

Pleistocene burrows in the Mar del Plata area (Argentina) and their probable builders

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Structures discovered near Mar del Plata are attributed to palaeoburrows built by fossil animals on the basis of morphological patterns, transgressive boundaries in relation to the sedimentary units, and the presence of claw marks on the walls and roofs. They are discrete features of several metres in length, and with subrounded cross sections. Their diameters range from 0.80 to 1.80 m, with the width generally exceeding the height. These structures occur in Pleistocene deposits containing mammals referable to the Ensenadan and Lujanian Ages. Several Xenarthra are good candidates as builders of these burrows. Palaeoburrows were attributed before to the large Pleistocene armadillos *Propraopus*, *Eutatus*, and *Pampatherium*. We consider the possibility that the mylodontid ground sloths were responsible for excavating the burrows. The similar diameters of the burrows and the sloths are consistent with this observation. Anatomical, allometric, and biomechanical analysis of sloths limbs indicates that they were well designed to perform such activity. The shape of some claw marks preserved on the sides and roof of the burrows fits the form of their hand skeleton. Thus, the mylodontid sloths *Scelidotherium* and *Glossotherium* are considered as possible builders for the large late Cenozoic burrows present in the Pampean region.

Key words: Pleistocene, burrows, Mylodontidae, Xenarthra, South America.

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Introduction

Mammalian burrows of different sizes are commonly mentioned, but not specifically described, in the literature referred to the late Cenozoic deposits of the Buenos Aires

Province (Argentina), especially in the coastal region (Ameghino 1908; Frenguelli 1921, 1928; Kraglievich 1952). In the last decade some specific studies have been performed. Genise (1989) and Scognamillo (1993) analyse and describe in detail small burrows of approximately 13 cm of diameter, found in the coastal cliffs of Mar del Plata area (Buenos Aires Province) and attributed to the fossil rodent *Actenomys*.

Large structures with diameters of approximately 1 m were studied in the proximity of La Plata, NE of Buenos Aires Province (Imbellone & Teruggi 1988; Imbellone *et al.* 1990), and Rio Grande do Sul in southern Brazil (Bergqvist & Maciel 1994). In Mar del Plata, Quintana (1992) reported a burrow of the same diameter, providing the first morphological description of this kind of tunnels. This was of particular interest because it was branched, 23 metres long, with some tracks on the walls and the roof, and devoid of sedimentary filling. The construction of all these large burrows was attributed to giant armadillos (Dasypodidae and Pamphathiidae).

In recent years several larger burrows were discovered in the area of Mar del Plata. Zárate *et al.* (1998) examined these large structures focusing on their stratigraphic and sedimentological implications. In this paper, we analyze faunistic, morphological, biomechanical, and ichnological evidence to propose their probable builders in a palaeoecological context. The term burrow or palaeoburrow is used following Bergqvist & Maciel (1994), i.e., including both palaeocaves (hollows) and crotovines (filled with sediments).

Stratigraphy, morphology, and fillings of the burrows

Although the burrows in late Cenozoic sediments near Mar del Plata have been known for more than a century, they were not described nor interpreted until very recently. Zárate *et al.* (1998) recorded and described 42 structures in the Mar del Plata area (Buenos Aires Province) (Fig. 1). The time range of these burrows extends from the Pliocene to the late Pleistocene, and possibly until as recently as late glacial maximum–late glacial times. Based on the shallowest empty burrows found in the area, Zárate *et al.* (1998) estimated a probable depth of 5–6 m from the surface. Thus, the structures are stratigraphically transgressive, which constrains the chronological resolution of their time of formation, the prevailing palaeoenvironmental conditions when formed, and estimations of their relative abundance at any stratigraphic level.

The stratigraphic relationships, sizes, and closed boundaries are the main criteria for field recognition of these structures (Zárate *et al.* 1998). Once the contextual framework has been established based on these criteria, the sedimentary fillings and the associated faunal remains are further applicable criteria to aid in determining the origin.

The structures, formed in cohesive material composed of very fine sandstone or siltstones (loess-like sediments), are located either in floodplain or in interfluvial palaeoenvironments. The tunnels are filled with thinly stratified fine sands and silts alternating with laminated clay layers.

