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Paleoecology and diversity of Pliocene to Pleistocene fossorial mammals in the Pampean region of Argentina based on a quantitative analysis of fossil burrows

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ABSTRACT

Pliocene and Pleistocene sedimentary successions in the Pampean region of Argentina contain abundant and diverse fossil mammalian burrows. In this paper, we report fossil burrows from eight localities from near Miramar to the northern area of Mar del Plata, spanning the Early Pliocene to the Late Pleistocene, and analyze burrow size patterns. The minimum width of each fossil burrow was measured as an indicator of its diameter. Available allometric equations for extant burrowing vertebrates were used to estimate the body size of potential producers based on burrow diameter. Size distribution patterns indicate that, in the Early Pliocene to Early Pleistocene levels, small burrows (attributed to rodents, typotheres, and small armadillos) were abundant, while medium- to large-sized burrows (attributed to large cingulates) were less common. In the Middle to Late Pleistocene levels, small burrows are very scarce, and medium-sized burrows are most abundant, together with giant burrows (attributed to ground sloths). Our findings indicate a significant size diversity for Pliocene–-Pleistocene burrowing mammals in the studied area, from small rodents to giant ground sloths. Although present in Pliocene to Early Pleistocene times, the largest ground sloths began to build subterranean galleries only later in the Middle to Late Pleistocene. Small burrowers were comparatively less active during that time. These patterns are discussed in the light of paleoclimate and paleoecology of the putative guild of extinct burrowers, to develop working hypotheses for future studies. A paleoclimatic shift from Pliocene Climate Optimum to more arid and colder conditions from the Late Pliocene to Late Pleistocene, and the incursion of large predators to the region, are proposed as major factors promoting large ground sloths to adopt a fossorial lifestyle.

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1. Introduction

Digging is common among terrestrial vertebrates, and many taxa are well-suited for this activity, including lungfish, salamanders, frogs, turtles, lizards, snakes, crocodiles, birds, and mammals. These substrate modifications can span from shallow, simple daybeds to highly complex tunnel systems (Butler, 1995). Although most extant mammals can dig for different purposes, only a few excavate complex tunnels, and are termed fossorial mammals (Hildebrand, 1985; Reichman and Smith, 1990). They include echidnas, marsupial moles and wombats, armadillos, hedgehogs, rodents, aardvarks, pangolins, and carnivorans, and comprise solitary and eusocial taxa (Hasiotis et al., 2007). Many other vertebrates take advantage of abandoned burrows and can be termed secondary fossorials. The impact of burrows on the environment has made many fossorial animals to be considered ecological engineers (Marchetti et al., 2024). Fossoriality grants burrowers (and secondary fossorials) ecological advantages and disadvantages (Hildebrand, 1985).

In the terrestrial fossil record, burrows and dens ascribed to vertebrates have been known since the Devonian, their putative producers spanning from lungfish to sauropod dinosaurs (see Voorhies, 1975; Hasiotis et al., 2007; Marchetti et al., 2024). The diameter of these biogenic structures spans from centimeters to tens of centimeters, not surpassing 50 cm until early Neogene (e.g. Damiani et al., 2003; Hasiotis et al., 2007; Varricchio et al., 2007; Modesto and Botha-Brink, 2010; Simpson et al., 2010; Martin and Varricchio, 2011; Colombi et al., 2012; Krapovickas, 2012; Krapovickas et al., 2013; Fiorelli et al., 2018; Cardonato and Melchor 2018). Fossil burrows are commonly found in the terrestrial late Cenozoic (Neogene–Quaternary) sequences of South America. They range in size from small to giant, with some reaching diameters of up to 2 m, with an increasing size trend from the Miocene until the late Pleistocene (Cardonatto and Melchor, 2018). Large to giant fossil burrows have been described from the late Miocene to the Late Pleistocene in Argentina (e.g. Quintana, 1992; Zárate et al., 1998; Isla and Dondas, 2001; Dondas et al., 2009; Genise and Farina, 2012; Melchor et al., 2012; Cenizo et al., 2016; Krapovickas and Tauber, 2016; Cardonatto and Melchor, 2018; Toledo et al., 2023; Arregui et al., 2024), Uruguay (Varela et al., 2023), and Brazil (e.g. Buchmann et al., 2009; Lopes et al., 2017; Frank et al., 2023; Bechtel et al., 2024). Therefore, Plio—Pleistocene fossil burrows of South America are unique by their enormous size, reaching up to four times the size of the largest known non-anthropic, biogenic excavations recorded.

In the Argentinean Pampean area, fossil burrows are frequent along the cliffs of the Atlantic coast of Buenos Aires province (Zárate et al., 1998; Vizcaíno et al., 2001; Dondas et al., 2009; Beilinson and Taglioretti, 2013). They were early noted by Ameghino (1908), Frenguelli (1928), and Kraglievich (1952), but not thoroughly described until later by Genise (1989) and Zárate et al. (1998). These fossil burrows usually show discrete boundaries with the host rock, being either sub-circular or elliptical in section. Although longitudinal sections are common, they have not been often reported and, in some rare cases, plan views are recorded. The fossil burrows were recorded in either aeolian (loess) and loess-like sediments, as well as fluvial siltstones and sandstones, and were filled with laminated sand and siltstones. Vertebrate bones are commonly recovered from these fillings, ranging from isolated pieces to partially articulated skeletons (e.g., Elissamburu et al., 2011; MLT pers. obs.). Quintana (1992), Genise (1989), Zárate et al. (1998), Elissamburu et al. (2011), Genise and Farina (2012), and Cardonatto and Melchor (2018) provided previous approaches to quantification of these fossil burrows. Zárate et al. (1998) described diameter ranges of fossil burrows from Pleistocene successions at the Mar del Plata sea cliffs, showing that fossil burrows of ~100 cm were the most common, followed by fossil burrows of ~190 cm.

Regarding putative producers, previous studies have attributed these fossil burrows to various animal groups: armadillos, rodents, and typotheres have been considered as producers of the smaller fossil burrows (Genise, 1989; Scognamillo, 1993; Fernández et al., 2000; Elissamburu et al., 2011), while the largest ones were attributed to cingulates such as large armadillos, pampatheres, glyptodonts, and ground sloths (Quintana, 1992; Zárate et al., 1998; Bargo et al., 2000; Vizcaíno et al., 2001; Cardonato and Melchor 2018).

