Special Issue: The Apidima Legacy Collections: New Analyses and Interpretations

New Insights Into the Small Mammal Assemblage (Eulipotyphla, Rodentia, Lagomorpha) from the Apidima Cave C Legacy Collection: Taxonomy and Preliminary Paleoenvironmental Interpretations

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ABSTRACT

The Apidima Cave complex (Mani, Peloponnese, Southern Greece) is of exceptional paleoanthropological significance, containing unique fossil human remains and associated fauna. While these hominin discoveries have drawn considerable attention, much of the faunal assemblage, particularly the small mammals, has remained understudied. In this study, we re-examine the small mammal assemblage (Eulipotyphla, Rodentia, and Lagomorpha) from the Apidima Cave C legacy collection, excavated in the 1970s–1980s. We provide a detailed systematic description of the identified taxa and infer the paleoenvironment surrounding the site using Habitat Weighting and Taxonomic Habitat Index, supported by comparison with other Late Pleistocene small mammal assemblages from Greece. The small mammal assemblage is represented by the order Eulipotyphla including, *Erinaceus* sp., *Talpa europaea,* and *Crocidura leucodon.* The rodent assemblage comprises *Chionomys nivalis, Microtus* (two or three species), *Apodemus epimelas, Apodemus sylvaticus/flavicollis,* and *Nothocricetulus migratorius.* Two lagomorph species were recognized, *Lepus timidus* and *Lepus europaeus.* The composition of the small mammal assemblage indicates the existence of diverse biomes, including open areas, rocky environments, and forest patches in the vicinity of the site. The occurrence of *L. timidus* marks the currently southernmost presence of the species in Europe, and along with that of the snow vole (*C. nivalis*), suggests a phase with colder climatic conditions in the Apidima Cave C sequence. Considering the nature of the assemblage, which lacks stratigraphic context for the origin of the specimens, we consider an ecological palimpsest affected by time-averaging as a plausible explanation. Additional material recovered from stratified contexts will provide more reliable information in the future.

INTRODUCTION

The study of fossil small vertebrates assemblages has been widely employed in paleoenvironmental research (e.g., Alvarez-Vena et al. 2021; Andrews 1990; Bañuls-Cardona and López-García 2016; Cuenca-Bescós et al. 2005; Fagoaga et al. 2021; López-García et al. 2017; Marquina-Blasco et al. 2021). Due to their abundance in archaeological and paleontological deposits, combined with their high levels of habitat specialization and restricted home ranges, small mammals serve as effective indicators of local past climates and environments (García-Alix et al. 2008; Minwer-Barakat et al. 2005). Despite the demonstrated value of small mammal assemblages for reconstructing local paleoenvironments (i.e., Cuenca-Bescós et al. 2005; Jovanović et al. 2022; Piñero et al. 2016; Rey-Rodríguez et al. 2022; Suárez-Bilbao et al. 2017), such analyses remain relatively limited for the Pleistocene of Greece (with few exceptions: see Chatzopoulou 2014; Kolendrianou et al. 2020; 2023, among others). A common approach in studies of small mammal faunas from archaeological or paleontological sites is describing the environmental preferences or characteristics of the small mammal fauna as part of the paleoenvironmental discussion (Chatzopoulou 2014; Piskoulis 2021; Vasileiadou et al. 2003). Small mammals, especially voles, can also play an important role in the Early and Middle Pleistocene in biochronological correlation (van der Meulen 1973). This gap is particularly evident in archaeological contexts, where research has traditionally prioritized lithic, macrofaunal, and hominin remains. Consequently, the potential of small mammal studies to address paleoenvironmental aspects and to complement broader faunal and archaeological datasets remains in many cases unexplored. This is also the case in the Apidima Cave complex, even though there are abundant microfaunal remains within the legacy faunal collections from the site.

The studied assemblage comes from Apidima Cave C, which is part of the Apidima Cave complex, located in the Mani Peninsula (Peloponnese, Southern Greece) (Figure 1). Investigations were conducted by the Anthropological Museum (Medical School, National and Kapodistrian University of Athens) under the direction of Prof. Theodoros Pitsios during the 1970s and 1980s. The site comprises five karstic caves, designated A–E, located on a steep coastal escarpment (see Figure 1). The investigations of Pitsios in four (A–D) of these depressions revealed the presence of Quaternary deposits and led to the recovery of significant paleoanthropological remains (Harvati et al. 2019; 2026; Naumann et al. 2026; Pitsios 1995, 1999) as well as lithic assemblages broadly attributed to the Middle and Upper Paleolithic (Darlas 1995; Harvati and Delson 1999; Lombardo et al. 2026a; 2026b; Pitsios 1999; see also Harvati et al. 2026 [this issue]). The larger mammal fauna from the caves has been studied by Lax (1995) and Tsoukala (1999), providing the taxonomic identification and a preliminary taphonomic evaluation, while the taphonomy of Cave A was recently studied in detail by Roditi et al. (2016). However, no detailed study has been conducted on small mammal assemblages yet. Among the four investigated contexts, Apidima Cave C appears to contain the richest small mammal assemblage, providing the opportunity to investigate its taxonomic composition and contribute to the reconstruction of past habitats in the vicinity of the site.

Apidima Cave C, currently situated at 18 meters above sea level, yielded lithic artifacts, faunal remains, and human skeletal elements. Previous work on a limited number of lithic artifacts tentatively attributed the assemblage to the Aurignacian (Darlas 1995). Lombardo et al. (2026a [this issue]) conducted a detailed techno-typological examination of the lithic assemblage and placed it within the Proto-aurignacian variability. Among the most remarkable paleo-