The morphology of the structures is characterised by discrete boundaries and subcircular to slightly elliptical cross-sections. Some of them show flat floors and arched roofs. Longitudinal sections are also frequent, but not usually reported, possibly because they have been misinterpreted as fluvial features. Their maximum width

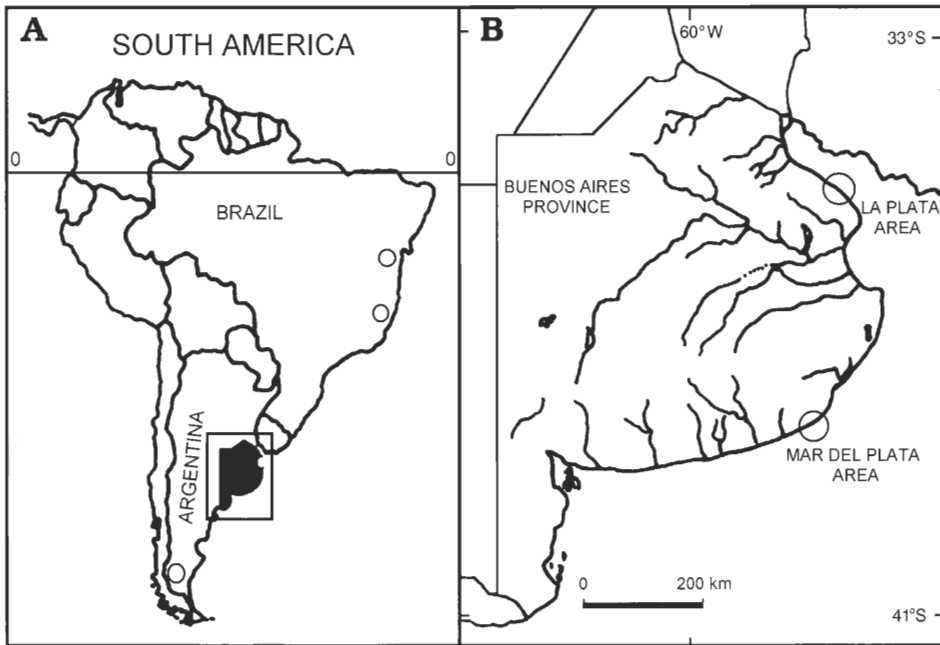


Fig. 1. A. Map of South America showing the location of Buenos Aires Province (in black) and the approximate areas of natural caves with ground sloths remains (open circles). B. Map of Buenos Aires Province showing the areas where large Pleistocene burrows (open circles) were found.

varies between 0.80 and 1.80 m, and usually the width slightly exceeds the height (Fig. 2). Tunnels recently discovered in Mar del Plata and devoid of sedimentary filling reach up to 1.80 m in width and 40 m in length. The major size variation might reflect different animal diggers; size variations between 15–30 cm are possibly caused by measurement of width along a plane oblique to the longitudinal axis of the structure (due to difficulty in interpretation of the true axis); those between 5 and 10 cm are attributable to measurement error caused by boundaries that are difficult to distinguish from the surrounding sediments.

Associated fauna

A large number of mammalian taxa have been recorded from the late Cenozoic exposures along the Mar del Plata-Miramar sea-cliffs. There is an extensive account of them in a recent compilation edited by Alberdi *et al.* (1995). Many taxa can be discarded as the builders of these burrows as they do not show adaptations to dig (proboscideans, artiodactyls, perissodactyls, litopterns, most notoungulates, and some large carnivores). Others are too small (rodents, notoungulates such as hegetotheres, and other carnivores).

On the other hand, many representatives of the superorder Xenarthra fulfill both requirements: they have morphological adaptations to dig and they are large enough. They comprise three main lineages: cingulates, including armadillos (*Dasypodidae*

and Pamphathiidae) and their relatives the glyptodonts; vermilinguas, the anteaters (Myrmecophagidae); and tardigrades, the ground sloths (Mylodontidae and Megatheriidae), relatives of the highly specialised living tree sloths (Bradypodidae and Megalonychidae).

