



Large mammal burrows in late Miocene calcic paleosols from central Argentina: paleoenvironment, taphonomy and producers

María Cristina Cardonatto¹ and Ricardo Néstor Melchor²

¹Departamento de Geología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Santa Rosa, La Pampa, Argentina

²Instituto de Ciencias de la Tierra y Ambientales de La Pampa, Universidad Nacional de La Pampa and Consejo Nacional de Investigaciones Científicas y Técnicas, Santa Rosa, La Pampa, Argentina

ABSTRACT

Large cylindrical sediment-filled structures interpreted as mammal burrows occur within the loess-paleosol sequence of the late Miocene Cerro Azul Formation of central Argentina. A total of 115 burrow fills from three localities were measured. They are typically shallowly dipping, subcylindrical, unbranched structures with rounded ends and lacking enlargements. The horizontal diameter of the burrows range between 0.15 and 1.50 m, with most of the burrows in the interval of 0.39 to 0.98 m. Geometric morphometric analysis of transverse cross-sections support their distinct subcircular and elliptical (horizontally flattened) shapes. Burrow fills are typically laminated in the lower part and massive in the upper part. The laminated intervals reflect pulses of flowing water entering the abandoned burrow during moderate rains, whereas massive intervals reflect mass flow input of dense sediment-water mixtures during heavy rains that produced sheet floods. Approximately 1% of the burrows contained fragmentary, disarticulated and weathered mammal bones that were introduced in the open burrow by currents along with other sedimentary particles. Analysis of the tetrapod burrow fossil record suggests that Miocene burrows, including those studied herein, reflect a remarkable increase in the average size of the fossorial fauna. We conclude that large late Miocene mammals dug burrows essentially as a shelter against environmental extremes and to escape predation. The simple architecture of the burrows suggests that the producers essentially foraged aboveground. Several mammal groups acquired fossorial habits in response to cold and seasonally dry climatic conditions that prevailed during the late Miocene in southern South America. The considerable range of horizontal diameters of the studied burrows can be attributed to a variety of producers, including dasypodids, the notoungulate *Paedotherium minor*, Glyptodontidae and *Proscelidodon* sp.

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Corresponding author

María Cristina Cardonatto,
mccardonatto@exactas.unlpam.edu.ar

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INTRODUCTION

Fossil vertebrate burrows are relatively common biogenic structures and the oldest convincing evidence of tetrapod burrows are Early Permian (Asselian-Artinskian)

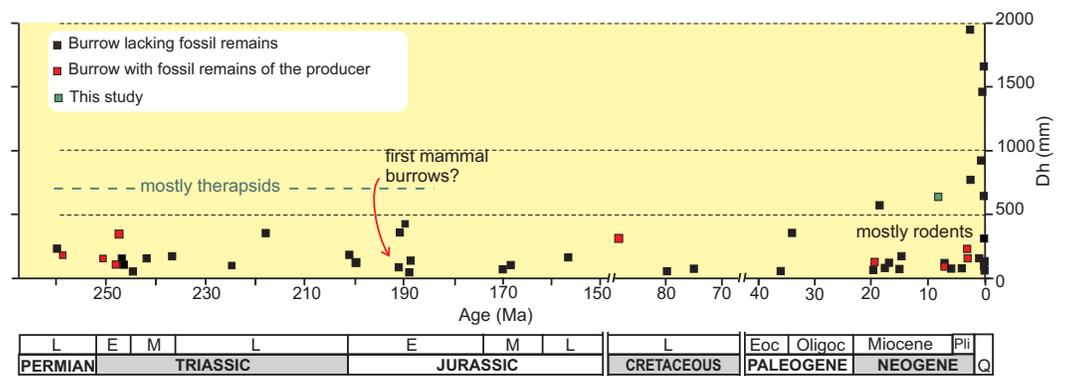


Figure 1 Plot of horizontal diameter of fossil tetrapod burrows vs age. Plot of the average horizontal diameter (Dh) of fossil tetrapod burrows in the published literature against the age of the hosting rock, distinguishing between burrows with remains that were interpreted as belonging to the producer, those lacking bone remains and the present study. Note that the age axis contains two gaps in the Cretaceous and Paleocene. Source of information on [Article S1](#). Image credit: Ricardo N. Melchor and María C. Cardonatto.

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lyosphorid amphibian burrows from Kansas, USA (*Hembree, Martin & Hasiotis, 2004*). Most pre-Cretaceous tetrapod burrows have been attributed to therapsids, in part on the basis of the finding of articulated skeletons in a few Late Permian-Early Triassic burrows (*Smith, 1987; Groenewald, Welman & MacEachern, 2001; Damiani et al., 2003; Modesto & Botha Brink, 2010*). A common architecture for Permian to Jurassic tetrapod burrows is a shallowly inclined ramp with a rounded and not enlarged end, of reduced horizontal diameter (*Fig. 1*), with discrete scratch marks, always showing a horizontally flattened elliptical cross-section, and commonly with a bilobed bottom (e.g., *Damiani et al., 2003; Sidor, Miller & Isbell, 2008; Riese, Hasiotis & Odier, 2011; Liu & Li, 2013; Melchor & Loope, 2016; Krummeck & Bordy, 2018*). Most of Jurassic tetrapod burrows occur in eolian sequences including the oldest subhorizontal burrow systems that have been assigned to primitive mammals from the Early Jurassic Navajo Sandstone of USA (*Riese, Hasiotis & Odier, 2011*) (*Fig. 1*). In contrast, there is a dearth of reports of Cretaceous tetrapod burrows which could possibly be due to the more equable climates that existed for most of this period. An exceptional occurrence for the Late Cretaceous is the unique dinosaur burrow containing an adult and two juvenile remains of ornithomimids, further suggesting denning behavior and parental care (*Varricchio, Martin & Katsura, 2007*).

Most Cenozoic tetrapod burrows have been attributed to mammals, mainly to Rodentia and Xenarthra (e.g., *Voorhies, 1975; Martin & Bennett, 1977; Benton, 1988; Gobetz & Martin, 2006*), whereas a few examples are related to Carnivora (e.g., *Hunt, Xiang-Xu & Kaufman, 1983; Hembree & Hasiotis, 2008*). The record of Paleogene tetrapod burrows is meager and may also be linked to dominantly benign climate conditions (*Fig. 1*). The Miocene record of tetrapod burrows is more varied and abundant, with a diversification of the architectural patterns and behavioral strategies that, commonly, appeared under stressed volcanoclastic and eolian environments. The early Miocene volcanoclastic floodplains of Nebraska, USA, witnessed the appearance of (1) the celebrated vertical

helical burrows ending in a ramp and terminal chamber named *Daimonelix* (e.g., [Barbour, 1892](#); [Martin & Bennett, 1977](#)), as well as (2) smaller, complex subhorizontal rodent burrow systems with terminal chambers and subcircular cross-section ([Gobetz & Martin, 2006](#)), and (3) the first carnivore den ([Hunt, Xiang-Xu & Kaufman, 1983](#); [Hunt, 1990](#)). Also in the early Miocene, the coastal dunes of Germany preserved the oldest fossil food cache ([Gee, Sander & Petzelberger, 2003](#)). The main tetrapod burrowing innovation during the middle Miocene is represented by cylindrical, subhorizontal, unbranched tunnels with a meniscate backfill interpreted as foraging tunnels of small Dasypodidae from southern South America ([Melchor et al., 2012](#); [Melchor et al., 2016](#)). Pliocene burrows are small (horizontal diameter less than 250 mm) and those from the Atlantic coast of the Buenos Aires province, Argentina have received a considerable attention, because they are common and a significant number of the burrows contains bone remains (e.g., [Genise, 1989](#); [Quintana, 1992](#); [Fernández, Vassallo & Zárate, 2000](#); [Elissamburu, Dondas & De Santis, 2011](#)). These are subcircular burrows assigned to rodents and notoungulates. The Pleistocene megafauna of South America is also reflected in the burrow trace fossil record in the form of huge tunnels (up to 2 m wide), with horizontally flattened elliptical cross-sections from Argentina and Brazil (e.g., [Quintana, 1992](#); [Vizcaíno et al., 2001](#), [Buchmann, Pereira Lopez & Caron, 2009](#), [Genise & Farina, 2012](#); [Frank et al., 2012](#); [Frank et al., 2015](#)). The smaller burrows are attributed to Dasypodidae and Pamphathiidae and the larger to ground sloths. It has been suggested that the adoption or generalization of burrowing behavior by large Pleistocene herbivorous mammals may reflect the arrival of large carnivorans after the Great American Biotic Interchange, just before the Pliocene-Pleistocene boundary ([Soibelzon et al., 2009](#)).

A trend towards larger diameter burrows is evident from the early Miocene to the late Pleistocene (see [Fig. 1](#)). Pre-Miocene burrows attain a maximum average horizontal diameter (Dh) of 420 mm (the examples from the Navajo Sandstone described by [Loope, 2006](#)); however, most are in the range of 100–200 mm. From the Miocene on, burrows with an average horizontal diameter in excess of 500 mm are recorded ([Fig. 1](#)), including those studied herein. The Neogene record also includes more common and smaller burrows (Dh \sim < 200 mm) that are mostly attributed to rodents and small Dasypodidae ([Fig. 1](#)).

In this context, the tetrapod burrows from the late Miocene Cerro Azul Formation are the largest pre-Pleistocene tetrapod burrows and can help to understand the reasons for acquisition of burrowing habits in large Cenozoic mammals from South America. These structures have been partially and briefly described ([Genise et al., 2013](#)), but a detailed description has yet to be done and is an objective of this study. The purposes of this work are: (1) to infer the likely producers of these late Miocene large burrows and (2) to interpret the taphonomic processes involved in the preservation of the burrow casts and its paleoecological and paleoenvironmental meaning.

MATERIAL & METHODS

The studied localities with late Miocene burrows are distributed in a latitudinal belt of approximately 25 km ([Fig. 2](#)): Salinas Grandes de Hidalgo (SG, 37°12'55"S, 63°35'25"W; 100 masl); Laguna Chillhué (LC, 37°19'15.13"S; 64°14'31.52"W; 145 masl); and Laguna La

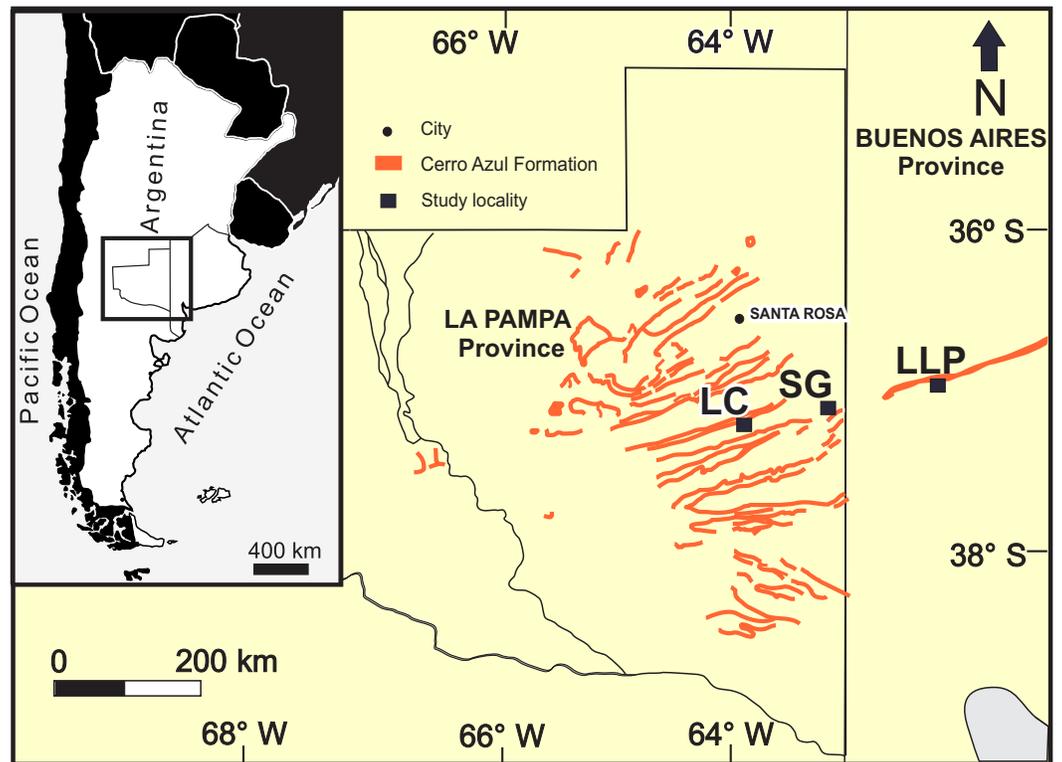


Figure 2 Study area. Study area in central Argentina (inset), outcrops of the Cerro Azul Formation and localities in La Pampa and Buenos Aires provinces. LC: Laguna Chillhué, SG: Salinas Grandes de Hidalgo, LLP: Laguna La Paraguaya. Modified from *Cardonatto et al. (2016)*.

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Paraguaya near Carhué city (LLP, $37^{\circ}5'53.57''\text{S}$; $62^{\circ}47'34.98''\text{W}$; 101 masl). The first two localities belong to La Pampa province, whereas the remaining is located in the adjacent Buenos Aires province. The burrow fills appear in outcrop as transverse to oblique, longitudinal, tangential and plan view exposures.

Another locality of the Cerro Azul Formation, a roadcut in national road 154 (R154, $37^{\circ}49'28.5''\text{S}$, $64^{\circ}4'8.9''\text{W}$), has been previously described as having vertebrate burrows (*De Elorriaga & Visconti, 2001*). However, this locality is not considered herein because the burrows probably postdate significantly the deposition of the unit. The reasons for this inference are: (1) burrow diameters are considerably larger than those described herein (Dv up to 2.25 m) and more consistent with burrows attributed to a large Pleistocene megafauna (e.g., *Vizcaino et al., 2001*; *Frank et al., 2012*); and (2) the burrow cut the carbonate nodules of the capping calcrete. Although absolute dating of the calcrete is not available, it has been suggested that the calcretization process significantly postdates the deposition of the Cerro Azul Formation (*Vogt, Carballo & Calmels, 1999*; *Melchor & Casadio, 2000*; *Visconti et al., 2010*). The main argument for this inference is that the calcrete is developed in sedimentary sequences ranging in age from late Miocene to Pleistocene.

Standard measurements in burrows were horizontal diameter (Dh), vertical diameter (Dv), preserved length, mean azimuth of burrow fill and inclination of fill laminae. The

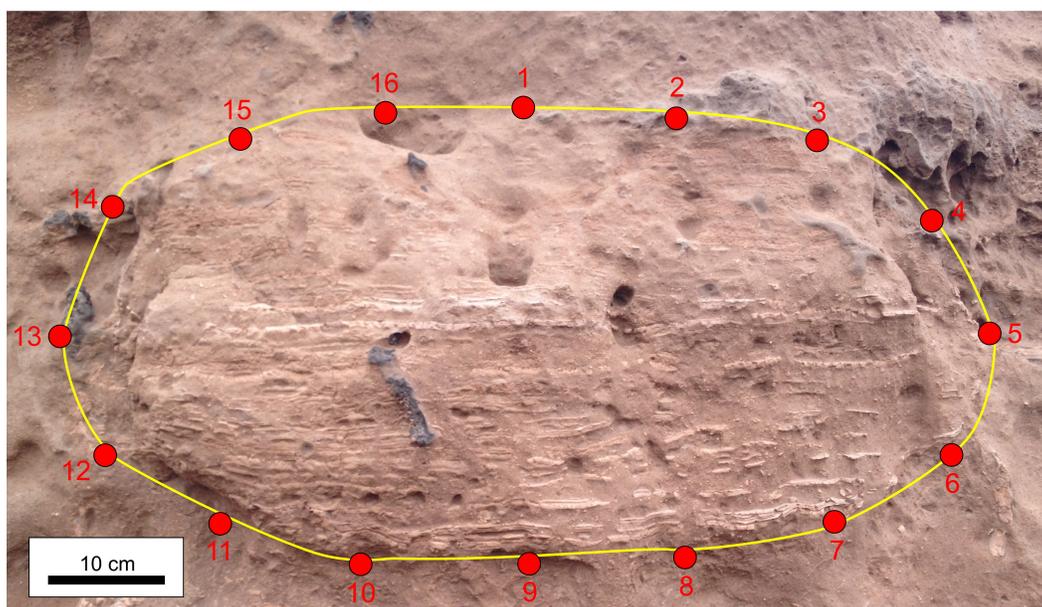


Figure 3 Example of location of landmarks. Location of landmarks (red points) on burrow fills preserved in cross section. Photo credit: Ricardo Néstor Melchor.

