

Late Miocene mammalian burrows in the Camacho Formation of Uruguay reveal a complex community of ecosystem engineers

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ABSTRACT

We report fossil mammal burrows from backshore beach facies in the Camacho Formation of southern Uruguay, of Late Miocene (Huayquerian SALMA) age. The presence of desiccation cracks and rhizoliths indicate the occurrence of relatively extended periods of subaerial exposure and the incipient development of vegetation. The analysis of the burrows' spatial extent, size, and structure reveals the existence of exceptionally well-preserved and intercrossing tunnel systems. We show the existence of different size classes of burrows, which indicate that at least four different taxa were responsible for their construction. Considering the inferred body masses of the trace makers obtained from allometric relationships and the body masses of taxa recovered for the Camacho Formation, the burrows may have been produced by a combination of the following mammals: one of several rodents, notoungulates, cingulates, folivorans, and a carnivoran. The fossil association represents an exceptional case of a community of ecosystem engineers in the Late Miocene of southeastern South America.

1. Introduction

Fossil vertebrate burrows are relatively common in the fossil record and burrowing behaviour was probably present in mammals since their origins (Damiani et al., 2003). Most Cenozoic burrows are attributed to mammal taxa, namely Rodentia, Xenarthra, and Carnivora (Cardonatto and Melchor, 2018). Paleogene burrows are scarce and show relatively simple structures. In the Miocene, the record becomes more abundant, with burrows becoming much more diverse both in size and complexity (Cardonatto and Melchor, 2018). This trend is often associated with the increase of harsh environments, with burrows being present in volcaniclastic and aeolian environments. In South America, the oldest unequivocal mammal burrow was reported from the Middle Miocene of Argentina, and represents cylindrical, subhorizontal, unbranched tunnels with a meniscate backfill interpreted as foraging tunnels of small Dasypodidae (Melchor et al., 2012). Considerable larger burrows, also unbranched, were reported from the Late Miocene of Argentina, and were interpreted as shelters against predation and environmental extremes produced by xenarthrans or notoungulates (Cardonatto and

Melchor, 2018). Complex tunnel systems in South America are also reported from the Late Pliocene of Argentina, with some branching systems including chambers that are mostly attributed to rodents (Elissamburu et al., 2011).

The study of fossil burrows provides important insights regarding the behaviour of the involved vertebrates. Burrowing behaviour has been often associated with a response to the environment or the increase of predation pressure, while in other cases, burrowing has been interpreted to be related to food acquisition and nesting (Reichman and Smith, 1990; Kinlaw, 1999). Furthermore, complex tunnel systems have been interpreted as evidence of non-solitary behaviour, providing information on the presence of complex social interactions between individuals (Weaver et al., 2021).

In the present study, we report recently discovered mammal burrows from a fossil site assigned to the Camacho Formation (Late Miocene) and located in Southern Uruguay. We describe the burrows' extent, size, and structure, as well as their potential makers, the depositional context, and the environment in which these taxa lived. The results provide insights regarding the behaviour of some South American extinct fauna and their

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role as important ecosystem engineers.

2. Geological setting

The reported burrows are located in Punta San Gregorio, west of the town of Kiyú, San José, southern Uruguay (34°41'14"S; 56°49'16"W; Fig. 1). These fossil burrows are exposed in plan view on the abrasion platform, corresponding to the Camacho Formation (Goso and Bossi, 1966). According to its land mammal fossil assemblage, it has been assigned to the Late Miocene, Huayquerian South American Land Mammal Age (sensu Pascual et al., 1965) or regional Stage/Age (sensu Cione and Tonni, 1995) (9.0–6.8 Ma).

The Camacho Formation is commonly exposed in the southwestern coastal cliffs of Uruguay, in the Colonia and San José departments. It comprises a clastic succession of very fine to coarse sandstones, siltstones, and argillaceous claystones (Sprechmann et al., 1994, 2000; Perea and Martínez, 2004; Perea et al., 2013). It has been associated with a highstand eustatic event, regionally known as the Paranaense transgression or Paranaense Sea (Sprechmann et al., 2000).

The Camacho Formation has been partly correlated with the Paraná Formation from northeastern Argentina, based on geological features and fossil invertebrates (del Río et al., 2018). However, it also has been correlated with the overlying lower member of the Ituzaingó Formation, mainly based on its mammal assemblage (Perea et al., 2020a). ⁸⁷Sr/⁸⁶Sr stable isotope analyses on invertebrates from the Camacho Formation have provided considerable disparate values, with calculated ages within the Middle and Late Miocene (18–17 Ma, Sprechmann et al., 2010; 7.2–6.0 Ma, del Río et al., 2018; 15–13 Ma and 11–9 Ma,

Soibelzon et al., 2019). We consider the Late Miocene assignment as the most conservative approach based on the available information, and therefore, subscribe to that proposed age for the discussion of our results.

The Camacho Formation includes two members: the lower San Pedro and the upper Cerro Bautista members. The San Pedro Member is composed predominantly by bioturbated greyish-green sandy siltstones interbedded with thin levels of sandstones, and is related to subtidal, low energy, coastal environments, disturbed by storms and occasional tidal influence (Perea and Martínez, 2004). It should be noted that outcrops of this member in the San José Department were previously described by Francis and Mones (1965) as the Kiyú Formation, or proposed to be the base of the Raigón Formation by Bossi and Navarro (1991). In the Colonia Department, these deposits are characterised by the abundance of ichnofossils, interpreted as invertebrate burrows, marine invertebrates, and some vertebrates (Sprechmann et al., 1994; Perea and Martínez, 2004; Perea et al., 2013).

In contrast, the greatest diversity of terrestrial vertebrates, including rodents, xenarthrans, and notoungulates, is recorded in the fine sediments at the base of the Kiyú and Puerto Arazatí cliffs, at the San José Department (Perea et al., 2020a). In this area, facies related to a regressive phase have been recognised, characterizing a shallow marine environment on a siliciclastic shelf. In addition, in Puerto Arazatí, a beach backshore environment, as well as episodic subaerial exposure of these deposits have been inferred by the presence of the *Psilonichnus* Ichnofacies and trace fossils assigned to sarcosaprophagous insects, recorded in some specimens of glyptodonts (Perea et al., 2020b).

The Cerro Bautista Member is composed of white fine to very fine

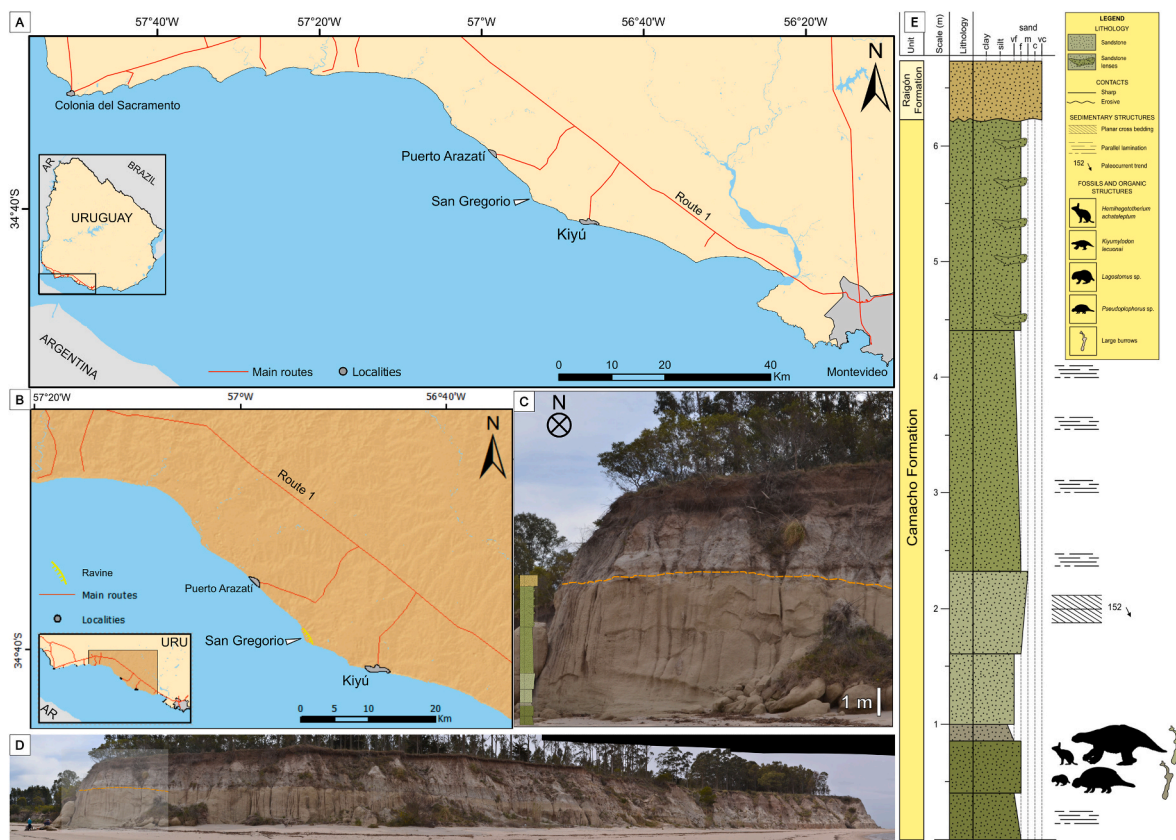


Fig. 1. Geological and geographical context and stratigraphic section of the Camacho Formation at Punta San Gregorio. A. Geographic context of the south-western Uruguayan coast, with the main localities mentioned in this study. (B) Close-up view of the Kiyú-Puerto Arazatí coast, with the principal cliffs of Punta San Gregorio marked. (C) Typical exposures of the Camacho Formation at Punta San Gregorio; the erosive unconformity with the overlying Raigón Formation is highlighted by a dashed line. (D) Panoramic north view of the coastal cliff. The greyish area represents the exposures shown on C. The erosive unconformity is slightly dipping east. (E) Stratigraphic section of the Camacho Formation, including the position of vertebrate fossils and burrows. Only the base of the overlying Raigón Formation is represented.

sandstones interbedded with fossil-bearing conglomerates. Also, thin packages of massive greenish grey claystones can be found at the base. Outcrops of this member are exclusively found in the Colonia Department. This unit comprises shallow internal platform deposits, estuarine channels and plains, proximal tempestites, and intertidal and beach deposits (Perea and Martínez, 2004).

