuchi and Busch, 1992). Other rodents, such as the North American pocket gopher (*Geomys bursarius,* Geomyidae) backfills old tunnels of the system while excavating new ones to avoid the risk of predator exposure (Andersen, 1987; Sparks and Andersen, 1988; Thorne and Andersen, 1990). In one example, during the excavation of 112 m of new tunnels, a total of 77 m of tunnels were backfilled (Thorne and Andersen, 1990). The African silvery mole-rat (*Heliophobious argenteocinereus,* Bathyergidae) backfills up to 64% of its tunnel system (Šumbera et al., 2008). But still, these

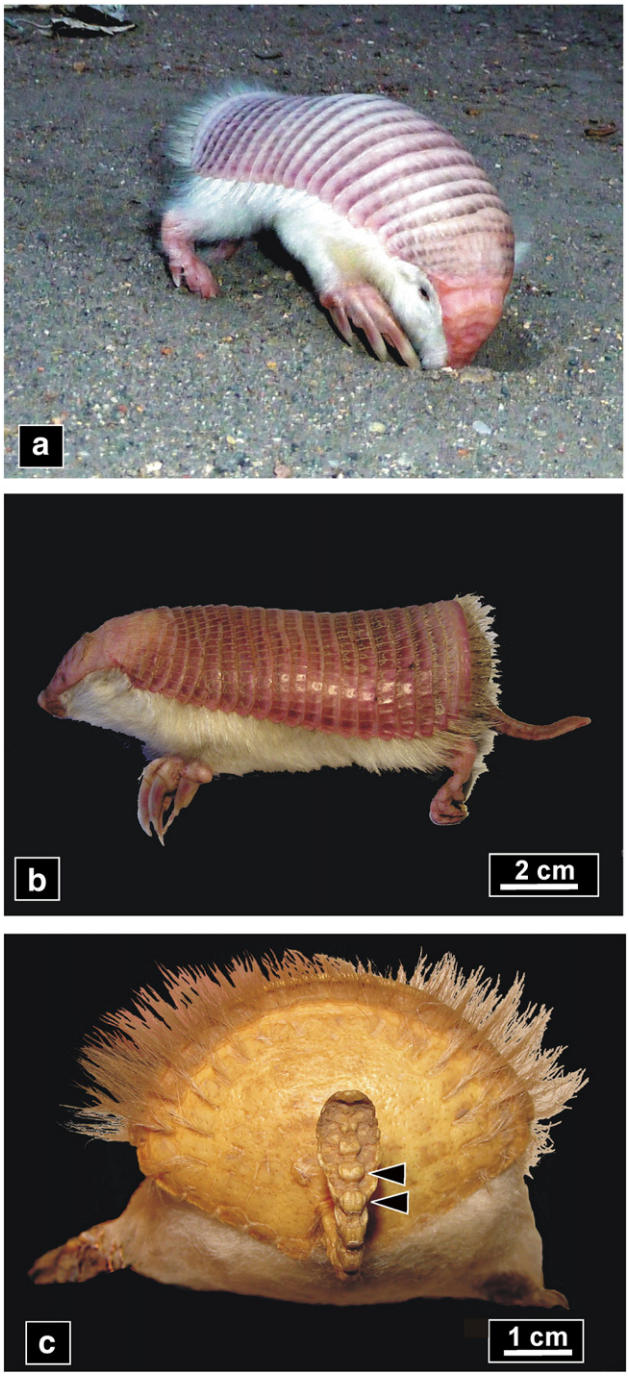

Fig. 13. Views of *pichiciegos* (*Chlamyphorus truncatus*) specimens. (a) Live *pichiciego* starting to dig a burrow. Note the large claws on the forelimb and the position of the tail. (b) Lateral view of a dead individual. Note the blunt, curved end. (c) Detail of the fan-shaped rump plate and protuberances (arrowed) in the tail of a dead pichi ciego. Figures (a) and (b) show the *pichi ciego* maintained in a terrarium during 8 months (Superina, 2011). Figure (d) is from an uncatalogued specimen from the Museo Provincial of Historia Natural de La Pampa.

rodents produce branching burrow systems that are incompatible with *N. meuleni*.