Recent papers consider the possibility of armadillos as the builders of large burrows. Quintana (1992) proposed two dasypodids, *Eutatus seguini* and *Propaopus* sp., or a pamphathid, *Pamphathium typum*, as probable builders of a palaeocave in Mar del Plata area. This has also been suggested for burrows in other areas of southern South America. Near La Plata (NE of Buenos Aires Province, Argentina), Imbellone and Teruggi (1988) and Imbellone *et al.* (1990) also tentatively attributed some burrows (with diameters of approximately 1 m) to *Eutatus seguini* or *Pamphathium typum*. Bergqvist & Maciel (1994) described large crotonines (about 1 m width) in Rio Grande do Sul (southern Brazil) which they attributed to the pamphathes *Pamphathium* and *Holmesina*, and to the extinct dasypodid *Propaopus*. Living armadillos are powerful diggers and scratchers that usually live in underground burrows. Their skeletons show all the adaptations required for a digger. The skull is low and narrow, the limb bones present strong processes and scars for muscle attachment, and the ungual phalanges are wide and relatively flat (usually one or two are more specialised). Both *Eutatus* and *Propaopus* are approximately the same size as the largest living armadillo *Priodontes maximus*, so they must have been close to 50 kg in body mass (Fariña & Vizcaíno 1997), and a maximum transverse body diameter of about 50 cm. Both show the same skeletal adaptations, more or less developed to the same degree, so they can easily be identified as diggers.

Pamphathes are larger than dasypodid armadillos. *Pamphathium typum* must have reached 200 kg and its estimated maximum transverse diameter was about 80 cm. It appears that they were not as good diggers as dasypodids. Edmund (1985) described limbs of pamphathes as being intermediate in proportions and specialisation between those of glyptodonts and the living armadillo *Dasypus*, including graviportal adaptations for the hind limb. The three central fingers of the manus are equally developed, and no especially developed claws are present. The relative length of the olecranon process is considerably less than in the fossorial armadillos. A long olecranon process improves the moment arm of triceps, which acts as an extensor of the forearm. Within mammals, this design is appropriate for diggers, such as the armadillos. Even in some unspecialised clades of mammals, species that are known to dig more frequently show relatively longer olecranon processes than those that do not dig (Vizcaíno *et al.* 1999).

The largest burrows have been attributed to other xenarthrans. Frenguelli (1921: p. 343) mentioned the large glyptodonts *Glyptodon*, *Neuryurus*, and *Doedicurus* (Cingulata, Glyptodontidae) and, even more, emphasised that frequently there were remains of these animals in those burrows. The transverse diameters of these glyptodonts range between 90 and 140 cm, and their masses between 800 and 1800 kg (Fariña *et al.* 1998). Kraglievich (1934) considered that glyptodonts were not functionally suited to dig. Although there is no specific study on the matter, Quintana (1992)

Fig. 2. Palaeoburrows in the Mar del Plata (Playa Santa Isabel) seacliffs. **A.** Frontal view of an eroded palaeoburrow with stratified internal filling at the background; scale bar 0.2 m. **B.** Tunnel section running parallel to the sea-cliff face exhibiting open ends; scale bar 1.8 m. **C.** Protruding internal filling of a palaeoburrow with host sediments removed by erosion; scale bar 0.2 m.