The stratigraphic range of fossil burrows encompass from Pliocene, a period during which Earth shifted from comparatively warm conditions to a cooling climate, and then to the intense glacial-interglacial fluctuations characteristic of the Pleistocene (Cione et al., 2015). The study and interpretation of fossil burrows and the diversity of their putative producers throughout this paleoclimatic shift is essential to understand sedimentological, taphonomic, and stratigraphic aspects of the late Cenozoic record (Zárate et al., 1998), but also the paleoecology of this unique ecosystem with large and giant-sized burrowing mammals.

The goal of this study was to record and analyze overall patterns of variation in size of fossil burrows exposed along the sea cliffs of the southeastern Atlantic coast of Buenos Aires province. The resulting patterns were discussed in the context of body size and other paleoecological information (e.g. metabolism and diet) about their likely producers, with a focus on the largest fossil burrows.

1.1. Study area

The burrows occur in late Pliocene-Pleistocene continental deposits exposed along the sea cliffs between the cities of Santa Clara del Mar and Miramar in the SE sector of Buenos Aires province (Fig. 1 and Table 1). Due to the lateral continuity and thickness of the exposures, particularly south of Mar del Plata, the area provides the best exposed and most complete stratigraphic record to interpret the late Cenozoic history of the Pampean Plain, allowing the reconstruction of the pampean landscape in time. The outcrops are characteristic for the abundance of vertebrate fossil remains. The mid-Pliocene succession is composed of loess and loess-like deposits with well-developed paleosols. The late Pliocene—Pleistocene succession mainly consists of fine sandstone beds and some debris and mud facies accumulated in floodplain environments, complex and welded paleosols associated with calcrete layers (Zárate, 1989; Zárate and Fasano, 1989).

2. Materials and methods

In several field seasons, a total of 145 burrows were identified and individually photographed and measured (Figs. 2 and 3; Table 1; Suppl. data) along approximately 50 km, from Barrio Atlántida to San Eduardo del Mar in the Buenos Aires province, Argentina. The sampling localities were chosen based on the accessibility of the cliff walls from the beaches. The measurements were taken in situ using metric tapes. The minimum diameter was used to ensure conservative estimates (Suppl. data). We analyzed the diameter distribution of the total fossil burrow sample, and of the Pliocene and Pleistocene subsamples. The data was organized into size classes separated by major gaps, supported by non-parametric methods as k-means clustering (Suppl. data). Allometric equations from White (2005) were utilized to estimate the body size of the putative burrowers (Suppl. data). We calculated the average of the body mass (**BM**) estimates by using the equations for solitary fossorial, colonial fossorial, and semifossorial mammals, computed on mammalian data from White's (2005) appendix. All calculations were performed in the statistical suite R (R Core Team, 2024) and for plots the package *ggplot2* (Wickham, 2016) was used.

3. Results

The sample showed a striking diversity in fossil burrow sizes, from 7.5 cm to 220 cm (Figs. 4 and 5). The modes of the total sample were 15 cm and 80 cm, and no major gaps were detected. Distribution was dominated by abundant small to large Pliocene fossil burrows, and medium to giant Pleistocene ones (Fig. 6 and Suppl. data). Three main fossil burrows size groups were represented in the Early Pliocene–Early

Pleistocene levels: a large abundance of small burrows (7.5–27 cm), followed by medium (32.5–65 cm) and large burrows (68–112 cm). No burrows larger than 112 cm were recorded in these Early Pliocene–Early Pleistocene levels. On the contrary, the Middle-Late Pleistocene levels presented scant small burrows (12–27 cm), followed by medium and large (40–100 cm) burrows, and finally a "tail" of several burrows surpassing 120 cm up until 220 cm were present (Suppl. data). In addition, the lower Pliocene levels, corresponding to Chapadmalal Formation (sampled mostly at LPAL and SEDM), concentrated most of small fossil burrows, with scarce medium and large ones. Upper Pliocene to Early Pleistocene levels (sampled at MARQ, PES and SISA), corresponding to Vorohue Formation and Punta San Andrés Formation (Kraglievich, 1952, 1953), showed a decline in small fossil burrows and an increase in representation of medium and large ones.

Summarizing, in the Early Pliocene–Early Pleistocene levels, there was a remarkable abundance of small-medium fossil burrows and absence of giant fossil burrows. In contrast, in the Middle-Late Pleistocene levels showed a scarcity of small fossil burrows, and a dominance of medium-large fossil burrows followed by giant ones. Large and medium fossil burrows were abundant in both time-bins.

BM estimates of producers obtained via White's (2005) equations were depicted in Figs. 7 and 8. In the Early Pliocene–Early Pleistocene levels there was small burrowers ranging from less than 100 g to ~3 kg, accompanied by a few medium burrowers ranging from 5.6 kg to 50 kg, and a great diversity of large burrowers from ~60 kg to ~300 kg.

For Middle–Late Pleistocene levels, recorded at Santa Clara Formation, small burrowers were under-represented, and it is remarkable a large diversity of medium and large burrowers ranging from ~70 kg to ~300 kg, followed by a diversity of giant burrowers surpassing 380 kg up to almost 3 t.