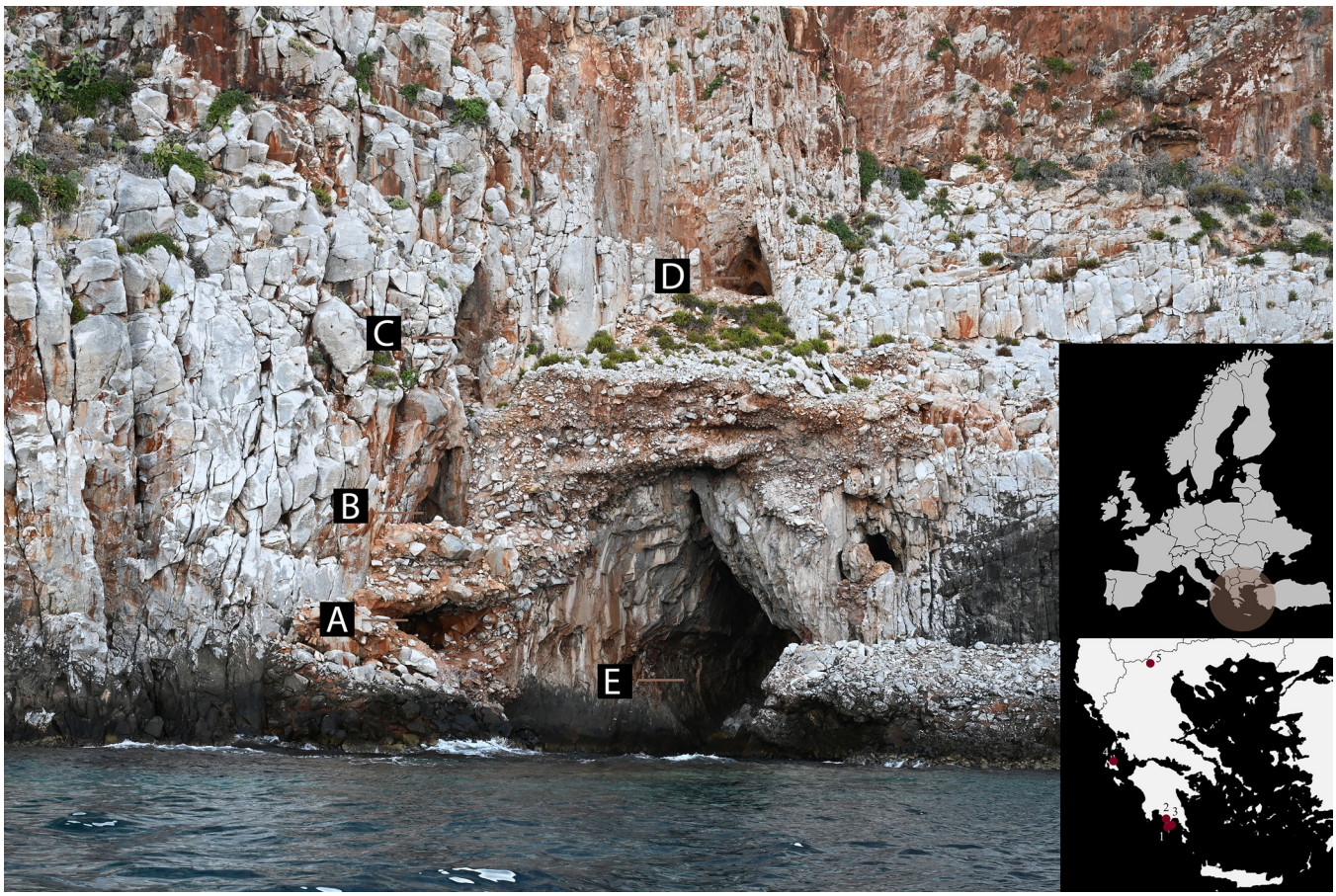

Figure 1. The five karstic complexes of Apidima (A–E) in Mani (Peloponnese, Southern Greece) and the Late Pleistocene sites mentioned in the text: 1) Apidima caves, 2) Kalamakia cave, 3) Melitzia cave, 4) Panthera cave, and 5) Almopia cave.

anthropological discoveries from the site is a partial human skeleton, hypothesized to represent an Upper Paleolithic burial (Karakostis et al. 2026 [this issue]; Mompherratou and Pitsios 1995; Naumann et al. 2026 [this issue]; Pitsios 1985, 1995). Recent direct dating of two human teeth, as well as of two fragmentary postcranial elements associated with the burial, through U-series analysis, indicated a minimum age of 11.7 ka b2k (Harvati et al. 2021), while radiocarbon dating of shells from the legacy collection of Cave C returned ages ranging from 21,120 ka cal BP to 31,940 ka cal BP (Harvati et al. 2026 [this issue]). The large mammal assemblage of Cave C shows the greatest taxonomic diversity among the four caves, including the carnivorans *Panthera pardus* (leopard), *Lynx lynx (*Eurasian lynx), *Felis silvestris* (European wildcat), *Vulpes vulpes (*red fox), *Meles meles* (European badger), and *Martes foina* (beech marten), the ungulates *Capra ibex* (alpine ibex), *Megaloceros* sp. (giant deer), *Dama dama* (fallow deer), and *Cervus elaphus* (red deer), as well as an elephantid (Tsoukala 1999). The small mammals recovered from the sieving of the sediment are the material studied in this research. Archival materials from the Museum of Anthropology and the original excavators report three stratigraphic layers in Apidima Cave C (see also Supplementary Figure 1); However, the small mammal assemblage lacks stratigraphic and spatial information. Hence, the chronological span of the small mammal remains and their association with other finds from the cave are uncertain.

The present work aims to provide a detailed taxonomic analysis of the small-mammal assemblage from the legacy collection of Apidima Cave C (hereafter referred to as API. LC-C) and to help understand the paleoenvironmental context during the site formation. As such, the study aims to add new information to the growing regional small mammals baseline, which is essential for understanding environmental variability and biodiversity in southern Greece during the Pleistocene.

MATERIALS AND METHODS

The studied materials are housed at the Anthropological Museum (Medical School, National and Kapodistrian University of Athens, Greece). Sediments were sieved using 2.5mm and 19.0mm wire mesh screens (Lax 1995; Pitsios 1985). The coarse mesh sizes used for sieving are inadequate for recovering remains of smaller-sized, taxa such as Soricidae, Gliridae, or isolated Murid teeth and have most likely resulted in an underrepresentation of micromammals in the assemblage. It is also unclear to what extent

detailed washing and sorting procedures were employed, as isolated teeth or very small elements are largely absent. The isolated teeth that do exist show evidence of recent breakage, suggesting they once belonged to more complete cranial elements. A total of 994 specimens was recorded. All specimens were examined using a Leica Wild M10 stereomicroscope at 10–40x magnification. Some specimens exhibited a lower degree of mineralization and a lighter color, suggesting they might be more recent and were therefore excluded from the study. Mechanical and ultrasonic attempts to further clean the surface of the specimens from breccia and adhering sediment have been unsuccessful.

Dental nomenclature follows Furió Bruno (2007) for Erinaceidae, Costes et al. (2022) for *Talpa*, Reumer (1984) for Soricidae, Van de Weerd (1976) for Muridae, Hir (1992) for Cricetidae, Nadachowski (1991) and Van der Meulen (1973) for Arvicolinae, and Callou (1997), Palacios and Lopez-Martinez (1980), and Suchentrunk and Davidovic (2004) for Lagomorpha. Chiroptera were not recognized in the old collection, yet they have been identified during our study (Hilson 2005). Cranial and postcranial material has been recorded and analysed for leporids. The study of rodents and insectivores (except for *Talpa*) was limited to cranial and dental remains. Molars are indicated with m, and premolars with p, upper teeth with upper-case letters, and lower teeth with lowercase letters.