The surface texture observed in the casted interval of the *tuquera* (Fig. 11c–f) can be interpreted as scratch traces produced by alternate strokes of the forelimbs, as described for *C. mendocinus* (Camin et al., 1995), whereas tooth traces are absent. As a consequence, a dominant scratch-digging mechanism commonly found in *Ctenomys* species inhabiting sandy friable soils is envisaged, whereas chisel-tooth digging is more frequent in species burrowing in harder clayey soils (e.g., Camin et al., 1995; Giannoni et al., 1996; Vassallo, 1998). A smooth floor and the preservation of scratch traces only on the ceiling and sides of the burrow are in agreement with the construction of an open burrow that is repeatedly trampled. These features further differentiate *Ctenomys* burrows from *N. meuleni*. Here, they can be linked to the presence of a single tuco-tuco and, probably, to a relatively "young" tunnel. In comparison, the smooth walls and bilobed floor in the studied *M. australis* burrow systems may indicate multiple occupants and "old" burrow systems. The presence of shallow steps on the ceiling of the burrow cast (Fig. 11f) may correspond to burrowing increments after one or more digging cycles followed by transport of loosened soil to the surface (e.g. Camin et al., 1995).

The Miocene burrows from the Río Negro Formation were attributed to tuco-tucos by Angulo and Casamiquela (1982). This interpretation was based on the assignation of tubular structures of similar diameter from the Pliocene Monte Hermoso Formation (south of Buenos Aires province) to rodent burrows by Frenguelli (1931), as well as comparisons with extant *tuqueras*. Although these authors were aware of the younger body fossil record of *Ctenomys*, they also considered the Río Negro Formation Pliocene in age, and thus had no conflict for such an attribution. The phylogeny of the Ctenomyidae indicates that extensive cladogenesis of *Ctenomys* took place only by the Pleistocene (Reig et al., 1990; Lessa et al., 2008; Verzi et al., 2010), whereas the oldest *Ctenomys* is Pliocene (Verzi et al., 2010). The ichnofossil record of Ctenomyidae (Genise, 1989) also starts in the Pliocene with burrows of the ancestral *Actenomys priscus* from the Chapadmalal Formation (Buenos Aires province). The evolution of octodontoid burrow types (Genise, 1989; Lessa et al., 2008) and the burrow characters analyzed below are not consistent with the attribution of the late Miocene specimens of *N. meuleni* to *Ctenomys*, as had been proposed by Angulo and Casamiquela (1982).

8.2.3. The pichiciego hypothesis

Analysis of the neoichnological (including field and laboratory observations) and morphological information on potential trace makers of *N. meuleni* points towards Chlamyphorinae as the more likely producers. The most relevant reasons are the fully subterranean habits of this taxon involving the excavation of long, unbranched, horizontal burrows in sand, and its habits of backfilling the burrow, a behaviour that has not been observed in the rodents discussed above. A subterranean predator, such as the *pichiciego*, needs to constantly move around belowground in search of food, excavating tunnels only to reach preys, which are never used again. In contrast to this, tuco-tucos and southern cavies, which are herbivores that forage aboveground, use their more permanent burrows for dwelling and reproduction. The meniscate structure of the fill can be explained by the packing of sediment with the rump plate, which also results in a massive rim of sediment in the burrow fill (sediment pushed against the burrow wall but not vibrated).

