



# Ants and xenarthrans involved in a Quaternary food web from Argentina as reflected by their fossil nests and palaeocaves

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## LETHAIA



Genise, J.F. & Farina, J.L. 2011: Ants and xenarthrans involved in a Quaternary food web from Argentina as reflected by their fossil nests and palaeocaves. *Lethaia*, Vol. 45, pp. 411–422.

Quaternary (Ensenadan stage-age) deposits of the Miramar Formation from the Buenos Aires sea coast near Mar del Plata (Argentina) are well known for bearing long horizontal tunnels produced by xenarthrans, either ground sloths or armadillos. Little known is that, in some cases, these palaeocaves cross-cut social insect nests. Nests of two studied palaeocaves can be attributed to ants based on the presence of abundant ant remains, filling of chambers and organic-rich linings. Insect remains show part of a food web composed of army ants (*Neivamyrmex*) preying on leaf-cutting ants (*Acromyrmex*), *Pheidole* and other soil invertebrates. The other main component of this web is represented by the xenarthrans feeding on these ants. The facultative foraging function of xenarthran palaeocaves is supported by the common record of these extended horizontal tunnel systems similar to other subterranean foraging mammals, the presence of insect nests cross-cut by them and the extended myrmecophagy among xenarthrans. Xenarthran foraging burrows, despite their high-energy cost, would have been favoured by abundance of underground ant nests during Quaternary times and harsh climate. This climate would have produced the scarcity of insects on surface and longest periods of underground activity by xenarthrans, involving the extension of shelter burrows for adult and possibly juvenile feeding. □ *Ant fossil nests, Argentina, Buenos Aires, food web, Quaternary, xenarthran palaeocaves.*

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Plio-Pleistocene deposits of the Buenos Aires seacoast near Mar del Plata are well known for bearing palaeocaves, the production of which is attributable to mammals. The palaeocaves can be basically grouped in small examples (11–13 cm in diameter), which preserve enough fossil remains inside them to allow attribution to rodents (Genise 1989; Scognamiglio *et al.* 1998; Fernández *et al.* 2000); and larger examples (90–210 cm wide). These may be reliably attributed to ground sloths, where their diameter exceeds 90 cm, and where the scratches on walls are bidactyl (e.g. Zárate *et al.* 1998; Vizcaíno *et al.* 2001; Dondas *et al.* 2009); or to armadillos (Pampatheridae or Dasypodidae) where diameters are smaller and scratch marks tridactyl (Dondas *et al.* 2009). The first records of these caves date back to Ameghino (1908), Frenguelli (1928) and Kraglievich (1952). Similar palaeocaves from southern Brazil were attributed to armadillos because of the preservation of marks produced by carapaces (Buchmann *et al.* 2009).

Less analysed by the literature (or supported only by brief paragraphs) are suggestions of the functionality of these caves. Vizcaíno *et al.* (2001) mentioned escape against predators, regulation of temperature or

physiological constraints, typical agents of mammal caves used for shelters. However, it remains unlikely that mostly horizontal and branched caves reaching lengths of about 70 m in Brazil and 40 m in Argentina (and even longer ones inferred) can be interpreted only as shelters.

In this contribution, we present data recovered from field work inside two large palaeocaves from the Pleistocene Miramar Formation of Mar del Plata (Argentina) that support the idea that some of these caves could have had a foraging purpose, for exploiting underground ant nests as modern xenarthrans do. Although Dondas *et al.* (2009) has mentioned this idea for some caves, it was not supported by data. To rectify this, presented herein are the location and description of the caves and interpretations and contents of nests found inside. The objectives of this contribution are: (1) to describe and document two mammal palaeocaves bearing insect nests; (2) to describe and interpret insect nests cross-cut by these mammal palaeocaves; (3) to analyse possible producers of insect nests and the relationships among them; and (4) to test the hypothesis that some of these palaeocaves were facultative foraging tunnels.

## Material and methods

Data presented herein were recovered during 3 days of fieldwork at two different palaeocaves (Fig. 1). The existence of these palaeocaves was communicated to the Museo Municipal Lorenzo Scaglia of Mar del Plata by the landowners, who had discovered them by chance. The former was the same as described by Quintana (1992) from the Miramar Formation (Pleistocene, Ensenadan stage-age) at Barrio Alfar (38° 05'17' S; 57° 33'27' W) of Mar del Plata (Buenos Aires province, Argentina). However, no mention to insect nests was included in that publication, although they were recorded in field notes from 14 and 17 November, 1987 (by C Quintana, JFG, JLF and J Puerta). During this work, the filling of tunnel D illustrated by Quintana (1992; fig. 1) was removed, measures were taken and hand samples of nests were collected for a further analysis in laboratory.

The second cave studied was the same mentioned by Dondas *et al.* (2009) from the Miramar Formation at Barrio Las Margaritas (37°54'52'S; 57°35'48' W) of Mar del Plata. Data and pictures of the cave, and particularly of insect nests, were recovered by one of us (JLF) for further laboratory analysis on 17 October 2005 during field work carried out with Dondas *et al.* (2009).

## Results

### Palaeocaves

The following descriptions are based on field observations made by us, and as such, they may differ to some point with those already published by Quintana

(1992) and Dondas *et al.* (2009). Alfar palaeocave (Fig. 2A) was composed of a H-shaped burrow system developed in a horizontal plane. It was accessed by a 5-m deep man-made shaft that intersected the roof of the palaeocave near the middle of the long branch (Fig. 2B). The H was composed of a long, bending branch, 23 m long and 0.90 m wide in average (Fig. 2E), having two dead ends showing scratch marks. This long branch cross-cut two structures, about 40 cm long and 60 cm high, and consisted of a boxwork of chambers and tunnels, interpreted herein as social insect nests, which extend from the lateral wall to the roof of the palaeocaves (Fig. 2D). The nests were located in irregular concavities occurring in the smooth walls of the palaeocave. Parts of these areas were stained with a dark colour. Scratch marks were also present in the lateral walls of the long branch (Fig. 2F). It was connected with a smaller one by means of a short perpendicular tunnel, 1.3 m long (Fig. 2C). The second, smaller, 3-m long, branch, showed both extremes filled with sediments at the time the fieldwork started. One of them was dug out, revealing a short blind tunnel showing scratch marks at its end (Fig. 2G), whereas the other was probably the original access to the cave from where the fillings entered. Purportedly, this filled tunnel was inclined, reaching the palaeosol surface.