4. Discussion

4.1. Variation and diversity of fossil burrows sizes and of BM estimates

As described, the size distribution of analised Plio—Pleistocene fossil burrows presented some notable patterns. First, there is a remarkable continuity in fossil burrow size (Figs. 4, 5 and 6): no major gaps could be recognized, challenging easy definitions of burrow groups. This variety suggests an astonishing diversity of putative burrowing animals, including almost all possible BMs from tiny rodents of less than 1 kg to giant sloths of several tonnes. The diversity of putative burrowers (Fig. 8) in Pliocene and Pleistocene times in the Pampean area includes rodents from 0.5 (e.g. *Microcavia*) to ~9 kg (*Lagostomus*), typotheres of ~2 kg (*Paedotherium*), small to large armadillos (e.g. *Chorobates*, *Chaetophractus*, ~5 kg; and *Macroeuphractus* and *Propraopus*, ~50 kg), pampatheres (~200 kg), and ground sloths from ~900 kg (e.g. *Scelidotherium*) to larger forms. However, the actual diversity of burrow sizes suggests that other tetrapods could have engaged in burrowing behavior too. For example, some burrows rendered BM estimates larger than largest armadillos but smaller than pampatheres; while other BM estimates were larger than pampatheres but smaller than ground sloths (Fig. 8). It is possible that some of these burrowers excavated galleries or chambers larger than predicted for their BM (see later), but also that juvenile pampatheres and ground sloths excavated burrows as well. Burrowing by juvenile individuals was also proposed for rodents by Elissamburu et al. (2011). It is feasible that other medium-large animals, such as carnivorans, mesotheriids, tayassuids, and glyptodonts, were secondary fossorials, capable of digging or expanding abandoned fossil burrows for fitting their necessities (Shockey et al., 2007; Soibelzon et al., 2009; Cenizo et al., 2016). Pampatheres have been proposed as lacking marked fossorial adaptations (Edmund, 1987), in spite of ichnological evidence as claw marks indicating their presence and activities inside some burrows (Quintana, 1992; Arregui et al., 2024). Similarly, although digging abilities of glyptodonts has been considered limited (Quintana, 1992; Milne et al., 2009), Cardonatto and Melchor (2018) and Varela et al. (2023) discussed late Miocene glyptodonts as putative fossil burrow producers. Further research is needed in this regard.

Another interesting pattern is observed in BM estimates: those for small and medium-large fossil burrows correspond overall with the inferred BMs of most known putative burrowers recorded at those levels (rodents, typotheres, and cingulates). Conversely, some of the largest BM estimates for top giant fossil burrows appear to exceed the inferred mass of their putative builders (Fig. 8). For example, among Pampean digging mylodonts the most well-known genera are *Scelidotherium* and *Glossotherium*, with size estimates about 900 kg and 1200 kg respectively (Fariña et al., 1998; Bargo et al., 2000; Toledo et al., 2017; Barbosa et al., 2023). *Catonyx* was slightly larger (~1600 kg; Toledo et al., 2017). In contrast, some BM estimates based on fossil burrows' diameter surpass the 3 tons, reaching BMs of the supposedly less-digging (*Lestodon*) and non-digging (*Megatherium*) giant sloths (Bargo et al., 2000). Several possible scenarios arise: 1) Giant burrows were produced by giant

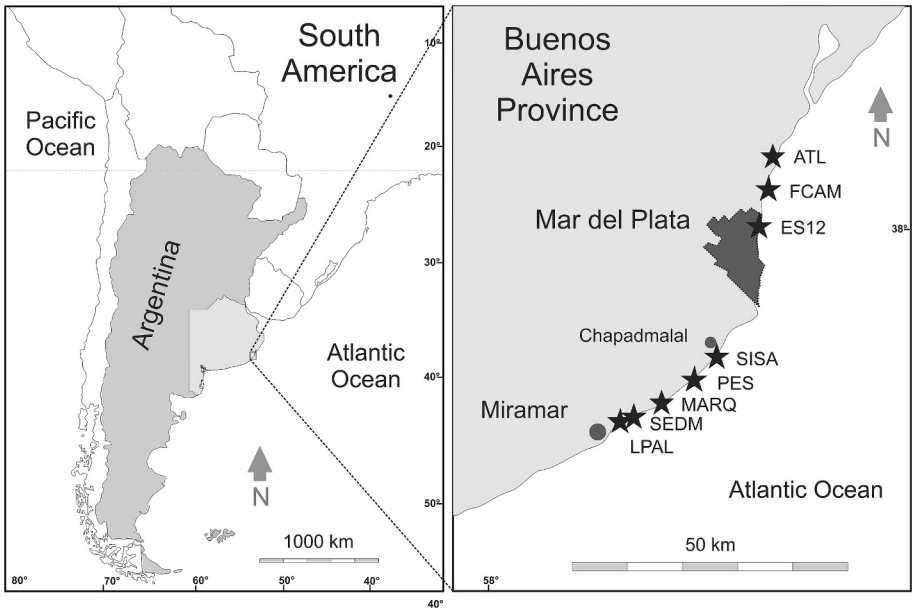

Fig. 1. Map showing localities of the Buenos Aires Province where Pliocene and Pleistocene fossil burrows were studied. Localities abbreviations as in Table 1.

ground sloths such as *Megatherium* and *Lestodon*, which were previously unknown as diggers; 2) Giant burrows were produced by large ground sloths like *Scelidotherium, Glossotherium* and *Catonyx*, inferred as burrowers, but which excavated burrows wider than expected for their BM; 3) Giant burrows were produced and expanded by several ground sloth individuals living as a group in the same tunnel, or along the time through different generations (Frank et al., 2015). Gregariousness has been described for ground sloths (see Tomassini et al., 2020) and giant burrows (up to 7 m in maximum diameter) recorded in Brazil have been ascribed to ground sloths, putatively for group accommodation (Frank et al., 2015). Possible factors influencing a burrow wider than expected for the BM could include that large and giant burrowers, being comparatively less agile and flexible, would need more space to maneuver inside the burrow (White and Seymour, 2021), especially if newborns and young individuals were housed in the burrow too. In addition, large and giant animals, having greater thermal inertia (McNab, 1985), would need more space for burrow ventilation to avoid overheating.

4.2. Paleoecological implications of the burrow diameter variation from Pliocene to Pleistocene

As explained early, burrow size ranges from dominant small fossil burrows and abundant large ones in the Early Pliocene to dominant medium-large fossil burrows in the Late Pliocene to Early Pleistocene, and finally to abundant medium-large burrows accompanied by giant ones in Middle-Late Pleistocene. This indicates a notable trend toward increasing size in these biogenic structures (early reported by Frenguelli, 1928). However, the diversity of potential burrowers shows similar compositions along the Pliocene and Pleistocene, including disparate digging morphotypes such as small rodents, typotheres, cingulates of different sizes, and mylodontid ground sloths (see Vizcaíno et al., 2004; Cione et al., 2015). This similarity in the diversity of mammalian digging morphotypes in the studied area and levels suggests a behavioral turnover among the largest burrowers, the ground sloths. According with the available evidence, they did not produce burrows during the Pliocene and Early Pleistocene but they did during the Middle–Late Pleistocene.