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mean azimuth was measured using a compass and considering the burrow fill boundary and dominant plunge of laminated fill. When changes of dip direction or inclination were observed in a single burrow fill they were recorded separately. Burrow diameter (especially D_h) was measured orthogonal to the main axis of the structure. The horizontal diameter was obtained from almost all types of exposures (except for longitudinal ones), whereas the vertical diameter was mostly an apparent value, except for the rare transverse sections, where it can be considered the true vertical diameter. At each location, GPS coordinates were recorded; the burrow fills were photographed and sketched.

The burrow fills exposed in transverse section ($n = 24$) were used for a 2-D geometric morphometric analysis. From field photographs, the outline of the burrow boundary was sketched in Corel DrawTM. These images were used to build a file with the TPSutil software. Burrow cross section outlines were oriented with respect to the top and bottom of the hosting bed and treated as symmetrical outlines. For each image a total of 16 type II landmarks (*Slice et al., 2008*) were digitised using the TPSdig2 software- Landmark 1 and 9 were positioned in the intersection of the burrow outline and the maximum vertical axis, whereas landmarks 5 and 13 resulted from the intersection of the maximum horizontal axis with the burrow outline. The remaining landmarks were arranged with an equidistant pattern on the burrow outline (*Fig. 3* and *Article S2*). Landmarks were aligned using the Procrustes superposition method (*MacLeod, 2009*) and the principal component analyses (PCA) using MorphoJ software. Results are presented by eigenvalue diagrams and PC scores, along with transformation grids.

From scaled sketches of transverse sections of burrow fills, the cross-sectional area of the burrow was estimated using ImageJ software. This cross-sectional area was used to estimate the body mass of the producer using the allometric relations of [Wu et al. \(2015\)](#).

At each locality, a detailed sedimentary log was measured and samples of host rock and burrow fill were collected for petrographic analysis. Also, at selected locations a detailed sedimentologic log of the burrow fill was measured. Mammal bones found *in situ* within burrow fills were recorded and collected for preparation and taxonomic identification. Fossil bones found outside burrows were not recorded or collected. Fossil remains from La Pampa province collected during this study are housed at the Paleontological Collection of the Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Santa Rosa city, La Pampa, Argentina, under the acronym GHUNLPam. Fossil material collected in burrows from Laguna La Paraguaya locality (Buenos Aires province) are housed at the Museo Histórico Regional de Guaminí “Coronel Marcelino E. Freyre” under the acronym MHG-P. Field work was approved by the Dirección Provincial de Museos y Preservación Patrimonial, under the Project “Vertebrados del Mioceno tardío-Plioceno en el área de las lagunas encadenadas del oeste de la provincia de Buenos Aires. Aportes a la bioestratigrafía del Cenozoico tardío de la Región Pampeana”, permit nr. 2015-3-P-156-2.

Geological setting

The Cerro Azul Formation outcrops are located in the north-western, central, and eastern part of La Pampa province and adjacent western Buenos Aires province, Argentina ([Linares, Llambías & Latorre, 1980](#); [Folguera & Zárate, 2009](#); [Visconti et al., 2010](#)). The unit is characterized by a monotonous succession of loess containing moderately developed paleosols ([Fig. 4](#)) that has been assigned to the late Miocene (Huayquerian Land Mammal age) essentially on the basis of its mammal remains ([Montalvo & Casadio, 1988](#); [Verzi, Montalvo & Vucetich, 1999](#); [Verzi, Montalvo & Tiranti, 2003](#)). In particular, the formation is considered as representing the interval between 10 and 5.7 Ma ([Cione et al., 2000](#); [Verzi, Montalvo & Deschamps, 2008](#)). The maximum exposed thickness in outcrop is 54 m, although the unit reaches about 180 m in the subsurface ([Visconti et al., 2010](#)). The formation is essentially composed of structureless, light brown (5YR 6/4), pale reddish brown (10R 5/4) or grayish orange pink (5YR 7/2), sandy siltstones and fine-grained sandstones, showing moderate selection and common carbonate cementation.

RESULTS

Sedimentology of the burrow—bearing sections

Macroscopic features of the studied sections are very similar to those of the classical localities of the Cerro Azul Formation outcrops (e.g., [Visconti et al., 2010](#); [Genise et al., 2013](#); [Cardonatto et al., 2016](#)), especially those of the Salinas Grandes de Hidalgo and Laguna La Paraguaya. Paleosol profiles are typically composed of two horizons ([Fig. 4](#)). The upper horizon is a clayey siltstone that is distinguished by the presence of subangular blocky, granular or prismatic peds and a darker color (5 YR 6/4) than the underlying horizon. Carbonates are rare except for the local occurrence of calcareous rhizoliths. This upper horizon can be compared with a Bt horizon and its thickness averages 0.60 m (range

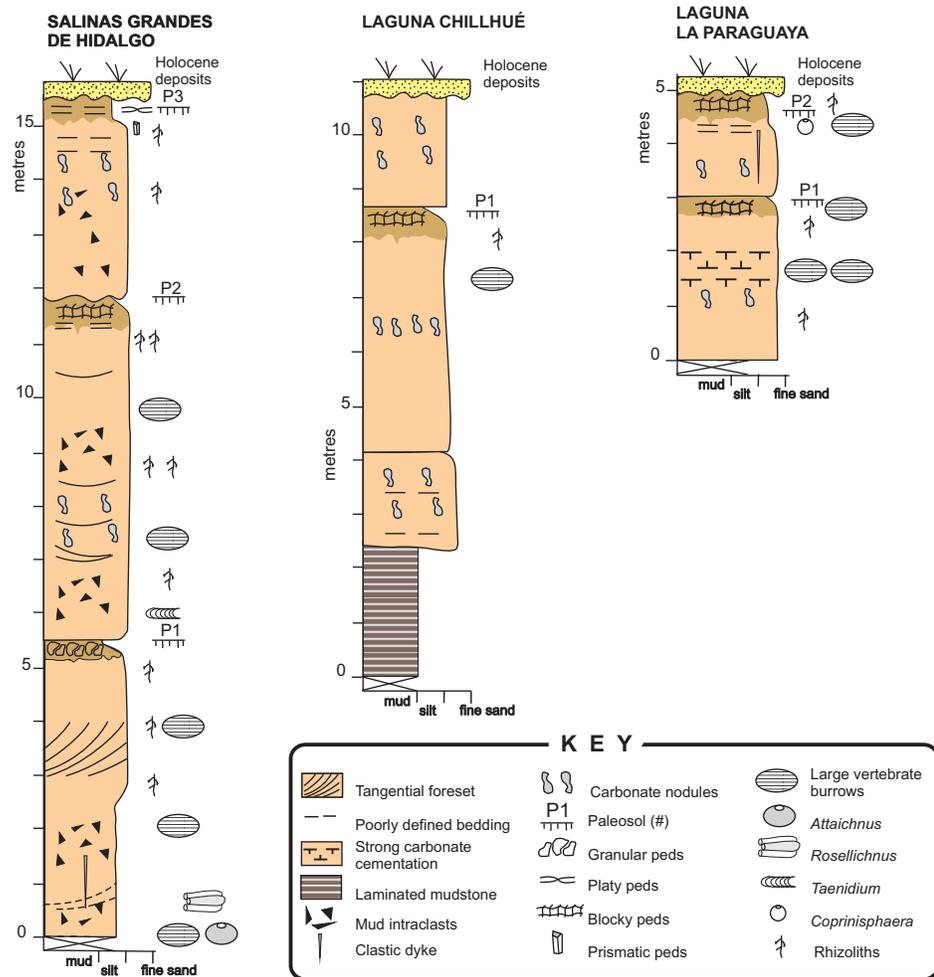


Figure 4 Sedimentary logs. Detailed sedimentary logs of the measured sections from the study localities. Image credit: Ricardo Néstor Melchor.

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= 0.35–1.00 m, $n = 5$), which is very close to the average for the formation (*Cardonatto et al., 2016*).

The lower horizon is characterized by lighter colored (5 YR 7/2), siltstone to fine-grained sandstone with pervasive carbonate cementation, both in the form of nodules and rhizoliths. Rhizoliths are small to medium sized and commonly 1–30 mm in diameter. The lower horizon can be up to more than 5 m thick and contain relicts of primary sedimentary structures, like tangential cross-bedding or horizontal bedding, as seen in the Salinas Grandes de Hidalgo section (*Fig. 4*). Mudstone intraclasts are common throughout. The remains of primary sedimentary structures and carbonate cementation suggest comparison with a Bk or Bk/C horizon. The trace fossils described in this paper occur in both horizons.

The section at Laguna Chillhué also contains similar paleosols (*Fig. 4*) and differs from the other localities by the presence of a 2 m thick, dark-red, laminated mudstone interval in the lower part of the section (*Montalvo et al., 1995*). The presence of a mudstone interval

in the lower section of the Cerro Azul Formation has been questioned by [Lorenzo, Mehl & Zárte \(2013\)](#), who supposed a younger age for this mudstone interval on the basis of geomorphological inferences. However, at this location the laminated mudstone interval is overlain, through a normal sedimentary contact, by lithologies typical of the Cerro Azul Formation containing mammal remains of Huayquerian (late Miocene) age, with no evidence of reworking. Vertebrate burrow fills were not observed in the laminated mudstone interval.

Description of large burrow fills

A total of 115 fossil burrows were measured from three localities: 53 from Salinas Grandes de Hidalgo, 59 from Laguna La Paraguaya, and three from Laguna Chillhué (see [Table S1](#)). The studied burrow fills are distinguished on the basis of the presence of a thinly laminated siltstone to mudstone interval that contrasts with the structureless host rock. When the upper part of the fill is massive and similar in grain size to the host rock, the upper burrow boundary is indistinct. Burrow fills exhibit an induration, composition and cementation similar to the hosting rocks, suggesting that they are too of late Miocene age. At Laguna La Paraguaya locality, the preferential carbonate cementation of the burrow fills resulted in 3-D exposures ([Fig. 5A](#)). At this locality the density of fossil burrows is locally high and may be difficult to find unburrowed intervals. Cross-cutting relationships between two or more burrows are common ([Figs. 5B, 5C](#)).

Size and plan view pattern

Observed horizontal diameter (D_h) ranges from 0.15 to 1.50 m ($n = 112$) and the frequency distribution suggests a roughly normal distribution where three subpopulations can be distinguished ([Fig. 6](#)). The small subpopulation has a D_h from 0.15 to 0.34 m (8 %), the intermediate subpopulation has a D_h from 0.39 to 0.98 m (84 %), and the large subpopulation exhibits a D_h from 1.05 to 1.50 m (8 %).

In plan view exposure, which is found only at SG and LLP localities ($n = 78$), a number of morphologies can be distinguished ([Fig. 7](#)). (1) The more common are straight to slightly curved burrows (89 % of cases), which exhibits a $D_h = 0.15\text{--}1.15$ m, showing a uniform inclination of internal laminae (ranging from $\approx 0^\circ$ to 27°), the maximum height difference between the proximal and distal portion of a burrow is 0.6 m, and the maximum preserved length is 5.18 m ([Figs. 7A, 7B](#)). Some burrow fills in this category display a decrease in inclination of internal laminae toward more distal positions (i.e., from 27° to 8°). (2) A sinuous burrow that displays two opposite curves in plan view was recorded in 5% of the cases ([Figs. 7C, 7D](#)). The horizontal diameter of sinuous burrow ranges from 0.42 to 0.80 m, dip of internal laminae is subhorizontal to slightly inclined (up to 8°), and the maximum observed length is 8 m. (3) The third plan view pattern is a C-shaped curve observed in 6% of the burrows, with an horizontal diameter ranging from 0.44 to 0.72 m ([Figs. 7E 7F](#)), which commonly appears as a ramp with a height difference of up to 0.55 m, the inclination of internal laminae can be uniform (from 3° to 12°) or show a shallowing toward the distal position (from 14° to subhorizontal).

In a few cases, the distal portion of burrow showed a lateral expansion of up to 23% of the D_h , commonly having a subhorizontal lamination ([Figs. 7G, 7H](#)). Other burrow

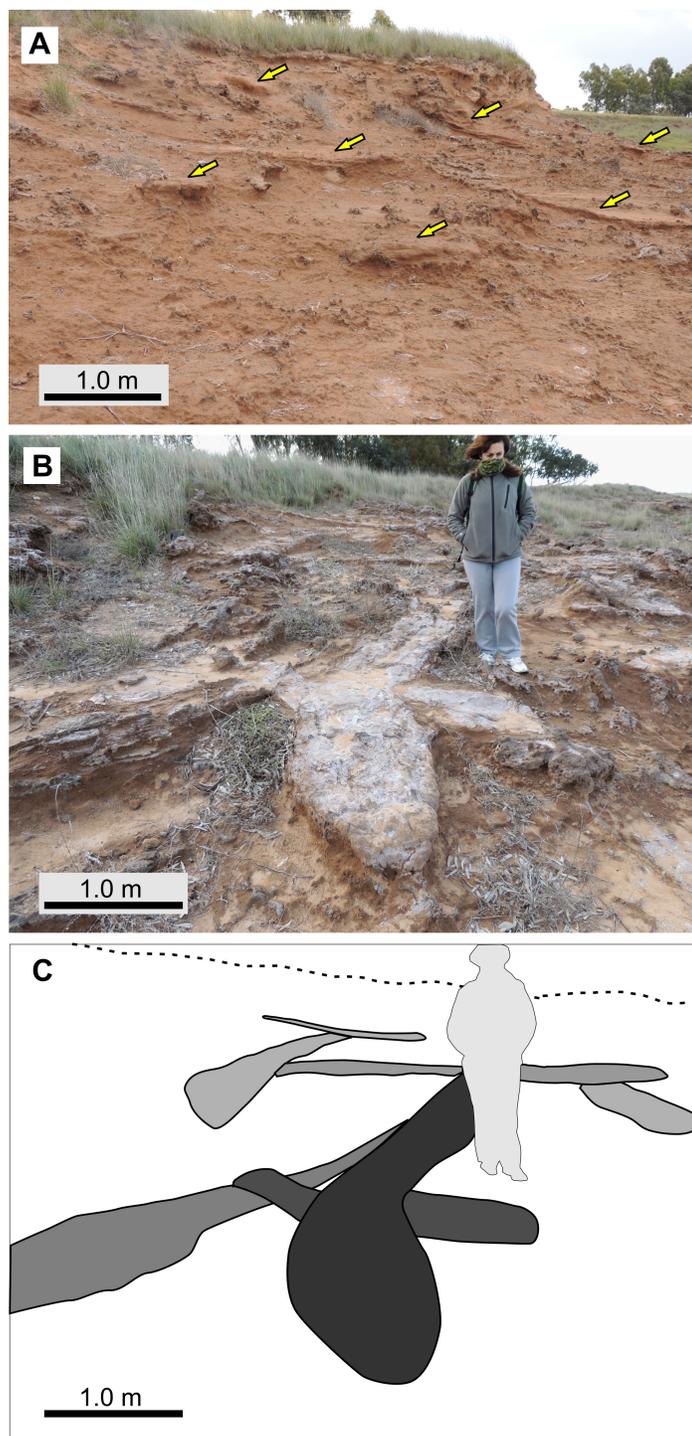


Figure 5 Abundance and cross-cutting relationships of burrows, from LLP locality. (A) General view of the outcrop showing several burrows (yellow arrows). (B–C) Field view and diagram of cross-cutting relationships between different fossil burrows (distinguished in C with different shades of gray). Photo and image credit: Ricardo Néstor Melchor.