At the site where the burrows were found, the San Pedro Member composes the abrasion platform of the beach and the base of the coastal cliffs. This site is remarkable for the lack of invertebrate fossils and the large number of vertebrate body fossils collected during, at least, the last 50 years. Interestingly, due to the present coastal dynamics of sand deposition and tides, the fossil burrows remain almost entirely covered by sand or water most of the time and were never registered before. The section exposed at the coastal cliffs also comprises the overlying Raigón (Pliocene-Pleistocene) and Libertad (Pleistocene) formations (Fig. 1E).

3. Materials and methods

Field activities were carried in order to expose, record, and study the burrows. Regarding the geology of the site, standard sedimentological techniques were employed to study the sediments inside and outside the burrows. A granulometric analysis of the sediments both inside and outside the burrows was performed and any potential sedimentary structure was recorded and described. The fossil contents, both outside and inside the burrows, were collected, prepared, and analysed in order to identify them. The fossil burrows were measured and mapped, allowing for the recognition of bifurcations, chambers, and connections. Since the burrows are observed in plan view, only the horizontal diameter (Dh) was recorded in all the registered burrows. Moreover, all the recognised chambers were measured considering both their maximum and minimum horizontal diameters (Dh_{\min} and Dh_{\max}). A DJI Mavic Pro drone was used to take pictures from different altitudes in order to properly record the extension and connections between the preserved burrows. Furthermore, the taxa collected in the site and those in other outcrops of the Camacho Formation were studied in order to explore potential makers of the burrows. For this purpose, the location of the collected fossils (those taxa found inside burrows are *a priori* more probable to be the builders), as well as the body mass of the taxa and the size of the burrows were evaluated.

Since all of the observed burrows are exposed in plan view, only the Dh measurements were considered for quantitative analyses. Considering that there is a high concentration of fossil burrows at the site, and their spatial connections and relationships are not always evident due to differential preservation or variations in depths, we measured every tunnel section despite its connection to others through chambers or bifurcations. Thus, we did not make any *a priori* assumptions about burrow groupings to avoid potential biases due to these issues. On the other hand, we performed a Mixture analysis to objectively address the existence of subgroups among the studied burrows. We fitted univariate Gaussian mixture models to the Dh data using the R package mixR (Yu, 2022). The models were fitted using the function “mixfit”, allowing for unequal variances between components. Model selection was performed with the function “select” based on the Bayesian Information Criterion (BIC), a criterion that penalizes the addition of parameters in order to avoid overfitting (Nasserinejad et al., 2017). In general, a model with a lower BIC value is preferred and a difference greater than 2 is considered as significant for the consideration of a model over others (Raftery, 1995). The results of the best mixture model were used to describe the different size groups among the studied tunnels, as well as to classify each tunnel to a size group. Finally, the tunnels were plotted in plan view according to their group assignment in order to consider the spatial distribution of the size groups and their potential associations.

For the estimation of the body masses of the potential makers of the burrows, we used the allometric regression obtained by White (2005). Since all the Dh measurements were obtained in plan view and the depth level of the observed longitudinal cut of the burrow can be considered as

random, the measurable apparent horizontal diameter does not represent the actual maximum diameter of the burrows but a transversal length somewhere between the true horizontal diameter and the minimum transversal length at the top or bottom of the tunnel. Therefore, to better represent the actual Dh, we used both the mean and 95th percentile of the obtained Gaussian distributions for each burrow size category for the estimation of body mass ranges of potential makers. Moreover, considering that all burrows are exposed only in plan view, we assumed a circular section for the estimation of burrow area to maximize burrow sampling. Furthermore, we obtained the body masses of the taxa registered for the Camacho Formation from published sources and estimated the body masses of the remaining taxa employing the allometric equations used in Fariña et al. (1998) or geometric similarity to comparable taxa. Finally, we compared the estimated body masses in order to define the potential makers of the different sizes of burrows.

4. Results

4.1. Sedimentology of the section

The Punta San Gregorio section is exclusively composed of sandstone through its 6.2 m of thickness. They can be massive, laminated, or cross-bedded. The facies association of very fine to fine, massive, and parallel laminated sandstones stands out, denoting medium to low energy conditions. In the lower third, an association of planar cross-bedded medium-grained sandstone shows higher energetic conditions. In the upper third some massive, coarser-grained sandstone lenses are developed, but without internal traction structures. The significant grain size contrast between the top and the overlying erosive base of the Raigón Formation suggests an important environmental change. These patterns have been interpreted as a transition from a beach backshore, for the lower 2.5 m, to foreshore until the top of the section. Additionally, at the active abrasion plain several post depositional structures have been recognised. Desiccation and syneresis cracks developed on very fine sandstones are consistent with shallow environments and subaerial exposure of the basal levels (Figs. S1A and B). The incipient development of vegetation, evidenced by the presence of rhizoliths, also points to relatively extended periods subaerial exposure (Figs. S1C and D).

4.2. Description of the burrows

Fossil burrows were identified along the abrasion platform in a stretch of 305 m parallel to the coastline. Likewise, burrows were recorded from the proximity of the cliff to the coastline, covering several metres. Several clusters with higher densities of tunnels were identified, but burrows occurred almost entirely along the studied zone. In general, the tunnels showed infills similar to the hosting sediments, with slightly different colorations often being the only character that distinguished them.

Several macroscopic samples were taken from the infill and walls of different tunnels. Commonly, the sediments are very fine to fine sand, not coarser than medium sand. Compositionally, quartz is the most frequent mineral. Subordinately, amphibole, iron oxides, and potassic feldspar are part of the coarse fraction. All the levels have a cement-supported texture, mainly by calcite. In the infill it can reach up to 40%, giving a higher relative cohesion than the surrounding rocks (Fig. S2). The colour difference is associated with changes in the cement composition or impurities, rather than different mineralogy. A significant characteristic of the infill is the presence of millimetric clay-walled rhizoliths at 10–15% (Figs. S1C and D). They usually have a vermicular shape in different directions and are of whitish to pinkish colour. These root traces suggest subaerial exposure and a poorly developed palaeosol horizon (Retallack, 2001).

The burrows comprised several different sizes and shapes, as well as the presence of different chamber-like structures (Fig. 2; 3). In plan

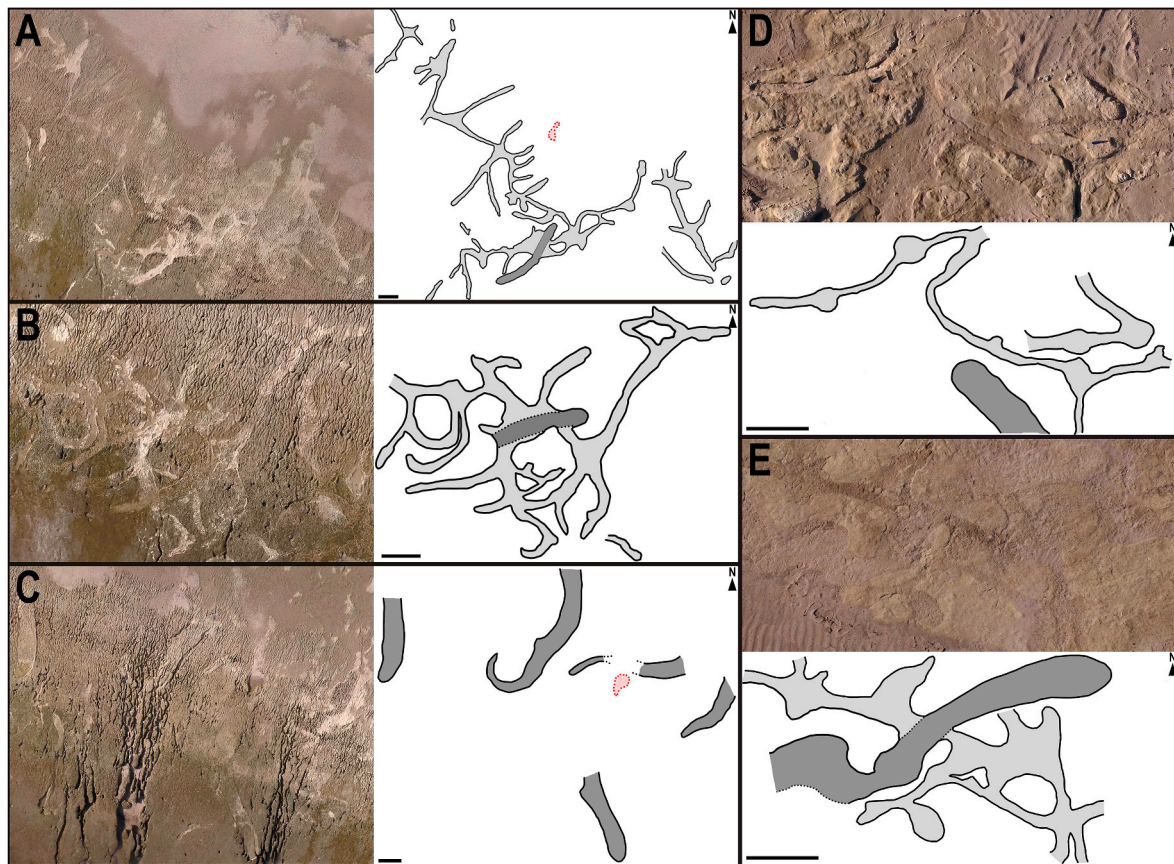


Fig. 2. Fossil burrows in plan view. Bigger burrows cutting through smaller ones can be seen in A, B, and E. Locations of body fossils of *Nothrotheriidae* indet. (A) and *Pseudoplohophorus* sp. (B) are shown in red. Scale equals 1 m (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