The taxonomic identification of the specimens follows biometric and morphological criteria established in the relevant literature. For Erinaceidae, we rely on the diagnostic features recorded in Furió et al. (2015), López Jiménez et al. (2020), Marchetti et al. (2000), Popov (2004), and Rzebik-Kowalska (2006). Identification of *Talpa* specimens is based on Marchetti et al. (2000), Maul (2001), Popov (2004), Reumer (1996), Rzebik-Kowalska (2000, 2006), and van Cleef-Roders and van den Hoek Ostende (2001). Specimens of Soricidae have been identified following Koufos et al. (2001), Reumer (1984, 1986), and Rofes and Cuenca-Bescós, (2010); the classification of Cricetinae relies on Bogićević et al. (2011), Lozano-Fernández et al. (2019), Maul and Parfitt, (2010), Popov (1989, 2000), Pradel (1989), Rey-Rodríguez et al. (2022), Tsoukala and Chatzopoulou (2005), and Van der Meulen (1973). Arvicolinae specimens were classified after the criteria outlined in Bogićević et al. (2012), Chaline et al. (1999), Chatzopoulou (2014), Dimitrijević (1991), Marchetti et al. (2000), Marković (2008), Maul (2001), Maul and Parfitt (2010), Nadachowski (1982), and Popov (1989, 2000). Finally, the identification of Muridae follows Chatzopoulou (2014), Lozano-Fernández et al. (2019), Marchetti et al. (2000), Maul (2001), Maul and Parfitt (2010), Popov (1989, 2000), Siori et al. (2014), Suata-Alpaslan (2011), Van de Weerd (1973), and Van der Meulen (1973), while Leporidae classification is based on Fladerer et al. (2023), Miracle and Brajković (2010), Suchentrunk and Davidovic (2004), and Veitschegger et al. (2015).

Taxonomic abundances are reported using Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI), following Lyman (2008). Articulated specimens were recorded separately. MNI is calculated based on the most common dental element, considering its side.

For the paleoenvironmental analysis, we applied two quantitative approaches—the Taxonomic Habitat Index (THI) (Andrews 2006; Evans et al. 1981) and Habitat Weighting (HW) (Cuenca-Bescós et al. 2009; 2010). For HW, we calculated the MNI for each taxon using dental material. Habitats were classified into six categories following the IUCN Red List (https://www.iucnredlist.org/resources/spatial-data-download) in accordance with Luzi et al. (2022), Rey-Rodríguez et al. (2022), and Rogall et al. (2025). The habitat categories are the following: a) forest, including forested and wooded areas and forest margins, b) shrubland, including shrublands, bushlands and thickets dominated by woody shrubs, c) grassland, with grass-dominated open areas with minimal woody vegetation, d) wetland with environments where water periodically or permanently covers the soil, e) desert characterized by areas of very low precipitation and sparse of absent vegetation, and f) rocky, where the environment includes rocky or stony substrates. Each taxon was assigned a score of 1.00, divided equally among the habitats it occupies today, following the protocol of Rey-Rodríguez et al. (2022). Both THI and HW rely on present-day distributions of the taxa, which is appropriate here since all species in the assemblage also occur today.

The only taxon identified at the genus level and used in both methods is *Erinaceus* sp., as there is no other representative of this genus identified at a species level. Its habitat preferences were based on *E. concolor* and *E. roumanicus,* the species that are currently present in Greece, as well as *E. europaeus,* which appears in the fossil record. Only *E. europaeus* occupies grasslands; the other two taxa are restricted to forest and shrubland (Amori et al. 2021; Gazzard and Rasmussen 2024).

RESULTS

SYSTEMATIC PALEONTOLOGY

Mammalia Linnaeus, 1758
Order Lagomorpha Brandt, 1855
Family Leporidae Gray, 1821
Subfamily Leporinae Trouesart, 1880
Genus *Lepus* Linnaeus, 1758

Species *Lepus timidus* Linnaeus, 1758

Material

Right upper incisor; 3 right p3.

Description

The upper incisor has a quadratic cross-section, and the buccal furrow is filled with cementum (Figure 2a-b). The p3 has a trapezoidal outline, an angular entoconid, and lacks undulations in the distal border of the protoconid. Two of the specimens lack an anteroflexid and have a greater

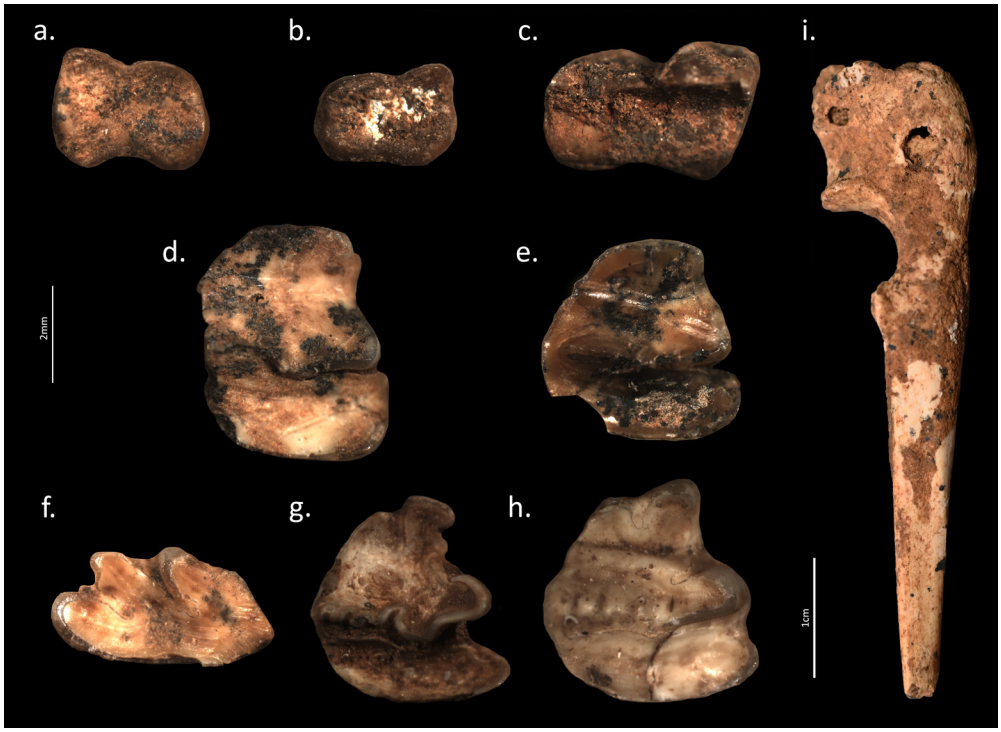

Figure 2. Lepus *remains identifiable to species level from API.LC-C.* Lepus timidus *(a, b, d, e): a) left upper incisor, b) right upper incisor, d-e) left p3;* Lepus europaeus *(c, f, g, h, i): c) right upper incisor, f) left P2, g-h) left p3, i) partially complete ulna (medial view). All dental elements are shown in occlusal view (scale bar 2mm for dental elements, 1cm for ulna).*

mesio-distal development than the third one, which shows a developed anteroflexid and an underdeveloped lingual anteroconid (Figure 2d-e).