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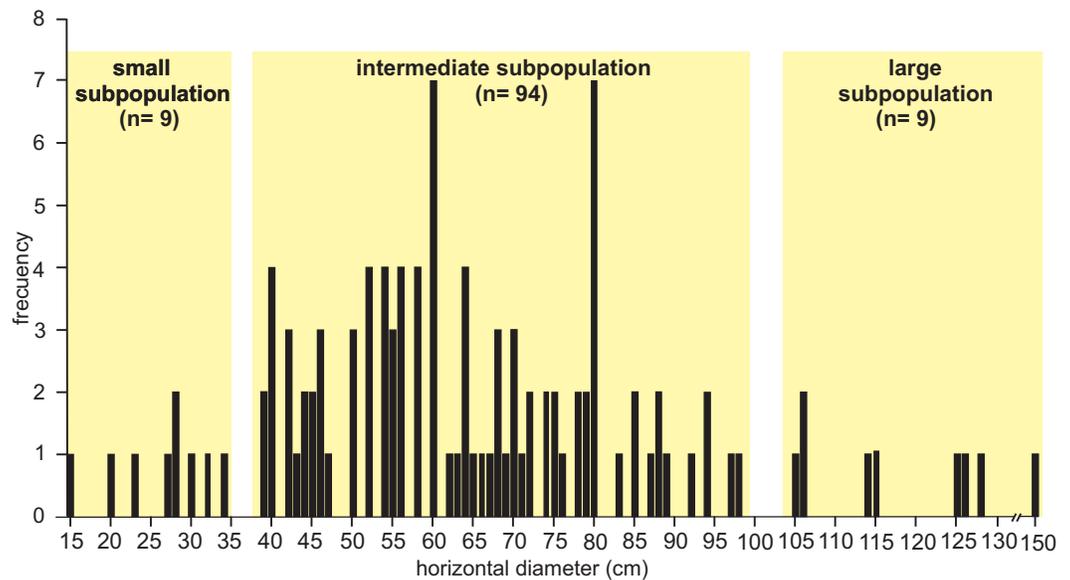


Figure 6 Histogram of horizontal diameter. Histogram showing the frequency distribution of horizontal diameter (Dh) for the studied fossil burrows. Three subpopulations can be distinguished. Image credit: María Cristina Cardonatto.

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fills exhibit a rounded end with no enlargement that can be accompanied by an upward bending of mudstone laminae against the walls of the burrow.

Cross-sectional shape and body mass

The analysis of the well defined cross-sectional shape of burrows ($n = 24$ from all localities) suggest a distinction between elliptical (with the major axis subhorizontal) and subcircular cross-sections. Elliptical cross-sections are more common ($n = 18$) and the corresponding Dh ranges from 0.39 to 1.50 m (belonging to the intermediate and large subpopulations, Fig. 6), with an average Dv/Dh ratio of 0.55. The burrows with elliptical cross-section include a few cases ($n = 4$) with a flat bottom and convex top. The subcircular cross-sectional shape ($n = 6$) is represented in the intermediate subpopulation with a Dh ranging from 0.39 to 0.56 m, and an average Dv/Dh ratio of 0.88.

Morphometric analyses suggest that 90.13 % of the variation is explained by the first two principal components (Fig. 8B), and deformation grids range from elliptical (score = -0.12) to subcircular (score = 0.17) (Fig. 8A).

Body mass estimates of the producers of the burrow on the basis of the cross-sectional area (using the method by Wu *et al.*, 2015) suggest that there are two ranges (Table S1). Most of the estimates ($n = 18$) belongs to the intermediate subpopulation with a range from 37 to 439 kg, whereas the remaining estimates comes from the large subpopulation ($n = 7$) with a range 708 to 1,623 kg. Burrows with subcircular cross-section from the intermediate subpopulation, are linked with a producer having body mass from 92.84 to 186.0 kg.

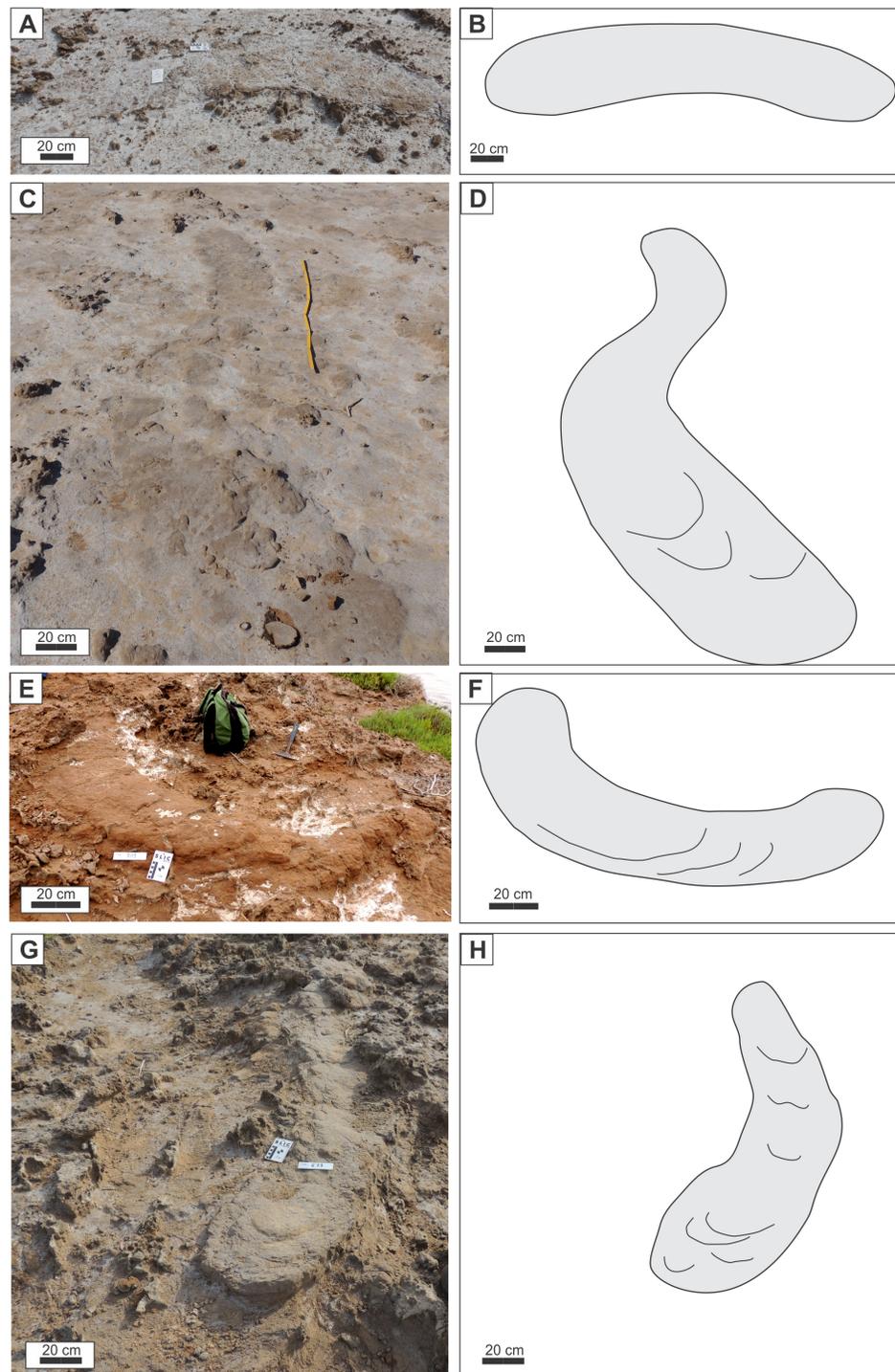


Figure 7 Burrow morphology in plan view. (A–B) Field photograph and diagram of slightly curved burrow. (C–D) Field photograph and diagram of sinuous burrow. (E–F) Field photograph and diagram of “C” shaped burrow. (G–H) Field photograph and diagram of burrow with slightly enlarged and rounded end. Curved lines in the diagrams represent weathered laminae. Photo credit: Ricardo Néstor Melchor. Image credit: María Cristina Cardonatto.

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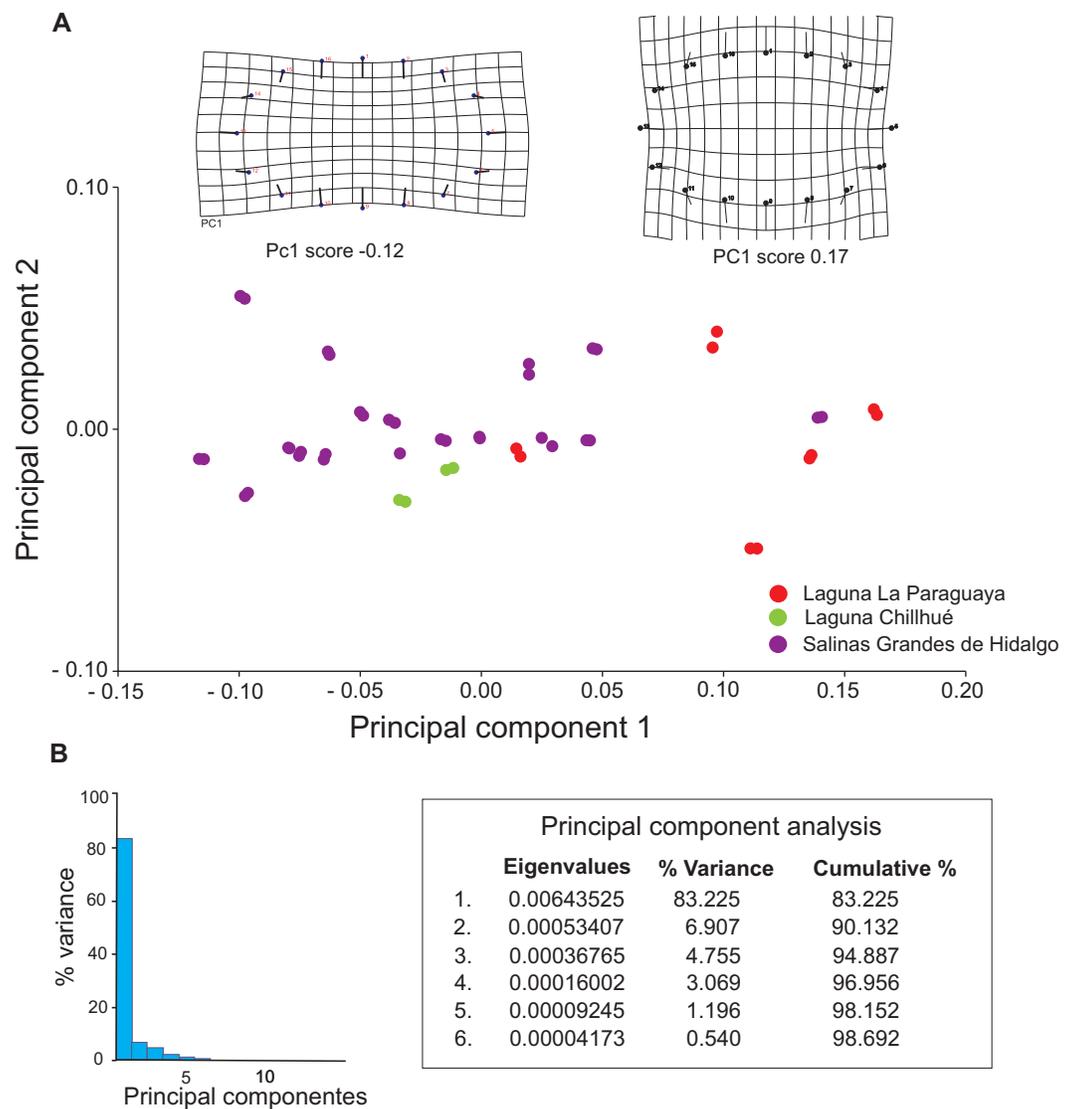


Figure 8 Results of geometric morphometric analysis of fossil burrows preserved in cross section. (A) Plot of principal components 1 and 2, distinguishing by study locality, and deformation grids for elliptical (PC1 score -0.12) and subcircular (PC1 score 0.17) shapes. (B) Histogram of variance of principal components. Image credit: María Cristina Cardonatto.

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Orientation and inclination

Readings of plunge azimuths of burrow fills from all localities are variable but most values are located in the northeast to southeast quadrants (i.e., between $N20^\circ$ and $N140^\circ$) (Figs. 9A, 9C). The average dip angle of all measured burrows with respect to the paleohorizontal is 7.25° and ranges from nearly 0 to 27° (Fig. 9B). Most orientation data come from the intermediate subpopulation ($D_h = 0.39\text{--}0.98$ m) and especially from LLP locality.

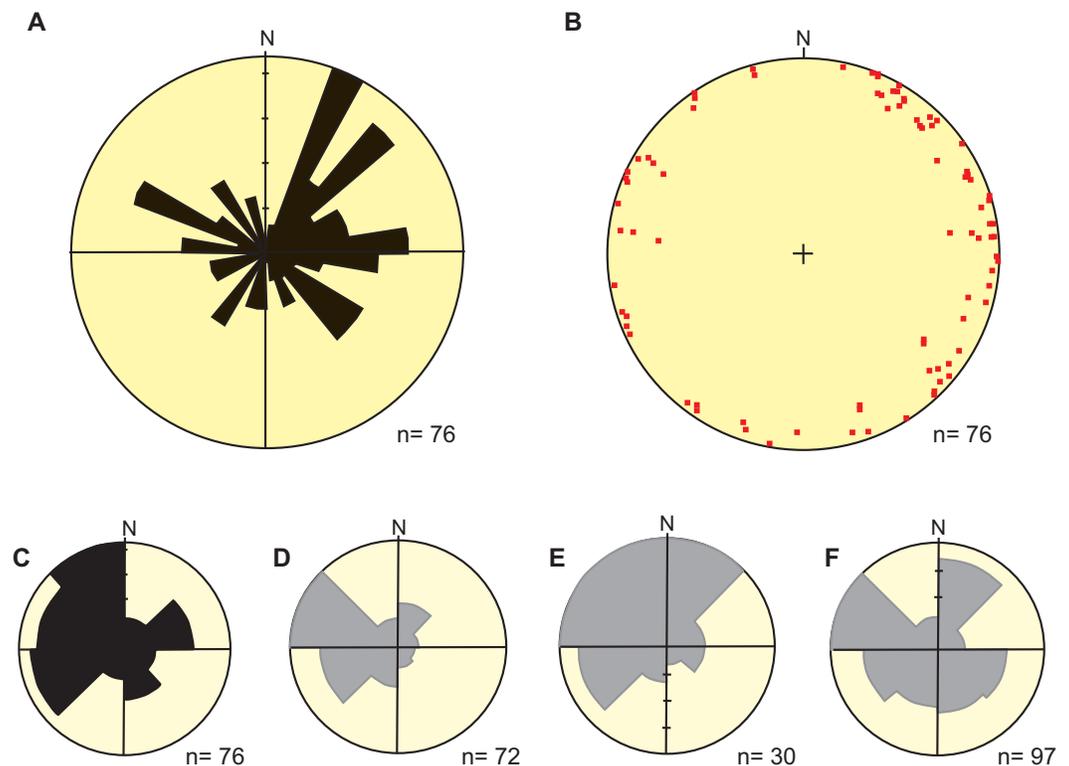


Figure 9 Orientation of fossil burrows compared with modern data from dasypodid burrows. (A) Rose diagram showing the dip azimuth of fossil burrows. (B) Equal area projection of dip azimuth and dip angle of fossil burrows. (C) Entrance orientation of fossil burrows, assuming that it is located at 180° of measured dip azimuth. The data in A–C is from SG and LLP localities, those from the remaining locality are preserved only in cross-section. (D) Entrance orientation of several species of dasypodid burrows from semiarid settings of northern-central Argentina build from data by [Crespo \(1944\)](#). (E) Entrance orientation of *Dasypus hybridus* burrows from a grassland setting in Uruguay build from data by [González, Soutullo & Altuna \(2001\)](#). (F) Entrance orientation of *Chaetophractus villosus* burrows from cultivated land in Buenos Aires province, Argentina build from data by [Abba, Udrizar & Vizcaino \(2005\)](#). Image credit: Ricardo Néstor Melchor.