When comparing the horizontal width of menisci in *N. meuleni* with the width of the rump plate of *pichiciegos* (Table 1), the larger size of the former can be explained by the side to side movement while packing noted in the captive individual observed for this study, as well as by Rood (1970). The aspect ratio of an ellipse fitted on the dorsal view of prepared *pichiciego* rump plates is within the range of the aspect ratio of an ellipse fitted on menisci of *N. meuleni* in plan view (Table 1). The outline of menisci in *N. meuleni* displays a close similarity with the rump plate of *C. truncatus* (compare Figs. 6a and 13b), including a segmented lower portion that may result from the lateral movement of the animal when compacting the sand (compare Figs. 5a and 13c), and a convex festooned upper part that matches the bristles of hair on the dorsal border of the rump plate (compare Figs. 5f and 13c). Additional bioglyphs observed in the concave surfaces of menisci are paired, rounded pits. Their size and the separation between adjoining pits match the protuberances on the ventral side of the tail of pichiciegos (Table 1, Figs. 5c, d, e, 13c). The features of ridges on the external wall of *N. meuleni* (Figs. 4g, h, 6g, h)

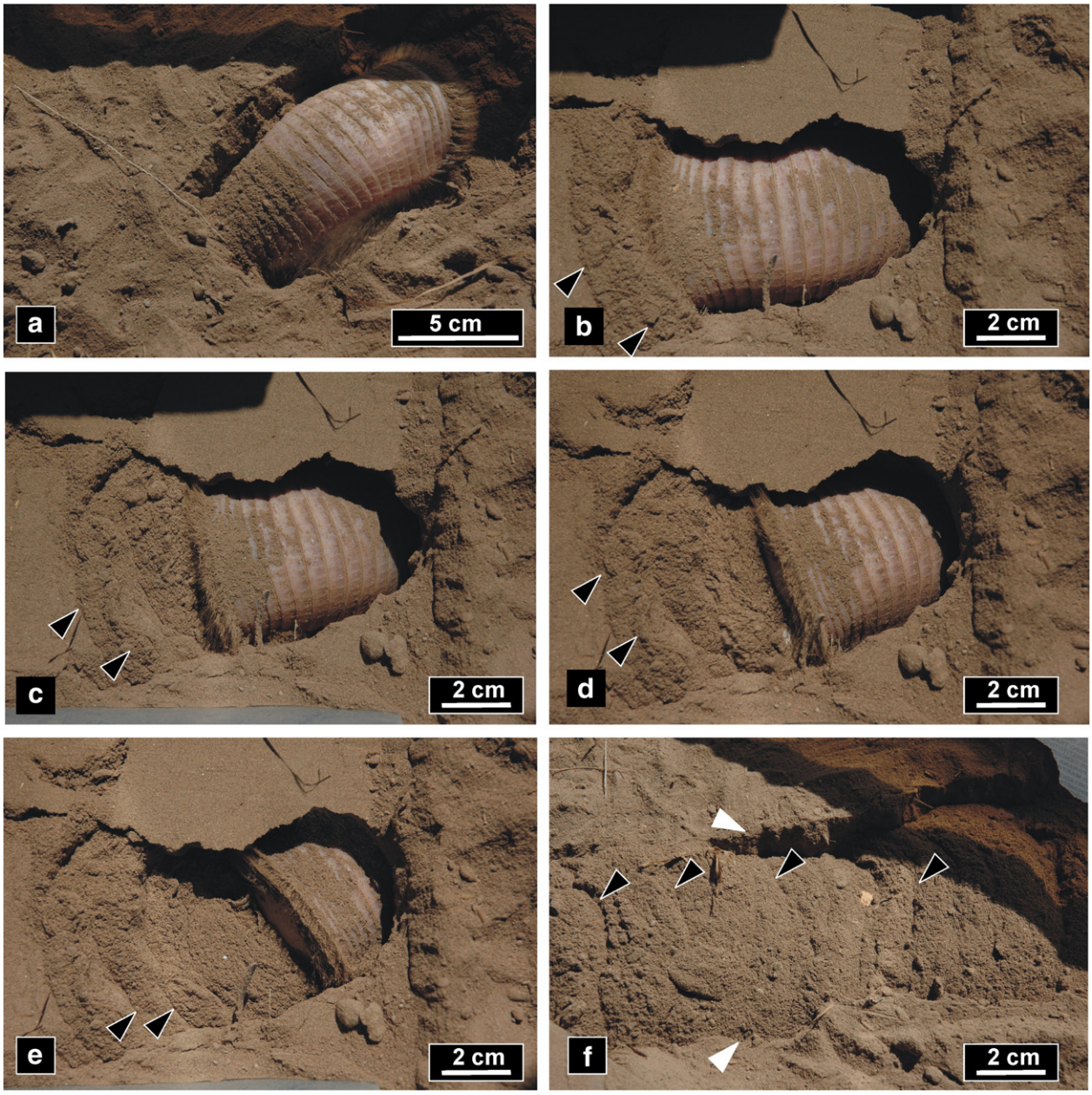

Fig. 14. Views of a captive-kept *pichiciego* digging in its terrarium. (a) Partly buried *pichiciego* initiating a shallow burrow (the head is pointing toward the lower left corner). (b) to (e) Sequence of pictures showing the progression of a shallow excavation. The head points toward the upper right corner. In figures (b) to (d) the animal is compacting the sand with its pelvic scute, in figure (e) it is loosening sand at the end of the tunnel. Arrows indicate the meniscate backfill. (f) Shallow burrow dug and backfilled by the *pichiciego* in the terrarium. The black arrows point to some of the individual menisci and white arrows to burrow margin.

are also consistent with their production by a *pichiciego*, both by comparison with the size of its forelimbs and claws (Fig. 13a, b) and because of the preservation of ridges on the burrow floor (Fig. 6g, h). The lack of root traces in the burrow wall of *N. meuleni*, and its presence in fossil burrows that are interpreted as open excavations (e.g., Martin and Bennett, 1977; Gobetz, 2006), is suggestive of a foraging trace fossil with well compacted fill, instead of a living burrow space