view, most of the tunnels showed straight or semi-straight sections, although some occurrences of curved and sinusoidal sections were observed (Fig. 2). In transversal view, the sampled burrows showed sections that were from a flattened oval to an “inverted U” shape, with a tendency of smaller ones having the former and larger ones showing the latter shape (Fig. 3D and E). Furthermore, different sizes, evidenced by the maximum measurable diameter, were clearly visible among the exposed burrows. The presence of bifurcations was registered almost exclusively in the smaller tunnels, which showed not only simple bifurcations, but also places where three or more burrows branched off from the same section (Fig. 2A,B,D; 3 A,C). In a similar manner, the presence of clear chambers where the burrow became wider, either branching off laterally from a tunnel, in the middle of a section associated with multiple branches, or as a terminal chamber, was consistently associated with the smaller burrows (Fig. 2D; 3C). On average, the recorded chambers measured 38.89 cm and 46.43 cm for D_{\min} and D_{\max} , respectively. On the other hand, the larger burrows that were recovered from the site showed more simple designs, most of the time showing straight or semi-straight sections that ended in a terminal chamber that was barely wider than the burrows maximum diameter (Fig. 3B). Finally, some of the larger burrows were registered as “cutting” through the smaller tunnel systems, as can be seen in Fig. 2A,B,E.

4.3. Burrows size analysis and estimated body mass of potential makers

A total of 243 burrows were measured (Table S1). The range of D_h for the studied burrows was 10.4–116 cm. The mixture analysis provided the best fit for the model with four components, supporting the existence of four significantly different subgroups among the burrows according to their D_h . The best fitted model (four components, unequal

variances) showed a BIC of 1877.40, while the models with three and five components showed BICs of 1880.98 and 1892.46, respectively ($\Delta\text{BIC} = 3.58$ and 15.6, respectively). Taking into account that according to Raftery (1995) a $\Delta\text{BIC} > 2$ shows positive evidence in favour of the more complex model, we considered the four-component model for the following analyses. The mean and standard deviation of each recovered component were 15.25 ± 2.22 , 25.44 ± 1.76 , 34.79 ± 4.71 , and 70.23 ± 17.29 cm, respectively. The estimated proportions of each component were, from the smallest to the largest burrows, 0.43, 0.21, 0.24, and 0.12. Accordingly, the smallest burrows were more abundant and showed less variations in D_h , while larger burrows were increasingly less common and showed more spread in D_h values (Fig. 4).

Assuming the allometric relationship described by White (2005), we estimated the following body mass ranges of the potential makers for each of the burrow size categories: 1.9–4.2, 9.3–13.8, 24.3–50.8, and 211.2–723.9 Kg.

4.4. Preserved vertebrates remains and body mass of taxa found in the camacho formation

Body remains of vertebrates are commonly found in the same level that the burrows are located. During the field work, several specimens were collected. The recorded taxa were: *Lagostomus* sp., *Pseudoplohophorus* sp., and *Nothrotheriidae* indet. Most of the specimens were found outside the burrows in the hosting sediments, with only a single specimen assignable to the genus *Lagostomus* found within a tunnel (Fig. 3F; S3A) and some indeterminate fossil fragments found within a second tunnel (Fig. S3B). Furthermore, an incomplete carapace assignable to *Pseudoplohophorus* sp. was found in relative spatial association with a burrow in a section where the burrow’s limits were not clearly visible

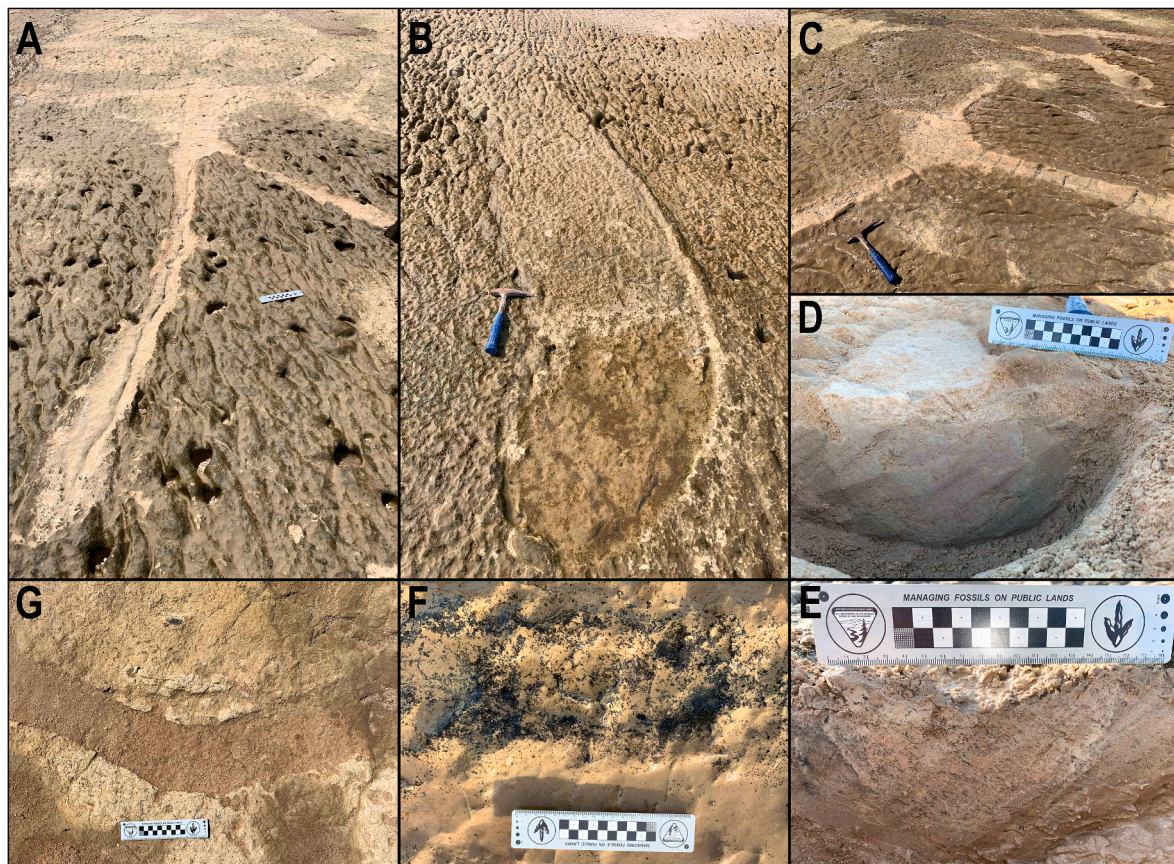


Fig. 3. Examples of fossil burrows in the studied zone. A: bifurcation in small burrows. B: large burrow showing ending without a clear enlarged chamber. C: small burrow system showing a central chamber with three tunnels. D: section of a burrow showing an approximate circular shape. E: section of a burrow showing the similar, massive infilling. F: *Lagostomus* sp. specimen found inside a burrow. G: burrow showing several smaller (1–2 cm) burrows branching out.

(Fig. 2C; S3C). Finally, a *Nothrotheriidae* indet. specimen was found close to a cluster of small burrows, but no clear association to them was noticeable (Fig. 2A; S3D).

The revision of the available literature and the new estimations of body masses for the taxa occurring in the Camacho Formation that could be considered as potential makers of the burrows showed a wide spectrum of sizes (Table S2). The smallest potentially-burrowing mammals of the Camacho Formation would be represented by rodents (*Lagostomus* and *Prodolichotis*) and armadillos (*Doellotatus* and *Proeuphractus*) with body masses lower than 10 kg. On the other hand, the largest potentially-burrowing taxa were represented by rodents (*Isostylomys* and *Arazamys*), glyptodonts (*Pseudoplohophorus*), and ground sloths (*Kiyumylodon*, *Lestobradys*), with genera reaching body masses higher than 200 kg.