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Composition of burrow fills

The vertebrate burrows are easily spotted in the field because of the distinctive laminated structure of the infilling sediments that contrasts with the structureless host rock. The filling is composed of an alternation of laminated claystone and siltstone with massive fine-grained sandstone and siltstone containing floating claystone intraclasts. Laminated intervals are a few millimeters to about 50 mm thick, whereas massive intervals tend to be thicker. Most of the burrow fills display a laminated interval in the lowermost part of the fill, with the upper part massive, especially in the Salinas Grandes de Hidalgo locality (Figs. 10A–10C). A few burrows display a poorly defined lamination to massive structure throughout (Fig. 10D). Claystone and siltstone laminae at the bottom of the structure typically deflect upwards against the burrow wall, which is a good criterion to distinguish burrow fills that are mostly exhumed by erosion. Laminae tend to be horizontal but successive laminated packages resting at low angles were also identified. Individual laminae

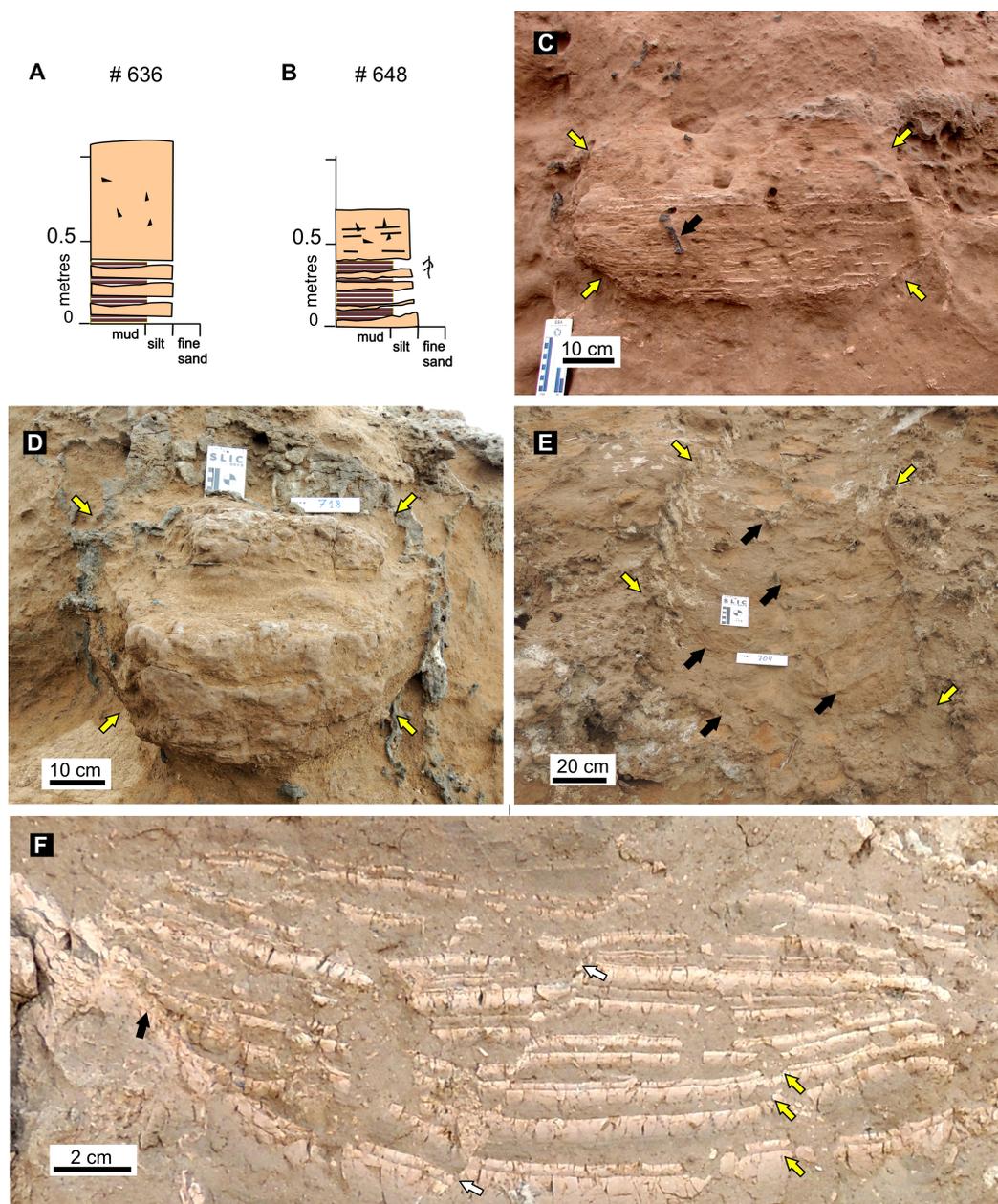


Figure 10 Features of fossil burrow fills. (A–B) Detailed sedimentary logs of the fill of selected burrows (see Table S1 for information on these burrow fills). References as for Fig. 4. (C) Cross-section of laminated to massive burrow fill # 648 from SG, represented in (B). Elliptical outline of fill indicated by yellow arrows, black arrow point to subvertical rhizolith cutting the laminated fill. (D) Cross-section of burrow fill # 714 from LLP. Subcircular outline of poorly laminated to massive burrow fill indicated by yellow arrows. (E) Pseudomeniscate structure in burrow fill # 704 from LLP seen in plan view. Yellow arrows point the outline of the burrow and black arrows to individual pseudomenisci. (F) Detail of laminated burrow fill (# 632 from SG) showing direct grading in siltstone to claystone laminae (yellow arrows), syndimentary fault (white arrows) and onlap of clay laminae on burrow wall (black arrow). Image credit: Ricardo Néstor Melchor.

Full-size DOI: 10.7717/peerj.4787/fig-10

are normally graded (typically siltstone grading to claystone), and locally disrupted giving a brecciated aspect. Both synsedimentary faulting and deformation were identified (Fig. 10F). A pseudomeniscate structure was identified in two cases (one from Salinas Grandes de Hidalgo and the other from Laguna La Paraguaya). This structure is composed of massive siltstone or fine-grained sandstone arranged in adjacent crescent-shaped bodies with the convex margin pointing downslope that span the full width of the fill (Fig. 10E). Horizontal width of individual pseudomeniscate bodies taken parallel to the burrow axis is 120 mm.

Associated ichnofossils

Only the ichnofossils found within or very close to the burrow fills are considered. We found within the fills abundant rhizoliths and rare smaller vertebrate burrows, vertebrate footprints and ?*Rosellichnus* isp. In the paleosol adjacent to the fills we found *Taenidium barretti*, *Attaichnus kuenzelli* and *Coprinisphaera* isp.

Calcareous rhizoliths, including rhizocretions and root casts, are abundant and were recorded in all studied localities. Rhizoliths are arranged in vertical, oblique and subhorizontal position (Fig. 10C). Rhizoliths are submillimeter to 30 mm thick and the maximum preserved length is 500 mm. Rhizoliths occurring inside burrow fills are similar in shape and cementation to those of the hosting rock.

A single small burrow (Fig. 11A) that cuts the laminated interval of a larger vertebrate burrow fill was identified at Salinas Grandes de Hidalgo (# 638). The 43 mm in diameter structure displays a subcircular outline and a poorly laminated siltstone fill.

A partially eroded burrow fill from Laguna La Paraguaya (# 708) exposed an internal bedding plane of the filling showing closely spaced elliptical depressions with a noticeable marginal rim (Fig. 11C). These are tentatively interpreted as footprints of a quadrupedal animal composing a 316 mm wide trackway. If this is a trackway a pace angulation of 112° and a stride length of 600 mm can be inferred. Measurements on individual footprints indicate that average footprint length is 144 mm, average footprint width is 93 mm, and the marginal rim is of uniform thickness and about 50 mm wide.

A group of five subcircular rings in the upper part of a burrow fill (# 659A from SG) is tentatively identified as a cluster of bee cells and compared with the ichnogenus *Rosellichnus* (Fig. 11D). The presence of the ichnogenus at this locality, although at other section, was already documented by *Cardonatto et al. (2016)*.

Adjacent to the burrow fills at Salinas Grandes de Hidalgo, several specimens of *Attaichnus kuenzelli* were identified, in some cases very close, but no cross-cutting relationship were seen. A few specimens of *Taenidium barretti* also occur at this locality, in the form of subcylindrical burrows, 12 mm wide and 80 mm long with an average meniscus thickness of 2.2 mm. At Laguna La Paraguaya we also found two specimens of cemented and compact spherical chambers (diameter 18.7–23.0 mm) with a large emergence hole (10–11 mm) assigned to *Coprinisphaera* isp. (Fig. 11B).

Bone remains found within burrow fills

Mammal bones within the burrow fills are scarce (only 1% of burrows contained fossil remains) and usually appear disarticulated and poorly preserved, in some cases with

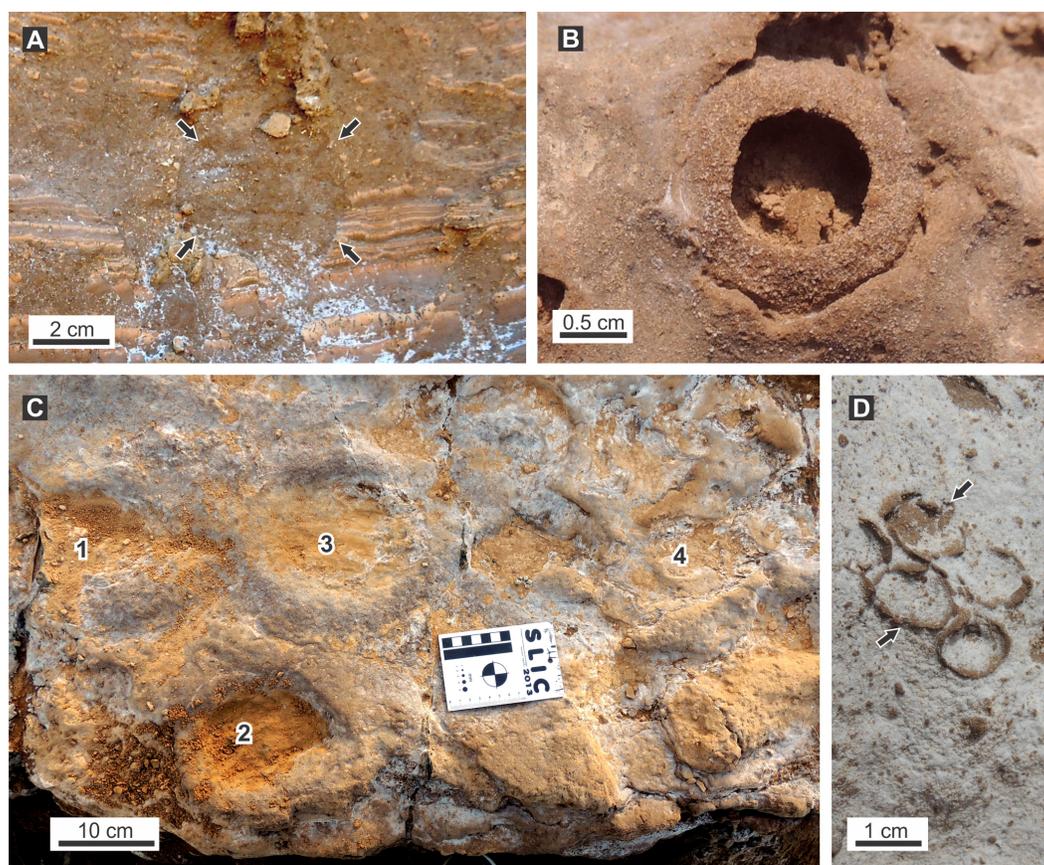


Figure 11 Ichnofossils associated with burrow fills. (A) Small burrow fill (black arrows) cutting the laminated fill of a larger mammal burrow from SG locality. (B) *Coprinisphaera* isp. from LLP locality. (C) Tetrapod footprints on the top of laminated fill of a burrow from LLP locality. Numbers refers to individual footprints. (D) ?*Rosellichnus* isp. (arrowed) inside a burrow fill from SG. Photo credit: Ricardo Néstor Melchor.

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signs of abrasion (Fig. 12A). The fossil remains from the SG locality are *Proscelidodon* sp. and Glyptodontidae indet., whereas the rest of the fossil material was found at LLP locality, including: *Paedotherium minor* (two specimens), *Doellotatus* sp., *Eosclerocalyptus* sp., Mesotheriinae indet., Glyptodontidae indet. (three specimens), and undeterminate mammals (two specimens). For details about the taxonomy and illustrations of mammal remains, see Article S3 and Fig. S1. The only articulated remains are glyptodont osteoderms found at Laguna La Paraguaya (# 702) that are assigned to *Eosclerocalyptus* sp. (Fig. 12B), and remains of a carapace with several articulated osteoderms from the same locality (# 670) assigned to Glyptodontidae indet. *Proscelidodon* sp. remains (including a hemimandible with teeth and postcranial elements) appeared disarticulated but associated within a single burrow fill. The fossil remains display different degree of weathering and corrosion, as well as biostratinomic fractures.

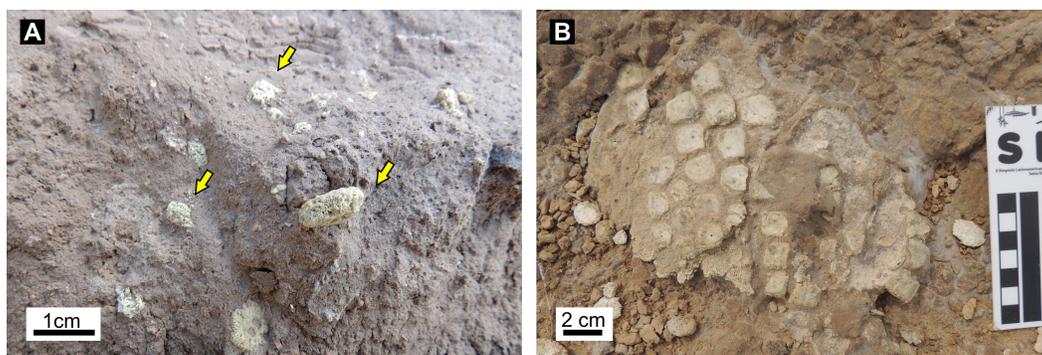


Figure 12 Bone remains inside burrow fills. (A) Close-up of isolated, weathered and fragmentary glyptodontid osteoderms from a vertical section of a burrow fill from SG locality. The burrow boundary is not shown in the photograph. (B) Partly articulated osteoderms of *Eosclerocalyptus* sp. found inside a burrow fill from LLP locality. Photo credit: Ricardo Néstor Melchor.

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DISCUSSION

Producers

The studied fossil burrows are unbranched and display a significant variation in the horizontal diameter, which ranges from 0.15 m to 1.5 m (Fig. 6). The simple, ramp type morphology of the studied burrows suggests that the animals foraged aboveground (e.g., Reichman & Smith, 1990). In order to infer the likely producers of the fossil burrows there are several constraints that need to be considered: (1) the faunal remains found inside the burrow fills; (2) the fossorial mammals that were recorded in the Cerro Azul Formation, especially those from the studied localities; (3) the size of burrows, as expressed by the Dh; and (4) the overall architecture and cross-section of burrows (including the Dv/Dh ratio) and the extrapolated body mass of its digger. The surface ornamentation of burrows is commonly a very useful clue to the producer (e.g., Seilacher, 2007); however, it is not preserved in the studied cases.