or a passively-filled excavation. An open burrow that suffered the repeated passage of its occupant (or its occupants, in the case of social species) would lose these bioglyphs produced during initial excavation due to trampling. The width of parallel ridges, width of individual ridges, and the separation between ridges on the walls of *N. meuleni* match the forelimb width, claw width, and separation between claws, respectively, of *C. truncatus* (Table 1).

Minoprio's (1945) statement that *C. truncatus* only digs burrows in aeolian sand, avoiding clayey deposits, is not fully consistent with the occurrence of *N. meuleni* at Gran Salitral because the latter burrowed from sand-silt sediments on the margin of lacustrine deposits down into more compacted and clayey calcareous mudstone deposits (Fig. 7a). *N. meuleni* are densely grouped at the Prospecting Pit site (Fig. 7b, c) and also in some blocks at La Loberia and El Faro localities (Fig. 6e), which seems to contrast with the solitary habits and current scarcity of the *pichiciego*. A possible explanation is that the high density resulted from the overprinting of burrows produced at different times in the interdune deposit. In addition, the cross-cutting of *N. meuleni* burrows is more consistent with the work of a surface-forager like *C. truncatus*.

Minoprio (1945, Fig. 17) indicated that part of the *pichiciego* tunnels may remain empty and that a mound may be found near the entrance of temporary refuge and probing burrows. In contrast to this, all recorded specimens of *N. meuleni* are meniscate backfilled tunnels. The apparent lack of empty tunnels in the fossil material and

Table 1
Comparison of burrow system features of southern cavies (*Microcavia australis*), tuco-tucos (*Ctenomys azarae*), and *pichiciego* (*Chlamyphorus truncatus*) with the ichnotaxon *Nagtuichnus meuleni*. Source of information for southern cavies and tuco-tucos are neoichnological observations at Gran Salitral. For *pichiciego*, the information is either derived from observations on a captive-kept individual (Superina, 2011), or from [(1)]Minoprio (1945) or [(2)]measurements from preserved specimens at the Museo Provincial de Historia Natural de La Pampa. The width of the forelimb, as well as the width and separation of claws are given for comparison with the size and morphology of the sets of parallel ridges (interpreted as scratch traces) observed in *N. meuleni*.