5. Discussion

5.1. Fossil burrows diversity and potential makers

The results showed a clear differentiation among the preserved burrows, with size (measured as Dh) being the main factor for their recognition. The lack of a clear normal distribution and the existence of size gaps also support the existence of these groupings among the tunnels, since a normal distribution without clear gaps would be expected for burrows made by a single taxon considering the expected body size distribution of a mammal population. Furthermore, the frequencies at which each burrow size class was recorded varied considerably between size classes, with smaller tunnels being more frequent than larger ones. This difference in the frequency of each size class is expected since smaller animals tend to have larger populations and therefore would be

more abundant (White et al., 2007). Another aspect that was different among the recorded burrows was the presence or lack of bifurcations and differentiated chambers, with the smaller traces having several interconnected tunnels and chambers while the larger ones showed simpler patterns often lacking bifurcations altogether and showing almost indistinguishable terminal chambers. These patterns support the involvement of different taxa in the making of the burrows as, for example, smaller social taxa like some rodents tend to construct complex tunnel systems with different entries and several chambers often used for different purposes (Lacey et al., 2000; Cardonato and Melchor, 2021), while larger taxa like the giant armadillo *Priodontes maximus* excavate simple burrows and has solitary habits (Desbiez and Kluyber, 2013).

The Camacho Formation in Southern Uruguay has been geochronologically constrained to the Late Miocene based on the most recent data (11.63–5.33 Mya; Perea et al., 2020a). As mentioned before, several vertebrates have been recorded for the formation, including representatives of many typical South American mammalian clades like marsupials, xenarthrans, notoungulates, and litopterns (Perea et al., 2020a), as well as several rodents, and, interestingly, some of the first representatives of the North American mammal fauna that arrived in South America during the Great American Biotic Interchange (Soibelzon et al., 2019). However, most of the recorded taxa come from historical collections, with precise stratigraphic context often being absent, and only a handful of taxa were recorded in association with the fossil burrows during our fieldwork. This situation poses certain challenges for confidently defining the taxa responsible for the trace fossils, which is further complicated by the complex arrangement of the burrows and their diversity. Considering this, our estimations of the body mass of the potential makers based on burrow size and the body mass estimations of

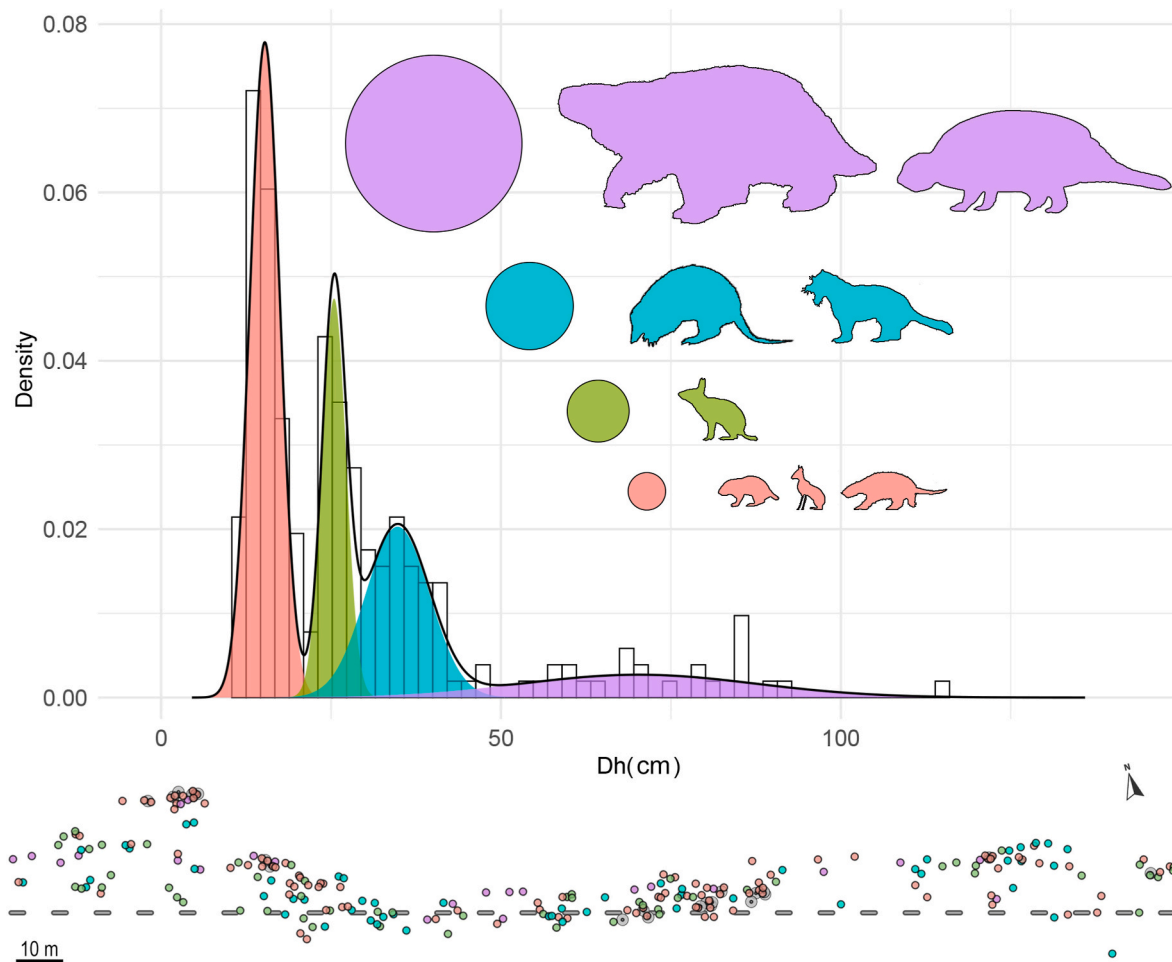


Fig. 4. Top: Size distribution of the sampled burrows and results of the mixture model that recovered four different size categories (potential makers discussed in the text are shown for comparison). From top to bottom and left to right: *Kiyumylodon*, *Pseudoplohophorus*, *Ringueletia*, *Cyonasua*, *Hemihegetotherium*, *Lagostomus*, *Prodolichotis*, and *Proeuphractus*. Bottom: Spatial distribution of the sampled burrows (colours correspond to size categories, grey circles indicate measured chambers, and the horizontal line depicts the approximate coastline). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

the taxa recorded on the Camacho Formation provide a baseline for the identification of the potential makers for each burrow size class.

The smaller burrows registered at the site provided an estimated body mass of 1.9–4.2 Kg for their potential makers, which is compatible with two rodents recorded for the Camacho Formation, *Lagostomus* sp. and *Prodolichotis* sp., and the armadillo *Proeuphractus limpidus*. The genus *Lagostomus* is recorded from the Late Miocene to the present day, with the extant species *L. maximus*, commonly known as viscachas (Rasia and Candela, 2017). Extant viscachas (~5 kg) are recognised to be good diggers, producing complex systems of tunnels where several individuals form colonies (Jackson et al., 1996). Furthermore, several extinct species of the genus have been recorded for the Late Miocene in the region, and most of them show smaller sizes when compared to *L. maximus* (Rasia et al., 2020). Moreover, complex systems of fossil burrows were described by Cardonatto et al. (2023) and assigned to *Lagostomus* in the Late Miocene-Early Pliocene of Argentina. On the other hand, the genus *Prodolichotis* is related to the extant *Dolichotis*, commonly known as maras (Madozzo-Jaén, 2019). Maras are known for their adaptations to life on steppes and good running capacity, and a monogamous breeding system that is maintained for life (Campos et al., 2001). Maras are not recognised as especially good diggers, but they can dig tunnel systems for couples and offsprings to occupy, although they also use previously built burrows by other taxa (Campos et al., 2001). On the other hand, the presence of *Proeuphractus limpidus* in the Camacho Formation is also worth mentioning, since the phylogenetically related

extant *Euphractus sexcinctus* is known for its digging ability and omnivorous diet (Redford and Wetzel, 1985). However, considering the complexity of the smaller burrow systems found at the site, which is compatible with a relatively highly social species, and the fact that *Lagostomus* remains where found within one burrow, we propose this genus as the most probable maker of these burrow systems.

The second burrow size category provided an estimated body mass of 9.3–13.8 Kg, which overlaps with the predicted body mass of *Hemihegetotherium achataleptum*. *Hemihegetotherium achataleptum* is a member of the Hegetotheriidae, a family within the South American order Notoungulata, which shows a considerable morphological convergence with hares (Cassini et al., 2012). Like other members of the Hegetotheriinae, *H. achataleptum* was probably a good runner, but also had the capacity to dig burrows, either for protection from predators or nesting (Croft, 2016). In fact, a phylogenetically related taxa, *Paedotherium* sp., has been proposed as the maker of fossil burrows in southern Buenos Aires Province, Argentina (Elissamburu et al., 2011). Interestingly, the fossil burrows attributed to *Paedotherium* for the Pliocene of Argentina were frequently found in association with smaller burrows, in that case assigned to the rodent *Actenomys priscus*. This combination is particularly interesting considering the close spatial association of the two smaller burrow size classes recovered in our study, which almost match the mean horizontal diameters reported by Elissamburu et al. (2011). These kinds of assemblages would indicate that these pairs of taxa could make their burrows within the same space, making complex

intermingled tunnel systems or using parts of the other taxa's burrow system. Another potential explanation that should not be ruled out is the possible contribution of juvenile individuals in burrowing activities, although the clear gap in the burrow size distribution would not be explained by this hypothesis. On the other hand, it should be noted that the Pachyarmatheriidae *Neoglyptatelus uruguayensis*, although a bit bigger than the estimated body mass based on tunnel diameter, could also be responsible of some of the burrows considering its phylogenetic closeness to other specialised burrowers within the Xenarthra (Fericola et al., 2017).