Faunal remains found in burrow fillings

In general, bone remains found inside a burrow can be considered as belonging to its producer or occupant only if they are articulated, disarticulated but still closely associated, nearly complete, are commonly found in a terminal portion and fit the size (cross-sectional diameter) of the burrow (e.g., Smith, 1987; Groenewald, Welman & MacEachern, 2001; Damiani et al., 2003). The remains found inside the studied burrows do not fulfill any of these criteria. In most cases, these bone remains have been passively introduced and it is uncertain if they belong to the producers. The remains are essentially fragmentary, disarticulated, with evidence for abrasion and weathering (Fig. 12A, Fig. S1); suggesting that they spent some time at the surface and then were introduced into the burrows by currents along with other sedimentary particles. The fragmentary and disarticulated state of *Doellotatus* sp. and one of the specimens of *Paedotherium minor* and the considerably small size of the animals (body mass about 1–2 kg, Table 1) in comparison with the containing burrows; further suggest that these remains were introduced by currents. In the case of

Table 1 Body mass estimate of producers. Relationship between cross-sections and body mass of the putative producers, estimated body mass according to Wu et al. (2015). See estimate of cross-sectional area and body mass for every burrow in Table S1.

Range of burrow Dh (m)	Estimated body mass (kg)	Fossil remains inside burrow fill	Potential burrow producer	Body mass of potential producer (kg)
0.15–0.34	1–13	<i>Paedotherium minor</i>	<i>Paedotherium</i>	1.86 (Elissamburu, 2004)
			<i>Doellotatus</i>	Less than 1 (Vizcaíno & Fariña, 1999)
			<i>Chasicotatus</i>	Less than 1 (Scillato-Yané, Krm-potic & Esteban, 2010)
			<i>Proeuphractus</i>	2–3 (Perea & Scillato-Yané, 1995)
			<i>Chorobates</i>	1–10 (Vizcaíno & Fariña, 1999)
			<i>Lagostomus</i>	1–10 (Vizcaíno & Fariña, 1999)
0.39–0.94	37–439	Mesotheriinae indet.	<i>Mesotheriinae</i>	20.88–60.13 (Croft, Flynn & Wyss, 2004)
			<i>Eosclerocalyptus</i> sp.	More than 100 (Vizcaíno & Fariña, 1999)
			<i>Glyptodontidae</i> indet.	More than 100 (Vizcaíno & Fariña, 1999)
			<i>Glyptodontidae</i> indet.	More than 100 (Vizcaíno & Fariña, 1999)
			<i>Macrochorobates</i>	10–100 (Vizcaíno & Fariña, 1999)
			<i>Macroeuphractus</i>	10–100 (Vizcaíno & Fariña, 1999)
			<i>Proscelidodon</i> sp.	581.8 (De Esteban-Trivigno, Mendoza & De Renzi, 2008); 850 (Bargo et al., 2000); 1,057 (Fariña, Vizcaíno & Bargo, 1998). Body mass of <i>S. leptocephalum</i>
			<i>Paedotherium minor</i> <i>Doellotatus</i> sp.	
1.05–1.5	708–1,623	<i>Glyptodontidae</i> indet.	<i>Glyptodontidae</i>	More than 100 (Vizcaíno & Fariña, 1999)
			<i>Proscelidodon</i>	581.8 (De Esteban-Trivigno, Mendoza & De Renzi, 2008); 850 (Bargo et al., 2000); 1,057 (Fariña, Vizcaíno & Bargo, 1998). Body mass of <i>S. leptocephalum</i> .

Notes.

Dh, horizontal diameter.

Proscelidodon sp., the bones are disarticulated but associated, which suggest that they can belong to a single specimen, and the partial horizontal diameter of the burrow match the size of this ground sloth. The only articulated remains are fragments of the dorsal carapace of *Glyptodontidae* that occur in burrows large enough to hug these animals (Dh = 0.78 to 1.50 m) (Table 1). In consequence, the unique remains that can belong to the producer of the burrows are *Proscelidodon* sp. and those of *Glyptodontidae*.

Fossorial mammals of the Cerro Azul Formation and size of burrows

The mammals with fossorial habits recorded in the Cerro Azul Formation include xenarthrans, notoungulates and rodents (e.g., [Goin, Montalvo & Visconti, 2000](#); [Cerdeño & Montalvo, 2001](#); [Urrutia, Montalvo & Scillato-Yané, 2008](#)). Among the Xenarthra, the Glyptodontidae, Dasypodidae and Mylodontidae display fossorial adaptations. The same is true for Mesotheriidae and Hegetotheriidae (Notoungulata); and Caviidae, Octodontidae, and Chinchillidae (Rodentia). Below we discuss the potential producers for each size class of the burrows ([Table 1](#)) as expressed by the horizontal diameter and cross-sectional area of the burrows.

For the small subpopulation ($D_h = 0.15\text{--}0.34$ m, 8% of cases), with a body mass ranging from 1 to 13 kg, the likely candidates are the notoungulate *Paedotherium minor*, the dasypodids *Doellotatus*, *Chorobates*, *Proeuphractus*, and *Chasicotatus*; and the rodent *Lagostomus*. *Paedotherium* (Hegetotheriidae) is a medium-sized rodent-like ungulate native to South America. This taxon is very common in the Cerro Azul Formation, both in La Pampa and Buenos Aires provinces (e.g., [Montalvo, Tomassini & Sostillo, 2016](#)). Articulated remains of this genus have been found within Pliocene burrow casts (about 0.16–0.22 m wide) from the Atlantic coast of Buenos Aires province (e.g., [Genise, 1989](#); [Scognamillo, 1993](#); [Elissamburu, Dondas & De Santis, 2011](#)) and a morphofunctional analysis of its postcranial skeleton suggest a digging capacity ([Elissamburu, 2004](#)).

The Dasypodidae show a neotropical geographic distribution and were important components of the late Miocene-Pliocene South American fauna ([Scillato-Yané, 1982](#); [Ortiz Jaureguizar, 1998](#)). Dasypodids exhibit fossorial habits and were abundant during the late Miocene in the Pampean region of Argentina, suggesting preference for open environments and well drained soils ([Scillato-Yané et al., 2013](#)). Most dasypodids recorded in the Cerro Azul Formation were small- to medium-sized, with body mass in the range 1–10 kg for *Doellotatus*, *Chasicotatus*, *Proeuphractus* and *Chorobates* ([Table 1](#)). In particular, the holotype of *Chasicotatus ameghinoi* is a nearly complete carapace about 150 mm wide ([Scillato-Yané, Krmpotic & Esteban, 2010](#)), which match the lower size range of the small subpopulation. Modern dasypodid burrows are usually simple ramps lacking significant enlargements (e.g., [González, Soutullo & Altuna, 2001](#); [Abba, Udrizar & Vizcaino, 2005](#)), which is similar to the architecture of the fossil burrows.

In the same localities of *Paedotherium*-bearing burrows from the Atlantic coast of the Buenos Aires province, there are also burrows containing articulated remains of *Lagostomus* that partially overlap in diameter with those containing *Paedotherium* remains ([Genise, 1989](#); [Elissamburu, Dondas & De Santis, 2011](#)). The extant *Lagostomus maximus* (plains vizcacha) is well known for its digging adaptations and for living in communal burrow systems (e.g., [Jackson, Branch & Villarreal, 1996](#)). Plains vizcacha burrow systems show an average entrance horizontal diameter of 0.26 m and a range of 0.17–0.37 m ([Llanos & Crespo, 1952](#)), which matches the range of the small subpopulation. However, extant *L. maximus* burrow systems have several entrance ramps that typically converge into a central chamber or a much more complex architecture (e.g., [Llanos & Crespo, 1952](#); [Rafuse et al., in press](#)), which contrast with the simple ramp type morphology of the fossil burrows. The 43 mm in diameter subcircular burrow identified in the fill of a larger burrow at

Salinas Grandes de Hidalgo (# 638) is probably related to a caviomorph rodent (Caviidae or Octodontidae).

For the dominant intermediate subpopulation ($D_h = 0.39\text{--}0.94$ m, 83% of measured burrows), with an estimated body mass ranging from 37 to 438 kg, the likely candidates are the Mesotheriinae (Mesotheriidae, Notoungulata); *Eosclerocalyptus*, *Coscinocercus*, and *Aspidocalyptus* (Xenarthra, Glyptodontidae); *Macrochorobates* and *Macroeuphractus* (Xenarthra, Dasypodidae); and *Proscelidodon* (Xenarthra, Mylodontidae). The fossil remains found in this size range that are likely candidates are those of Glyptodontidae and *Proscelidodon* sp. (Table 1). There are two Mesotheriinae species recognized for the late Miocene of central Argentina: *Pseudotypotherium subinsigne* and *Typotheriopsis silveyrai* (Cerdeño & Montalvo, 2001). These species exhibited a small to medium size (20.88 to 60.13 kg after Croft, Flynn & Wyss, 2004) (Table 1). The Mesotheriidae shows modifications in the appendicular skeleton that suggest a scratch-digging habit and fossorial adaptations and are envisaged as having used its hypsodont teeth to cut roots and break the substrate, to aid digging with claws (Shockey, Croft & Anaya, 2007).

Kraglievich (1934) and Quintana (1992) suggested that glyptodonts were not functionally suited for digging. However, a geometric morphometric study of the limb bones of five glyptodont species of Miocene and Pleistocene age and comparison with extant armadillos led Vizcaíno et al. (2011) to conclude that were generalized diggers, as modern Dasypodini and Euphractini. Generalized diggers are species that dig short burrows for protection or in search of food and that feed on the surface or just below it by making 'food probes' (Abba, Udrizar & Vizcaíno, 2005). In order to assess if glyptodonts were likely producers of the fossil burrows we compared the width of the dorsal carapace and the dorsal carapace height / width ratio with comparable values of the fossil burrows. Dorsal carapace width of Miocene-Pliocene glyptodonts range between 0.40 and 0.77 m (Perea, 2005; Vizcaíno et al., 2011; Zurita et al., 2011), well in the range of horizontal diameter of the fossil burrows. Information on the ratio between carapace height and width for Miocene-Pliocene glyptodonts is incomplete, and similar data for Pleistocene South American glyptodonts (Duarte, 1997; Zurita et al., 2010) average 0.87 (range = 0.78–0.91; $n = 4$). In our case study, glyptodonts are considered good candidates for constructing the subcircular burrows of the intermediate subpopulation, which are 0.39–0.56 m wide and display an average D_v/D_h ratio of 0.88. Regarding the large dasypodids *Macrochorobates* and *Macroeuphractus*, the available body mass estimates suggest a range of 10 to 100 kg (Vizcaíno & Fariña, 1999) and little is known about their paleoecology.

Among the mylodontids, the Scelidotherinae, endemic to South America (McDonald, 1987; Taglioretti et al., 2014); are only represented for the Huayquerian—Chapadmalian SALMAs (late Miocene to early Pliocene) by *Proscelidodon*, a ground sloth related to open environments with grasslands, under temperate and warm climate (Miño Boilini et al., 2011; Pujos et al., 2012; McDonald & Perea, 2002). A digging habit was inferred for *Proscelidodon* after a morphofunctional study of a Montehermosian (latest Miocene-early Pliocene) forelimb (Aramayo, 1988). Body mass estimates are only available for Pleistocene scelidotherines (Table 1) and range from 584 to 1,057 kg (De Esteban-Trivigno, Mendoza & De Renzi, 2008; Bargo et al., 2000; Fariña, Vizcaíno & Bargo, 1998). These would be

maximum estimates for late Miocene scelidotherines because the primitive Mylodontidae were smaller and there seems to be a trend toward progressively larger sizes in the Pleistocene (e.g., [McDonald & Perea, 2002](#)). Large Pliocene-Pleistocene fossil burrows near Mar del Plata city (Buenos Aires province) have been attributed to mylodonts on the basis of the finding of bone remains inside the fill ([Frenguelli, 1955](#)) and using the surface ornamentation of the burrows ([Zárate et al., 1998](#); [Dondas, Isla & Carballido, 2009](#)).

For the large subpopulation, with a Dh ranging from 1.05 and 1.50 m (9% of cases) and an extrapolated body mass of 700–1,600 kg, the more likely producer is *Proscelidodon* sp. and, secondarily, the Glyptodontidae.

To summarize, the studied fossil burrows can be attributed to several producers, according to their horizontal diameter. The more likely producers of the studied fossil burrows are: (1) for the small subpopulation, the smaller dasypodids (*Doellotatus*, *Chasicotatus*, *Proeuphractus* and *Chorobates*) on the basis of body mass, the fossorial habit and architecture of modern dasypodid burrows and, secondarily, *Paedotherium minor*. (2) For the intermediate and large subpopulations, the Glyptodontidae and Mylodontidae (*Proscelidodon* sp.) are good candidates as these were the largest representatives of the late Miocene burrowing fauna of the Cerro Azul Formation. The Glyptodontidae were generalized diggers, like modern dasypodids, and exhibited a carapace fitting especially the subcircular burrows. *Proscelidodon* sp. is also a likely candidate of the elliptical and larger burrows. For the intermediate subpopulation, probably the large dasipodids (*Macrochorobates* and *Macroeuphractus*) and Mesotheriinae should be considered.

Taphonomy of burrows

The horizontally laminated and massive fill of the burrows suggest that the material entered the excavation passively, that is after the burrow had been fully excavated, and without any assistance by the digger. The infill also indicates that the burrows were abandoned and received sediments in successive small pulses and large catastrophic events. Although we cannot discard some secondary input of dust by wind, most of the filling of the burrows is related to water transport as indicated by the well laminated and normal graded siltstone to mudstone laminae (Figs. 10A–10C, 10F). Laminated intervals are linked to successive pulses of sediment-laden water that eventually ponded in the terminal tracts of the burrows. This is in agreement with the interpretation by [Imbellone, Teruggi & Mormeneo \(1990\)](#) of similar Quaternary burrows and experimental results by [Woodruff & Varricchio \(2011\)](#). Experiments by [Woodruff & Varricchio \(2011\)](#) indicate that well-laminated fills were obtained by adding small amounts of sediment-water mixtures entering at a low angle (5°) into the burrow. In contrast, *en masse* pouring of the sediment-water mixture at high angle (30°) produced a massive and poorly sorted sediment fill, whereas *en masse* pouring at a low angle (5°) produced thicker graded beds ([Woodruff & Varricchio, 2011](#)). *En masse* filling experiments also produced “arcuate structures” ([Woodruff & Varricchio, 2011](#)) that are very similar to the pseudomeniscate structures described herein. Both features are comparable to “arcuate surface ridges” produced in experimental debris flows that reflect the pulsatory nature of experimental and natural debris flows ([Major, 1997](#)). The experiments by [Woodruff & Varricchio \(2011\)](#) lend further support to the interpretation of

the massive intervals as result of catastrophic input of large volume of unsorted sediment. As the burrows are related to an essentially flat landscape and no fluvial channel deposits were observed in any of the studied localities, the sediment pulses should be related with rainfall. We speculate that one or more laminae may result from moderate to heavy precipitation events. In contrast, massive intervals can be related to single heavy downpours producing sheet flooding, which can generate hyperconcentrated flows (e.g., [Smith & Lowe, 1991](#)) capable of transporting enough material to fill, at least, the terminal portion of a burrow in a single event. High-energy sheet floods can also saturate burrow walls and produce roof collapse.