Dondas *et al.* (2009) mentioned and located the palaeocave at Barrio Las Margaritas as the only example of their Type III morphology. However, no pictures or drawings were supplied, and other characters, such as scratch marks or insect nests, were not described. The illustration of their Type III caves is from palaeocaves at the coastal cliffs, 6 or more kilometre far from this locality, whereas other undescribed Type III palaeocaves are mentioned from the excavation of a sewage outfall (Dondas *et al.* 2009). There are no measures of length (1-m wide), whereas scratch marks are described as produced by three digits.

The Las Margaritas palaeocave (Fig. 3A) was composed of a more or less straight entrance tunnel, about 3-m long and 1-m wide (Fig. 3C), branching at one end into two secondary tunnels. The right one, curved and about 4 m long, showed a lateral, short (1 m), blind tunnel, whereas the left one, about 3-m long, was curved and directed backwards to the entrance. The entrance tunnel, at the other end, was oriented upwards to finally intersect the extant soil surface by means of a man-made excavation (Fig. 3B). The three branching tunnels were gradually filled with sediments (Fig. 3E) up to their complete concealment at their ends. Four insect nests, which were exposed in pits of the walls, were cross-cut by the entrance and the three branching tunnels respectively (Fig. 3D, F, G, H).

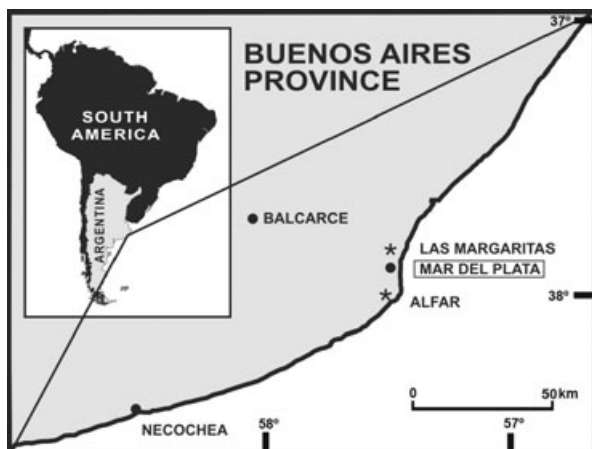
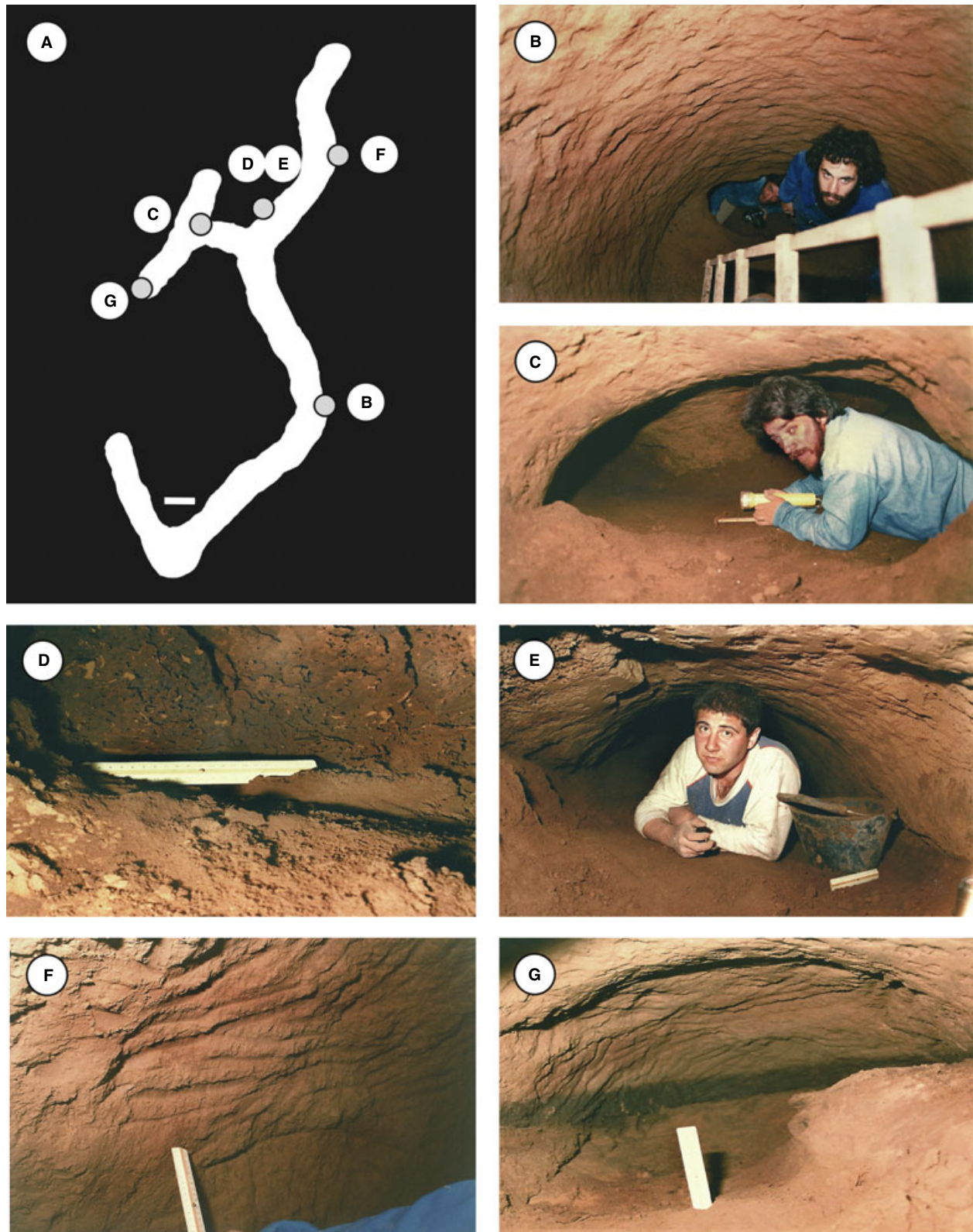


Fig. 1. Map showing the location of the Alfar and Las Margaritas palaeocaves.