The third burrow size class produced a body mass estimation of 24.3–50.8 Kg for the potential maker, which overlaps with several of the taxa recorded for the Camacho Formation, namely the Cingulata *Ringueletia* sp. and *Kraglievicha paranensis*, the Caviidae *Cardiatherium orientalis*, and the Procyonidae *Cyonasua* sp. considering the cingulates, the pampatheriid *K. paranensis* could be considered the least adapted for digging since members of this group lack important morphological adaptations for digging (Edmund, 1985; Vizcaíno et al., 2001). The rodent *Cardiatherium orientalis* would not represent a good digger either based on the behaviour of its extant relatives, like the capybara (*Hydrochoerus hydrochaeris*; Mones and Ojasti, 1986). On the other hand, the dasypodid *Ringueletia simpsoni* has been described as a good digger, and several fossil burrows have been assigned to this taxon in Argentina (Cenizo et al., 2016). In fact, a fossil burrow described by Cenizo et al. (2016) was assigned to *R. simpsoni*, and allowed the authors to infer that other taxa reutilised the burrow, as well as the existence of predator-prey relationships among taxa. Furthermore, one of the predators described by Cenizo et al. (2016) was the procyonid *Cyonasua lutaria*, which clearly supports the possible involvement of *Cyonasua* sp. in the fossil burrows described in the present study.

Finally, the largest burrows found at the site would correspond to a maker with a body mass of 211.2–723.9 Kg, which overlaps with the predicted body mass of some of the largest mammals recorded in the Camacho Formation, including rodents, armadillos, and sloths. Two large rodents are registered for the Camacho Formation, the Dinomyidae *Isostylomys intermedius* and *Arazamys castiglioni* (Rinderknecht et al., 2011). Neither of them could be considered a specialised digger based on the behaviour of their extant relatives, although particular adaptations to teeth-digging have been proposed for *Josephoartigasia monesi*, another giant Dinomyidae found in the Pliocene of Southern Uruguay (Cox et al., 2015). On the other hand, there are two large armadillos (order Cingulata) recorded for the Camacho Formation that are close to the estimated body mass (although smaller than the prediction based on burrow diameter), the Pampatheriidae *Vasallia* sp. and several species of the genus *Pseudoplohophorus*, a member of the Glyptodontinae whose infrageneric classification still lacks consensus. While armadillos are often specialised diggers (Vizcaíno et al., 1999), the adaptations for digging in most pampatheres and glyptodonts are often less well-defined, specially in the giant forms (Milne et al., 2009). Despite this, a partial carapace of the glyptodont *Pseudoplohophorus* sp. was found in clear association to one of the large burrows, thus, this taxon should not be entirely ruled out as a potential maker. In fact, an estimation of the Index of Fossorial Ability for this taxon shows that it was probably a more capable digger than its Pleistocene giant relatives (Vizcaíno et al., 1999; see. Supp. Mat.). Finally, the largest taxa recorded for the Camacho Formation are sloths, with three species with estimated body masses larger than 500 Kg, the Megalonychidae *Pliomorphus mutilatus* and the Mylodontidae *Kiyumylodon lecuonai* and *Lestobradys sprechmanni*. *Pliomorphus mutilatus*, as other megalonychids, should not be considered a good digger, and although its size would exclude an arboreal lifestyle, it was probably more adapted to feeding and partially climbing on trees (Casali et al., 2023). On the other hand, some Mylodontoidea are considered clear examples of digging adaptations within sloths, with several taxa showing morphological characters related to digging capacity (Pujos et al., 2012; Patiño et al., 2021). In fact, several Late Pleistocene taxa have been proposed as the makers of giant fossil

burrows found in Argentina and Brazil, with the Scelidotheriidae *Scelidotherium leptocephalum* and the Mylodontidae *Glossotherium robustum* and *Lestodon armatus*, which are commonly found in Uruguay (Varela and Fariña, 2016), as the most probable species responsible for these extensive galleries (Vizcaíno et al., 2001; Frank et al., 2015). Furthermore, recently discovered large fossil burrows in the Late Miocene of Central Argentina have been attributed to the scelidotheriid *Proscelidodon* sp. (Cardonatto and Melchor, 2018). Despite the relative geographical proximity and similar age, no scelidotheriid has been recovered in the Camacho Formation to date, so a direct comparison to the Argentinian fossil burrows is not possible. Despite this, the two recorded mylodontids have a close phylogenetic relationship to the Late Pleistocene specialised diggers mentioned before (Varela et al., 2019), and probably possessed similar morphological adaptations for digging, making them compelling candidates as makers of the large burrows. On the contrary, although lacking precise body mass estimations, the unidentified nothrotheriid found in proximity to the burrows could be discarded as an apt digger considering that members of the family Nothrotheriidae, including the genus *Pronothrotherium* registered for the Camacho Formation, are not recognised as good diggers (Pujos et al., 2012).

5.2. New insights on the palaeoenvironments and ecosystems of the region during the Late Miocene

The finding of these extensive burrow systems in the Punta San Gregorio site has important implications for the understanding of the palaeoenvironmental evolution of the region in the Late Miocene. As mentioned before, the Camacho Formation has been traditionally considered of marine origin and correlated with the Paranaense transgression (Sprechmann et al., 2000). However, the occurrence of mammal burrows and continental vertebrates remains, as well as other evidence of subaerial exposure like rhizoliths and desiccation or syneresis cracks in outcrops of the unit in the eastern coast of the San José Department, shows that at least during some time in the Late Miocene, this region was above sea level and mammalian communities thrived in this coastal setting (an artistic depiction of the site during the Late Miocene is shown in Fig. 5). This is interesting considering the geochronological data available for the Camacho Formation, which mostly represent the Colonia Department outcrops, where marine invertebrates are abundant, but are almost non-existent for the eastern San José Department sites (Perea et al., 2020a). The preservation of subaerial surfaces and poorly developed palaeosols can indicate at least one non-depositional episode in the unit, still poorly constrained. So far, the chronostratigraphic framework remains unclear, but with significant differences between the western and south-eastern localities of the Camacho Formation.

Furthermore, the finding of the fossil burrows poses new challenges for the recognition of stratigraphic levels and the assignment of fossil provenance, especially considering that burrowing taxa are known to act as taphonomic agents, often mixing, accumulating, and altering bone remains (Rafuse et al., 2019; Álvarez et al., 2020). In this regard, further studies improving the biostratigraphic correlations of the Camacho Formation, as well as new absolute ages would be crucial to improve our knowledge regarding the relationships between western and eastern outcrops, as well as their correlation to other Late Miocene Formations in the region.

The palaeoecological implications of the reported trace fossils extend beyond the new information on the behaviour of specific taxa. The extensive fossil tunnel systems uncovered at the Punta San Gregorio site provide unique information on many aspects of a Late Miocene mammal community where several taxa undoubtedly had important impacts on the ecosystem. In this aspect, burrowing taxa have been recognised as important ecosystem engineers that modify their environment through the mobilisation of soil and the generation of new underground spaces (Zhang et al., 2003). Furthermore, many authors have proposed that



Fig. 5. Artistic depiction of Punta San Gregorio during the Late Miocene. Several of the taxa discussed in the text are shown in association with the extensive burrow systems. Image composed using a combination of digital art and AI-generated (DALL·E 3) images (credit: LV).

certain borrowers can be considered as keystone species, whose activity has important effects over several other taxa (Beca et al., 2022). In fact, in some cases, certain taxa are highly dependent on the structures generated by burrowing taxa.

For example, in North America, the gopher tortoise (*Gopherus polyphemus*) produces large burrows that directly or indirectly affect a plethora of other species, including invertebrates and vertebrates like arthropods, amphibians, reptiles, birds, and mammals, with several of these species depending on the burrows for their survival (Kinlaw and Grasmueck, 2012). In South America, the giant armadillo *Priodontes maximus* is responsible for the construction of large burrows that are visited and used by many other taxa (Desbiez and Kluyber, 2013). Likewise, rodents like the plains viscacha or the prairie dogs generate extensive tunnel systems that increase biodiversity and modify the environment, improving soil properties and available forage biomass (Ceballos et al., 1999; Martínez-Estévez et al., 2013; Villarreal et al., 2008). Many more examples exist in the world today, and several authors have emphasised the role of these taxa in their ecosystems, as well as the importance of their conservation in order to maintain biodiversity and ecosystem services (Davidson et al., 2012). This is relevant considering the reduced diversity in burrowing taxa in South America in the present when compared to other continents (Beca et al., 2022). In contrast, the extensive modification of the environment evidenced by the fossil burrows is not unrealistic considering the high diversity of several clades known for their digging adaptations, like Rodentia, Xenarthra, and Notoungulata. In this sense, the Punta San Gregorio site shows a flourishing community of burrowing mammals in the Late Miocene of South America, and provides an important baseline that allows the comparison with the present state, where many taxa have become extinct during the last tens of thousand years (Fariña et al., 2013). In fact, several species within Cingulata and Folivora became extinct as recently as 11 ka ago, at the end of the Pleistocene, and undoubtedly many of these were capable diggers that probably acted like

keystone ecosystem engineers (Vizcaíno et al., 2001; Frank et al., 2015). Furthermore, the Late Miocene, and the Tortonian specifically, represents a time when several South American clades maintained high diversity (Brandoni, 2013; Prevosti et al., 2013; Varela et al., 2019; Croft et al., 2020), which is clearly reflected in the recovered taxa in the Camacho Formation. On the other hand, the climate during this time was generally warmer and more variable than today, which makes the Miocene a key time to study climate change and biotic responses since many aspects resemble the global changes occurring today (Steinthorsdottir et al., 2021).