Our studies also support the generalization that well laminated burrow fills will not contain remains of the producer and that massive fills of the whole burrow or most of the lower part have a greater chance of containing remains of the tetrapod that dug the burrow, as proposed by [Scognamillo \(1993\)](#) and [Groenewald, Welman & MacEachern \(2001\)](#). For the laminated burrow fills, the most likely scenario is that the burrow was vacated or, if the animal died inside, it may result scavenged and/or weathered, which produces incomplete and disarticulated remains. In the case of a massive fill, both live entombing ([Scognamillo, 1993](#); [Groenewald, Welman & MacEachern, 2001](#)) and fast burial after death ([Woodruff & Varricchio, 2011](#)) are required to produce a nearly articulated and complete skeleton. Massive fills in the upper half of the burrow will not preserve remains of its producer.

The episodic nature of the filling processes is evidenced by the laminated fill and further supported by the presence of footprints in the surface of some laminae and the cluster of bee cells (?*Rosellichnus* sp.) found inside the fill. These trace fossils suggest that partially filled burrows with a surface communication were explored or reoccupied by other tetrapods and used by bees to nest. Alternatively, the bee cells may be constructed after the complete filling of the burrow in the soil profile. Among the presumed producers of burrows of intermediate size, the outline and size of the footprints match those of Pleistocene glyptodonts but are quite different from those of ground sloths (compare [Aramayo et al., 2015](#)). Disruption of laminae composing the fill of the burrows is explained by drying and cracking of mud after a flood event, whereas synsedimentary faulting can be related to trampling by tetrapods.

Attaichnus kuenzelli occur profusely in the SG locality, in some cases very close, but never were cut by a large mammal burrow. These relationships suggest that the producers of the burrows were apparently not foraging on *A. kuenzelli*, considered a nest chamber of leaf-cutting ants ([Genise et al., 2013](#)).

Paleoecological and paleoenvironmental meaning

Detailed inferences about the paleoecological and paleoenvironmental meaning of the studied large mammal burrows can be gained through sedimentological study of the hosting rocks, analysis of orientation of fossil burrows and considering the associated trace fossils. This information, along with the potential producers will help to understand the reason for acquisition of burrowing habits in large late Miocene mammals.

Sedimentology

Thick, monotonous, massive continental successions of siltstone showing moderate to good sorting with associated paleosols, as those described for the Cerro Azul Formation, are typical of loess deposits, whose dominantly eolian origin is well established (e.g., [Johnson, 1989](#); [Pye, 1995](#)). The presence of pedogenic calcite is indicative of well-drained soil profiles in sub-humid, semi-arid, and arid climates with low rainfall (less than 800 mm/yr) and high evapotranspiration (see review in [Sheldon & Tabor, 2009](#)). Previous estimation of mean annual precipitation for the development of the paleosols of the Cerro Azul Formation is 449 ± 147 mm ([Cardonatto et al., 2016](#)). Paleosols showing a Bt horizon and blocky or prismatic peds can be compared with mollisols ([Cardonatto et al., 2016](#)). Some paleoenvironmental constraints can also be derived from the composition of the mammal fauna, and the stable isotopic composition of enamel teeth. Vertebrate remains of the Cerro Azul Formation, mainly notoungulates and rodents, suggest that these sediments were deposited in open landscapes like steppes or herbaceous plains ([Montalvo et al., 2008](#)). Carbon isotope composition from late Miocene herbivorous enamel teeth from Salinas Grandes de Hidalgo and nearby localities indicates a dominance of C3 plants in lowland areas ([MacFadden, Cerling & Prado, 1996](#)), which are favoured in climates with a cool growing season ([Ehleringer, Cerling & Helliker, 1997](#))

Orientation of burrows

Comparison with orientation data from modern Dasypodidae burrows can help to interpret the orientation pattern of fossil burrows. As xenarthrans are imperfect homeotherms, their body temperatures do change with the environment (e.g., [McNab, 1980](#); [McNab, 1985](#)). It has been suggested that the burrow entrance orientation of armadillos avoid prevailing winds and both uniform and preferential orientation has been documented (e.g., [McDonough & Loughry, 2008](#)). The cases of no preferential orientation are related to the invasive armadillo *Dasypus novemcinctus* from southern USA (Texas, Alabama, Oklahoma) and Belize ([Clark, 1951](#); [Zimmerman, 1990](#); [Platt, Rainwater & Brewer, 2004](#); [Sawyer et al., 2012](#)). All these cases are mostly related to forested areas. Studies documenting a preferred orientation of Dasypodidae burrows are from Argentina, Uruguay and Brazil, involving open environments and several species ([Crespo, 1944](#); [Carter & Encarnaçao, 1983](#); [González, Soutullo & Altuna, 2001](#); [Abba, Udrizar & Vizcaíno, 2005](#); [Ceresoli & Fernandez-Duque, 2012](#)). The pioneer study by [Crespo \(1944\)](#) included three localities from western Argentina, ranging from $27^{\circ}37''\text{S}$ to $34^{\circ}13''\text{S}$ with annual precipitation ranging from less than 200 mm to 500 mm. The vegetation ranges from low bushes, to shrubland and psammophilous grassland with sparse trees. These localities belong to the Monte and Espinal biogeographic provinces (e.g., [Roig, Roig-Juñent & Corbalán, 2009](#)) and the included armadillo species are: *Chaetophractus vellerosus*, *C. villosus* and *Zaedyus pichiy*. A compilation of the entrance orientation data from the three localities of [Crespo \(1944\)](#) suggests a dominant entrance orientation toward the west ([Fig. 9D](#)). This distribution is remarkably similar to the fossil burrows if we assume that entrance orientation was at 180° of dipping azimuth ([Fig. 9C](#)). Dominant surface wind patterns in northern Argentina are humid and sometimes hot winds from the east and north (e.g., [Barros et al., 2015](#)),

whereas cold winds are from the south. In consequence, the orientation pattern described by *Crespo (1944)* from open environments of the semiarid region of Argentina can be interpreted as preferential orientation of entrances avoiding dominant hot and cold winds. Similar patterns of armadillo burrow entrance orientation avoiding prevailing winds were documented by *Carter & Encarnaçao (1983)* in Minas Gerais, Brazil; *González, Soutullo & Altuna (2001)* in Uruguay (Fig. 9E); *Abba, Udrizar & Vizcaino (2005)* in Buenos Aires province of Argentina (Fig. 9F); and *Ceresoli & Fernandez-Duque (2012)* in Formosa province, northern Argentina. Alternative explanations for this preferential orientation are that, as the armadillos seek food following an odour in the wind, they tend to approach a site from downwind and dig in the lee side (*Carter & Encarnaçao, 1983*) and to maximize sun exposure during cold winters (*Ceresoli & Fernandez-Duque, 2012*). In particular, the most adequate example to evaluate the orientation of the fossil burrows is the data from dasypodid burrows by *Crespo (1944)*, which were collected in open semiarid settings similar to those of the late Miocene of central Argentina. In consequence, it is possible to propose that the late Miocene wind pattern of central Argentina was similar to the present one with hot winds from the east and north and cold winds from the south.

Associated trace fossils

The trace fossil assemblage of the Cerro Azul Formation is of low diversity and abundance and dominated by insect trace fossils (*Celliforma*, *Rosellichnus*, *Fictovichnus*, *Rebuffoichnus* and *Teisseirei*), and was compared with the *Celliforma* ichnofacies (*Cardonatto et al., 2016*). The *Celliforma* ichnofacies is typical of well-drained calcareous paleosols developed under low vegetation coverage (*Genise et al., 2010; Genise et al., 2016*). The reduced size of associated rhizoliths suggests that the vegetation was dominated by scrubs with minor participation of herbaceous plants.

The local occurrence of cemented *Coprinisphaera* at LLP and additional occurrences of fossil dung-beetle brood balls (*Quirogaichnus coniunctus* *Laza, 2006*) from the formation in a nearby locality (*Laza, 2006*) is indicative of the presence of the *Coprinisphaera* ichnofacies, suggesting herbaceous communities and wetter climatic conditions (*Genise et al., 2016*) for the easternmost locations of the formation.

Burrowing habits in large late Miocene mammals

Mammal burrows are typically constructed as shelters from environmental extremes and predators, and also for food storage, foraging and reproduction (e.g., *Reichman & Smith, 1990; Kinlaw, 1999*). From these common uses of burrows, protection from environmental extremes and predators are more likely for the studied fossil burrows and no evidence supporting the remaining functions is available. Top predators during deposition of the Cerro Azul Formation are the Phorusrhacidae (*Cenizo, Tambussi & Montalvo, 2012; Vezzosi, 2012*) that occupied the role of large carnivorans, as well as the Sparassodonta (*Goin, Montalvo & Visconti, 2000*).

However, the main factor controlling the occurrence of large mammal burrows during the late Miocene (Fig. 1) is herein related to environmental changes. It has been suggested that different mammal groups acquired fossorial habits during the Cenozoic as a response to the expansion of open, savanna-like environments under cold, dry and seasonal climates

(Nevo, 1979; Nevo, 1995; Nevo, 2011). During the late Miocene (the Huayquerian SALMA), southern South America experienced a global cooling as response to the increase in the Antarctic ice sheet (Zachos et al., 2001) and the uplift of the Andes (e.g., Amidon et al., 2017), which favored cold and seasonally dry climatic conditions. This regional framework is confirmed by the inferences on the sedimentology, faunal remains and invertebrate ichnology of the studied succession. This evidence suggests open environments, with well-drained soils and low vegetation coverage, and a semiarid and seasonal climate. Considering that the more likely candidates for the largest burrows are xenarthrans (Glyptodontidae and Mylodontidae), which are imperfect homeotherms (e.g., McNab, 1980; McNab, 1985), the necessity and convenience for excavating an underground refuge is clear. In addition to escape from predation, these animals used burrows to avoid extremely cold or warm climatic conditions in order to conserve energy and water, and to breed because of the particular physiology of xenarthrans (Vizcaíno et al., 2001).

CONCLUSIONS

Subcylindrical structures with a laminated fill occurring in a late Miocene loess-paleosol sequence from central Argentina are interpreted as burrows of fossorial mammals. The burrows occur associated with calcareous paleosols developed under a semiarid climate in a flat landscape. A detailed analysis of more than one hundred structures permitted to conclude that:

1. The more common geometry is a shallow ramp with a rounded end, lacking bifurcations.
2. The ample variation of the horizontal diameter of the burrows, along with cross-sectional shape and inferred body masses suggest that several producers were involved.
3. The smaller burrows ($D_h = 0.15\text{--}0.34$ m, 8% of cases, body mass ranging from 1 to 13 kg) were produced by small dasypodids and, secondarily, by the notoungulate *Paedotherium minor*.
4. For the dominant burrows exhibiting an intermediate ($D_h = 0.39\text{--}0.94$ m, 83% of measured burrows, producer body mass of 37 to 438 kg), and large horizontal diameter ($D_h = 1.05\text{--}1.50$ m, 9 % of measured burrows, producer body mass of 700–1,600 kg), the Glyptodontidae and Mylodontidae (*Proscelidodon* sp.) are the best candidates. The Glyptodontidae are related to the subcircular burrows of intermediate size and *Proscelidodon* sp. would be the producer of the elliptical and largest burrows.
5. About 10% of the burrow fills contained fragmentary, disarticulated, abraded and weathered bone remains that were introduced into the burrows by aqueous currents and do not belong to the excavator of the burrow.
6. After abandonment, the burrows received sediments from the surface that progressively filled the structure. The filling process was produced dominantly by several pulses of sediment laden currents related to moderate rains (well laminated fill) and *en masse* input of dense sediment-laden currents related to heavy rains producing sheet flooding (massive fill). During filling, the abandoned burrows were visited or reoccupied by other tetrapods and used by bees to nest,

7. In general, it is not considered likely that well laminated burrow fills will contain remains of the producer, whereas massive fills have a greater chance of containing remains of the tetrapod that dug the burrow.
8. The main factor explaining the appearance of large mammal burrows in the late Miocene are environmental changes, including the appearance of open environments with low vegetation and semiarid and seasonal climate.

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- María Cristina Cardonatto conceived and designed the experiments, performed the experiments, analyzed the data, contributed materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft, and prepared the Systematic Paleontology section.
- Ricardo Néstor Melchor conceived and designed the experiments, performed the experiments, analyzed the data, contributed materials/analysis tools, prepared figures and/or tables, approved the final draft, and conducted sedimentologic study.

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Data Availability

The following information was supplied regarding data availability:

The raw data are provided in the [Supplemental Files](#).

Supplemental Information

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REFERENCES

- Abba AM, Udrizar DE, Vizcaíno SF. 2005.** Distribution and use of burrows and tunnels of *Chaetophractus villosus* (Mammalia, Xenarthra) in the eastern Argentinean pampas. *Acta Theriologica* **50**:115–124 DOI [10.1007/BF03192624](https://doi.org/10.1007/BF03192624).
- Amidon WH, Fisher GB, Burbank DW, Ciccio PL, Alonso RN, Gorin AL, Silverhart PH, Kylander-Clark ARC, Christoffersen MS. 2017.** Mio-Pliocene aridity in the south-central Andes associated with Southern Hemisphere cold periods. *Proceedings of the National Academy of Sciences of the United States of America* **114**:6474–6479 DOI [10.1073/pnas.1700327114](https://doi.org/10.1073/pnas.1700327114).
- Aramayo SA. 1988.** Nuevos restos de *Proscelidodon* sp. (Edentata, Mylodontidae) del Yacimiento Monte Hermoso (Plioceno inferior a medio) provincia de Buenos Aires, Argentina. Estudio morfológico funcional. *Actas Segundas Jornadas Geológicas Bonaerenses* **1**:99–107.
- Aramayo SA, Manera de Bianco T, Bastianelli NV, Melchor RN. 2015.** Pehuen Co: updated taxonomic review of a late Pleistocene ichnological site in Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* **439**:144–165 DOI [10.1016/j.palaeo.2015.07.006](https://doi.org/10.1016/j.palaeo.2015.07.006).
- Barbour EH. 1892.** Notice of new gigantic fossils. *Science* **19**:99–100.
- Bargo MS, Vizcaíno SF, Archuby FM, Blanco RE. 2000.** Limb bone proportions, strength and digging in some Lujanian (Late Pleistocene-Early Holocene) mylodontid ground sloths (Mammalia, Xenarthra). *Journal of Vertebrate Paleontology* **20**:601–610 DOI [10.1671/0272-4634\(2000\)020\[0601:LBPSAD\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2000)020[0601:LBPSAD]2.0.CO;2).
- Barros VR, Boninseña JA, Camilloni IA, Chidiak M, Magrín GO, Rusticucci M. 2015.** Climate change in Argentina: trends, projections, impacts and adaptation. *Wiley Interdisciplinary Reviews: Climate Change* **6**:151–169.
- Benton MJ. 1988.** Burrowing by vertebrates. *Nature* **331**:17–18 DOI [10.1038/331017a0](https://doi.org/10.1038/331017a0).
- Buchmann FS, Pereira Lopez R, Caron F. 2009.** Icnofósseis (paleotocas e crotovinas) atribuídos a mamíferos extintos no sudeste e sul do Brasil. *Revista Brasileira Paleontological* **12**:247–256 DOI [10.4072/rbp.2009.3.07](https://doi.org/10.4072/rbp.2009.3.07).