Remarks

Species-level identification within *Lepus* is based primarily on dental elements, particularly on the incisors, the P2, and the p3 (Fladerer et al. 2023).

The quadratic cross-section of the upper incisor and the fact that the buccal furrow is filled with crown cementum are features diagnostic for *L. timidus* and distinguish it from *L. europaeus* (Callou 1997; Fladerer et al. 2023; Miracle and Brajković 2010). The dimensions of the upper incisor (Supplementary Table 1) fall within the documented range for *L. timidus* (Fladerer et al. 2023; Miracle and Brajković 2010).

The p3 are compared to Late Pleistocene leporid species, including some endemic species, such as *L. granatensis* (Iberian hare) from Granada. In *L. granatensis*, the occlusal surface typically exhibits a well-developed anteroflexid and a protoconid that lacks crenulations (Palacios and Lopez-Martinez 1980). This differs from most API.LC-C specimens, where the presence of a developed anteroflexid is usually accompanied by distinct enamel undulations. Similarly, *L. castroviejoi*, another Iberian species, shows crenulations on the protoconid, weakly developed anteroflexid and paraflexid, with a broad and open protoflexid (Palacios and Lopez-Martinez 1980). All the above features are not present in the API.LC-C material.

According to Vismara (2012), the convexity of the lingual wall in p3 is not a reliable feature to distinguish *L. corsicanus* from *L. europaeus*, as both exhibit an intermediate degree of convexity. In contrast, *L. timidus* is typically characterized by a flat to slightly convex lingual wall and a generally square occlusal outline, while *L. capensis* displays a highly convex lingual wall.

The dimensions of the p3 do not show any clear biometric distinction between *L. europaeus* and *L. timidus* in the API.LC-C sample. The dimensions of these two species tend to overlap substantially (Miracle and Brajković 2010).

Species *Lepus europaeus* Pallas, 1778

Material

Two left and 5 right upper incisors; 1 left and 1 right P2; 3 lower incisors; 2 left and 4 right p3; two ulnae.

Description

In the upper incisors, the buccal furrow is not filled with crown cement, and the cross-section is consistently rectangular (Figure 2c). The mesial border of the lobes is rounded, with the lingual lobe typically more pronounced. In one specimen, the lingual lobe is notably more developed and has a more pointed outline.

The P2 shows a well-developed lagicone and deep paraflex and hypoflex valleys (Figure 2f). Notably, in one specimen, the paraflex exhibits additional enamel folds at

its base and crenulations are present on the mesial hypercone. The mesoflexus is distinctly V-shaped.

Even though most of the lower incisors from API.LC-C are fragmented, two of them are adequately preserved. They have a trapezoid shape and a wider width than length, not being rectangular.

All the p3 show crenulations at the internal side of the hypoconid. The specimens are wide, although the mesial lobe of the tooth is smaller. The lingual side of the entoconid is rounded, and the hypoflexid is very short. They all have anteroflexid, which is not always that deep (Figure 2g-h).

Most of the studied ulnae do not preserve the olecranon (possibly gnawed). In the two specimens in which the olecranon is preserved, it is high, robust, and strong (Figure 2i).

Remarks

All upper incisors show the characteristic rectangular cross-section, a usually pointy, larger than the other, mesial lobe, a "V"-shaped buccal furrow, and they lack cement within the groove. These features are considered as diagnostic of *L. europaeus* (Miracle and Brajković 2010). The dimensions of the API.LC-C upper incisors (see Supplementary Table 1) fall within the size range reported for *L. europaeus* (Fladerer et al. 2023; Miracle and Brajković 2010). Most specimens are relatively large, while one of them aligns with the smaller-sized *L. europaeus*. All the aforementioned characters are similar to those of *L. europaeus* (Callou 1997; Fladerer et al. 2023; Miracle and Brajković 2010).

Differences between P2 of *L. europaeus* and *L. timidus* have been studied by several researchers (Fladerer et al. 2023; Palacios and Lopez-Martinez 1980; Vismara 2012), who detected differences in the mesoflexus. In *L. timidus* it is generally deeper and more defined compared to the shallower, less distinct mesoflexus in *L. europaeus*; the distal-buccal angle of the tooth is slightly pronounced in *L timidus*, and significantly pronounced in *L. europaeus*; the lingual protrusion of the centrocone is more extensive in *L. timidus* than in *L. europaeus*, where it appears slightly lingually protruding; the distal wall is convex in *L. europaeus* but concave in *L. timidus* (Vismara 2012). A deep, "V"-shaped mesoflexus, along with a developed lagicone and well-defined valleys, a convex distal wall, as seen in API.LC-C material, is more commonly associated with *L. europaeus* (Fladerer et al. 2023; Palacios and Lopez-Martinez 1980).

The trapezoidal shape of the lower incisors and the wider, rather than rectangular, length-width ratio are described as characteristics of *L. europaeus* (Fladerer et al. 2023). A possibly juvenile specimen is also assigned to *L. europaeus* based on its dimensions. Similar to the upper incisors, the difference between *L. europaeus* and *L. timidus* in the lower incisors concerns the Length/Breadth ratio, with *L. timidus* being smaller and more quadratic (Miracle and Brajković 2010).

The internal crenulations of the hypoconid, the rounded lingual side of the entoconid and the short hypoflexid of the p3 are characters attributed to *L. europaeus* (Palacios and Lopez-Martinez 1980).

Studies distinguishing *L. europaeus* and *L. timidus* based on the postcranial skeleton are very limited. Nevertheless, Veitschegger et al. (2015) pointed out differences in the olecranon of the ulna, which is larger and more robust in *L. europaeus*, contrary to the small and slender morphology of *L. timidus*. The specimens from the API.LC-C assemblage resemble those of *L. europaeus* (e.g., Figure 2i).

Lepus sp.

Material

Ten lower incisors; 3 fragments of hemimandibles with the incisor; 1 left and 8 right p3; 2 left, 1 right, and 4 unknown orientations of upper incisors; 2 left and 10 right P2; 2 palatal ridges; and the remaining postcranials including the rest of the ulnae.

Description

The upper incisors are either too damaged or covered with breccia. Most of the specimens assigned to *Lepus* sp. either lack distinctive characters (e.g., the molars and premolars except for P2 and p3) or are not adequately preserved (fragmented or covered with breccia). A few exceptions are described here, such as the p3 specimen, which shows a trapezoidal outline and an angular entoconid, and lacks undulations.

One P2 is buccal-lingually compressed, exhibits an underdeveloped lagocine and a well-developed hypercone. Most valleys are deep, with the paraflexus and the mesoflexus appearing as broad, shallow grooves.

Remarks

The preservation of the incisors does not allow any assignment at species level. The p3 shares several diagnostic traits with *L. timidus*, including a trapezoidal outline, angular entoconid, and absence of undulations. However, a paraflexid, typically rare in *L. timidus* may be present, though the occlusal surface is partially obscured by breccia.