The shift in burrow size distribution may be consistent with the overall transition from warmer to cooler climatic conditions after the M2 glaciation and the mid-Pliocene Warm Period (Westerhold et al., 2020; Cione et al., 2015), which potentially influenced the ecological requirements and burrowing behavior of these mammals. Adopting a fossorial lifestyle could result in key ecological advantages. Burrows serve as microhabitats that provide a haven for resting, protecting from weather, aestivation/hibernation, escaping predators, and rearing offspring, thereby enhancing survival and reproductive success (Hildebrand, 1974, Feldhamer et al., 2020). Burrows are more humid and thermostable than the ground surface (Hildebrand, 1985; Reichman and Smith, 1990), not only through the day but also along the year (see Hasiotis et al., 2007), which is important for low-metabolism mammals such as large armadillos, pampatheres and ground sloths living in seasonal environments. It also provides access to food sources such as tubers, roots and soil invertebrates (Genise and Farina, 2012).

During the Pliocene—Pleistocene the largest members of the burrowing guild in the Pampean plains were all xenarthrans. Among extant xenarthrans, armadillos are the burrowers par excellence (McDonough and Loughry, 2008); they burrow for foraging, resting, protecting themselves from weather, escaping from predators, and raising offspring

Table 1
Stratigraphy of studied localities and levels, including equivalences between regional and international times. Ages and stratigraphy follow proposals by Kraglievich (1952, 1953, 1959); Schnack et al. (1982); Zárate (1989); Bidegain et al. (2005); Gómez-Samus (2016).

Locality	Abbrev.	Stratigraphy and references	South American Chronostratigraphy	International Chronostatigraphy	Antiquity	GPS coordinates	Outcrop length (m)
North							
Barrio Atlántida	ATL	Santa Clara Fm. (Schnack et al., 1982); (Gómez-Samus, 2016)	Upper Ensenadan /Bonaerian	Middle Pleistocene (Upper Calabrian) - Late Pleistocene	800–120 ka	37°51′9.52"S / 57°30′23.26"W	1275
Felix U Camet	FCAM	Santa Clara Fm. (Schnack et al., 1982); (Bidegain et al., 2005); (Gómez-Samus, 2016)	Upper Ensenadan /Bonaerian	Middle Pleistocene (Upper Calabrian) - Late Pleistocene	800–120 ka	37°54′26.44"S / 57°31′23.76"W	470
Espigón 12	ES12	Santa Clara Fm. (Schnack et al., 1982); (Bidegain et al., 2005)	Upper Ensenadan /Bonaerian	Middle Pleistocene (Upper Calabrian) - Late Pleistocene	800–120 ka	37°57′49.48"S / 57°32′24.69"W	760
South							
Santa Isabel	SISA	Barranca de los Lobos Fm. - Vorohue Fm. (Kraglievich, 1952, 1953) // San Andrés Allofm., lower allomember, alocapes: a1, a2, a3 (Zárate, 1989)	Barrancalobean - Vorohuean	Late Pliocene (Upper Piacenzian) - Early Pleistocene (Gelasian)	2.8–2.4 ma	38°11′42.98"S / 57°40′8.08"W	1100
Playa Escondida	PES	Barranca de los Lobos Fm. - Vorohue Fm. (Kraglievich, 1952, 1953) // San Andrés Allofm., lower allomember, alocapes: a1, a2, a3 (Zárate, 1989)	Barrancalobean - Vorohuean	Late Pliocene (Upper Piacenzian) - Early Pleistocene (Gelasian)	2.8–2.4 ma	38°13′29.16"S / 57°43′16.61"W	1420
Marquesado	MARQ	Chapadmalal Fm. - Vorohue Fm. (Kraglievich, 1952, 1953, 1959) // Playa Los Lobos Allofm. a6 to a7? - San Andres Alloform. Lower allomember a3	Chapadmalalan - Vorohuean	Late Pliocene (Middle Piacenzian) - Early Pleistocene (Gelasian)	3.0–2,8 ma / 2.6–2.4 ma	38°13′49.05"S / 57°44′7.29"W	470
San Eduardo del Mar	SEDM	Chapadmalal Fm. - Vorohue Fm. (Kraglievich, 1952, 1953, 1959) - Playa San Carlos Allofm. a5 Playa Los Lobos allofm P7 (Paleosoil) - Punta San Andres Alloform. a2-a3?	Chapadmalalan - Vorohuean	Late Pliocene (Middle Piacenzian) - Early Pleistocene (Gelasian)	3.5–2.4 ma	38°14′14.77"S / 57°45′20.02"W	750
Las Palomas	LPAL	Chapadmalal Fm. (Kraglievich, 1952, 1953) // Playa San Carlos Allofm. a3 - Playa Los Lobos Alloform. P6 (Zárate, 1989)	Chapadmalalan	Early Pliocene (Upper Zanclean) -Late Pliocene (Middle Piacenzian)	3.74–3.04 ma	38° 8′58.12"S / 57°36′54.01"W	210

(McDonough and Loughry, 2008). Their burrows can be quite long, either simple or complex, and with multiple entrances (Abba et al., 2005). Like all extant xenarthrans, armadillos are low-metabolism mammals (McNab, 1980, 1985) whose body temperatures can be strongly influenced by atmospheric temperatures (Abba et al., 2011). Hibernating has been recorded in the Patagonian piche *Zaedyus pichiy*, the extant xenarthran having the southernmost distribution, as a strategy for surviving cold season via entering torpor (Superina and Boily, 2007; Superina, 2008). Increment in burrowing behavior as a strategy to enhance thermoregulation during cold seasons has been documented in the long-nosed armadillo *Dasypus hybridus* (González et al., 2001) and in the Patagonian piche (Superina and Boily, 2007; Superina, 2008).

According to Woolnough and Steele (2001: p. 35), "The long-term gains of living in a burrow need to exceed the initial energetic cost of burrow construction and maintenance." In this sense, it has been proposed that a low metabolic rate can compensate for the high energetic costs of burrowing (Vleck, 1979). As mentioned above, temperature can be a key factor also for extinct xenarthrans given their estimated low-metabolic rate (McNab, 1985), although BM-dependent thermal inertia has to be accounted for. Disadvantages related to digging and inhabiting extensive burrows include a great expenditure of energy in their construction, limitation to evaporative cooling due to high underground humidity, reduced visibility and mobility, low oxygenation, and risk of entrapment during floods (Hildebrand, 1985; Marchetti et al., 2024). Ground sloths were also inferred to be low-metabolism animals, which could compensate for the enormous costs of digging (Vleck, 1979) and prevent overheating when inside the burrow (White, 2003), although evidence indicating ground sloths would have a higher metabolism than expected was published recently (Varela et al., 2024). Nevertheless further research on this topic is needed since extinct ground sloths were quite different in size and morphology from extant relatives feasible as functional and ecological models (see Vizcaíno et al., 2018, 2023).