5.3. Gregariousness, social behaviour, and interactions among taxa

The extensive and intermingled systems recovered for the smaller burrows, as well as the presence of several chambers, supports the existence of social behaviour in the responsible taxa. This kind of social burrowing is relatively common in rodents (Lacey et al., 2000), but its occurrence in notoungulates cannot be discarded considering the lack of extant relatives and their size compatibility with the burrows. In this sense, the fossil record of burrowing social behaviour in mammals is not extensive, particularly for South America. In fact, the oldest record of mammal fossil burrows similar to those of extant social rodents is registered for the Oligocene of Mexico (Guerrero-Arenas et al., 2020), while similar records for South America have been dated to the Late Pliocene (Elissamburu et al., 2011). The newly reported fossil burrows represent one of the oldest records of a gregarious social behaviour related to burrowing activities for the region. On the other hand, the largest burrows showed more simple designs, which are clearly similar to those of extant xenarthrans (Redford and Wetzell, 1985; Desbiez and Kluyber, 2013; Cardonatto and Melchor, 2023) and would indicate a relatively solitary behaviour for these taxa. Considering all this, the findings support the existence of diverse and well-developed burrowing behaviours in several taxa before the main pulse of the South American

Biotic Interchange (GABI), which has been often proposed as one potential explanation for the development of burrowing behaviour in taxa like the giant cingulates and folivorans (Genise, 1989; Vizcaíno et al., 2001).

The newly found fossil burrows are also relevant for the understanding of the interactions among taxa present in the region during the Late Miocene. As mentioned above, the spatial association of the two smaller size classes is strikingly similar to those reported for the Late Pliocene by Elissamburu et al. (2011) and supports the co-existence of at least two distantly related taxa and the potential sharing of space, in this case by the rodent *Lagostomus* sp. and the notoungulate *Hemihegetotherium achataleptum*. Moreover, Cardonatto and Melchor (2018) also reported associations of burrows of different sizes for the Late Miocene Cerro Azul Formation of central Argentina, which could be tentatively correlated to the Camacho Formation.

Previous research on extant taxa has shown that the presence of more than one burrowing ecosystem engineer in the same region enhances their effects on landscape heterogeneity and biodiversity (Davidson and Lightfoot, 2006). This is particularly interesting, considering that the Late Miocene has often been associated with high mammalian diversity in the region, and the Camacho Formation has been proposed to have a high number of endemic taxa that have been proposed to be the product of the partial isolation of southern Uruguay during the Paranaense transgression (Perea et al., 2013). Furthermore, the close association of these burrow sizes could also indicate the reutilization of abandoned tunnels by other taxa, which is commonly seen in many extant taxa, as well as the potential dependence of certain taxa on these biostructures (Jones et al., 1994). For example, the burrows of extant burrowers like the giant armadillo *Prionomys maximus* are visited by many taxa, including mammals, reptiles, and birds, providing key resources for their survival (Desbiez and Kluyber, 2013). Moreover, not only vertebrates have relevant interactions with burrowing taxa. Research has shown that the burrows of the prairie dog *Cynomys gunnisoni* have an important effect on the overall diversity of arthropods (Bangert and Slobodchikoff, 2006). Similarly, Cardonatto and Melchor (2020) showed that the burrows of the rodent *Tympanoctomys barrerae* are extensively used by invertebrates in La Pampa, Argentina. Interestingly, several of the studied burrows at Punta San Gregorio have smaller burrows (~1–2 cm wide; Fig. 3G) branching out from them, showing a striking similarity to those reported by Cardonatto and Melchor (2020) in extant rodent burrows.

Finally, it is worth mentioning the possible occurrence of burrows associated with predation, as some of the larger burrows were found apparently cutting through the smaller burrow systems (Fig. 2A,B,E). As mentioned before, this behaviour would not be extraordinary considering it is seen in extant taxa like certain armadillos and procyonids but is relatively uncommon in the fossil record. The presence on the Camacho Formation of one procyonid, *Cyonasua* sp., within the size range predicted for these burrows makes it a probable maker, especially considering the involvement of the closely related *Cyonasua lutaria* in similar predatory behaviour in the Pliocene of Argentina (Cenizo et al., 2016). Furthermore, the armadillo *Proeuphractus limpidus*, although assignable to a smaller burrow size class, should not be discarded. In fact, the predation of turtle nests by armadillos, probably *E. sexcinctus*, has been reported in beaches of the Northern Coast of Brazil (Gandu et al., 2013). Moreover, the fossil *Macroephractus*, a close relative of *Proeuphractus*, has been distinguished for its significant adaptations for carnivory and potential digging capacity (Vizcaíno and De Iuliis, 2003). The lack of articulated fossil remains within the burrows makes these assignments difficult and new findings would be important for the confirmation of these hypotheses.

6. Conclusions

In this work, we present a new fossil site located in southern Uruguay where a great amount of fossil burrows are preserved along a fauna

representative of the Late Miocene of southeastern South America. The diversity of the recovered burrows, both in terms of size and morphology, supports the existence of several taxa involved in their creation and adapted to digging and fossoriality. Despite the specific assignment for the fossil burrows, the reported findings uncover a complex community of burrowing taxa with different behaviours and interactions, encompassing a clear example of a highly engineered ecosystem in the fossil record and providing a unique opportunity to continue improving our knowledge regarding these kinds of adaptations and their evolution in contexts of global change. Future research expanding on the geographic and temporal extent of the fossil burrows, while also integrating different approaches will be crucial to better understand the biology of the Late Miocene South American fauna, addressing their diversity, trophic relationships, and ecological and biogeographical context in a key moment in the history of the continent at the onset of the Great American Biotic Interchange.

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Authors contributions

Luciano Varela: Conceptualization, Investigation, Methodology, Formal analysis, Resources, Visualization, Funding acquisition, Writing – Original Draft. Ximena Martínez-Blanco: Conceptualization, Investigation, Methodology, Resources, Writing – Original Draft. Raúl Ugalde: Investigation, Resources, Visualization, Writing – Original Draft. P. Sebastián Tambusso: Investigation, Resources, Writing – Original Draft. Carolina Lobato: Investigation, Formal analysis, Resources, Writing – Original Draft. Claudio Gaucher: Investigation, Resources, Writing – Review & Editing. Richard A. Fariña: Investigation, Resources, Writing – Review & Editing.

Declaration of competing interest

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

Data availability

All the data used in the study is available in the manuscript or in the Supplementary Material

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Appendix A. Supplementary data

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References

- Álvarez, M.C., Rafuse, D.J., Bellinzoni, J.E., Kaufmann, C.A., 2020. Armadillos as taphonomic agents of archaeological sites in the Pampas Region, Argentina. *J. Archaeol. Sci. Rep.* 31, 102293. <https://doi.org/10.1016/j.jasrep.2020.102293>.