The P2 preserves morphological features commonly observed in *L. timidus*, such as a broad mesoflexus and paraflex, an underdeveloped lagicone, and a well-developed mesial hypercone (Fladerer et al. 2023). However, the mesial-distal compression contrasts with Koby's (1959) observation that *L. timidus* preserves a greater mesial-distal length. Given that only a single specimen is available, we assign this specimen to *Lepus* sp.

Comparative studies of postcranial elements from Middle Pleistocene localities (Fostowicz-Frelik and Gasparik 2008), along with the criteria suggested by Callou (1997), were used to exclude the presence of *Oryctolagus* (rabbits) in the API.LC-C assemblage. Due to the lack of comparative material to distinguish the *Lepus* species (except for ulnae as suggested by Veitschegger et al. 2015), the postcranial lagomorph material is attributed to *Lepus* sp.

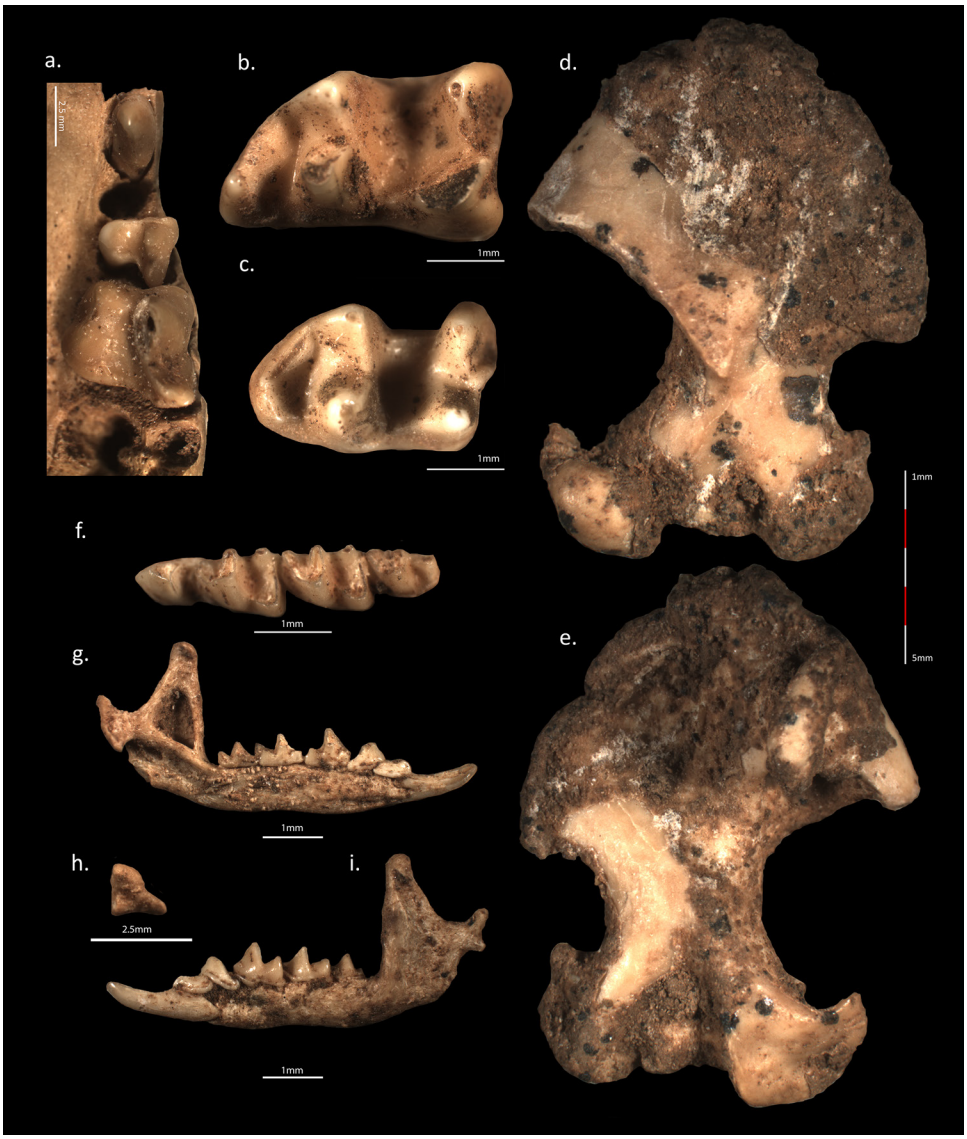

Figure 3. Eulipotyphla remains from API.LC-C. Erinaceus *sp. (a-c): a) fragment of maxilla with left C, P2, and P3, b) right m1, c) right m2 in occlusal view;* Talpa europaea *(d-e): left humerus in anterior (d) and posterior (e) views;* Crocidura leucodon *(f-i): left hemimandible in occlusal (f), lingual (g), and buccal (i) views; posterior view of the condylum (h) (scale bar as reported on each case).*

Order Eulipotyphla Waddell, 1999
Family Erinaceidae Fisher von Waldheim, 1817
Subfamily Erinaceinae Fisher von Waldheim, 1817
Genus *Erinaceus* Linnaeus, 1758

Erinaceus sp.

Material

Maxilla fragment with C, P2, and P3; right P2; right p2; right m1; left m1; left m2.

Description

The studied teeth are well preserved, slightly worn, with only the P3 of the maxilla being moderately broken. In occlusal view, the P2 shows a sub-triangular outline with a concave distal border (Figure 3a). It exhibits a well-developed paracone and a less prominent metacone. The protocone is rounded, and there is no evidence of a hypocone.

The occlusal surface of the P3 is sub-rectangular with a distinct extension in the disto-buccal side (see Figure 3a). The premolar is largely unworn, with minor breakage of the paracone. The paracone and metacone are the highest cusps, whereas the lingual cusps are shorter and more rounded.

The p2 is attached to a hemimandible fragment and is supported by two robust roots. The entoconid and the hypoconid are underdeveloped. The protoconid is robust and is the highest cuspid, connected to the paraconid through a pronounced crest that originates relatively high above the lingual base of the tooth. The metaconid is also connected to the protoconid by a transverse ridge, forming the basin between the paraconid and the joined meta- and protoco-

nid. There is a prominent inclining cingulum on the distal side, which almost reaches the hypolophid. No mesial or lingual cingula are present. On the labial side, a faint cingulum extends distally toward the protoconid. In a lingual view, the mesial valley is positioned significantly higher than the distal one.

The m1 is broad and has a distinct paraconid, entoconid, and hypoconid, all of which are more robust than the metaconid and the protoconid (Figure 3b). The valley between the entoconid, hypoconid, and paraconid is notably wide and deep in contrast to the shallow valley situated between the metaconid and protoconid and the paraconid. The lingual valleys close near the base of the crown, whereas the buccal valleys are closed at a higher level. There is no valley separating the protoconid and paraconid; instead, they are connected by a ridge situated above the level of the distal valley. A straight buccal cingulum is present. An inclined mesial cingulum is visible in the anterior view, originating from the entoconid. In the distal view, the cingulum continues straight until it reaches the base of the paraconid, where it terminates. No lingual cingulum is present.