*Fig. 2.* Alfara palaeocave. A, sketch of the palaeocave showing the location of pictures B to G. Scale bar = 1 m. B, the man-made access shaft (Carlos Quintana and JFG for scale). C, the entrance of the perpendicular tunnel between the long and the short branches, showing its cross section (JFG for scale). D, one of the ant nests located at the wall of the long branch. E, long branch showing its cross section (JLF for scale). F, scratch marks in the wall of the long branch. G, short blind tunnel with the fillings partially dug out, showing scratch marks at the end. Rule = 20 cm.

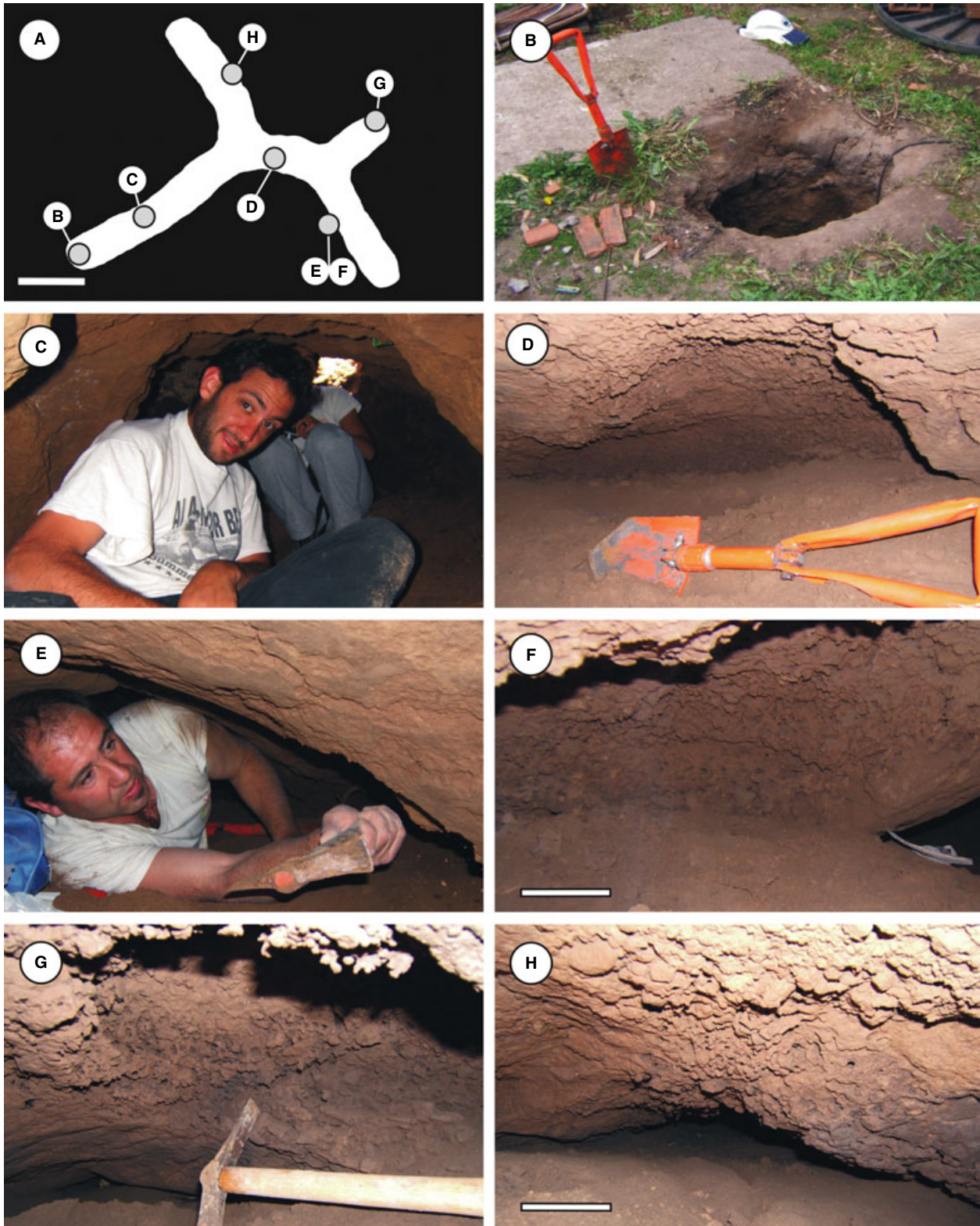


Fig. 3. Las Margaritas palaeocave. A, sketch of the palaeocave showing the location of pictures B to H. Scale bar = 1 m. B, man-made entrance of the palaeocave. Shovel = 60 cm. C, entrance tunnel showing its cross section (José L. Carballido for scale). D, ant nest at the bend of the right secondary tunnel. Shovel = 60 cm. E, JLF excavating the ant nest from the right tunnel. Note the sediments at the floor partially filling the tunnel. F, ant nest from the right tunnel. Scale bar = 15 cm. G, ant nest at the end of the short, blind tunnel connected to the right one. Hammer = 30 cm. H, ant nest from the left secondary tunnel. Scale bar = 15 cm.