The increase of digging behavior among ground sloths can be discussed in the light of paleoclimatic and paleoecologic differences between Pliocene-Early Pleistocene and Middle-Late Pleistocene. Although showing deteriorating conditions since the mid-Pliocene Climate Optimum, the climate during the Chapadmalalan Age (~4—3.2 Ma, Cione et al., 2015) was still humid and warm. In contrast, after the Marplatan-Barrancalobian (~3.2—2.95 Ma, Cione et al., 2015) faunal turnover, climate conditions developed colder and more arid during the Late Pliocene and the Pleistocene (Westerhold et al. 2020). A fossorial

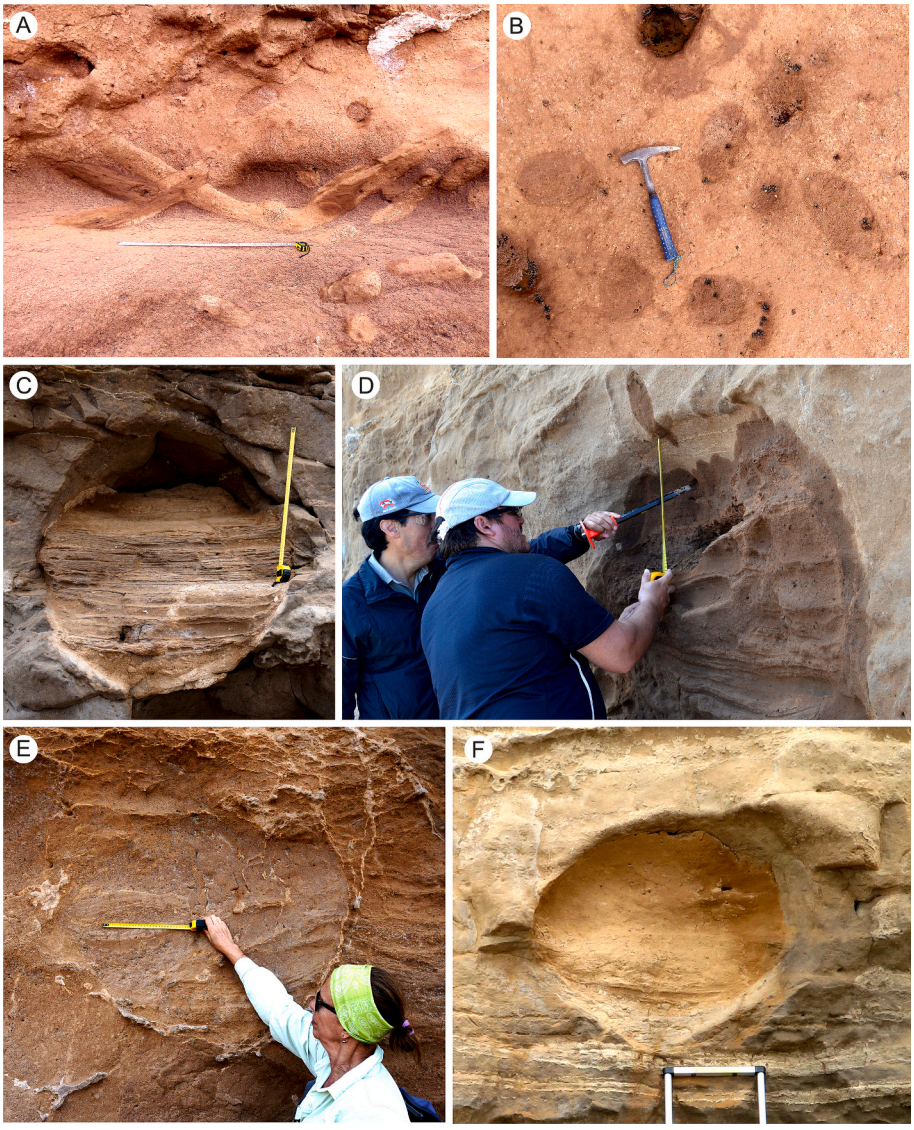

Fig. 2. Early Pliocene–Early Pleistocene fossil burrows as being sampled during fieldwork for this study. **A** and **B**, small burrows at **LPAL**; **C**, medium burrow at **SISA**; **D**, measuring a large burrow at **MARQ**; a large burrow at **MARQ**; **F**, a large burrow at **SISA.**

lifestyle could have provided ground sloths, and other large xenarthrans, protection from cold and dry surface conditions, as well as access to additional food resources when surface vegetation changed due to the expansion of steppe environments (Vizcaíno et al., 2001). In this sense, Marchetti et al. (2024), analyzing the evolution of fossoriality among extant vertebrates, describe burrowing becoming a strategy to endure a shift to more seasonal and arid climates during the early Permian; and a similar increase in burrow diversity and complexity is recorded in the aftermath of the early Triassic extinction event. More recently, Martin (2017) describes an increase in burrowing behavior among extant crocodiles in response to long-lasting droughts in wetlands in Georgia (US). Thus, we propose that ground sloths and other large xenarthrans were able to survive through the Late Pliocene—Early Pleistocene climate shift to colder and dryer conditions by expanding their ecological tolerance via the construction of new microhabitats, the burrows. The arrival of large carnivorans such as saber-toothed cats (*Smilodon*) and short-faced bears (*Arctotherium*) could have increased the pressure for digging shelters (Vizcaíno et al., 2001; Soibelzon et al., 2009). Fossoriality can be viewed as a behavioral alternative to migrating to more suitable environments. Among folivorans, the Pampean ground sloths, such as scelidotheres and other mylodontids, showed a suite of morphofunctional features, including a bulky limb musculature (see Cuenca Anaya, 1995; Bargo et al., 2000; Vizcaíno et al., 2001) that enabled them to be powerful burrowers. These sloths would already have the morphofunctional tools necessary to expand their putative burrowing behavior into a fossorial lifestyle, but this behavior seems to have been triggered by the context.

