Paleocaves exhumed from the Miramar Formation (Ensenadan Stage-age, Pleistocene), Mar del Plata, Argentina

Alejandro Dondas a,*, Federico I. Isla b, José L. Carballido b

a Museo Municipal de Ciencias Naturales “L. Scaglia”, Plaza España, 7600 Mar del Plata, Buenos Aires, Argentina
b Instituto de Geología de Costas y del Cuaternario, Universidad Nacional de Mar del Plata, Casilla de Correo 722, 7600 Mar del Plata, Argentina

A R T I C L E   I N F O

Article history:
Available online 19 July 2009

A B S T R A C T

Exhumed organic megastructures are analyzed in this paper. Large paleocaves (0.7–2.1 m width and 0.7–1.5 m height) are related to the digging of Xenarthra (Mammalia) that lived in the Pampas during the Pleistocene. Some of these burrows are completely filled by sediment, and others are found partially empty. They occur within the city of Mar del Plata and its surroundings, mostly restricted to the Miramar Formation. Three types of galleries have been identified. The larger caves (type I) are related to the digging activity of mylodontids (e.g. Glossotherium). Type II caves are related to smaller mylodontids (Scelidotherium leptocephalus). Other caves of similar size are attributed to the dasypodid Pampatherium (type III). The number of digits recognized in scratch marks on the cave walls helped to distinguish between mylodontid and dasypodid activities. The abundance of these caves has been interpreted in relation to water availability in the surroundings of the Tandilia Range, flooding potential, and shelter to avoid predation by carnivores. The paleobiologic and paleoecological significance of the structures assigned to ants or termites, and cave reoccupation by specimens of Arctotherium latidens (Ursidae, Tremarctinae), are also discussed.

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1. Introduction

Crotovina structures described in the coastal cliffs of Mar del Plata (Fig. 1) at the beginning of the 20th century (Ameghino, 1908; Frenguelli, 1928; Kraglievich, 1952) have been only partly studied. Although Frenguelli initially pointed to large glyptodontids (Mammalia, Edentata) as being responsible for the caves, he later suggested that the mylondontids (Mammalia, Mylodontidae) were the dwellers of the larger ones.

Quintana (1992) described an empty paleocave exhumed 4 m below the ground, south of the city of Mar del Plata. He tentatively assigned these excavations to some Dasypodidae (Mammalia, Edentata), as Eutatus sp. (Euphractinae, Eutatini), Propaopus sp. (Dasypodidae) or Pampatheriidae (Pampatherium sp.) More recently, and based on the dimensions of some caves and the sizes of scratch marks, the mylondontids Scelidotherium sp. or Glossotherium sp. (Tardigrada, Mylodontidae) were recognized as the excavators of the larger caves (Zárate et al., 1998; Vizcaíno et al., 2001).

In the present paper, the caves are described in detail, including evidence from the ocean coastal cliffs, and also from excavations to depths of 10–17 m (Base Spyrznal, Fourth Sewage Collector, a quarry at 389 km of National Road 2). Based on their sizes and marks from the walls, the effective dwellers of these caves are indicated or suggested.

2. Materials and methods

Between 1999 and 2006, sixteen caves have been exhumed in the city of Mar del Plata and its neighborhoods. They occurred mainly in the Miramar Formation (Ensenadan stage). As these caves are “time transgressive”, it is possible to identify them in the underlying stratigraphic units (Vorohué and San Andrés formations, sensu Kraglievich, 1952; Zárate and Fasano, 1989). During the Bonarian stage, it was also possible that some caves could have been dug down to the Miramar Formation sediments (Fig. 2).

Caves were located by means of GPS and using street names within the city of Mar del Plata. The Gauss-Kruger coordinates (the system used in Argentina) were calculated in order to place them into an Arc View environment (PALEOGIS, Dondas et al., 2001). Using GIS, the caves could be geographically related to fossiliferous localities where mammal bones have been sampled during many years. Several caves were discovered during the
construction of a new sewage collector, using pneumatic hammers, at 10 m depth. Several caves were recognized and described, some of them completely filled with sediment but others only partially (Isla and Dondas, 2001). Transverse dimensions of the caves (horizontal and vertical) and length were measured. Within the caves, various structures were recorded by photographs, including scratch marks corresponding to paws, anthills and oxidation of the roof of the caves. Scratch marks have been also preserved as gypsum casts. This sampled material was deposited at the Museum of Natural Sciences “Lorenzo Scaglia” of Mar del Plata.

Large burrow types are recognized considering the different size variables (width, height and length). Small and very common burrows, undoubtedly dug by rodents such as Ctenomys sp., were discarded from the analysis. Scratch marks were an unavoidable characteristic. Three types of burrows were considered.