### Associated insect nests

In both palaeocaves, the nests were composed of a boxwork of chambers and tunnels and lacked an external wall and regular shapes. Areas occupied by these boxworks ranged in size from 40 to 75-cm long and 30 to 60-cm high (Figs 2, 3). In the Alfar boxworks, the chambers are mostly flat, 4 to 10-mm high, the longest measured was 10-cm long, and in some cases horizontally arranged (Fig. 4A, B). There are small diameter (1 to 2 mm) passages connecting chambers. The walls show a lining, which is darker than the matrix and in some parts shows a bad preserved pelletal structure including insect remains (Fig. 4C, D). Part of the system was empty, whereas many chambers were filled with insect remains and two types of pellets (Fig. 4E): (1) light, up to 2 mm long, composed mostly of agglutinated coarse grains of quartz, feldspar and plagioclase; and (2) dark ones, most of them up to 1 mm long, composed mostly of organic matter, which in some cases included also coarse grains or insect remains (Fig. 4F). Chamber fillings also contain a large amount of loose arthropod remains, mostly insects (Fig. 4G). Among them, ant body parts such as heads, thoraxes, abdomens, antennae and legs were the most abundant, belonging to *Neivamyrmex* sp. (Fig. 5A), *Acromyrmex* sp. (Fig. 5B), *Pheidole* sp. (Fig. 5C) and *Solenopsis* sp. (Fig. 5D). In a counted sample of 161 ant heads, 93 belonged to *Neivamyrmex* (57.8%), 42 to *Acromyrmex* (26.8%), 16 to *Pheidole* (10%) and seven to *Solenopsis* (five winged individuals according to the presence of ocelli; 5%). Beside ants, the most abundant remains belonged to Rhyparochromidae (Hemiptera, Heteroptera, Lethaeini; Fig. 5E). Other remains included few body parts of Tenebrionidae, Staphylinidae, Histeridae, Scarabaeidae, Aphodiidae and Carabidae (Coleoptera); Cydnidae and Enicocephalidae (Hemiptera, Heteroptera; Fig. 5F); Apicotermiteinae (Isoptera, Termitidae; Fig. 5G), mites (Fig. 5H), spiders, and scorpions (Fig. 5I).

In the Las Margaritas boxworks, the chambers were more irregularly arranged and shaped, perhaps due to preservational or weathering differences with those of Alfar. No small diameter passages were observed. The walls show a lining darker than the matrix, but lighter than that of the Alfar boxworks. No insect remains were observed in the lining. Part of the system was empty, whereas other parts were concealed with consolidated fillings, and still other parts were filled with loose sandy material arranged in pellets bearing very few insect remains. The recognizable ones included nine heads of *Neivamyrmex*, (and other body parts, including an almost complete specimen; Fig. 5A) and one of *Solenopsis* sp., a leg of *Acromyrmex* sp., a thorax

of *Pheidole* sp. (Hymenoptera, Formicidae) and a mandible of Scarabaeidae (Coleoptera).

## Discussion

### *Palaeocave producers*

Frenguelli (1928) was the first to attribute one of these large palaeocaves to a ground sloth (*Scelidotherium*). Later, Quintana (1992) attributed the Alfar palaeocave to some Cingulata, either Pamphtheridae or Dasypodidae, depending on the width of the tunnels (up to 1.20 m), without analysing in detail the scratch morphology. Subsequently, Zárate *et al.* (1998) documented the presence of bydactyl scratch marks, further supporting attribution to ground sloths (see also Isla & Dondas 2001; Vizcaino *et al.* 2001, Dondas *et al.* 2009). In addition, Zárate *et al.* (1998) claimed that some of these palaeocaves could be diachronic because of their large size and the lack of record of the location of their entrances. Isla & Dondas (2001), extended this statement and considered that all palaeocaves were diachronic, and as such that they were excavated by mammals younger than the deposits. However, it cannot be applied as a general rule for all palaeocaves, particularly when the stratigraphical boundaries of the pampean sediments are not easily distinguished, even less inside palaeocaves. Herein, they are only tentatively considered to be from the Ensenadan stage-age just following Isla & Dondas (2001), although further studies are needed to more precisely establish the units and ages involved.

Isla & Dondas (2001) mentioned different types of large palaeocaves from a sedimentological study accomplished in the construction of a sewage pipeline at Mar del Plata. Following former contributions, they attributed these palaeocaves to ground sloths and armadillos based on size and scratch marks. They recorded ten caves in a section of 5 km along the pipeline. Buchmann *et al.* (2009) described similar palaeocaves from southern Brazil, attributing some of them to Cingulata based on the finding of traces left by a carapace, which ruled out ground sloths as possible producers. These types of traces were not found in Argentinean palaeocaves.

Finally, Dondas *et al.* (2009) grouped large caves in three types according to their size and scratch marks on the walls, but no detailed descriptions or illustrations were provided. Only scratch marks and cross sections at the coastal cliffs are depicted. Type I palaeocaves, the larger ones described from Base Spyrzmal, Km 389 and streets Colón and Arenales, are attributed to ground sloths such as *Scelidotherium* and *Scelidodon*. Type II caves, including cross sections in the