	Microcavia australis	*Ctenomys azarae*	*Chlamyphorus truncatus*	*Nagtuichnus meuleni*
Burrow system architecture	Subhorizontal to sloping, Y or T-shaped, terminal chamber	Subhorizontal, branched burrow system (segments sloping less than 20°), main tunnel, lateral and *cul-de-sac* tunnels	Highly variable, including short blind burrows, horizontal burrows with entrance and exit, and rare burrows with terminal chamber [(1)]	Mostly horizontal to oblique, unbranched burrows
Burrow system size	1.5 m long by 0.63 m wide	6 m long by 3.7 m wide	Several metres	Up to 2.5 m long
Burrow fill	Open burrow. Urine and feces on burrow floor.	Mostly open burrow, plugged entrances, shallow steps on ceiling	Meniscate backfilled, menisci of uniform thickness of 8.1–11.6 mm (mean: 10.1 mm). Range of meniscus thickness/burrow width ratio: 0.18–0.23 (mean: 0.20)	Two-zoned meniscate backfill. A central meniscate core surrounded by a discontinuous massive outer layer. Menisci of uniform thickness of 7.8–22.6 mm (mean 13.2 mm). Range of meniscus thickness/burrow width ratio: 0.12–0.30 (mean: 0.21)
Burrow cross-section	Flat or bilobed floor and convex ceiling, average width/height ratio = 1.2	Circular (width/height ratio: 1.0) or slightly flattened floor with convex ceiling	Circular?	Circular, width/height ratio = 1.05
Burrow diameter	53–124 mm wide, 53–95 mm high	56–80 mm wide, 58–79 mm high, average width/height ratio = 1.0	Entrance 60–70 mm wide [(1).] Burrow 42.9–56.5 mm Meniscus width unknown	46–78 mm, average: 63.7 mm Menisci horizontal width = 50.5–67.5 mm
Wall	Smooth walls, except for sides of chambers, and knobs. Insect burrows. Sets of up to four parallel ridges, 9–17.8 mm wide, separation of ridges 2.4–5.3 mm Ridge width 2.6–4.0 mm	Chevron pattern on ceiling and sides, floor smooth Sets of up to four parallel ridges 16.1–21 mm wide, separation of ridges 4–6.5 mm Ridge width: 2.5– 4.2 mm	Surface texture unknown Forelimb width: 10–17.9 mm (four digits), separation of claws: 4.1–8.4 mm [(2)] Claw width: 2–4.7 mm [(2)]	Floor and sides with parallel ridges, chevron pattern in floor. Sets of up to three parallel ridges, 17–20 mm wide, separation of ridges 5–11 mm. Ridge width: 2.8–5 mm
Chamber	Dimensions in mm (length: height:width): 150:101:108 to 190:90:125	None found	Rare [(1)]	None found
Bioglyphs	Rounded knobs with radial scratch-traces on burrow ceiling Criss-cross pattern in chamber		Fan-shaped pelvic shield. Tail protuberances: 2–2.9 mm, distance between protuberances: 6.4–8.9 mm	Meniscus surface with a polygonal lower half and convex festooned upper half. Paired pits in concave side of menisci, pits range in diameter from 2 to 4.8 mm, distance between pits 6–11 mm
Setting	Nabkha (vegetated dune)	Low relief, sparsely vegetated sandy deposits (dry interdune)	Low relief, sparsely vegetated sandy deposits (dry interdune)[(1)]	Damp to dry interdune

the variable colour (and composition) of menisci at the Prospecting Pit site (Fig. 7a–c) can be explained by the digging mechanism used by *C. truncatus*, as revealed by observations of a captive-kept individual and shown in Fig. 14a–f. The mound near the entrance is the first material excavated when the animal starts digging (see also Minoprio, 1945, p. 50). The amount of sand in the mound should approximately equal the volume of the tunnel necessary to hold the entire animal plus an empty space, smaller than its body length, that is used to move the decompacted sediment from the front end to the rear end of the tunnel and allows the animal to breathe (Fig. 14e). As a consequence, the material used to form the menisci can be excavated by the *pichiciego* from a range of depths (linked with burrow inclination) that roughly compares with its body length. In this scenario, the mixing of two or more layers of sediments of different composition (i.e. brown siltstone and whitish calcareous mudstone at the Prospecting Pit site, Fig. 7f) in different proportions can produce menisci of contrasting coloration. Another potential source of whitish or mixed material in the fill of *N. meuleni* are former burrows.