A



B



C

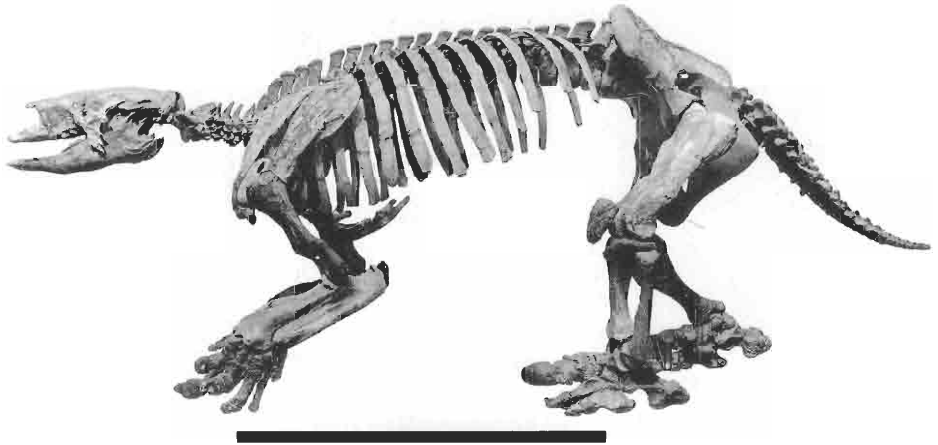


Fig. 3. Skeleton of the ground sloth *Scelidotherium leptcephalum* (from Lydekker 1894). Scale bar 1 m.

concur with Kraglievich, arguing that the carapace is relatively rigid (in comparison with armadillos) and fused to the pelvic girdle, the dorsal and lumbar vertebrae are fused forming a tube, and they lack other structures in the skull and limbs typical of burrowing mammals.

Mylodonts as burrowers

Frenguelli (1928: pp. 77, 89; 1955) reported a burrow filled with volcanic ash that he attributed to the ground sloth *Scelidotherium* (Tardigrada, Mylodontidae) since the animal was found within it. Interestingly, this assignment has not been mentioned since.

Even though many researchers emphasized that the legs of mylodontids (Figs. 3, 4) were well adapted for digging (Owen 1842, 1851; Winge 1941; Aramayo 1988; McDonald 1987, 1995; Cuenca Anaya 1995; White 1997), they considered them mainly used to dig for food. Moreover, Cuenca Anaya (1995) extensively described the forelimb of *Scelidotherium* and asserted that it was clearly adapted for digging, but he rejected the possibility of fossoriality based only on its large size. The body mass, maximum transverse diameter and length of *Scelidotherium* were approximately 800 kg (Fariña *et al.* 1998), 100 cm and 270 cm, respectively. The same figures for *Glossotherium* were 1200 kg (Fariña *et al.* 1998), 120 cm and 325 cm.

The morphology of the manus of some mylodontids (*Glossotherium*, *Proscelidodon*, and *Scelidotherium*) was extensively described by Cartelle (1980), Aramayo (1988) and Cuenca Anaya (1995), respectively. The carpus, metacarpus and first phalanges are closely articulated forming a shovel-like structure, and the most remarkable feature is the great development of the second and third fingers, specially the unguinal phalanges (Fig. 5A, B). The other fingers are reduced and carry no unguinal phalanx in the scelidotheres. In *Glossotherium*, they are reduced too, but the first finger is less reduced and retains an unguinal phalanx. The functional analyses by Aramayo (1988) and Cuenca Anaya (1995) indicate that the forearm and the manus of the scelidotheres were able to

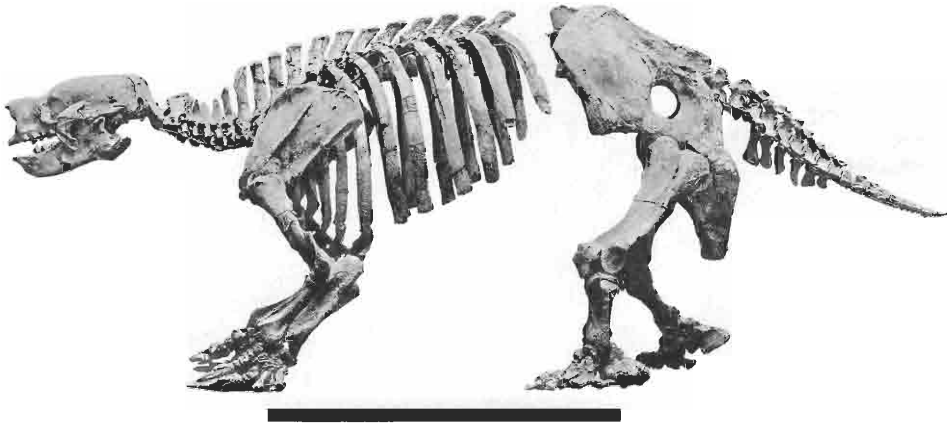


Fig. 4. Skeleton of the ground sloth *Glossotherium robustum* (from Lydekker 1894). Scale bar 1 m.

perform ample movements of flexion, extension, pronation and supination, which Aramayo (1998) correlates with digging habits.