The m2 resembles the m1 in the overall morphology (Figure 3c). It lacks a lingual cingulum, while a continuous and straight cingulum is present on the buccal side. Like in the m1, the crown preserves the general structural pattern; however, the paraconid is extremely reduced or entirely absent.

Remarks

The API.LC-C molars resemble the morphology of *Erinaceus*, as described in Hilson (2005) dilambdodont with low and broad cusps and a multicusped upper fourth premolar. The material is limited, making species-level identification nearly impossible. *Erinaceus* is the only hedgehog genus present in Greece (Gazzard et al. 2025). Within the genus, there are larger species such as the extinct *E. praeglacialis*, and the extant *E. europaeus* and *E. concolor*, as well as the smaller extinct taxon *E. samsonowici* (Vasileiadou and Doukas 2021). The size of the preserved molars is rather large, comparable to that of the larger-sized hedgehogs from the Late Pleistocene of Europe, such as *E. praeglacialis*, *E. europaeus*, and *E. concolor* (Berto et al. 2024; Furió et al. 2015; López Jiménez et al. 2020). The distinction among these species is based on the morphology of the upper first molar (Furió et al. 2015; Rzebik-Kowalska 2000), which are not present in API.LC-C. A revision of the taxonomy in fossil *Erinaceus* has already been proposed (Furió et al. 2015), as there are no unified criteria to differentiate Plio-Pleistocene *Erinaceus*. Additionally, species that are sympatric today, such as *E. europaeus* and *E. concolor*, can be distinguished only by karyotype (Rzebik-Kowalska 1994). There is only one alveolus in P2, a characteristic trait of the genus *Erinaceus* (Furió et al. 2015), which excludes the possibility of the African genus *Atelerix*, which is also absent from Greece. The only extant hedgehog species in Greece are *E. roumanicus* and *E. concolor*, whose territory is limited to some islands (Gazzard et al. 2025). In the fossil record, *E. samsonowici*, *E. praeglacialis*, and *E. europaeus* have been recorded (Vasileiadou and Doukas 2021). Pending additional diagnostic material, we assign the API.LC-C material to *Erinaceus* sp. for the moment.

Talpidae Gray, 1825
Talpinae Murray, 1866
Talpa Linnaeus, 1758

Species *Talpa europaea* Linnaeus, 1758

Material

Left humerus; fragment of right humerus.

Description

The two humeri from API.LC-C exhibit typical *Talpa* morphology, including a stocky shape and a prominent deltoid process (Figure 3d-e; Costes et al. 2022). One is complete and in good condition, while the other has a broken distal epiphysis.

Remarks

Identification of fossil *Talpa* species is typically based on humeral size. The dimensions of the complete humerus (Width of the distal epiphysis (DE)=8.46mm, Width of the diaphysis D=4.45mm) fall within the documented range for *Talpa europaea* (Chatzopoulou 2014; Maul and Parfitt 2010; Rzebik-Kowalska 2006), belonging to the larger individuals of the species similar to that of Untermassfeld (Figure 4; Maul 2001). Interspecific differences in the humerus have been reported between *Talpa occidentalis* (Spanish mole), *Talpa aquitania* (Aquitannian mole), and *T. europaea* (Costes et al. 2022). Most identifications, however, rely primarily on size. The dimensions of the specimen from API.LC-C fall clearly within the range of *T. europaea* (European mole), and they are close to that of *T. stankovici* (Balkan mole).

Family Soricidae Fischer 1814
Genus *Crocidura* Wagler 1832

Species *Crocidura leucodon* Hermann, 1780

Material

Two left hemimandibles with incisor–m3; left hemimandible with m1; right hemimandible with p4–m1; right hemimandible with m2–m3.

Description

There is one very well-preserved hemimandible with dentition that shows moderate tooth-wear. The remaining hemimandibles either lack teeth or have fully developed but broken dentition. Only the lower teeth are preserved in the hemimandibles, and one of them bears all the cheek teeth (Figure 3f-i). The teeth lack pigmentation, and when observable, the mental foramen is positioned slightly anterior to the m1. The *processus angularis* has a triangular outline. The lower incisor is monocuspid.

The a1 (first antemolar) is slightly elongated, having a triangular outline with a short mesial cuspid and a distinct

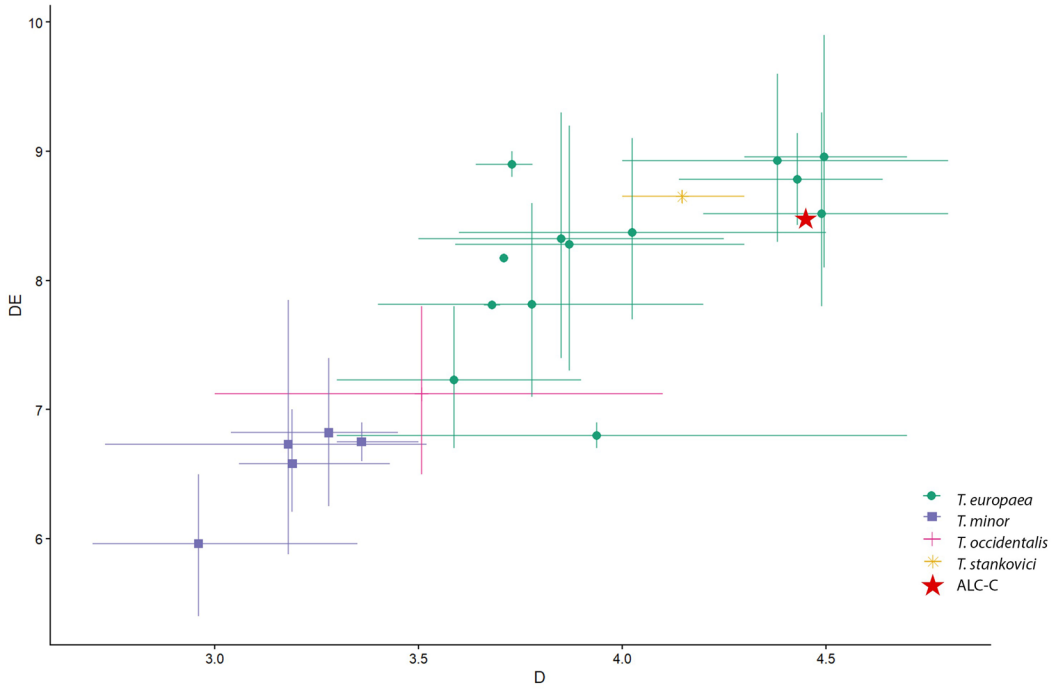

Figure 4. Metrical comparison of Talpa *humerus (D and DE) average values from API.LC-C with T*alpa europaea *and* Talpa minor. *Data from Cleef-Roders and Hoek Ostende (2001), Maul (2001), and Maul and Parfitt (2010 and references therein); see Supplementary Table 2. The lines indicate the min-max range taken from the literature.*

cingulum encircling the crown (see Figure 3f-i). The p4 has a subrectangular occlusal outline and bears a well-defined peripheral cingulum. The m1 and m2 have rather similar morphology, with the protoconid being the highest cuspid, and the lingual cuspids being shorter. The entoconid crest is low, the lingual cingulum is weak but present on the m1 and faint on the m2. In the m1, the buccal cingulum is robust and wavy in shape in the buccal re-entrant valley, whereas in the m2, it is also strong but straight. The m3 bears a single cuspid on the talonid, the hypoconid. Its buccal cingulum is straight and strong, whereas the lingual one is faint and nearly absent.