Energy expenditure in burrowing activities positively correlates with BM (Haussmann, 2017). For a large burrower, digging a shelter greater than its own size would imply a higher metabolic cost than for a smaller burrower (Woolnough and Steele, 2001). This is because, according to data from extant mammals, an animal's output power is related to the cross-sectional area of its muscles, but the sediment removed for building a burrow increases at a volumetric factor. Therefore, the maximum diameter of a burrow is unlikely to exceed the body diameter of the producer since digging a larger burrow would be an inefficient expenditure of energy (Vleck, 1979). Additionally, during the excavation, the animal typically compacts the lateral walls and roof of the burrow to enhance structural stability, an effort that becomes increasingly challenging in the context of a burrow larger than the burrower's own size.

It should be taken into account that published studies that measure burrowing energy cost address, in most cases, mammals of relatively small BM (e.g. Luna and Antinuchi, 2006; Zelová et al., 2010). The cost-

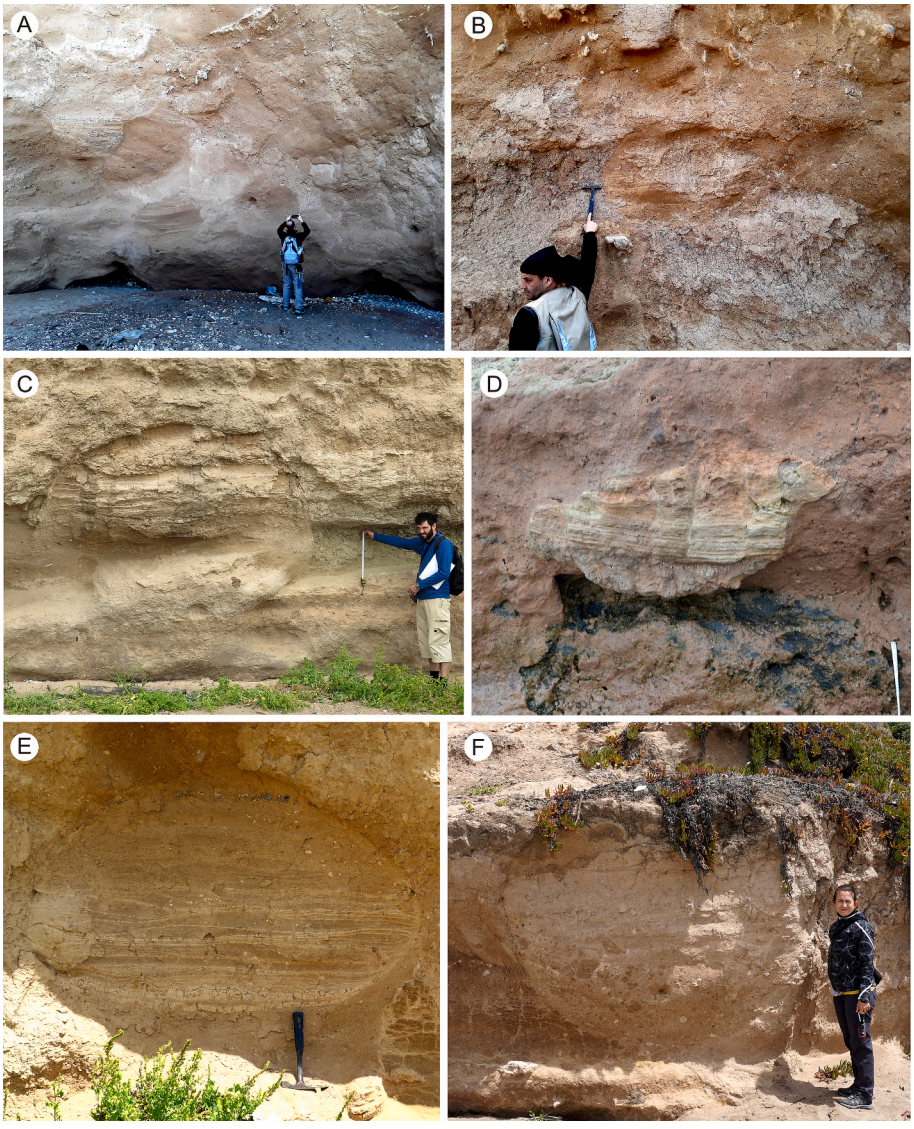

Fig. 3. Middle–Late Pleistocene fossil burrows as being sampled during fieldwork for this study. **A**, set of medium burrows at **FCAM**; **B**, medium burrow at **FCAM**; **C**, giant burrow at **ES12**; **D**, large burrow at **ATL**; **E**, large burrow at **ES12**; **F**, giant burrow at **ES12**.

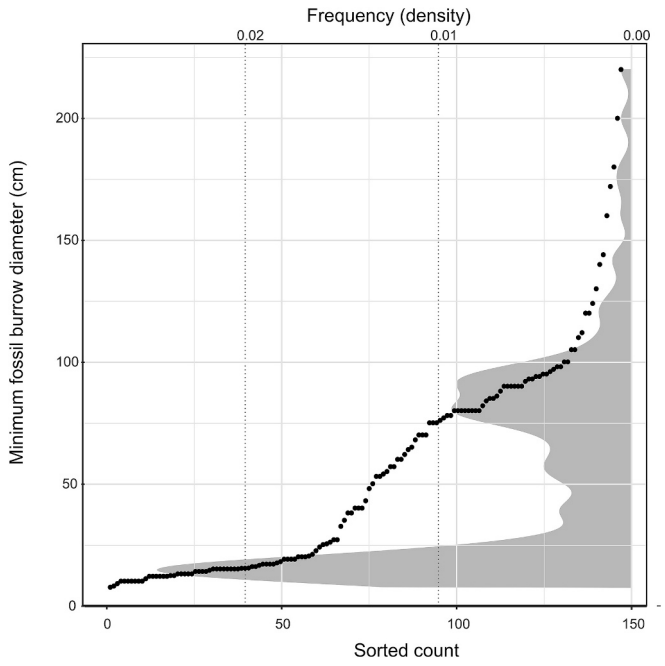

Fig. 4. Distribution of the minimum diameter of fossil burrows analyzed in this work, depicted as black circles sorted in ascending order. At right, a density plot of fossil burrows minimum diameter showing modal peaks.