Our own anatomical, allometric and biomechanical studies on Pleistocene mylodontids demonstrate that the limb bones of *Scelidotherium* (Fig. 3) and *Glossotherium* (Fig. 4), frequently recorded in the Mar del Plata area, were well designed to dig (Bargo *et al.* 2000) and are summarised as follows. In *Glossotherium* and *Scelidotherium*, values of strength indicators calculated on limb bones are equivalent or even higher than those of large modern galloping mammals, indicating that they are suited to withstand strong bending forces. However, the general morphology and proportions of the limbs, particularly of the manus and pes preclude them from such locomotion. Bargo *et al.* (2000) proposed that the strenuous activity implied by such tensions could be digging.

The large olecranon process of *Scelidotherium* and *Glossotherium* (Figs. 3–5) suggests that the forearm was better adapted for strength rather than speed. Additionally, the large, relatively flat, wide and straight ungual phalanges are also of an appropriate design for digging (White 1997). Application of an equation developed by Fariña *et al.* (submitted) to *Scelidotherium* and *Glossotherium* indicates that their elbows were three to four times longer than required merely for walking. Such values strongly suggest that the limbs were designed to perform other strenuous activities, such as digging, and include a safety factor (Alexander 1981).

Finally, the estimated position of the centre of mass in mylodontids, nearly over the hind feet, implies that a bipedal posture could easily have been attained. A bipedal, though not necessarily fully erect, posture is an essential requirement for digging, as the forelimbs must be liberated from their function of supporting the body weight so that they may act on the substrate. This applies especially when the tunnel runs horizontally. A good analogue may be the highly specialised armadillo *Priodontes maximus*, which walks essentially on its hindlimbs while maintaining the backbone roughly parallel to the ground, the forelimbs flexed, and the hands, turned posteriorly, dragging along the ground (Frechkop 1949).

The general body shape size and the form of skull are more tapered in *Scelidotherium* than in *Glossotherium*. This suggests that the former would be a better candidate to dig