Remarks

The lack of pigmentation on the tooth enamel, the underdeveloped talonid of m3 and the monocupsulate incisor are diagnostic characters of the subfamily Crocidurinae (Repenning 1967). The intermediate size, the lack of cuspids in the incisor, the tall cuspid in the p4, the sub-square p4 outline, and the strong, wavy buccal cingulum on the m1 are characteristic features of the genus *Crocidura* (Reumer 1984). The relatively large size of the API.LC-C specimen (Figure 5) and the buccal straight cingulum in the m2 beneath the buccal re-entrant valley, distinguish it from *C. suaveolens*, in which the cingulum forms a curve beneath the re-entrant, valley (Reumer 1996). The morphology of the API.LC-C *Crocidura* remains is consistent with that of *C. leucodon* described by Reumer (1996).

Family Cricetidae Fisher, 1817
Subfamily Cricetinae, Fisher, 1817
Tribe Cricetini Fisher, 1817
Subtribe Cricetina Fisher, 1817
Genus *Nothocricetulus* Lebedev et al., 2018

Species *Nothocricetulus migratorius* Pallas, 1973

Material

Right maxilla fragment with M1–M3; right maxilla fragment with M1; 9 left and 2 right hemimandibles with m1–m3; left hemimandible with m1–m2; right and left hemimandibles with m1; right hemimandible with m3; isolated m2.

Description

Some specimens are covered with breccia with limited features recognizable, such as the arrangement of the cuspids into parallel rows in the lower molars and ridges connecting the cuspids. Most of the specimens have breccia in a few spots. The stage of wear is mostly moderate; a few exceptions are very worn, and one is quite unworn.

The M1 is rectangular with the cusps arranged in two parallel rows. A mesial valley divides the anteroloph into two distinct lophs, although the breccia obscures much of the surface. The M2 has a sub-square shape, with a slightly developed posteroloph. The M3 has a more oval shape,

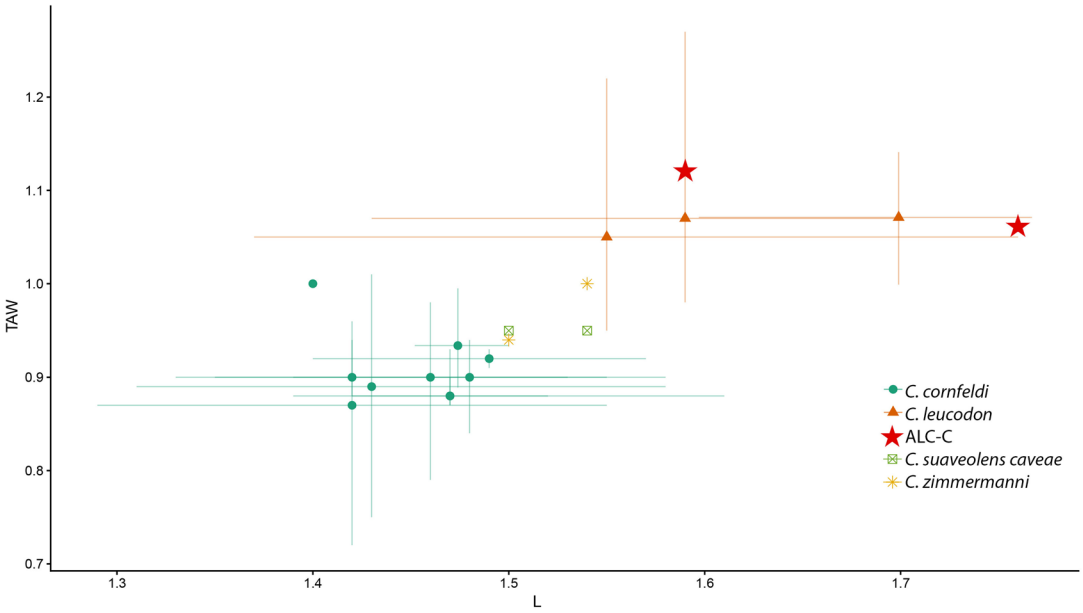

Figure 5. Metrical comparison of Crocidura *m2 width of the talonid (TAW) with the length (L) of the tooth of specimens from API. LC-C and* C. kornfeldi, C. leucodon, C. suaveolens caneae, *and* C. zimmermanni. *Data from Berto et al. (2024), Chatzopoulou (2014), Fanfani (1999), Koufos et al. (2001), Reumer (1984, 1986), Rofes and Cuenca-Bescós (2010), and Rzebik-Kowalska (2007); see Supplementary Table 3. The lines indicate the min-max range taken from the literature.*

with mesial lophs that are larger than the distal ones (Figure 6a).

The m1 is elongated, brachydont, and cuspidate, and shows a bisected anteroconid, forming two similarly sized cuspids separated by a shallow basin. The posterolophid is distinct but low. The m2 has a sub-orthogonal outline, lacks a mesolophid, and an ectolophid connects the protoconid with the hypoconid and entoconid. The m3 exhibits a rounded outline and has a weak mesiolingual cingulum (Figure 6b-c).

Remarks

The taxonomy of the genus *Cricetulus* was revised after the more recent molecular analyses that confirmed *Cricetulus migratorius* is genetically closer to *Cricetus* and the extinct *Allocricetus* than to other *Cricetulus* species. Based on these findings, a new genus, *Nothocricetulus,* was proposed to include *C. migratorius* (Lebedev et al. 2018). Horáček and Lebedová (2022) showed that morphological criteria, especially size, were insufficient for taxonomic assignment, providing the basis for subsequent molecular studies for identifying Late Pleistocene European hamsters. This need for molecular studies led Bujalksa et al. (2026) to study hamsters from central and eastern Europe. Their research shows that the Pleistocene fossil record of small-size hamsters of Europe includes the genus *Cricetiscus,* located mainly in central Europe, and *Nothocricetulus,* located further east, including eastern Europe and the Balkans (Bujalksa et al. 2026)

The size of the API.LC-C specimens indicates that they are too small to belong to *Cricetus* (Bogićević et al. 2011; Maul and Parfitt 2010; Popov 2000; Pradel 1989). Their dimensions fall within the range of *Nothocricetulus* and *Allocricetus,* although some approach the lower limits reported for *Mesocricetus* (Figure 7). However, the latter can be excluded based on dental morphological features; in *Mesocricetus,* the lower molars possess a mesolophid between the metaconid and entoconid, the mesolophid is weak on the m1, though more pronounced on the m2 and m3 (Bogićević et al. 2011). This feature is absent in all API.LC-C specimens. Additionally, *Mesocricetus* m2 has an oval outline, whereas *Nothocricetulus*, like the API.LC-C specimens, displays a more angular, sub-orthogonal shape (Kryštufek et al. 2009).