- Bangert, R.K., Slobodchikoff, C.N., 2006. Conservation of prairie dog ecosystem engineering may support arthropod beta and gamma diversity. *J. Arid Environ.* 67 (1), 100–115. <https://doi.org/10.1016/j.jaridenv.2006.01.015>.
- Beca, G., Valentine, L.E., Galetti, M., Hobbs, R.J., 2022. Ecosystem roles and conservation status of bioturbator mammals. *Mamm. Rev.* 52 (2), 192–207. <https://doi.org/10.1111/mam.12269>.
- Brandoni, D., 2013. Los mamíferos continentales del “Mesopotamiense” (Mioceno tardío) de Entre Ríos, Argentina. *Diversidad, edad y paleobiogeografía. Publicación Espec. - Asoc. Paleontol. Argent.* 14, 179–191.
- Bossi, J., Navarro, R., 1991. *Geología del Uruguay*. Departamento de Publicaciones de la Universidad de la República, Montevideo, p. 970.
- Campos, C.M., Tognelli, M.F., Ojeda, R.A., 2001. *Dolichotis patagonum*. *Mamm. Species* 652, 1–5.
- Cardonatto, M.C., Feola, S., Melchor, R.N., 2023. Neogene communal rodent burrow systems from central Argentina. *Hist. Biol.* 1–15. <https://doi.org/10.1080/08912963.2023.2228319>.
- Cardonatto, M.C., Melchor, R.N., 2021. Environmental influence on burrow system features of a colonial and fossorial rodent: implications for interpreting fossil tetrapod burrows. *Palaios* 36 (6), 225–245.
- Cardonatto, M.C., Melchor, R.N., 2023. Neoichnology of armadillos: keys for the paleoecological and behavioral interpretation of fossil tetrapod burrows. *Palaios* 38 (2), 57–75.
- Cardonatto, M.C., Melchor, R.N., 2018. Large mammal burrows in late Miocene calcic paleosols from central Argentina: paleoenvironment, taphonomy and producers. *PeerJ* 6, e4787. <https://doi.org/10.7717/peerj.4787>.
- Cardonatto, M.C., Melchor, R.N., 2020. Recognition of fossil nekha deposits: clues from neoichnology and sedimentology. *Palaios* 35 (7), 277–291. <https://doi.org/10.2110/palo.2020.024>.
- Casali, D.M., Boscaini, A., Gaudin, T.J., Perini, F.A., 2023. Morphological disparity and evolutionary rates of cranial and postcranial characters in sloths (Mammalia, Pilosa, Folivora). *Palaeontology* 66 (1), e12639. <https://doi.org/10.1111/pala.12639>.
- Cassini, G.H., Cerdeño, E., Villafañe, A.L., Muñoz, N.A., 2012. Paleobiology of santacruciana native ungulates (meridiungulata: astrapotheria, litopterna and Notoungulata). In: Vizcaíno, S.F., Kay, R.F., Bargo, M.S. (Eds.), *Early Miocene Paleobiology in Patagonia*. Cambridge University Press, Cambridge, pp. 243–286. <https://doi.org/10.1017/CBO9780511667381.015>.
- Ceballos, G., Pacheco, J., List, R., 1999. Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. *J. Arid Environ.* 41 (2), 161–172. <https://doi.org/10.1006/jare.1998.0479>.
- Kenzo, M., Soibelzon, E., Magnusson Saffer, M., 2016. Mammalian predator–prey relationships and reoccupation of burrows in the Pliocene of the Pampean Region (Argentina): new ichnological and taphonomic evidence. *Hist. Biol.* 28 (8), 1026–1040. <https://doi.org/10.1080/08912963.2015.1089868>.
- Cione, A.L., Tonni, E.P., 1995. Chronostratigraphy and “Land-Mammal Ages” in the Cenozoic of southern South America: principles, practices, and the “Uquian” problem. *J. Paleontol.* 69 (1), 135–159. <https://doi.org/10.1017/S002236000026998>.
- Cox, P.G., Rinderknecht, A., Blanco, R.E., 2015. Predicting bite force and cranial biomechanics in the largest fossil rodent using finite element analysis. *J. Anat.* 226 (3), 215–223. <https://doi.org/10.1111/joa.12282>.
- Croft, D.A., Gelfo, J.N., López, G.M., 2020. Splendid innovation: the extinct South American native ungulates. *Annu. Rev. Earth Planet Sci.* 48, 259–290. <https://doi.org/10.1146/annurev-earth-072619-060126>.
- Croft, D.A., 2016. *Horned Armadillos and Rafting Monkeys: the Fascinating Fossil Mammals of South America*. Indiana University Press.
- Damiani, R., Modesto, S., Yates, A., Neveling, J., 2003. Earliest evidence of cynodont burrowing. *Proc. R. Soc. B: Biol. Sci.* 270 (1525), 1747–1751. <https://doi.org/10.1098/rspb.2003.2427>.
- Davidson, A.D., Detling, J.K., Brown, J.H., 2012. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world’s grasslands. *Front. Ecol. Environ.* 10 (9), 477–486. <https://doi.org/10.1890/110054>.
- Davidson AD, Lightfoot DC. 2006. Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland. *Ecography* 29(5), 755–765. (doi:10.1111/j.2006.0906-7590.04699.x).
- del Río, C.J., Martínez, S., McArthur, J., Thirlwall, M., Pérez, L., 2018. Dating late Miocene marine incursions across Argentina and Uruguay with Sr-isotope stratigraphy. *J. South Am. Earth Sci.* 85, 312–324. <https://doi.org/10.1016/j.jsames.2018.05.016>.
- Desbiez, A.L.J., Kluyber, D., 2013. The role of giant armadillos (*Priodontes maximus*) as physical ecosystem engineers. *Biotropica* 45 (5), 537–540. <https://doi.org/10.1111/btp.12052>.
- Edmund, G., 1985. The fossil giant armadillos of North America (Pampatheriinae, Xenarthra=edentata). In: Montgomery, G.G. (Ed.), *The Evolution and Ecology of Armadillos, Sloths and Vermilinguas*. Smithsonian Institution Press, Washington, DC, pp. 83–93.
- 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. *Mastozool. Neotrop.* 18 (2), 227–238.
- Fariña, R.A., Vizcaíno, S.F., De Iuliis, G., 2013. Megafauna: Giant Beasts of Pleistocene South America. Indiana University Press.
- Fariña, R.A., Vizcaíno, S.F., Bargo, M.S., 1998. Body mass estimations in Lujanian (late Pleistocene-early Holocene of South America) mammal megafauna. *Mastozool. Neotrop.* 5 (2), 87–108.
- Fernicola, J.C., Rinderknecht, A., Jones, W., Vizcaíno, S.F., Porpino, K., 2017. A new species of *Neoglyptatelus* (Mammalia, Xenarthra, Cingulata) from the late Miocene of Uruguay provides new insights on the evolution of the dorsal armor in cingulates. *Ameghiniana* 55 (3), 233–252. <https://doi.org/10.5710/AMGH.02.12.2017.3150>.
- Francis, J.C., Mones, A., 1965. Sobre el hallazgo de *Cardiatherium taliceii* n.sp. (Rodentia, Hydrochoeridae) en la Playa Kiyú, Departamento de San José, República Oriental del Uruguay. *Kraglieviana* 1, 3–44.
- Frank, H.T., Althaus, C.E., Dario, E.M., Tramontina, F.R., Adriano, R.M., Almeida, M., Ferreira, G.F., Nogueira, R., Breier, R., 2015. Underground chamber systems excavated by Cenozoic ground sloths in the state of Rio Grande do Sul. *Braz. Rev. Bras. de Paleontol.* 18 (2), 273–284. <https://doi.org/10.4072/rbp.2015.2.08>.
- Gandu, M.D., López-Mendilaharsu, M., Goldberg, D.W., Lopez, G.G., Tognin, F., 2013. Predation of sea turtle nests by armadillos in the northern coast of Bahia, Brazil. *Mar. Turt. Newsl.* 139, 12–13.
- Genise, J.F., 1989. Las cuevas con *Actenomys* (Rodentia, Octodontidae) de la Formación Chapadmalal (Plioceno superior) de Mar del Plata y Miramar (Provincia de Buenos Aires). *Ameghiniana* 26 (1–2), 33–42.
- Goso, H., Bossi, J., 1966. Cenozoico. In: Boss, J. (Ed.), *Geología del Uruguay*. Universidad de la República, Montevideo, pp. 259–301.
- Guerrero-Arenas, R., Jiménez-Hidalgo, E., Genise, J.F., 2020. Burrow systems evince non-solitary geomysid rodents from the Paleogene of southern Mexico. *PLoS One* 15 (3), e0230040. <https://doi.org/10.1371/journal.pone.0230040>.
- Jackson, J.E., Branch, L.C., Villarreal, D., 1996. *Lagostomus maximus*. *Mamm. Species* 543, 1–6. <https://doi.org/10.2307/3504168>.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386. <https://doi.org/10.2307/3545850>.
- Kinlaw, A., Grasmueck, M., 2012. Evidence for and geomorphologic consequences of a reptilian ecosystem engineer: the burrowing cascade initiated by the gopher tortoise. *Geomorphology* 157, 108–121. <https://doi.org/10.1016/j.geomorph.2011.06.030>.
- Kinlaw, A.L., 1999. A review of burrowing by semi-fossorial vertebrates in arid environments. *J. Arid Environ.* 41 (2), 127–145. <https://doi.org/10.1006/jare.1998.0476>.
- Lacey, E.A., Patton, J.L., Cameron, G.N., 2000. *Life Underground: the Biology of Subterranean Rodents*. University of Chicago Press, Chicago.
- Madozo-Jaén, M.C., 2019. Systematic and phylogeny of *Prodolichotis prisca* (Caviidae, Dolichotinae) from the Northwest of Argentina (late Miocene-early Pliocene): advances in the knowledge of the evolutionary history of maras. *C. R. Pale* 18 (1), 33–50. <https://doi.org/10.1016/j.crpv.2018.07.003>.
- Martínez-Estévez, L., Balvanera, P., Pacheco, J., Ceballos, G., 2013. Prairie dog decline reduces the supply of ecosystem services and leads to desertification of semiarid grasslands. *PLoS One* 8 (10), e75229. <https://doi.org/10.1371/journal.pone.0075229>.
- Melchor, R.N., Genise, J.F., Umazano, A.M., Superina, M., 2012. Pink fairy armadillo meniscate burrows and ichnofabrics from Miocene and Holocene interdune deposits of Argentina: palaeoenvironmental and palaeoecological significance. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 350, 149–170. <https://doi.org/10.1016/j.palaeo.2012.06.026>.
- Milne N, Vizcaíno SF, Fernicola JC. 2009. A 3D geometric morphometric analysis of digging ability in the extant and fossil cingulate humerus. *J. Zool.* 278(1), 48–56. (doi:10.1111/j.1469-7998.2008.00548.x).
- Mones, A., Ojasti, J., 1986. *Hydrochoerus hydrochaeris*. *Mamm. Species* 264, 1–7.
- Nasserinejad, K., van Rosmalen, J., de Kort, W., Lesaffre, E., 2017. Comparison of criteria for choosing the number of classes in Bayesian finite mixture models. *PLoS One* 12 (1), e0168838. <https://doi.org/10.1371/journal.pone.0168838>.
- Pascual, R., Ortega Hinojosa, E.J., Gondar, D., Tonni, E.P., 1965. Las edades del Cenozoico mamífero de la Argentina, con especial atención a aquellas del territorio bonaerense. In: *Anales de la Comisión de Investigaciones Científicas de la provincia de Buenos Aires* 6, 165–193.
- Patiño, S., Perez Zepa, J., Fariña, R.A., 2021. Finite element and morphological analysis in extant mammals’ claws and quaternary sloths’ ungual phalanges. *Hist. Biol.* 33 (6), 857–867. <https://doi.org/10.1080/08912963.2019.1664504>.
- Perea, D., Martínez, S., 2004. *Estratigrafía del Mioceno-Pleistoceno en el litoral sur-oeste de Uruguay*. In: Veroslavsky, G., Ubilla, M., Martínez, S. (Eds.), *Cuencas Sedimentarias de Uruguay, Cenozoico*. Ediciones DIRAC, Montevideo, pp. 105–124.
- Perea, D., Rinderknecht, A., Ubilla, M., Bostelmann, E., Martínez, S., 2013. Mamíferos y estratigrafía del Neógeno de Uruguay. *Publicación Espec. - Asoc. Paleontol. Argent.* 14, 192–206.
- Perea, D., Verde, M., Montenegro, F., Toriño, P., Manzuetti, A., Roland, G., 2020b. Insect trace fossils in glyptodonts from Uruguay. *Ichnos* 27 (1), 70–79.
- Perea, D., Verde, M., Toriño, P., Montenegro, F., Ubilla, M., Manzuetti, A., 2020a. A complex association of invertebrates, vertebrates and trace fossils in the marine Camacho Formation (late Miocene of Uruguay): biostratigraphy and paleoenvironments. *Ameghiniana* 57 (3), 266–277. <https://doi.org/10.5710/AMGH.29.02.2020.3327>.
- Prevosti, F.J., Forasiepi, A., Zimic, N., 2013. The evolution of the Cenozoic terrestrial mammalian predator guild in South America: competition or replacement? *J. Mamm. Evol.* 20 (1), 3–21. <https://doi.org/10.1007/s10914-011-9175-9>.
- Pujos, F., Gaudin, T.J., De Iuliis, G., Cartelle, C., 2012. Recent advances on variability, morpho-functional adaptations, dental terminology, and evolution of sloths. *J. Mamm. Evol.* 19, 159–169. <https://doi.org/10.1007/s10914-012-9189-y>.
- Raftery, A.E., 1995. Bayesian model selection in social research. *Socio. Methodol.* 25, 111–163. <https://doi.org/10.2307/271063>.
- Rafuse, D.J., Kaufmann, C.A., Gutiérrez, M.A., González, M.E., Scheifler, N.A., Álvarez, M.C., Massigoge, A., 2019. Taphonomy of modern communal burrow systems of the Plains vizcacha (*Lagostomus maximus*, Chinchillidae) in the Pampas region of Argentina: implications for the fossil record. *Hist. Biol.* 31 (5), 517–534. <https://doi.org/10.1080/08912963.2017.1374957>.