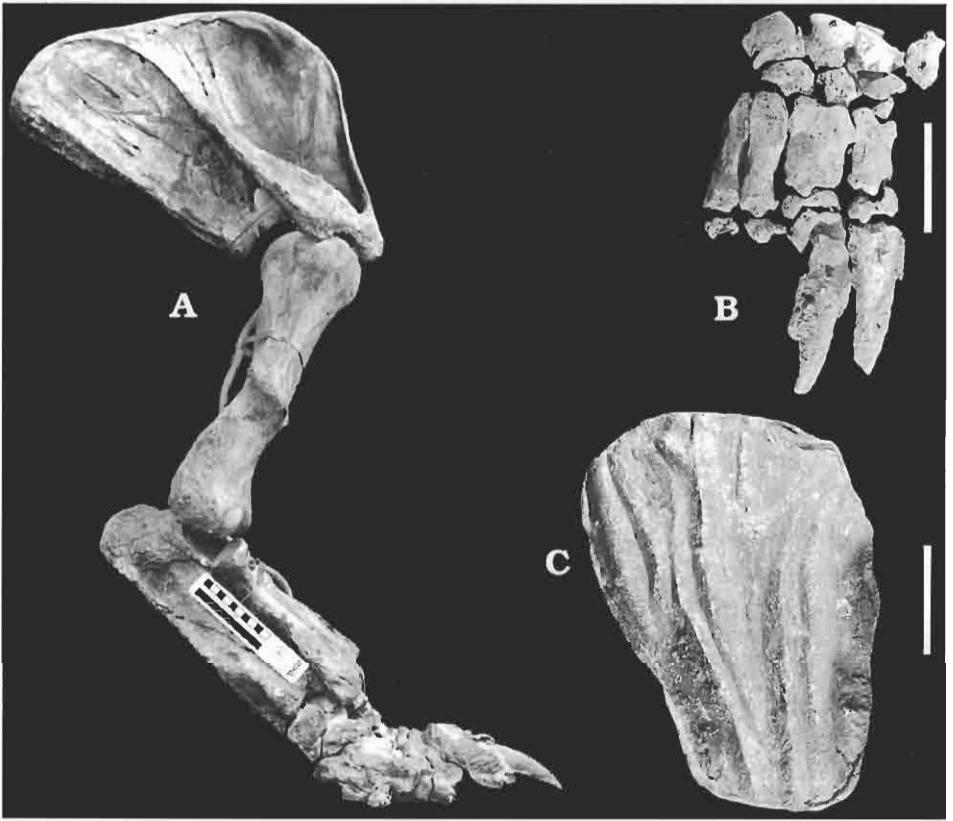


Fig. 5. A. Skeleton of the forelimb of *Glossotherium robustum*. B. Right manus of *Scelidotherium* (MLP 3-574). C. Cast of the claw marks found in the tunnel described by Quintana (1992; MMP 2c). Scale bars 10 cm.

its own tunnels. Those are features largely considered typical of fossorial mammals (Shimer 1903). Nevertheless, this interpretation about a differential fossorial ability between both forms is far from being definitive and needs further analyses.

Discussion

There is little doubt that the largest dasypodid armadillos *Eutatus* and *Propaopus* were the builders of many of the large burrows recorded in several localities in South America. Perhaps the gigantic pampatheres would have dug larger burrows, but it is not so clear that they were the builders of the largest structures found in the Mar del Plata sea-cliffs. More probably some type of mylodontid ground sloth, such as *Scelidotherium* or *Glossotherium*, could be suspected as responsible.

Once it is established that certain ground sloths are well suited for digging, and that the tunnels are dug in cohesive sediments, other evidence deserves to be considered. First, the size of the largest tunnels fits better with hypothesis that the sloths were responsible rather than armadillos. As described above, the largest dasypodid armadillos

have a maximum width of 50 cm. Consequently a tunnel of circular section of over 100 cm diameter implies that they should remove a volume of material equivalent to four times their body volume each time they progress their own body length during digging (assuming that the volume of the tail is not relevant). To minimise the energy expenditure when constructing a tunnel, the tunnel diameter is expected to be relatively constant and to approximate the general body diameter of the digger (Vleck 1979; Hickman 1990). The size of the tunnels suggests that the ground sloths were the likely builders.

Another piece of evidence are some tracks recorded in some palaeocaves. Casts of the tracks reported by Quintana (1992) are kept in the Museo Municipal de Mar del Plata 'Lorenzo Scaglia' (MMP 2C). They consist of pairs of parallel grooves of approximately 30 cm long and 4 cm wide (Fig. 5C). They fit well with the morphology of the manus of both *Glossotherium* and *Scelidotherium*, which evidently bore large claws on well-developed digits II and III (Fig. 5B). The tracks are too large to have been formed by the largest dasypodid armadillos, *Eutatus* and *Proptraopus*. Pampatheres were larger, but did not bear large, specialised claws, and digits II to IV were subequal in size and shape and carried strong pointed unguis (Edmund 1985). Thus they would produce three grooves on the substratum rather than two.

Thirdly, Frenguelli (1928) reported finding of remains of a *Scelidotherium* skeleton within a burrow filled by volcanic ash. This could be taken as strong circumstantial evidence, but actually only demonstrate that the animal was there, and not necessarily that it had built the burrow. However, the position of the tracks in the palaeocave walls and roofs strengthens the possibility that it dug the burrow.

As indicated above, the possibility of mylodontids as burrow-builders has not been postulated since Frenguelli (1928). Perhaps subsequent researchers did not note that brief report in his very extensive and mainly geological work. Possibly also the lack of appropriate examples among living mammals resulted in the assumption that an animal of that size could not be burrower.