2.1. Type I: giant burrows

Several caves have widths over 1.8 m, but never wider than 2.1 m (Fig. 3a). Their heights are approximately 140 cm. Scratch marks were horizontal, vertical or oblique with runs over 110 cm. The distance between digits is about 3–4 cm with a depth of 5–6 cm into the sediment. The cave exhumed at 389 km of National Road 2 was particularly important. Three specimens of Arctotherium latidens (female and siblings) were obtained from this location (Soibelzon et al., 2001, 2005). Associated with these remains, six Scelidotherium sp. skulls and one Scelidodon sp. skull were also found. Another cave exhumed at the intersections of Colón and Arenales streets was 15 m long, and contained large and incised scratch marks in different directions (Fig. 4).

The cave discovered at Base Spyrznal was about 2 m wide and 1.4 m high, with a total length of about 45 m. Its volume was
estimated at 100 m$^3$. A block 0.4 by 0.6 m was extracted to record the scratch marks assigned to a mylodontid.

2.2. Type II

Smaller burrows with horizontal diameters varying between 90 and 120 cm and vertical heights of 75–100 cm were also identified (Fig. 3b). These caves have scratch marks produced by two digits and runs of up to 30–40 cm. These types of burrows were described in Punta Mogotes (Quintana, 1992) and the GADA facilities. These burrows were carved by an animal that produced tracks from two digits. They are assigned to a small mylodontid, with the 1000 kg Scelidotherium leptcephalum the most likely one.

2.3. Type III

This type of structure is very similar to type II. In the Las Margaritas locality (37° 54’52”S; 57° 35’48”W) the cave was 1.0 m wide and 0.75 m high (Fig. 5). The scratch marks were completely different (vertical or oblique with runs not longer than 30 cm) and were produced by paws with three digits. Several sedimentary structures similar to anthills were recognized in the sediments in which these caves were dug. This type of digging is similar to the activity of the present large dasypodid “tatu carreta”, Priodontes maximus (Carter and Encarnaçao, 1983).

Considering the morphology of the caves, scratch marks and similarities of present-day behavior, these caves were assigned to Pampatherium typum, a 120–150 kg mammal that was either related to dasypodids or glyptodontids (De Iulis et al., 2000). Although the masticatory system of different Pampatheriidae suggests that they were grazers of coarse vegetation (De Iulis et al., 2000), the giant armadillos of the present Pampa plains are associated with termite colonies in 44% of the cases (Carter, 1983) (Table 1).

3. Discussion

The abundance of these caves is related to their stability, food supply for their builders and proximity to water, but avoiding flood-susceptible areas. The Tandilia Range, the rocky hills that meet the Atlantic Ocean at Mar del Plata, seems ideal in the sense that the relief must have enabled cave construction, ensuring water supply. The existing relief provides a physical detachment from the groundwater table and appropriate shelter to avoid predators.

Mylodontids are mammals that used to live in caves. In Southern Chile, Mylodon caves were initially studied by E. Nordenskjöld. Recently, radiocarbon dating showed that mylodontids occupied the cave between 15,439 and 12,938 B.P. (Tonni et al., 2003). Mylodontid digging capacity was repeatedly analyzed by many researchers (Owen, 1842; Cuenca Anaya, 1995; White, 1997), but analysis was restricted to their assumed ability to dig for bulbs or roots. More recently, several authors (Zárate et al., 1998; Bargo et al., 2000; Dondas et al., 2001; Vizcaíno et al., 2001) focused on Mylodontid ability to dig larger caves, which are common in southeastern Buenos Aires province. Anatomical, allometrical and
biomechanical analyses pointed to the particular digging capacity of Scelidotherium sp. and Glossotherium sp. (Bargo et al., 2000).

Distinction between II and III type caves is based on comparison of scratch marks. In type II caves, scratches of only two digits were assigned to mylodontids with reduced digits I, IV and V (Fig. 6). On the other hand, the scratches attributed to Pamphatherium sp. are the product of 3 digits in vertical–oblique short runs (Fig. 6).

In relation to the digging capacity, new studies have analyzed the eating aptitude of the extinct Tardigrada. Glossotherium robustum and Lestodon armatus were recognized as selective feeders by their narrow snouts that could eat roots and tubers due to their digging capacity (Bargo and Vizcaíno, 2000). However, these authors acknowledged that the lack of modern analogues did not allow good extrapolations.