Holocene and late Miocene specimens of *N. meuleni* may be attributable to *C. truncatus*. Although unlikely, we cannot discard the possibility that older specimens were produced by an unknown Chlamyphorinae. Chlamyphorinae is considered a major lineage of armadillos within Dasypodidae that diverged from its sister-group Tolypeutinae during the Oligocene (around 32 Ma; Delsuc et al., 2004; Möller-Krull et al., 2007). Their strictly subterranean lifestyle developed sometime between 32 and 17 Ma because of palaeoenvironmental changes that led to the development of more arid habitats in South America (Delsuc et al., 2012). The two extant, allopatric genera *Chlamyphorus* and *Calyptophractus* separated around the transition between early and middle Miocene (17 ± 3 Ma; Delsuc et al., 2012). In accordance with these data, the presence of late Miocene chlamyphorines as producers of *N. meuleni* is viable. The producer can be pinned down to *Chlamyphorus* because *Calyptophractus* developed, and is still restricted to, north of the Paraná river basin (i.e., much farther north than our study sites), while *Chlamyphorus* occurs south of it (Delsuc et al., 2012).

8.3. Comparison with similar structures

Large meniscate burrows attributed to vertebrates that share some features with *N. meuleni* have been described for rocks ranging in age from Permian to Recent, and are mainly known from aeolian successions (Ward, 1988; Smith, 1993; Loope, 2008; Schmeisser et al., 2009). The most similar structures are backfilled meniscate burrows described from aeolian dune and interdune facies of the Tsondab Sandstone of the Namib desert (Ward, 1988), which is Miocene to Holocene in age (Pickford et al., 1995). These 50 mm-wide structures are composed of menisci with an alternate arrangement, where the thickest part of successive menisci is displaced from the midline (Fig. 12 in Ward, 1988). The fill of these structures was, however, not described, and it is not known whether they bear surface ridges on the external wall. These trace fossils were assigned to the Namib golden mole (*Eremitalpa granti namibiensis*, Chrysochloridae) because

of the close similarity with its modern surface traces (Fig. 13 in Ward, 1988). The remaining aeolian case studies include burrows from USA that commonly have a massive fill of which a small portion is meniscate, namely those of the Jurassic Entrada Sandstone (Loope, 2008) and those of the interdune deposits of the Nebraska Sand Hills produced by the Medieval pocket gopher (Schmeisser et al., 2009). The latter example shares a few features with *N. meuleni*, including the average diameter of 65 mm, its occasional appearance in high density spots, and rare meniscate backfilling (Fig. 4D in Schmeisser et al., 2009). The only fluvial example was described by Smith (1993) as "septate burrows or trails" on rippled point bar paleosurfaces from the Upper Permian Beaufort Group of South Africa. These are 2–3 m long and 60–90 mm wide trace fossils, with a meniscate fill composed of fine-grained sandstone with slightly coarser interlayers (Fig. 24 in Smith, 1993).

The apparent resemblance of *N. meuleni* with the purported Namib golden mole burrows described by Ward (1988) and a common palaeoenvironmental setting for both trace fossils may indicate a behavioural convergence in subterranean insectivorous mammals that dig in friable, sandy substrates. Gasc et al. (1986) sustained that the Namib golden mole is not a "sand swimmer", as commonly thought, as its digging locomotion involves compaction and decompaction of sand. Although the details of the subsurface locomotion of *Chlamyphorus* (producer of *Nagtuichnus*) and *Eremitalpa* (possible producer of the Tsondab Sandstone burrows) differ, both are parasagittal scratchers, a feature only shared with one extant mammal, the Australian marsupial mole (*Notoryctes typhlops*, Chrysochloridae) (Holm, 1969; Gasc et al., 1986). The marsupial mole is also an insectivorous subterranean mammal that inhabits sandy deserts and actively backfills its burrows. This elusive small marsupial (body mass: 30–60 g) essentially builds horizontal, backfilled burrows with a circular cross-section (average width: 40 mm). Its burrows are more abundant in sandy dunes or sand flats at a depth ranging between 0.2 and 1.0 m, usually in association with spinifex grass (*Triodia* spp.), various acacias, and other shrubs. The marsupial mole also avoids digging in harder soils of the interdune areas, preferring dune crests and slopes (Benshemesh and Johnson, 2003; Benshemesh, 2004, 2008; Benshemesh and Schulz, 2008). It is, however, not known whether the marsupial mole burrow has a meniscate structure (cf. Benshemesh and Schulz, 2008).