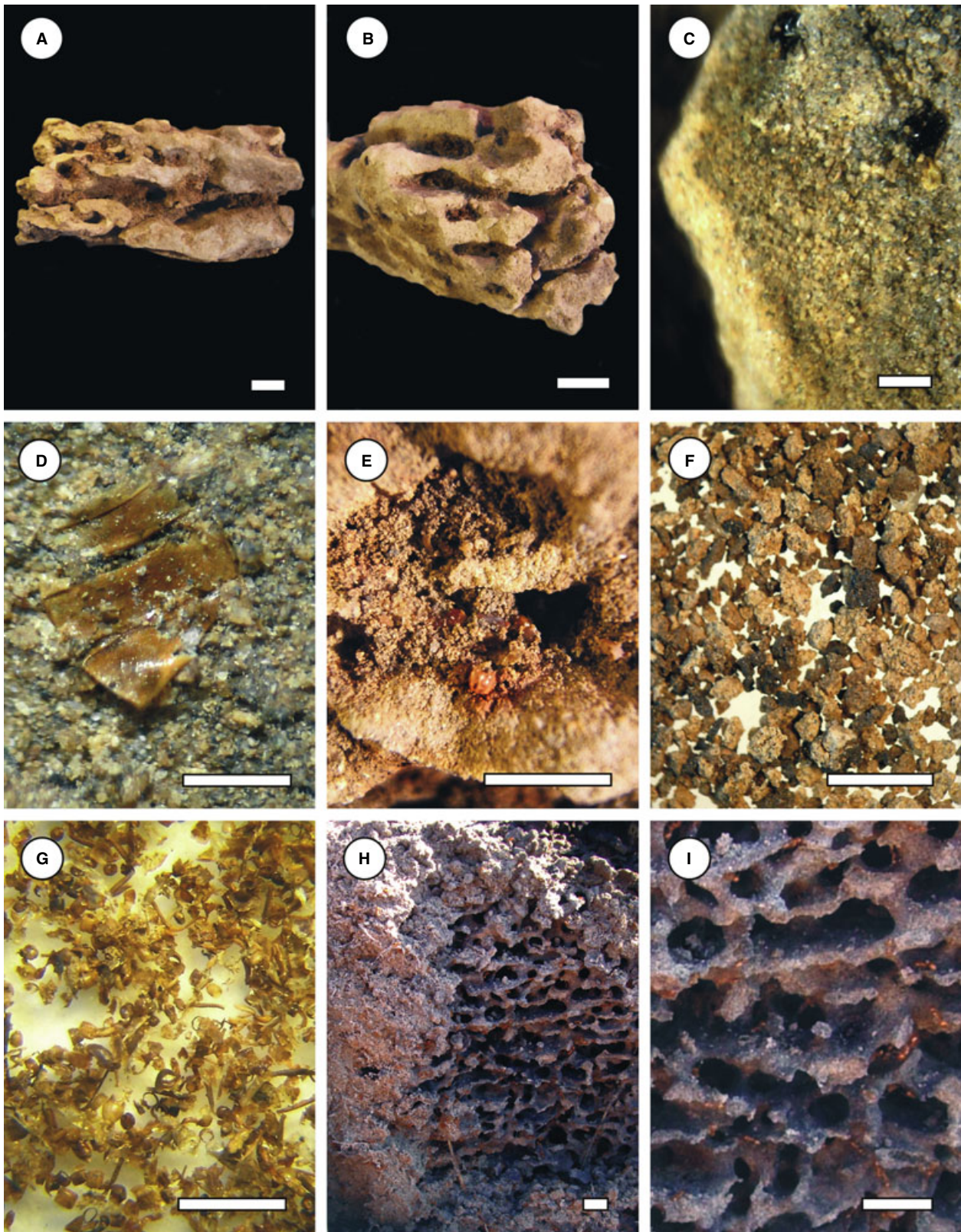


Fig. 4. Ant nests. A, B, detail of boxwork showing horizontally arranged chambers partially filled with sediments and insect remains. Scale bars = 1 cm. C, dark lining contrasting with the lighter rock matrix and preserving two black insect remains. Scale bar = 0.2 cm. D, abdominal sclerites entombed in the lining. Scale bar = 0.5 cm. E, detail of chamber fillings showing loose sediments and insect remains. Scale bar = 1 cm. F, light, mostly inorganic pellets and dark, mostly organic pellets. Scale bar = 1 cm. G, insect remains removed from the chamber fillings. Scale bar = 1 cm. H, extant nest of *Solenopsis* sp. in a sandy soil of La Pampa province. Scale bar = 1 cm. I, detail of the lining of the *Solenopsis*'s nest. Scale bar = 1 cm.