- Cardonatto MC, Sostillo R, Visconti G, Melchor RN. 2016.** The *Celliforma* ichnofacies in calcareous paleosols: an example from the late Miocene Cerro Azul formation, La Pampa, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* **443**:203–215 DOI [10.1016/j.palaeo.2015.11.036](https://doi.org/10.1016/j.palaeo.2015.11.036).
- Carter TS, Encarnação CD. 1983.** Characteristics and use of burrows by four species of armadillos in Brazil. *Journal of Mammalogy* **64**:103–108 DOI [10.2307/1380755](https://doi.org/10.2307/1380755).
- Cenizo MM, Tambussi CP, Montalvo CI. 2012.** Late Miocene continental birds from the Cerro Azul formation in the Pampean region (central-southern Argentina). *Alcheringa* **36**:47–68 DOI [10.1080/03115518.2011.582806](https://doi.org/10.1080/03115518.2011.582806).
- Cerdeño E, Montalvo CI. 2001.** Los Mesotheriinae (Mesotheriidae, Notoungulata) del Mioceno superior de La Pampa, Argentina. *Revista Española de Paleontología* **16**:63–75.
- Ceresoli N, Fernandez-Duque E. 2012.** Size and orientation of giant armadillo burrow entrances (*Priodontes maximus*) in western Formosa Province, Argentina. *Edentata* **13**:66–68 DOI [10.5537/020.013.0109](https://doi.org/10.5537/020.013.0109).
- Cione AL, Azpelicueta MM, Bond M, Carlini AA, Casciotta JR, Cozzuol MA, De la Fuente M, Gasparini Z, Goin FJ, Noriega J, Scillato-Yané GJ, Soibelzon L, Tonni EP, Verzi D, Vucetich MG. 2000.** Miocene vertebrates from Entre Ríos province, eastern Argentina. In: Aceñolaza FG, Herbst YR, eds. *Miocene vertebrates from Entre Ríos province, eastern Argentina. Serie correlación geológica*, vol. 14. San Miguel de Tucumán: El Neógeno de Argentina, 191–237.
- Clark WK. 1951.** Ecological life history of the armadillo in the eastern Edwards Plateau region. *American Midland Naturalist* **46**:337–358 DOI [10.2307/2421982](https://doi.org/10.2307/2421982).
- Crespo J. 1944.** Contribución al conocimiento de la ecología de algunos dasipódidos (Edentata) Argentinos. *Revista Argentina de Zoogeografía, Buenos Aires* **4**:7–39.
- Croft DA, Flynn JJ, Wyss A. 2004.** Notoungulata and Litopterna of the early Miocene Chucal Fauna, northern Chile. *Fieldiana, Geology* **50**:1–52.
- Damiani R, Modesto S, Yates A, Neveling J. 2003.** Earliest evidence of cynodont burrowing. *Proceedings of the Royal Society of London B: Biological Sciences* **270**:1747–1751 DOI [10.1098/rspb.2003.2427](https://doi.org/10.1098/rspb.2003.2427).
- De Elorriaga EE, Visconti G. 2001.** Crotovinas atribuibles a grandes mamíferos del Cenozoico en el sureste de la Provincia de La Pampa. In: *9º Reunión Argentina de Sedimentología*, vol. 1. Córdoba: Resúmenes, Asociación Argentina de Sedimentología, 63.
- De Esteban-Trivigno S, Mendoza M, De Renzi M. 2008.** Body mass estimation in Xenarthra: a predictive equation suitable for all quadrupedal terrestrial placentals? *Journal of Morphology* **269**:1276–1293 DOI [10.1002/jmor.10659](https://doi.org/10.1002/jmor.10659).
- Dondas A, Isla FI, Carballido JL. 2009.** Paleocaves exhumed from the Miramar formation (Ensenadan Stage-age, Pleistocene), Mar del Plata, Argentina. *Quaternary International* **210**:44–50 DOI [10.1016/j.quaint.2009.07.001](https://doi.org/10.1016/j.quaint.2009.07.001).
- Duarte RG. 1997.** Gliptodontes del Pleistoceno tardío de Agua de las Palomas, Campo del Pucará, Catamarca, Argentina. Variaciones morfológicas del caparazón de *Glyptodon reticulatus* Owen, 1845. *Ameghiniana* **34**:345–355.

- Ehleringer JR, Cerling TE, Helliker BR. 1997.** C4 photosynthesis, atmospheric CO₂, and climate. *Oecologia* **112**:285–299 DOI [10.1007/s004420050311](https://doi.org/10.1007/s004420050311).
- Elissamburu A. 2004.** Análisis morfométrico y morfofuncional del esqueleto apendicular de *Paedotherium* (Mammalia, Notoungulata). *Ameghiniana* **41**:363–380.
- Elissamburu A, Dondas A, De Santis L. 2011.** Morfometría de las paleocuevas de la “Fm.” Chapadmalal y su asignación a *Actenomys* (Rodentia), *Paedotherium* (Notoungulata) y otros mamíferos fósiles hospedantes. *Mastozoología Neotropical* **18**:227–238.
- Fariña RA, Vizcaíno SF, Bargo MS. 1998.** Body mass estimations in Lujanian (late Pleistocene—early Holocene of South America) mammal megafauna. *Mastozoología Neotropical* **5**:87–108.
- Fernández ME, Vassallo AI, Zárate M. 2000.** Functional morphology and paleobiology of the Pliocene rodent *Actenomys* (Caviomorpha: Octodontidae): the evolution to a subterranean mode of life. *Biological Journal of the Linnean Society* **71**:71–90 DOI [10.1111/j.1095-8312.2000.tb01243.x](https://doi.org/10.1111/j.1095-8312.2000.tb01243.x).
- Folguera A, Zárate M. 2009.** La sedimentación neógena continental en el sector extrandino de Argentina central. *Revista de la Asociación Geológica Argentina* **64**:692–712.
- Frank HT, Althaus CE, Dario EM, Tramontina FR, Adriano RM, Almeida ML, Ferreira GF, Nogueira R, Breier R. 2015.** Underground chamber systems excavated by Cenozoic ground sloths in the state of Rio Grande do Sul, Brazil. *Revista Brasileira de Paleontología* **18**:273–284 DOI [10.4072/rbp.2015.2.08](https://doi.org/10.4072/rbp.2015.2.08).
- Frank HT, Buchmann FS, Gonçalves De Lima L, Fornari M, Caron F. 2012.** Cenozoic vertebrate tunnels in southern Brazil. In: Netto RG, Carmona NB, Tognoli FM, eds. *Ichnology of Latin America: selected papers*. Vol. 2. Porto Alegre: Monografías da Sociedade Brasileira de Paleontología, 141–158.
- Frenguelli J. 1955.** Loess y limos pampeanos. *Serie técnica y didáctica*, vol. 7. La Plata: Universidad Nacional de La Plata, Facultad de Ciencias Naturales y Museo, 1–88.
- Gee CT, Sander PM, Petzelberger BEM. 2003.** A Miocene rodent nut cache in coastal dunes of the Lower Rhine Embayment, Germany. *Palaeontology* **46**:1133–1149 DOI [10.1046/j.0031-0239.2003.00337.x](https://doi.org/10.1046/j.0031-0239.2003.00337.x).
- Genise JF. 1989.** Las cuevas de *Actenomys* (Rodentia: Octodontidae) de la Formación Chapadmalal (Plioceno superior) de Mar del Plata y Miramar (Provincia de Buenos Aires). *Ameghiniana* **26**:33–42.
- Genise JF, Bedatou E, Bellosi E, Sarzetti LC, Sánchez MV, Krause JM. 2016.** The Phanerozoic four revolutions and evolution of paleosol ichnofacies. In: Mángano MG, Buatois LA, eds. *The trace-fossil record of major evolutionary events. Topics in Geobiology, vol 40*, Dordrecht: Springer-Verlag, 301–370.
- Genise JF, Farina JL. 2012.** Ants and xenarthrans involved in a Quaternary food web from Argentina as reflected by their fossil nests and palaeocaves. *Lethaia* **45**:411–422 DOI [10.1111/j.1502-3931.2011.00301.x](https://doi.org/10.1111/j.1502-3931.2011.00301.x).
- Genise JF, Melchor RN, Bellosi ES, Verde M. 2010.** Invertebrate and vertebrate trace fossils from continental carbonates. In: Alonso-Zarza AM, Tanner L, eds. *Carbonates in*

- continental settings: facies, environments and processes. Developments in Sedimentology*, vol. 61. Amsterdam: Elsevier, 319–369.
- Genise JF, Melchor RN, Sánchez MV, González MG. 2013.** *Attaichnus kuenzelii* revisited: a Miocene record of fungus-growing ants from Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* **386**:349–363 DOI [10.1016/j.palaeo.2013.06.004](https://doi.org/10.1016/j.palaeo.2013.06.004).
- Gobetz KE, Martin LD. 2006.** Burrows of a gopher-like rodent, possibly *Gregorymys* (Geomyoidea: Geomyidae: Entoptychtinae), from the early Miocene Harrison Formation, Nebraska. *Palaeogeography, Palaeoclimatology, Palaeoecology* **237**:305–314 DOI [10.1016/j.palaeo.2005.12.002](https://doi.org/10.1016/j.palaeo.2005.12.002).
- Goin FJ, Montalvo CI, Visconti G. 2000.** Los marsupiales (Mammalia) del Mioceno Superior de la Formación Cerro Azul (Provincia de La Pampa, Argentina). *Estudios Geológicos* **56**:101–126.
- González EM, Soutullo A, Altuna CA. 2001.** The burrow of *Dasytus hybridus* (Cingulata: Dasypodidae). *Acta Theriologica* **46**:53–59.
- Groenewald GH, Welman J, MacEachern JA. 2001.** Vertebrate burrow complexes from the Early Triassic *Cynognathus* Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa. *Palaios* **16**:148–160 DOI [10.1669/0883-1351\(2001\)016<0148:VBCFTE>2.0.CO;2](https://doi.org/10.1669/0883-1351(2001)016<0148:VBCFTE>2.0.CO;2).
- Hembree DI, Hasiotis ST. 2008.** Miocene vertebrate and invertebrate burrows defining compound paleosols in the Pawnee Creek Formation, Colorado, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology* **270**:349–365 DOI [10.1016/j.palaeo.2008.07.019](https://doi.org/10.1016/j.palaeo.2008.07.019).
- Hembree DI, Martin LD, Hasiotis ST. 2004.** Amphibian burrows and ephemeral ponds of the Lower Permian Speiser Shale, Kansas: evidence for seasonality in the midcontinent. *Palaeogeography, Palaeoclimatology, Palaeoecology* **203**:127–152 DOI [10.1016/S0031-0182\(03\)00664-3](https://doi.org/10.1016/S0031-0182(03)00664-3).
- Hunt RM. 1990.** Taphonomy and sedimentology of Arikaree (lower Miocene) fluvial, eolian, and lacustrine paleoenvironments, Nebraska and Wyoming: a paleobiota entombed in fine-grained volcanoclastic rocks. In: Lockley MG, Rice A, eds. *Volcanism and fossil biotas*. Vol. 244. Boulder: Geological Society of America, Special Paper, 69–111.
- Hunt RMJ, Xiang-Xu XUE, Kaufman J. 1983.** Miocene burrows of extinct bear dogs: indication of early denning behavior of large mammalian carnivores. *Science* **221**:364–366 DOI [10.1126/science.221.4608.364](https://doi.org/10.1126/science.221.4608.364).
- Imbellone P, Teruggi M, Mormeneo L. 1990.** Crotovinas en sedimentos cuaternarios del partido de la Plata. In: Zárata M, ed. *International symposium on loess*. Mar del Plata: CADINQUA, 166–172.
- Jackson JE, Branch LC, Villarreal D. 1996.** *Lagostomus maximus*. *Mammalian Species* **543**:1–6.
- Johnson SY. 1989.** Significance of loessite in the Maroon formation (Middle Pennsylvanian to Lower Permian), Eagle Basin, Northwest Colorado. *Journal of Sedimentary Research* **59**:782–791.

- Kinlaw A. 1999.** A review of burrowing by semi-fossorial vertebrates in arid environments. *Journal of Arid Environments* **41**:127–145 DOI [10.1006/jare.1998.0476](https://doi.org/10.1006/jare.1998.0476).
- Kraglievich L. 1934.** *La antigüedad pliocena de las faunas de Monte Hermoso y Chapadmalal, deducidas de su comparación con las que le precedieron y sucedieron.* Montevideo: Imprenta “El Siglo Ilustrado”, 136 p.
- Krummeck WD, Bordy EM. 2018.** *Reniformichnus katikatii* (new ichnogenus and ichnospecies): continental vertebrate burrows from the Lower Triassic, Main Karoo Basin, South Africa. *Ichnos* **25**:138–149 DOI [10.1080/10420940.2017.1292909](https://doi.org/10.1080/10420940.2017.1292909).
- Laza JH. 2006.** Dung-beetle fossil brood balls: the ichnogenera *Coprinisphaera* Sauer and *Quirogaichnus* (Coprinisphaeridae). *Ichnos* **13**:217–235 DOI [10.1080/10420940600843641](https://doi.org/10.1080/10420940600843641).
- Linares E, Llambías E, Latorre C. 1980.** Geología de la Provincia de La Pampa, República Argentina y Geocronología de sus rocas metamórficas y eruptivas. *Revista de la Asociación Geológica Argentina* **35**:87–146.
- Liu J, Li L. 2013.** Large tetrapod burrows from the Permian Naobaogou Formation of the Daqingshan Area, Nei Mongol, China. *Acta Geologica Sinica—English Edition* **87**:1501–1507 DOI [10.1111/1755-6724.12154](https://doi.org/10.1111/1755-6724.12154).
- Llanos AC, Crespo JA. 1952.** Ecología de la vizcacha (*Lagostomus maximus maximus* Blainv.) en el nordeste de la provincia de Entre Ríos. *Revista de Investigaciones Agrícolas* **6**:289–378.
- Loope DB. 2006.** Burrows dug by large vertebrates into rain-moistened Middle Jurassic sand dunes. *Journal of Geology* **114**:753–762 DOI [10.1086/507618](https://doi.org/10.1086/507618).
- Lorenzo FR, Mehl AE, Zárate MA. 2013.** Sedimentología y estratigrafía de depósitos del Mioceno tardío de los valles transversales de la provincia de La Pampa, Argentina. *Latin American Journal of Sedimentology and Basin Analysis* **20**:67–84.
- MacFadden BJ, Cerling TE, Prado J. 1996.** Cenozoic terrestrial ecosystem evolution in Argentina: evidence from carbon isotopes of fossil mammal teeth. *Palaeos* **11**:319–327 DOI [10.2307/3515242](https://doi.org/10.2307/3515242).
- MacLeod N. 2009.** Who is Procrustes and what has he done with my data. *Palaeontological Association Newsletter* **70**:21–36.
- Major JJ. 1997.** Depositional processes in large-scale debris-flow experiments. *Journal of Geology* **106**:345–366.
- Martin LD, Bennett DK. 1977.** The burrows of the Miocene beaver *Palaeocastor*, Western Nebraska, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology* **22**:173–193 DOI [10.1016/0031-0182\(77\)90027-X](https://doi.org/10.1016/0031-0182(77)90027-X).
- McDonald HG. 1987.** A systematic review of the Plio-Pleistocene Scelidotherinae ground sloth (Mammalia: Xenarthra: Mylodontidae). PhD thesis, University of Toronto, Toronto, Canada, 478 p.
- McDonald HG, Perea D. 2002.** The large Scelidotherine *Catonyx tarijensis* (Xenarthra, Mylodontidae) from the Pleistocene of Uruguay. *Journal of Vertebrate Paleontology* **22**:677–683 DOI [10.1671/0272-4634\(2002\)022\[0677:TLSCTX\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2002)022[0677:TLSCTX]2.0.CO;2).