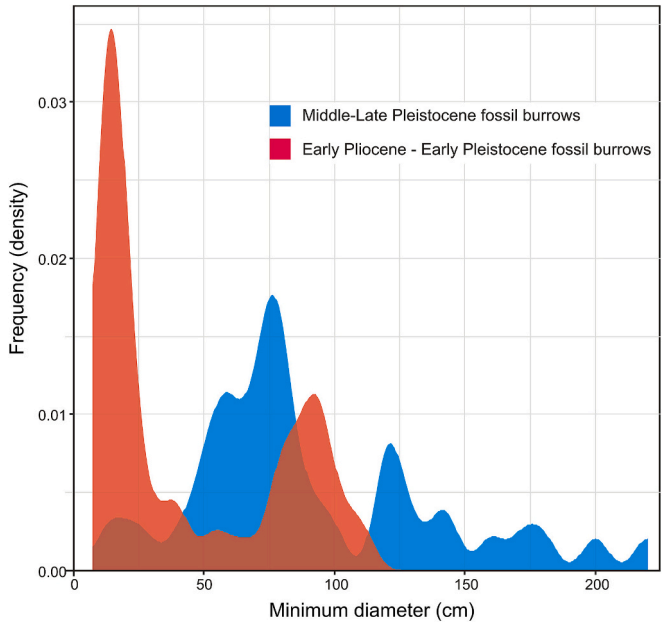

Fig. 5. Density plots of fossil burrow minimum diameter of the two time-bins represented by levels sampled in this work.

of-burrowing model, which predicts severe restrictions to the cross-sectional area of the burrow, was developed for underground foraging species, typically subterranean rodents whose galleries must be assiduously extended to access food sources since they either forage underground or do so by traveling short distances aboveground (Vleck, 1981; Lacey et al., 2000). This situation contrasts with that of fossorial mammals whose burrows' main purpose is sheltering, and where once built (although with a high energy expenditure) it would not require further extensions, or at least not with the frequency in which it occurs in those species that burrowing is the predominant foraging method. Based upon mesowear angle analysis, mixed feeding to grazing diets has been

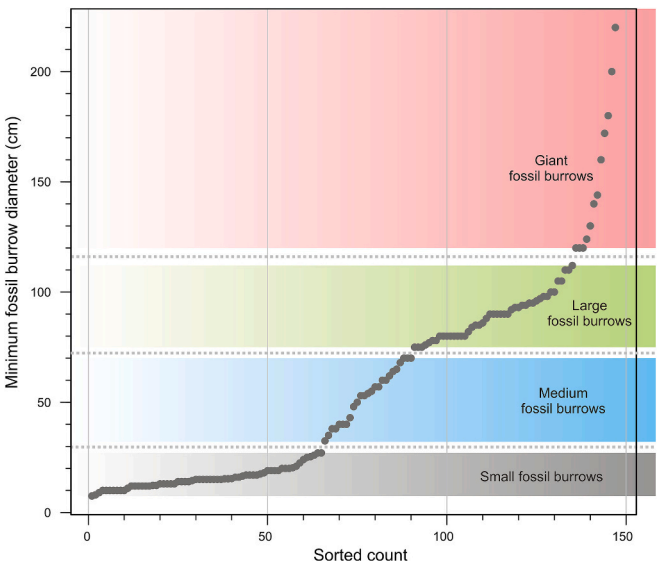

Fig. 6. Distribution, in ascending order, of minimum burrow diameters and their clasiffication into size classes according to methods applied in this work.

inferred for most mylodontid ground sloths, whereas grazing and possibly digging for roots was proposed for *Lestodon* and *Scelidotherium* (Saarinen and Karme, 2017). Although the consumption of items obtained by burrowing cannot be ruled out for the putative occupants of giant fossil burrows, they probably were not strict underground feeders. As mentioned above, in large fossorial mammals such as ground sloths, burrow diameters could be influenced not only by digging cost but by other requirements such as maneuverability and/or ventilation of the cave (White and Seymour, 2021).

According to Liow et al. (2008, 2009), organisms able to survive in situ to deteriorating environment changes have comparative greater advantage. These strategies, defined as "sleep or hide" by Liow et al. (2008), may have confer ground sloths, large to giant low-pacing herbivores, an extra opportunity to survive the cooler and drier conditions of the Pleistocene and avoid extinction. This advantage could extend to coeval fauna (secondary fossorials) which could make use of existing burrows (e.g. Cenizo et al., 2016), as happen nowadays with burrows dig by the giant armadillo *Priodontes maximus* (Desbiez and Kluyber, 2013).

5. Concluding remarks

This study sheds light on the behavior of organisms in the past and the interrelationship between them and their environment.

- The remarkable variety in size of fossil burrows recorded in this work indicates an outstanding diversity of burrowing animals, from small to giant, inhabiting the Pampean area at Plio—Pleistocene times.
- Early Pliocene to Early Pleistocene levels predominantly showed small and large fossil burrows (attributed mostly to rodents and cingulates), while Late Pleistocene levels exhibited a prevalence of medium to large-sized burrows along with the appearance of giant burrows associated with ground sloths. The emergence of large fossil burrows since the Late Pliocene and of giant burrows during the Late Pleistocene may indicate a response to climate shifts and the presence of new predators, as happened during the GABI.
- BM estimations for the possible producers showed departure from the expected values as diameter increases, suggesting different burrow uses among large and giant burrowers.