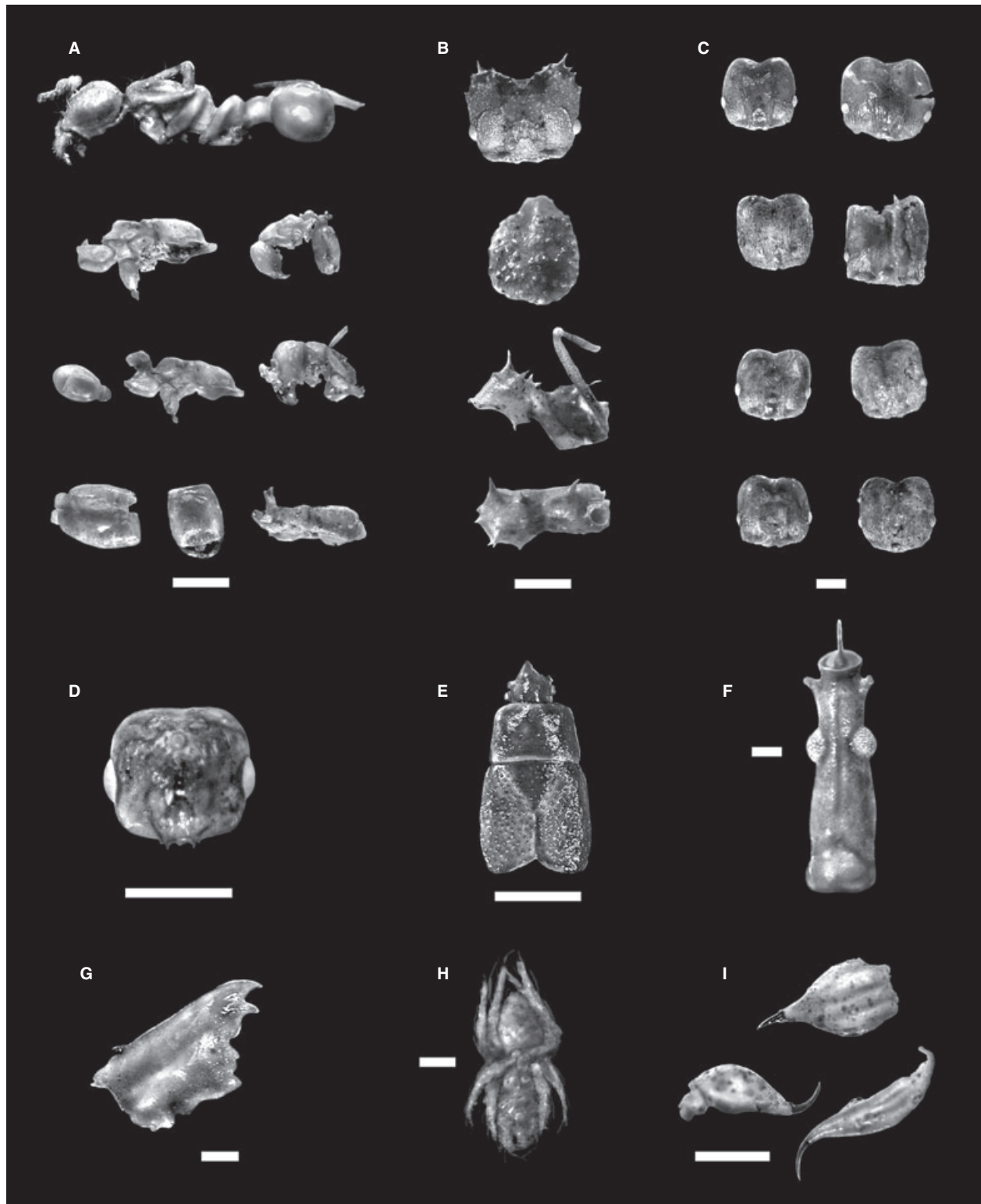


Fig. 5. Arthropod remains from Las Margaritas palaeocave (A) and Alfar palaeocave (A–I). A, an almost complete specimen of *Neivamyrmex* from Las Margaritas palaeocave and body remains from Alfar palaeocave. Scale bar = 1 mm. B, head and body parts of *Acromyrmex*. Scale bar = 1 mm. C, heads of *Pheidole*. Scale bar = 1 mm. D, head of *Solenopsis*. Scale bar = 1 mm. E, an almost complete body of Rhyparochromidae (Heteroptera). Scale bar = 1 mm. F, head of Enicocephalidae (Heteroptera). Scale bar = 0.1 mm. G, mandible of Apicotermittinae (Isoptera). Scale bar = 0.1 mm. H, a complete specimen of a mite. Scale bar = 0.1 mm. I, scorpion stings. Scale bar = 1 mm.

coastal cliffs, the palaeocave described by Quintana (1992) and one of GADA facilities, which is neither identified nor located in the map and commented along the text, are attributed to *Scelidothorium leptcephalum*. Under Type III, the only palaeocave mentioned was that of Barrio Las Margaritas, which was not illustrated with pictures or drawings, although other type III palaeocaves are depicted from the coastal cliffs (Dondas *et al.* 2009; fig. 5) and others are mentioned from the sewage outfall (Isla & Dondas 2001). There were no measures of length (only that they were 1-m wide), and scratch marks were described as produced by three digits, which induced these authors to attribute it to *Pampatherium typum*, a large Dasypodidae.

In summary, there is a consensus among former authors that these palaeocaves were produced by xenarthrans, either ground sloths (Alfar locality) or armadillos (Las Margaritas locality), which is followed herein.

#### *Insect nest producers and ichnotaxonomy*

Distinction between ant and termite fossil nests, within the Krausichnidae, is difficult. This is particularly true for structures composed of diffuse boxworks included in the rock matrix, which do not resemble the most typical nests of ants or termites (Genise 2004; Cosarinsky *et al.* 2005). In addition, identifications are also difficult because invasions, reoccupation and inquilinism of nests are common among ants and termites. The best-preserved Alfar boxwork shows characters that can be attributed to either ants or termite nests. However, the dominance of ant remains inside this structure, mainly army ants (*Neivamyrmex* sp.) and secondarily *Acromyrmex* sp. and *Pheidole* sp., along with other characters of its architecture suggest it is an ant nest, but with a complex history hidden behind it. Army ants (Ecitonini) are typical predators of soil arthropods, particularly social insects, and among them, leaf-cutting ants (Attini; LaPolla *et al.* 2002). During their migratory phase, *Neivamyrmex rugulosus* can establish their bivouacs inside raided nests, which are reached by underground passages. Superficial nests are more intensely preyed upon than deeply located ones, and *Pheidole* nests were also raided (LaPolla *et al.* 2002). Accordingly, the most likely assumption is that Alfar boxworks are army ant nests or other (*Pheidole* sp.?) raided nests, to where other preys of army ants such as *Acromyrmex* sp., winged *Solenopsis* sp., soil bugs, beetles and arachnids were carried.

In any case, it is necessary to analyse the possible age of insects contained in the fillings of these nests. The depth of the Alfar palaeocave and their nests, at

5 m, is a first argument against the nests being extant ones. Most extant ant and termite nests of this area are shallow, with the exception of leaf-cutter ant nests, which in any case reach up to 2 m. The same reasoning is also applicable for insect remains, as it is not expected that insects are found in the soil horizons some 5-m below ground. In addition, insect remains of similar preservation are included within the wall linings, indicating that remains and nests have the same age. The preservation of ant remains, particularly of cuticle, may respond to a combination of conditions produced by the unusual microenvironment of palaeocaves. For instance, high water tables or surface floodings transporting sediments inside the cave, as evidenced in Alfar (Quintana 1992), could result in anoxic conditions inside nests that precluded the presence of predators and scavengers and the decay of ant cuticles. Chitinophagous bacteria that degrade cuticle live almost exclusively in oxygenated environments (Martínez-Delclòs *et al.* 2004). The young age of these remains (500 ky to 2 Ma) may be another factor that aided in their preservation, as cuticle chitin can be still recognized as old as in Oligocene insects (Martínez-Delclòs *et al.* 2004). Also, favouring the preservation and anoxic conditions are the entombment and packing of body remains together with pellets inside filling of nests, the definite burial of the cave and the carbonate rich soil where it occurred.