- McDonough CM, Loughry WJ. 2008.** Behavioral ecology of armadillos. In: Vizcaíno SF, Loughry WJ, eds. *The biology of Xenarthra*. Gainesville: University Press of Florida, 281–293.
- McNab BK. 1980.** Energetics and the limits to a temperate distribution in armadillos. *Journal of Mammalogy* **61**:606–627 DOI [10.2307/1380307](https://doi.org/10.2307/1380307).
- McNab BK. 1985.** Energetics, population biology, and distribution of xenarthrans, living and extinct. In: Montgomery GG, ed. *The evolution and ecology of armadillos, sloths and vermilinguas*. Washington, D.C.: Smithsonian Institution Press, 219–232.
- Melchor RN, Casadio S. 2000.** Descripción Geológica de la Hoja 3766-III “La Reforma” (1:250.000), Provincia de la Pampa. *Servicio Geológico Minero Argentino, Boletín* **295**:1–56.
- Melchor RN, Genise JF, Umazano AM, Superina M. 2012.** Pink fairy armadillo meniscate burrows and ichnofabrics from Miocene and Holocene interdune deposits of Argentina: palaeoenvironmental and palaeoecological significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* **350–352**:149–170.
- Melchor RN, Loope D. 2016.** Communal therapsid burrows from interdune facies of the Lower Jurassic Navajo Sandstone, southern Utah, USA. In: Baucon A, De Carvalho CN, Rodrigues J, eds. *Abstract Book Ichnia*. Vol. 1. Indanha-a-nova: International Ichnological Association, 174.
- Melchor RN, Umazano AM, Perez M, Krause JM. 2016.** Endemic bioturbation: distinctive Neogene eolian trace fossil assemblages dominated by large meniscate burrows from Patagonia, Argentina. In: *Abstract Book Ichnia*. Vol. 1, 208.
- Miño Boilini AR, Tomassini RL, Oliva C, Manera de Bianco T. 2011.** Adiciones al conocimiento de *Proscelidodon* Bordas, 1935 (Mammalia, Xenarthra, Scelidotheriinae). *Revista Brasileira de Paleontologia* **14**:269–278 DOI [10.4072/rbp.2011.3.06](https://doi.org/10.4072/rbp.2011.3.06).
- Modesto SP, Botha Brink J. 2010.** A burrow cast with *Lystrosaurus* skeletal remains from the Lower Triassic of South Africa. *Palaios* **25**:274–281 DOI [10.2110/palo.2009.p09-077r](https://doi.org/10.2110/palo.2009.p09-077r).
- Montalvo CI, Casadio S. 1988.** Presencia del género *Palaeoctodon* (Rodentia, Octodontidae) en el Huayqueriense (Mioceno tardío) de la Provincia de La Pampa. *Ameghiniana* **25**:111–114.
- Montalvo CI, Melchor RN, Visconti G, Cerdeño E. 2008.** Vertebrate taphonomy in loess-palaeosol deposits: a case study from the late Miocene of central Argentina. *Geobios* **41**:133–143 DOI [10.1016/j.geobios.2006.09.004](https://doi.org/10.1016/j.geobios.2006.09.004).
- Montalvo CI, Tomassini RL, Sostillo R. 2016.** Leftover prey remains: a new taphonomic mode from the late Miocene (Cerro Azul Formation) in central Argentina. *Lethaia* **49**:219–230 DOI [10.1111/let.12140](https://doi.org/10.1111/let.12140).
- Montalvo CI, Visconti G, Púgener L, Cardonatto MC. 1995.** Mamíferos de Edad Huayqueriense (Mioceno tardío), Laguna Chillhué, provincia de La Pampa. In: 4° *Jornadas Geológicas y Geofísicas Bonaerenses (Junín)*, Actas. Vol. 1. Junín: Comisión de Investigaciones Científicas, 73–79.

- Nevo E. 1979.** Adaptive convergence and divergence of subterranean mammals. *Annual Review of Ecology and Systematics* **10**:269–308
DOI [10.1146/annurev.es.10.110179.001413](https://doi.org/10.1146/annurev.es.10.110179.001413).
- Nevo E. 1995.** Mammalian evolution underground. The ecological-genetic-fenetic interfaces. *Acta Theriologica* **3**:9–31.
- Nevo E. 2011.** Evolution under environmental stress at macro- and microscales. *Genome Biology and Evolution* **3**:1039–1052 DOI [10.1093/gbe/evr052](https://doi.org/10.1093/gbe/evr052).
- Ortiz Jaureguizar E. 1998.** Paleocología y evolución de la fauna de mamíferos de América del Sur durante la “Edad de las Planicies Australes” (Mioceno superior-Plioceno superior). *Estudios Geológicos* **54**:161–169.
- Perea D. 2005.** *Pseudoplohophorus absolutus* n. sp. (Xenarthra, Glyptodontidae), variabilidad en Sclerocalyptinae y redefinición de una biozona del Mioceno Superior de Uruguay. *Ameghiniana* **42**:175–190.
- Perea D, Scillato-Yané GJ. 1995.** *Proeuphractus limpidus* Ameghino, 1886 (Xenarthra, Dasypodidae, Euphractini): osteología comparada del cráneo y elementos de la coraza asociados (Neógeno del Uruguay). *Boletín de la Real Sociedad Española de Historia Natural* **90**:125–130.
- Platt SG, Rainwater TR, Brewer SW. 2004.** Aspects of the burrowing ecology of nine-banded armadillos in northern Belize. *Mammalian Biology* **69**:217–224
DOI [10.1078/1616-5047-00138](https://doi.org/10.1078/1616-5047-00138).
- Pujos F, Candela A, Galli CI, Coira BL, Reguero MA, De los Reyes M, Abello MA. 2012.** The Scelidotheriine *Proscelidodon* (Xenarthra: Mylodontidae) from the Late Miocene of Maimará (Northwestern Argentina, Jujuy Province). *Ameghiniana* **49**:668–674
DOI [10.5710/AMGH.20.11.2012.593](https://doi.org/10.5710/AMGH.20.11.2012.593).
- Pye K. 1995.** The nature, origin and accumulation of loess. *Quaternary Science Reviews* **14**:653–667 DOI [10.1016/0277-3791\(95\)00047-X](https://doi.org/10.1016/0277-3791(95)00047-X).
- Quintana CA. 1992.** Estructura interna de una paleocueva, posiblemente de un Dasypodidae (Mammalia, Edentata) del Pleistoceno de Mar del Plata (Provincia de Buenos Aires, Argentina). *Ameghiniana* **29**:87–91.
- Rafuse DJ, Kaufmann CA, Gutiérrez MA, González ME, Scheifler NA, Álvarez MC, Massigoge A. 2017.** Taphonomy of modern communal burrow systems of the Plains vizcacha (*Lagostomus maximus*, Chinchillidae) in the Pampas region of Argentina: implications for the fossil record. *Historical Biology* In Press
DOI [10.1080/08912963.2017.1374957](https://doi.org/10.1080/08912963.2017.1374957).
- Reichman OJ, Smith SC. 1990.** Burrows and burrowing behavior by mammals. *Current Mammalogy* **2**:197–244.
- Riese DJ, Hasiotis ST, Odier GP. 2011.** Synapsid burrows and associated trace fossils in the lower Jurassic Navajo Sandstone, Southeastern Utah, U.S.A. indicates a diverse community living in a wet desert ecosystem. *Journal of Sedimentary Research* **81**:299–325 DOI [10.2110/jsr.2011.25](https://doi.org/10.2110/jsr.2011.25).
- Roig FA, Roig-Juñent S, Corbalán V. 2009.** Biogeography of the Monte Desert. *Journal of Arid Environments* **73**:164–172 DOI [10.1016/j.jaridenv.2008.07.016](https://doi.org/10.1016/j.jaridenv.2008.07.016).

- Sawyer CF, Brinkman DC, Walker VD, Covington TD, Stienstraw EA. 2012. The zoogeomorphic characteristics of burrows and burrowing by nine-banded armadillos (*Dasypus novemcinctus*). *Geomorphology* 157:122–130.
- Scillato-Yané GJ. 1982. Los Dasypodidae (Mammalia-Edentata) del Plioceno y Pleistoceno de Argentina. Tesis Doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 159 pp. Inédita.
- Scillato-Yané G, Góis F, Zurita AE, Carlini A, González Ruiz L, Krmpotic C, Oliva C, Zamorano M. 2013. Los Cingulata (Mammalia, Xenarthra) del “Conglomerado osífero” (Mioceno Tardío) de la Formación Ituzaingó de Entre Ríos, Argentina. *Asociación Paleontológica Argentina, Publicación Especial*, Vol. 14, 118–134.
- Scillato-Yané GJ, Krmpotic CM, Esteban GI. 2010. The species of genus *Chasicotatus* Scillato-Yané (Eutatini, Dasypodidae). *Revista Mexicana de Ciencias Geológicas* 27:43–55.
- Scognamillo DG. 1993. Estructura de las cuevas de *Actenomys* (Rodentia: Octodontidae) de la Aloformación Playa San Carlos, Plioceno tardío (Barranca de los Lobos, Pdo. Gral. Pueyrredón): significado paleoecológico y estratigráfico. Licenciatura thesis, National University of Mar del Plata, Argentina, 32 pp.
- Seilacher A. 2007. *Trace fossil analysis*. Berlin: Springer, 226.
- Sheldon ND, Tabor NJ. 2009. Quantitative paleoenvironmental and paleoclimatic reconstruction using paleosols. *Earth-Science Reviews* 95:1–52
DOI 10.1016/j.earscirev.2009.03.004.
- Shockey BJ, Croft DA, Anaya F. 2007. Analysis of function in the absence of extant functional homologues: a case study using mesotheriid notoungulates (Mammalia). *Paleobiology* 33:227–247 DOI 10.1666/05052.1.
- Sidor CA, Miller MF, Isbell JL. 2008. Tetrapod burrows from the Triassic of Antarctica. *Journal Vertebrate Paleontology* 28:277–284
DOI 10.1671/0272-4634(2008)28[277:TBFTTO]2.0.CO;2.
- Slice DE, Bookstein FL, Marcus LF, Rohlf FJ. 2008. A glossary for geometric morphometrics web site. Available at <http://life.bio.sunysb.edu/morph/>.
- Smith R. 1987. Helical burrow casts of therapsid origin from the Beaufort Group (Permian) of South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 60:155–170 DOI 10.1016/0031-0182(87)90030-7.
- Smith GA, Lowe DR. 1991. Lahars: volcano-hydrologic events and deposition in the debris flow—hyperconcentrated flow continuum. In: Fisher RV, Smith GA, eds. *Sedimentation in volcanic settings*, vol. 45. SEPM Special Publication, 59–70.
- Soibelzon LH, Pomi LH, Tonni EP, Rodriguez S, Dondas A. 2009. First report of a South American short-faced bears’ den (*Arctotherium angustidens*): palaeobiological and palaeoecological implications. *Alcheringa* 33:211–222
DOI 10.1080/03115510902844418.
- Taglioretti M, Miño Boilini AR, Scaglia F, Dondas A. 2014. Presencia de *Proscelidodon patrius* (Xenarthra, Scelidotheriinae) en la Formación Chapadmalal (Plioceno superior), Mar del Plata, Buenos Aires, Argentina: implicancias bioestratigráficas. *Ameghiniana* 51:420–427 DOI 10.5710/AMGH.04.08.2014.2715.

- Urrutia JJ, Montalvo CI, Scilato-Yané GJ. 2008.** Dasypodidae (Xenarthra, Cingulata) de la Formación Cerro Azul (Mioceno tardío) de la provincia de La Pampa, Argentina. *Ameghiniana* **45**:289–302.
- Varricchio DJ, Martin AJ, Katsura Y. 2007.** First trace and body fossil evidence of a burrowing, denning dinosaur. *Proceedings of the Royal Society B: Biological Sciences* **274**:1361–1368 DOI [10.1098/rspb.2006.0443](https://doi.org/10.1098/rspb.2006.0443).
- Verzi DH, Montalvo CI, Deschamps C. 2008.** Biostratigraphy and biochronology of the Late Miocene of central Argentina: evidence from rodents and taphonomy. *Geobios* **41**:145–155 DOI [10.1016/j.geobios.2006.09.005](https://doi.org/10.1016/j.geobios.2006.09.005).
- Verzi DH, Montalvo CI, Tiranti SI. 2003.** Un nuevo *Xenodontomys* (Rodentia, Octodontidae) del Mioceno tardío de La Pampa, Argentina. Patrón evolutivo y bioestratigrafía. *Ameghiniana* **40**:229–238.
- Verzi DH, Montalvo CI, Vucetich MG. 1999.** Afinidades y significado evolutivo de *Neophanomys biphlicatus* (Rodentia, Octodontidae) del Mioceno tardío-Plioceno temprano de Argentina. *Ameghiniana* **36**:83–90.
- Vezzosi RI. 2012.** First record of *Procarriama simplex* Rovereto, 1914 (Phorusrhacidae, Psilopterinae) in the Cerro Azul Formation (upper Miocene) of La Pampa Province; remarks on its anatomy, palaeogeography and chronological range. *Alcheringa* **36**:157–169 DOI [10.1080/03115518.2011.597657](https://doi.org/10.1080/03115518.2011.597657).
- Visconti G, Melchor RN, Montalvo CI, Umazano AM, De Elorriaga EE. 2010.** Análisis litoestratigráfico de la Formación Cerro Azul (Mioceno superior) en la provincia de La Pampa. *Revista de la Asociación Geológica Argentina* **67**:257–265.
- Vizcaíno SF, Blanco RE, Bender JB, Milne N. 2011.** Proportions and function of the limbs of glyptodonts. *Lethaia* **44**:93–101 DOI [10.1111/j.1502-3931.2010.00228.x](https://doi.org/10.1111/j.1502-3931.2010.00228.x).
- Vizcaíno SF, Fariña RA. 1999.** On the flight capabilities and distribution of the giant Miocene bird *Argentavis magnificens* (Teratornithidae). *Lethaia* **32**:271–278.
- Vizcaíno SF, Zárate M, Bargo MS, Dondas A. 2001.** Pleistocene burrows in the Mar del Plata area (Argentina) and their probable builders. *Acta Palaeontologica Polonica* **46**(2):289–301.
- Vogt T, Carballo OC, Calmels AP. 1999.** Un esbozo de explicación de la génesis de las toscas de la meseta de La Pampa. In: *1° Congreso Argentino de Cuaternario y Geomorfología, Actas*. Santa Rosa: Asociación Argentina de Cuaternario y Geomorfología, 195–205.
- Voorhies MR. 1975.** Vertebrate burrows. In: Frey RW, ed. *The study of trace fossils*. New York: Springer-Verlag, 325–350.
- Woodruff DC, Varricchio DJ. 2011.** Experimental modeling of a possible *Oryctodromeus cubicularis* (Dinosauria) burrow. *Palaios* **26**:140–151 DOI [10.2110/palo.2010.p10-001r](https://doi.org/10.2110/palo.2010.p10-001r).
- Wu NC, Alton LA, Clemente CJ, Kearney MR, White CR. 2015.** Morphology and burrowing energetics of semi-fossorial skinks (*Liopholis* spp.). *The Journal of Experimental Biology* **218**:2416–2426 DOI [10.1242/jeb.113803](https://doi.org/10.1242/jeb.113803).

- Zachos J, Pagani M, Sloan L, Thomas E, Billups K. 2001.** Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**:686–693 DOI [10.1126/science.1059412](https://doi.org/10.1126/science.1059412).
- Zárate MA, Bargo MS, Vizcaíno SF, Dondas A, Scaglia O. 1998.** Estructuras biogénicas en el Cenozoico tardío de Mar del Plata (Argentina) atribuibles a grandes mamíferos. *Revista Asociación Argentina de Sedimentología* **5**:95–103.
- Zimmerman JW. 1990.** Burrow characteristics of the nine-banded armadillo, *Dasyus novemcinctus*. *Southwestern Naturalist* **35**:226–227 DOI [10.2307/3671550](https://doi.org/10.2307/3671550).
- Zurita AE, Oliva C, Dondas A, Soibelzon E, Isla FI. 2011.** El registro más completo de un Hoplophorini (Xenarthra: Glyptodontidae) para los Pisos/Edades Chapadmalalense-Marplatense (Plioceno tardío-Pleistoceno temprano). *Revista del Museo Argentino de Ciencias Naturales* **13**:69–75 DOI [10.22179/REVMACN.13.232](https://doi.org/10.22179/REVMACN.13.232).
- Zurita AE, Soibelzon LH, Soibelzon E, Gasparini GM, Cenizo MM, Arzani H. 2010.** Accessory protection structures in *Glyptodon* Owen (Xenarthra, Cingulata, Glyptodontidae). *Annales de Paléontologie* **96**:1–11 DOI [10.1016/j.annpal.2010.01.001](https://doi.org/10.1016/j.annpal.2010.01.001).