Dasypodids are known as dwellers and anteaters. The present “Giant armadillo”, P. maximus, is a well-known termite eater; their burrows are 44% related to termite mounds (Carter, 1983). At the same time, the termite mounds supply a way to exchange gases from the caves (Carter, 1983). However, “giant armadillo” is also the name given to the Pamphatheriidae family (Edmund, 1985). P. typum was a member of the Tolypeutinae family (Abrantes and Bergqvist, 2005; Abramantes et al., 2005), a subfamily to which also the extant P. maximus and Tolypeutes sp. belong, both termite eaters (Redfords, 1985). However, the phylogeny of “giant armadillos” is a subject of great controversy and requires a revision (De Iulis et al., 2000; Abramantes and Bergqvist, 2005).

Living giant dasypodids, such as P. maximus and the giant anteaters (Myrmecophaga tridactyla and Tamandua tetradactyla), are well-known termite eaters. The extinct small mylodontid, S. leptocephalum, is proposed as an animal capable of occasionally eating insect eggs. Obviously, a 1000 kg animal could not live only with a diet exclusively based on insects. The partially filled cave, exhumed during the construction of the Sewage outfall of Mar del Plata, contained structures similar to ant mounds, and similar to the structures described in the Miocene of La Pampa (Laza, 1982). S. leptocephalum could have eaten ants, but could have also taken advantage of their eggs or stored plant fragments. The tubular cranium of S. leptocephalum is also evidence to consider it an insectivorous animal, similar to anteaters and the aardvarks (Knuthing, 2005). Perhaps it could have taken advantage of eggs during the winter. Although these facts need further confirmation, S. leptocephalum could have been the largest mammal with a partial formicivore diet, considering that most large anteater mammals belong to the Xenarthra Superoorder (Table 2).

The Miramar Formation (Ensenadan stage-age) represents a change from units with a fauna dominated by small animals (the Vorohué and San Andrés formations) to sediments with large caves that belonged to large xenarthra (Frenguelli, 1928). These changes have been interpreted as caused by climate change (Tonni and Fidalgo, 1978; Prado et al., 1987; Cione and Tonni, 1995). However, a possible bias concerns the spatial resolution of the studied environments: the Vorohué and San Andrés formations are low-relief floodplain deposits, limited only to the neighborhoods of the Tandilia Range (Zárate and Fasano, 1989). The Miramar Formation is more extensive, including fluvial and subaerial sediments. The Vorohué and San Andrés formations have maximum thicknesses of 4–6 and 6 m, respectively (Kraglievich, 1952). The Miramar Formation has a maximum thickness of 34 m measured at the Miramar well (Frenguelli, 1928), although at the same cliffs in the General Pueyrredón County it has a maximum thickness of only 3 m (Kraglievich, 1952).

Regarding Pampean ages, several authors accept that the Ensenadan stage-age extends from about 2 Ma to less than 0.78 Ma, and that it is overlain by the Bonaerian stage-age (Cione and Tonni, 1995; Nabel et al., 2000). In recent years, this boundary has been proposed to be younger than previously estimated: 0.7 Ma (Tonni et al., 1999), 0.65 Ma (Rabassa et al., 2005; Soibelzon et al., 2005) and even 0.5 Ma (Verzi et al., 2004). However, other authors found

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**Table 1**

Dimensions of ancient burrows compared to present caves of *Priodontes maximus*.

<table>
<thead>
<tr>
<th>Type</th>
<th>Burrow width (cm)</th>
<th>Burrow height (cm)</th>
<th>Number of digits</th>
<th>Interdigit scratch mark (cm)</th>
<th>Caves</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>210</td>
<td>110</td>
<td>2</td>
<td>11</td>
<td>km 389; Colón and Arenales streets; Base Spyridal</td>
</tr>
<tr>
<td>II</td>
<td>140</td>
<td>75</td>
<td>2</td>
<td>4</td>
<td>Punta Mogotes; GADA</td>
</tr>
<tr>
<td>III</td>
<td>11</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>Las Margaritas; Serra de Canastra, Minas Gerais, Brazil</td>
</tr>
<tr>
<td><em>P. maximus</em>#</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Vizcaíno et al., 2001; #Carter, 1983; Carter and Encarnação, 1983.

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![Fig. 4](image-url)  
Scratch marks exhumed at the cave on the intersection of Colón and Arenales streets, Mar del Plata.