Beside its general architecture, some characteristics of the boxworks are also compatible with ant nests. The accumulation of waste material and detritus, such as removed soil, ant bodies, provision remains and pellets inside chambers of ant nests is a commonly recorded trait (Bruch 1917; Moser 1962; Zolessi & González 1974; Jonkman 1980; Coutinho 1984; Halfen & Hasiotis 2010), which is present in the Alfar boxworks. The other characteristic is the wall lining present in these boxworks, which is compatible with those found in ant nests of *Forelius chalybaeus* excavated in sandy soils (Bruch 1916; plate VI). Personal observations made by one of us (JFG) on nests of *Solenopsis* sp. excavated in sandy soils of Gran Salitral (La Pampa, Argentina) show that walls are lined with an organic-rich coating, which, judging for the lack of organic-rich horizons in the soil should be of faecal origin (Fig. 4H, I). Such lining is similar to that found in the boxworks associated with palaeocaves.

Although diagnostic characters are more poorly preserved in Las Margaritas nests, and insect remains are very few, they are similar to those of the Alfar nests, suggesting that army ants preying on leaf-cutting ants and/or *Pheidole* sp. were very common behaviours by Pleistocene times for this area.

Ichnotaxonomically, this type of boxworks in palaeosols cannot be placed clearly in any named



ichnogenus (Genise 2004). Fossil social insect nests including boxworks of interconnected chambers are included in *Syntermesichnus* Bown & Laza (1990), having different types of chamber arrangements that are lacking in the Alfar and Las Margaritas boxworks, and *Barberichnus bonaerensis* Laza (2006), which is more similar to these boxworks, but lacks the flat chambers horizontally arranged. Fossil ant and termite nests described from Pliocene and Pleistocene formations at Buenos Aires coastal cliffs by Laza (1995, 1997) and Genise (1999) differ from the material described herein. Nevertheless, the new evidence presented herein suggests that the empty central space of *Tacuruichnus farinai* may be the result either of an attack of a large mammal to a social insect nest, or may be the result of decay of the central hive as postulated originally (Genise 1999). Finally, the boxworks described and documented herein are completely different from *Attaichnus kuenzeli*, composed of spherical large chambers, and described by Laza (1982) from the Miocene Cerro Azul Formation of La Pampa, which was mentioned by Dondas *et al.* (2009) as associated with a palaeocave from Mar del Plata. In addition, the partial exposure of the nests inside the palaeocaves precludes the erection of a new ichnotaxon.

### Palaeocave function

Vizcaíno *et al.* (2001) considered the role of ground sloths as constructors of large palaeocaves postulating that their functions were escape from predation, and/or thermoregulation. However, the extraordinary length of these caves suggests that other function may have been involved. Based on the maximum length measured of a fragment of a palaeocave (70 m), Buchmann *et al.* (2009) suggested that some of these palaeocaves may reach hundred of metres.

Long horizontal tunnels by Marsupialia or Eutheria, usually forming networks, are foraging tunnels related with food location, whereas those composed of more simple shorter tunnels, in many cases with chambers, are used for shelter, involving protection from predators and daily temperature fluctuations, and food storage or breeding (Nevo 1979; Reichman & Smith 1990). Foraging tunnels may involve 80% of the total burrow system and may reach 250 m in length up to 40 cm of depth in the root zone (Nevo 1979). Long foraging tunnels are excavated by herbivorous rodents (Rodentia), insectivorous Australian marsupial moles (Marsupialia, Notoryctemorphia), South African golden moles (Insectivora, Chrysochloridae), true North Hemisphere moles (Insectivora, Talpidae) and Argentinean pigmy armadillos (Cingulata, Dasypodidae). Among the herbivorous rodents, South

American tuco-tucos (Rodentia, Ctenomyidae) excavate long and shallow horizontal tunnels to reach plants for feeding on them on surface (Busch *et al.* 2000; Lacey & Wieczorek 2003). African molerats (Rodentia, Bathyergidae) excavate also long and shallow horizontal foraging tunnels to feed underground, whereas nests, refuges from predators and chambers with thermoregulatory functions are found in deeper locations (Šumbera *et al.* 2008). North American pocket gophers (Rodentia, Geomyidae) can excavate about 1 m of foraging horizontal tunnels per day to reach underground parts of plants (Andersen 1987; Thorne & Andersen 1990). Less-known marsupial and golden moles excavate long tunnels seeking for adult insects, larvae and earthworms, whereas some species of the latter prefer termites and still others excavate tunnels among vegetation clumps where insect larvae concentrate (Holm 1969; Walker 1983; Reichman & Smith 1990). Horizontal tunnels of different species of true moles may reach 185, 550 and 270 m, respectively, (Hickman 1983a,b, 1984). Concerning xenarthrans, Minoprio (1945) confirmed that the pigmy armadillo mostly feed on insect larvae below ground, excavating long horizontal burrows, which in many cases collapse behind it (Rood 1970). In conclusion, why to excavate horizontally within the soil for up to 30 m as for the Alfar palaeocave, or up to 40 and 70 m recorded by Dondas *et al.* (2001) and Buchmann *et al.* (2009), once reached the necessary depth for avoiding predators and daily temperature fluctuations? The length of these palaeocaves as first-hand evidence, then, suggests that foraging may have been involved to some extent in their excavation.

Ichnological evidence of the presence of fossil nests of social insects cross-cut by the palaeocaves also supports the hypothesis that they would have the potential function, although not necessarily exclusive, of reaching social insect nests while digging below ground. The ichnological analysis of cross-cutting demonstrates that if insect nests would have been constructed after the cave, then they would not be opened to the palaeocaves exposing a large area of their boxworks. Furthermore, pits containing some of them are evidence that they might be excavated from the interior of the caves. A former mention of insect nests by Dondas *et al.* (2009) is confusing and unsupported by evidence. For Type II (Alfar) and Type III (Las Margaritas) palaeocaves, Dondas *et al.* (2009) mentioned the presence of 'anthills', a term that is usually applicable to epigeous mounds made by ants, in contrast with the underground condition of the caves. Enigmatically, these authors proposed, without any previous explanation, that *Scelidotherium leptocephalum* (the putative constructor of the Alfar palaeocave) was 'an animal capable of eating insect eggs',

although they disregarded it as a strictly myrmecophagous animal considering its large body size. They claimed that the partially filled cave exhumed during the construction of the sewage outfall of Mar del Plata (not recorded in the contribution or mentioned under type II section), contained structures similar to 'ant mounds' and similar to the 'structures described from the Miocene of La Pampa (Laza 1982)'. Such structures are spherical chambers named as *Attaichnus kuenzeli*, and interpreted as underground fungus gardens of leaf-cutting ants. In addition, Isla & Dondas (2001), and Dondas *et al.* (2001), who had described the palaeocaves exhumed in the sewage excavation, mentioned nothing about ant nests.