Three small insectivorous subterranean mammals (*Chlamyphorus*, *Eremitalpa*, and *Notoryctes*) seem to produce similar backfilled burrows, reflecting a behavioural convergence for living in friable and partially vegetated sandy desert areas. In terms of overall burrow architecture and diet of the producer, all these insectivorous mammals dig ephemeral structures in search of prey. In contrast, herbivorous rodents (like cavies and tuco-tucos) build permanent or semipermanent, open burrows of protracted usage.

9. Conclusions

1) The new ichnogenus and ichnospecies *Nagtuichnus meuleni* is proposed to include unbranched, large meniscate burrows showing a compartmentalized backfill. The fill is composed of a meniscate core and an outer massive and discontinuous layer of sediment. Other distinguishing features are a surface texture composed of sets of two or three parallel ridges on the external wall of the fill (and corresponding grooves in the host sediment), a particular outline of the menisci, and paired rounded pits in the concave surface of menisci.
2) The new ichnospecies is attributed to mammals, most probably to the pink fairy armadillo or *pichiciego* (*Chlamyphorus truncatus*, Dasypodidae). The key features that allow identification of the producer of *N. meuleni* are: (a) long, unbranched, backfilled burrows (suggesting fully subterranean habits) with a width compatible with extant *pichiciegos*, (b) the curvature and outline of menisci matching those of the rump plate of *C. truncatus*, (c) surface texture of the external wall of *N. meuleni* in the form of sets of parallel ridges that agree with claw width and separation of claws in the forelimbs of *pichiciegos*, (d) possible impression of the tail in the concave surface of menisci of *N. meuleni* that are of similar size and separation as the scales on the tail of *pichiciegos*.
3) *Nagtuichnus meuleni* occurs only in interdune deposits, and the particular ichnofabric developed in Holocene deposits of Gran Salitral could also be indicative of damp to dry interdune settings. The interval of the late Miocene–early Pliocene Río Negro Formation that contains *N. meuleni* is interpreted as damp and dry interdune deposit. *N. meuleni* was not found in associated thick cross-bedded sets (aeolian dune deposits). A similar palaeoenvironmental setting can be envisaged for the Holocene sediments of Gran Salitral. In this case, *N. meuleni* starts in dry interdune deposits and reaches down into the underlying wet interdune deposits.
4) During observation of burrow systems of *Ctenomys azarae* and *Microcavia australis* at Gran Salitral, some morphological signatures of potential application in palaeoichnological studies were identified. These include an open burrow with circular cross-section, heavily scratched ceiling and sides of tunnels with a chevron pattern, and smooth flat floor for *C. azarae*. *Microcavia australis* burrow systems display a plano-convex burrow cross-section with a bilobed floor, a smooth external wall, presence of rounded scratched knobs on the ceiling, a terminal chamber, and insect burrows in the wall.
5) The resemblance between burrow systems produced by Chlamyphorinae (*N. meuleni* and modern *Chlamyphorus truncatus* burrows), extant and purported fossil burrows of the Namib golden mole (*Eremitalpa*), and probably extant marsupial mole burrows (*Notoryctes*), reflects a behavioural convergence for living in friable and partially vegetated sandy desert areas (both dunes and interdunes).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.palaeo.2012.06.026. These data include Google map of the localities studied in this article.

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