Fossil burrows are ubiquitous features of southern South American late Cenozoic records at different settings, however their identification has been overlooked until recently, hence underestimating the

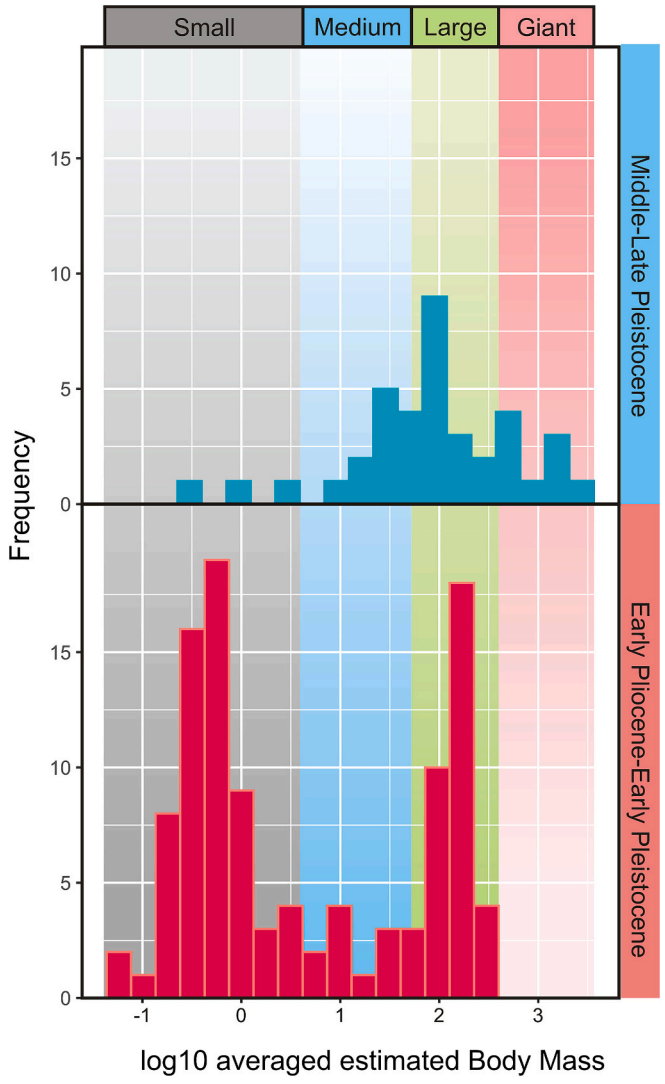

Fig. 7. Histograms of averaged BM estimates (log10), for the two time-bins sampled in this study, and their classification into size clases following the burrow's prior classification in this work.

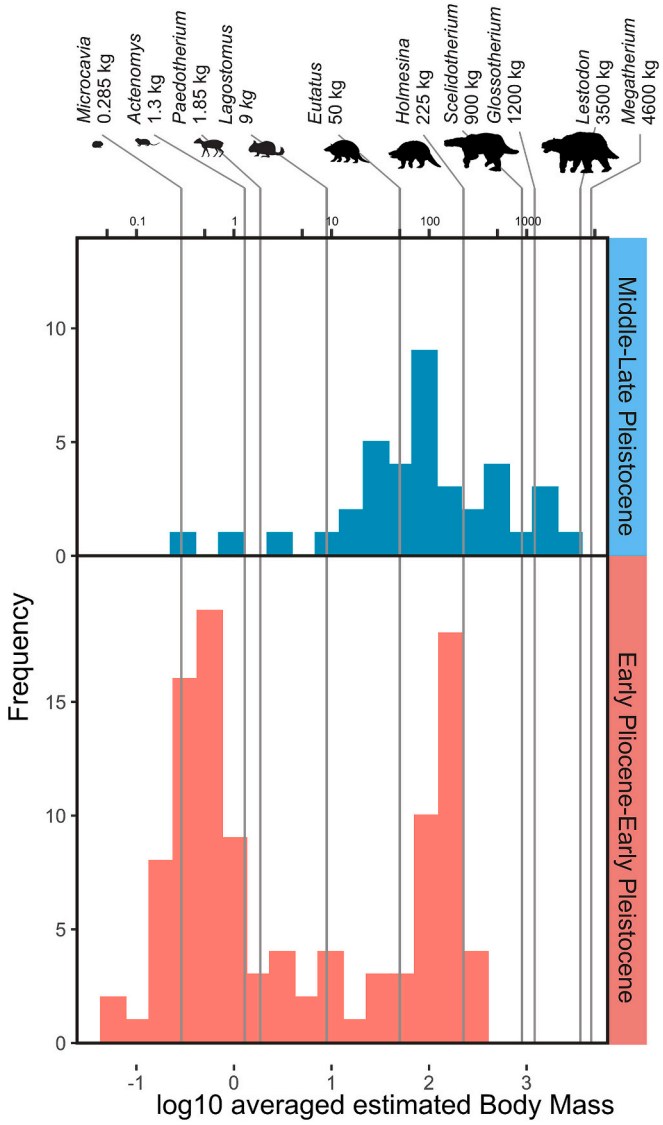

Fig. 8. Histograms of averaged BM estimates (log10), for the two time-bins sampled in this study. Overlayed, there are BM estimates for most well-known burrowing mammals recorded at the Plio-Pleistocene of the Pampean area, as available in the literature.

geomorphological role played by the fauna. Further research should explore the significance of large and giant burrows in the mode of life of extinct organisms, as well as their taphonomic and stratigraphic implications as time capsules encasing a distinct piece of history. Additionally, we encourage future evaluation of the importance of large and giant burrowing xenarthrans as significant ecosystem engineers during the Plio—Pleistocene of the Pampean region, even in the absence of modern analogues (Vizcaíno et al., 2017, 2023), marking an unprecedented event in the history of life.

CRediT authorship contribution statement

N. Toledo: Writing – original draft, Visualization, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **N.A. Muñoz:** Writing – original draft, Visualization, Resources, Methodology, Investigation, Data curation. **M. S. Bargo:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition. **V. Krapovickas:** Writing – original draft, Visualization, Resources, Methodology, Investigation, Funding acquisition. **M.L. Taglioretti:** Writing – review & editing, Visualization, Resources, Methodology, Investigation, Data curation. **L. M. Pérez:** Writing – original draft, Investigation, Data curation. **M.A. Zárate:** Writing – original draft, Resources, Investigation. **S.F. Vizcaíno:** Writing – original draft, Visualization, Resources, Investigation. **M. Arregui:** Writing – original draft, Visualization, Investigation. **A. Boscaini:** Writing – review & editing, Investigation. **F.I. Isla:** Writing – review & editing, Resources. **A.I. Vassallo:** Writing – original draft, Methodology. **F. Scaglia:** Resources, Data curation.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2024.112564.

Data availability

Data produced for this study would be available at the CONICET Institutional repository following this URL: http://hdl.handle.net/11336/245783

All authors approved the final version of the manuscript and are responsible for its content.

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