Considering the masticatory apparatus of mylodontids and their capabilities for excavation, Bargo & Vizcaino (2006) proposed that *Scelidotherium leptcephalum*, the supposed constructor of the Alfar palaeocave, fed on roots and tubers, which probably constitute a major part of its diet. However, despite this, xenarthrans is a group in which myrmecophagy is greatly extended, from strictly myrmecophagous groups as *Vermilingua* to some *Cingulata*, whose representatives are basically insectivorous, many of them showing a strong preference for ants or termites. Carter (1983) found that 48% of *Priodontes maximus* burrows, the larger extant armadillo, in a Brazilian grassland were associated to termite mounds, whereas in the brushland, this value reached up to 70%. Carter (1983) considered for her study burrows not associated with termite mounds as evidence on predation on other invertebrates, such as ants and worms. Redford (1985) recognized four groups of armadillos based on their food habitats, one of them including species of *Cabassous*, *Tolypeutes* and *Priodontes* that are exclusively ant or termite eaters.

The following observations support the hypothesis that these caves were produced for food location: (1) the common record of long horizontal tunnel systems (in contrast to slanted or vertical ones); (2) in some cases, the presence of social insect nests cross-cut by them; (3) the extended myrmecophagy among the potential producers of these palaeocaves; and (4) some anatomical traits as the tubular skull mentioned by Dondas *et al.* (2009). These also suggest that in this use they may be comparable with foraging burrows of subterranean mammals (Nevo 1979; Reichman & Smith 1990). The acquisition of fossorial habits in different groups of mammals was strongly favoured by the expansion of open habitats during the Cenozoic, a trend that was supposed to be reinforced by the drier climates of the Plio-Pleistocene (Nevo 1979). Accordingly, Zárate & Fasano (1989) proposed semiarid and cooler conditions during Ensenadan time, when steppe or prairie environments dominated, and Zárate

*et al.* (1998) considered that the Alfar palaeocave could have been excavated during the last maximum glacial.

Despite the strong evidence presented here to support the idea that some of these burrows could have had a foraging function, it is necessary to sound a note of caution to establish the limits of the present proposal. As Dondas *et al.* (2009) pointed out, it is impossible to imagine animals of several 100-kg feeding exclusively on ants, and excavating tunnels for this purpose in terms of the energy costs of burrowing, particularly for large mammals (Nevo 1979; Vleck 1979). However, if *Priodontes maximus*, having burrow diameters of up to 48.5 cm, are extended termite eaters (Carter 1983), then it is possible to ask why myrmecophagy should be ruled out as a putative function of the Las Margaritas palaeocave when it is 1 m in diameter (or even 75 cm considering the smaller diameter of the descending tunnel), and also attributed to an armadillo?

Feeding from ant nests below ground, as an alternative strategy, could be triggered and/or favoured by particular behaviours or environmental conditions, such as: (1) extension of tunnels for foraging purposes, favoured by the high density of ant nests, from former ones already excavated with other purposes, such as shelter or breeding; (2) extension of tunnels during harsh climatic conditions, when both mammals and insects avoid surface exposure – incidentally, colonies of ants constructing mounds migrate to the deepest part of nests during winter to avoid freezing (Bruch 1916); (3) completing the diet of ants harvested below ground with other insects or plants on surface as subterranean life favours food generalism due to the low harvestable food (Nevo 1979); (4) caves supported more than one individual, at least a family group, as sociality in subterranean mammals enhance the possibilities of locating food (Jarvis 1978); (5) the possibility of obtaining quick and safe food for juveniles without abandoning the cave, and thus decreasing the risk of predation; and (6) as ant nests are reconstructed if damaged only partly, the possibility of the same ant nest to be used repeatedly to feed juveniles inside caves, resulting in a sort of breeding, feeding and farming burrows.

## Conclusions

- Burrow systems composed of long horizontal tunnels produced by xenarthrans, (either ground sloths or armadillos), during Ensenadan stage-age of Buenos Aires province (Miramar Formation), Argentina, cross-cut boxworks that can be attributed to social insect nests.

- Nests can be attributed to ants based on the presence of abundant ant remains, filling of chambers and organic-rich linings. Insect remains are indicative of a food web composed of army ants (*Neivamyrmex* sp.) preying on leaf-cutting ants (*Acromyrmex* sp.), *Solenopsis* sp., *Pheidole* sp. and other soil invertebrates. The remaining component of this web is represented by the xenarthrans.
- The facultative foraging function of xenarthran palaeocaves is supported by the common record of these extended horizontal tunnel systems similar to other subterranean foraging mammals, the presence of insect nests cross-cut by them and the extended myrmecophagy among xenarthrans.
- Xenarthran foraging burrows, despite their high-energy cost, would have been favoured by abundance of underground ant nests during Quaternary times and harsh climate. This climate would have favoured longest periods of underground activity either by insects and xenarthrans, involving the extension of shelter burrows for adult, and possibly juvenile, feeding by the latter.

*Acknowledgements.* – This contribution was partially supported by grant PICT 2007-1972 from the FONCYT of Argentina to JFG. Authors thank the late José Puerta and Carlos Quintana for their assistance during fieldwork at the Alfar palaeocave and Alejandro Dondas, Jose Luis Carballido and Jimena Candido at Las Margaritas palaeocave. Also, Mirta González for observations on pellet composition, Marcela Cosarinsky for help with ant pellet morphology, Fabiana Cuzzo for ant identification and two anonymous reviewers for improving the original manuscript. Figures were composed by Daniel Speranza.

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