![Fig. 5](image-url)  
Three medium-sized paleocaves, with different type of erosion at their tops (black bars are 0.5 m long).
that the marine Belgranian highstand commonly separates both stages (Ameghino, 1908; Frenguelli, 1928; Cione et al., 2002; Parker et al., 2002). As this transgression has been dated by U/Th to 93.5 ± 3.5 ka and assigned to the Sangamonian highstand of 120 ka (MIS 5e; Isla et al., 2000), a significant gap (of about 400,000 years) would be regionally extended (as a “ravinement” surface in coastal sequences) between the Ensenadan–Bonaerian chronostratigraphical units, therefore challenging some magnetostratigraphic conclusions without the support of more precise dating. However, it should be taken into consideration that not all “Belgranense” marine units of Buenos Aires Province have been actually dated, making it likely that such sediments belong not only to the Sangamonian but perhaps also to one or more older interglacial periods. The subject is still open: continental and coastal sequences should be chronologically and stratigraphically correlated to each other wherever it is possible.

Some authors have stressed that large burrows are more common in the Miramar Formation than in the underlying

Table 2
Characteristics of living formicivore mammals.

<table>
<thead>
<tr>
<th>Order-family</th>
<th>Genus</th>
<th>Weight (kg)</th>
<th>Formicivoria</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tubulidentata</td>
<td>Orycteropus afer (Aardvark or earth pig)</td>
<td>40–65</td>
<td>Almost exclusive</td>
</tr>
<tr>
<td>Cingulata-Dasyopodidae</td>
<td>Priodontes maximus (Giant armadillo)</td>
<td>28–32</td>
<td>Not exclusive</td>
</tr>
<tr>
<td>Pilosa-Mirrmecophagidae</td>
<td>Myrmecophaga tridactyla; Tamandua tetradactyla (Giant anteater)</td>
<td>18–39</td>
<td>Exclusive</td>
</tr>
<tr>
<td>Pilosa-Megalonchidae</td>
<td>Choloepus didactylus (Linneaus’s two-toed sloth)</td>
<td>4–8</td>
<td>Not exclusive</td>
</tr>
<tr>
<td>Pholidota</td>
<td>Manis sp (Pangolin, Scaly anteater)</td>
<td>8–9</td>
<td>Almost exclusive</td>
</tr>
<tr>
<td>Monotremata</td>
<td>Tachyglossus aculeatus (Echidna, spiny anteater)</td>
<td>2.5–8</td>
<td>Exclusive</td>
</tr>
<tr>
<td>Marsupialia</td>
<td>Myrmecobius fasciatus (Numbat)</td>
<td>0.28–0.55</td>
<td>Exclusive</td>
</tr>
</tbody>
</table>

Fig. 6. Comparison of the paws of Glossothrium sp. (left) and Pampatherium sp. (right) (modified from Castelle et al., 1989) and their scratch marks (below). Black bar is 0.1 m long.
formations, such as Vorohué and San Andrés (Frenquelli, 1928). This is reasonable considering that these underlying formations represent floodplain facies (Zárate and Fasano, 1989), and therefore their fossil content is biased towards rodents and other small animals. On the other hand, the Miramar Formation is more extensive along the Pampas, and therefore may include larger animals belonging to different habitats.

These plains hosted several carnivorous genera during Ensenadan times. Smilodon sp. was thought to be dominant during the Middle Pleistocene and their bones are very common in the sediments of the Miramar Formation (Isla and Dondas, 2001). Among canids, several species lived together, particularly Protoconys scaglieri and Theriodictis platanus (Carnivora, Canidae); the latter has been considered as totally carnivorous (Prevosti et al., 2004). Among felids, Felis concolor was also common, whereas Panthera onca mesembrina Cabrera (larger than the present South American jaguar or “yaguareté”) is thought to have appeared towards the end of the Pleistocene. Some of these carnivorous animals would have taken advantage of these caves. The discovery of three specimens of A. latidens (Ursidae: Tremarctinae) in a filled gallery, discovered in a quarry excavated close to National Road 2 (km 389), suggests that these caves could have been reoccupied during younger times. These specimens were found in place, without evidence of transport or postmortem predation (Soibelzon et al., 2001). Mud cracks at the floor and oxidized stalactites at the roof suggest stability during a certain time.

4. Conclusions

1. Different types of caves have been identified according to their sizes and the scratch marks on their walls.
2. Mylodonids are assigned as the dwellers of the larger and medium caves. Medium-sized cingulates (Pampatherium sp.) are assumed to have built the smaller paleocaves, but they were even larger than present-day dasyopodid P. maximus.
3. Cave abundance in the city of Mar del Plata is related to hilly topography, water availability, lower flooding potential, and shelter, physical characteristics which are frequent in the southeastern end of the Tandilia Range.

Acknowledgments

Alfredo Carlini and Tracy Carter made useful comments about dasypodid behavior and their present caves, respectively.

References