- Rasia, L.L., Bonini, R.A., Candela, A.M., 2020. Nuevos registros de *Lagostomus* (Rodentia, Chinchillidae) en el Mioceno tardío de Argentina y su importancia bioestratigráfica. *Andean Geol.* 47 (2), 430–445. <https://doi.org/10.5027/andgeoV47n2-3270>.
- Rasia, L.L., Candela, A.M., 2017. Systematic revision of the vizcachas (Rodentia, caviomorpha, chinchillidae) from the chapadmalal formation, late Pliocene of Buenos Aires Province, Argentina. *Ameghiniana* 54 (1), 50–69. <https://doi.org/10.5710/AMGH.01.09.2016.3012>.
- Redford, K.H., Wetzel, R.M., 1985. *Euphractus sexcinctus*. *Mamm. Species* 252, 1–4. <https://doi.org/10.2307/3503786>.
- Reichman, O.J., Smith, S.C., 1990. Burrows and burrowing behavior by mammals. In: Genoways, H.H. (Ed.), *Current Mammalogy* 2. Plenum Press, New York, pp. 197–244.
- Retallack, G.J., 2001. Soils of the Past: an Introduction to Paleopedology. Blackwell Science, London, pp. 13–36. <https://doi.org/10.1002/9780470698716>.
- Rinderknecht, A., Enrique, B.T., Ubilla, M., 2011. New genus of giant Dinomyidae (Rodentia: hystricognathi: caviomorpha) from the late Miocene of Uruguay. *J. Mammal.* 92 (1), 169–178. <https://doi.org/10.2307/23259796>.
- Soibelzon, L.H., Riderknecht, A., Tarquini, J., Ugalde, R., 2019. First record of fossil procyonid (mammalia, Carnivora) from Uruguay. *J. South Am. Earth sci.* 92, 368–373. <https://doi.org/10.1016/j.jsames.2019.03.024>.
- Sprechmann, P., Martínez, S., Gaucher, C., 1994. Paleoeología y sedimentología de la Formación Camacho en el Departamento de Colonia (Mioceno Medio - superior, Uruguay). *Paleociencias del Uruguay* 2, 21–24.
- Sprechmann, P., Ferrando, A.L., Martínez, S., 2000. Estado actual de los conocimientos sobre la Formación Camacho (Mioceno medio?–superior?, Uruguay). In: Acenolanza, F.G., Herbst, R. (Eds.), *El Neógeno de Argentina*. Tucumán: INSUGEO, Serie Correlación Geológica, pp. 47–65.
- Sprechmann, P., Gaucher, C., Frei, R., 2010. Identificación del Burdigaliense (Mioceno temprano) en ostreidos procedentes de afloramientos de la Formación Camacho de Uruguay datados con 87Sr/86Sr. 10 Congreso Argentino de Paleontología y Bioestratigrafía y 7 Congreso Latinoamericano de Paleontología, (La Plata). *Acta* 1, 106.
- Steinthorsdottir, M., Coxall, H.K., De Boer, A.M., Huber, M., Barbolini, N., Bradshaw Cd, Burls, N.J., Feakins, S.J., Gasson, E., Henderiks, J., et al., 2021. The Miocene: the future of the past. *Paleoceanogr. Paleoclimatol* 36 (4), e2020PA004037. <https://doi.org/10.1029/2020PA004037>.
- Varela, L., Fariña, R.A., 2016. Co-occurrence of mylodontid sloths and insights on their potential distributions during the late Pleistocene. *Quat. Res.* 85 (1), 66–74. <https://doi.org/10.1016/j.yqres.2015.11.009>.
- Varela, L., Tambusso, P.S., McDonald, H.G., Fariña, R.A., 2019. Phylogeny, macroevolutionary trends and historical biogeography of sloths: insights from a Bayesian morphological clock analysis. *Syst. Biol.* 68 (2), 204–218. <https://doi.org/10.1093/sysbio/syy058>.
- Villarreal, D., Clark, K.L., Branch, L.C., Hierro, J.L., Machicote, M., 2008. Alteration of ecosystem structure by a burrowing herbivore, the plains vizcacha (*Lagostomus maximus*). *J. Mammal.* 89 (3), 700–711. <https://doi.org/10.1644/07-MAMM-A-025R1.1>.
- Vizcaíno, S.F., De Iuliis, G., 2003. Evidence for advanced carnivory in fossil armadillos (Mammalia: Xenarthra: Dasypodidae). *Paleobiology* 29 (1), 123–138. [https://doi.org/10.1666/0094-8373\(2003\)029<0123:EFACIF>2.0.CO;2](https://doi.org/10.1666/0094-8373(2003)029<0123:EFACIF>2.0.CO;2).
- Vizcaíno, S.F., Fariña, R.A., Mazzetta, G.V., 1999. Ulnar dimensions and fossoriality in armadillos. *Acta Theriol.* 44 (3), 309–320.
- Vizcaíno, S.F., Zárate, M., Bargo, M.S., Dondas, A., 2001. Pleistocene burrows in the Mar del Plata area [Argentina] and their probable builders. *Acta Palaeontol. Pol* 46 (2), 289–301.
- Weaver, L.N., Varricchio, D.J., Sargis, E.J., Chen, M., Freimuth, W.J., Wilson Mantilla, G. P., 2021. Early mammalian social behaviour revealed by multituberculates from a dinosaur nesting site. *Nat. Ecol. Evol.* 5 (1), 32–37. <https://doi.org/10.1038/s41559-020-01325-8>.
- White, E.P., Ernest, S.M., Kerkhoff, A.J., Enquist, B.J., 2007. Relationships between body size and abundance in ecology. *Trends Ecol. Evol.* 22 (6), 323–330.
- White, C.R., 2005. The allometry of burrow geometry. *J. Zool.* 265 (4), 395–403. <https://doi.org/10.1017/S0952836905006473>.
- Yu, Y., 2022. mixR: an R package for finite mixture modeling for both raw and binned data. *J. Open Source Softw.* 7 (69), 4031. <https://doi.org/10.21105/joss.04031>.
- Zhang Y, Zhang Z, Liu J. 2003. Burrowing rodents as ecosystem engineers: the ecology and management of plateau zokors *Myospalax fontanierii* in alpine meadow ecosystems on the Tibetan Plateau. *Mamm Rev.* 33(3–4), 284–294. (doi:10.1046/j.1365-2907.2003.00020.x).