The largest living fossorial mammal is the armadillo (*Oryzomys*, Order Tubulidentata), with a body mass up to 100 kg (Nowak 1991). However, this value does not necessarily reflect an upper size limit for fossorial mammals. The Australian Pleistocene giant wombat (*Phascolomys gigas*, Marsupialia) was even better adapted to dig than its well-known burrower living relatives (Stirling 1913). Following Rich (1990) it was the largest fossorial animal that ever lived. It was twice the height and length of any living wombat (Rich 1990) and, if geometric similarity is assumed it must have had a body mass about 200 kg to 300 kg, still much less than the pampean mylodonts. Perhaps, as postulated by Rayner (1996) with respect to the size of birds and the capability for flight, the upper limit of the body size for a fossorial mammal may be constrained by environmental and ecological rather than physical factors. Such factors may furnish clues for cave-building behaviour in some mylodontids. They are discussed as follows.

Glossotherium and *Scelidotherium* may, for example, have depended on burrows to escape predation. During the Pleistocene there were two large-sized carnivores, the sabre tooth cat *Smilodon* and the bear *Arctodus* (body masses: 350 kg and 300 kg, respectively; Fariña *et al.* 1998), that were possible predators of these sloths. The much

larger body size of the coexistent mylodontid *Lestodon* probably rendered at least the adult individuals immune to predation, as occurs today among elephants.

Another possibility includes climatic and physiological factors. It is possible that sloths used burrows to avoid alternatively excessively cold or warm climatic conditions and to conserve energy and water. During the early Pleistocene (most of the Ensenadan) the climate was warmer than today (Tonni & Cione 1995). The prevailing climate of the Pampean region during the last part of the Pleistocene (Lujanian) was mainly colder and much more arid than today, and a dry steppe developed in this area (Tonni & Cione 1997). In such an environment, the mylodontids may have needed a warmer and humid place to breed, or even to survive, during the colder season.

Living xenarthrans have low body temperatures, low basal rates of metabolism and high thermal conductance; these influence the geographical limits of their distributions (McNab 1985). Although there is no direct evidence of the energetics of mylodontids, it is worth noting that some Pleistocene mylodontids, such as *Mylodon*, are known to have occupied, at least seasonally, cooler environments further southward, near the southern extreme of continental Patagonia. Hibernation is not known to occur in living xenarthrans, but the Patagonian armadillo, *Zaedyus pichiy*, enters a state of torpor during winter, when the availability of insects, one of its main food resources, declines dramatically. McNab (1985) proposed that cold temperature tolerance of some ground sloths in North America (including *Glossotherium*), probably stemmed from a thick fur coat and continuously available food. However, only *Mylodon* (Moreno & Woodward 1899) and *Nothrotheriops* (Lull 1929) are known to have possessed a good thick fur coat. Nothing is known of the external appearance of *Scelidotherium* and *Glossotherium*, but it is conceivable that, if they did possess a poorer fur coat, they might have compensated by using caves, at least during unfavourable seasons. It might also be suggested that, as in living wombats (burrower marsupials with a very slow metabolic rate), burrows could help the ground sloths to reduce the need for water (Barboza 1995).

It is noteworthy that remains of late Pleistocene ground sloths, including many mylodontids, were found in natural caves and rockshelters. This suggests that the use of caves, whatever the reason, was a common behavioural pattern in ground sloths. Records of ground sloths in natural caves and caverns are specially abundant in Brazil, in the States of Bahia and Minas Gerais (Lund 1842; Winge 1915; Cartelle 1991). Ground sloths were also recorded in natural caves in cooler regions at higher latitudes and/or altitudes of Patagonia (Moreno & Woodward 1899; Scillato-Yané 1976) and Western North America (Akersten & McDonald 1991; McDonald *et al.* 1996). For North American forms, Akersten & McDonald (1991) proposed that the relatively stable environments of caves acted as an effective temperature buffer, explaining the frequent occurrence of sloth remains. Although Scillato-Yané (1976) proposed a physiological adaptation for cold-tolerance in Patagonian sloths, a behavioural adaptation such as that proposed for the North American ones is also plausible.

In the area of Mar del Plata, as in most of the remaining Pampean region, caves and rockshelters are restricted to some places of the Tandilia and Ventania mountain ranges of Buenos Aires, and other ranges flanking westward the Pampas. Thus, if the Pampean mylodontids needed to dwell in relatively closed shelters in such extensive plains environment, they would have had to built the cave shelters themselves, and they were well-adapted for that.

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