The genera *Allocricetus* and *Nothoricetulus* are similar in size; however, Hir (1993) noted that individuals of the extinct *Allocricetus bursae* possess an additional pre-anteroconid anterior to the anteroconid of m1, a feature that is absent in all API.LC-C specimens. Other extinct species of *Allocricetus* (e.g., *A. ehiki, A. eversmanni*, and *A. croaticus*) are distinguished by their larger size relative to API.LC-C specimens (Chatzopoulou 2014 and references therein).

In the scatterplot that compares the dimensions of the m1 from API.LC-C with specimens from other Upper Pleistocene localities in Greece and the Balkans, the API.LC-C specimens are closer to the larger-sized *Mesocricetus* (see Figure 7), even though they are morphologically similar to *Nothocricetulus migratorius.*

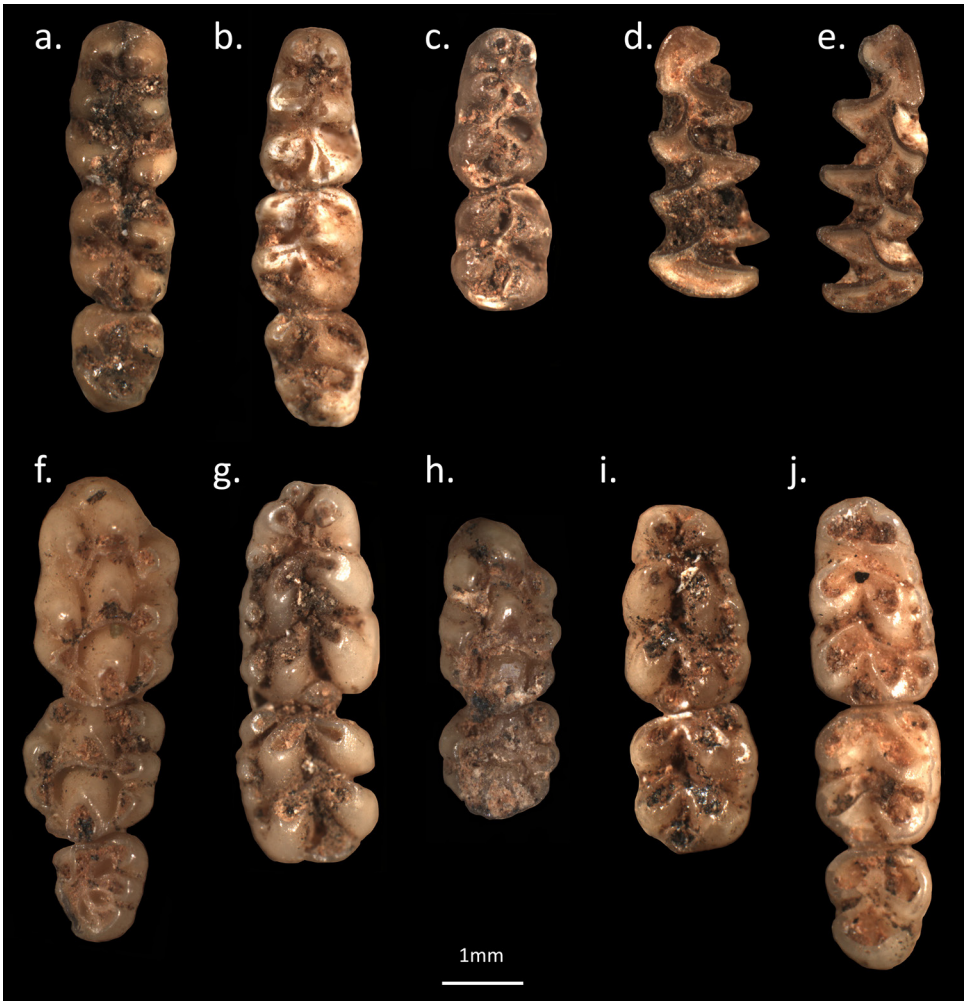

Figure 6. Rodent remains from API.LC-C in occlusal view. Nothocricetulus migratorius *(a-c): a) right M1-M3, b) left m1-m3, c) left m1-m2;* Chionomys nivalis *(d-e): d) left m1, e) right m1;* Apodemus epimelas *(f-g): f) right M1-M3, g) left m1-m2.* Apodemus sylvaticus/flavicollis *(h-j): h) right M1-M2, i) right m1-m2, j) right m1-m3 (scale bar 1mm).*

Subfamily Arvicolinae Gray 1821
Genus *Chionomys* Miller 1908
Subgenus *Chionomys* Miller 1908

Species *Chionomys nivalis* Martins, 1842

Material

Left and right hemimandibles with m1–m2; 2 left and 2 right hemimandibles with m1; 9 left and 8 right m1.

Description

The m1 from API.LC-C preserves four closed triangles, crown cementum in the re-entrant angles, lacks roots, and the enamel is thicker in the mesial than in the distal edges of the dental prisms (Figure 6d-e). T4 and T5 are separated, and most of the time T5 well separated from the AC. T6 and T7 are developed in most specimens but sometimes incipient. BRA4 and LRA5 are incipient or absent, and the anterior cap is short, either rounded or triangular pointed. The m2 consists of the posterior loop, and four alternating closed triangles.

Remarks

The separated T5 and T6, the development of T6 and T7 are traits of the morphotypes '*aquitanicus*' and '*nivalis,*' in which the difference is in the absence ('*aquitanicus*') or incipient development ('*nivalis*') of BRA4 and LRA5 (Alfaro-Ibanez 2025; Nadachowski 1991). The API.LC-C molars preserve these traits, and the BRA4 and LRA4 are sometimes absent and others incipient.

They are also very similar to the specimens from the Upper Pleistocene locality of Loutra Almopia Cave (LAC) in northern Greece (Chatzopoulou 2014). Compared with other Mediterranean or Balkan *Chionomys* species, the API.LC-C specimens differ from *Chionomys gud,* in which the T5, T6, and T7 are always confluent, and BRA4 is better developed than LRA5 (Nadachowski 1991). The dimensions of API.LC-C specimens are larger than Late Pleistocene and recent *C. nivalis* from the Balkans, including Greece (Bogićević et al 2012; Marković 2008; Popov 1989, 2000).

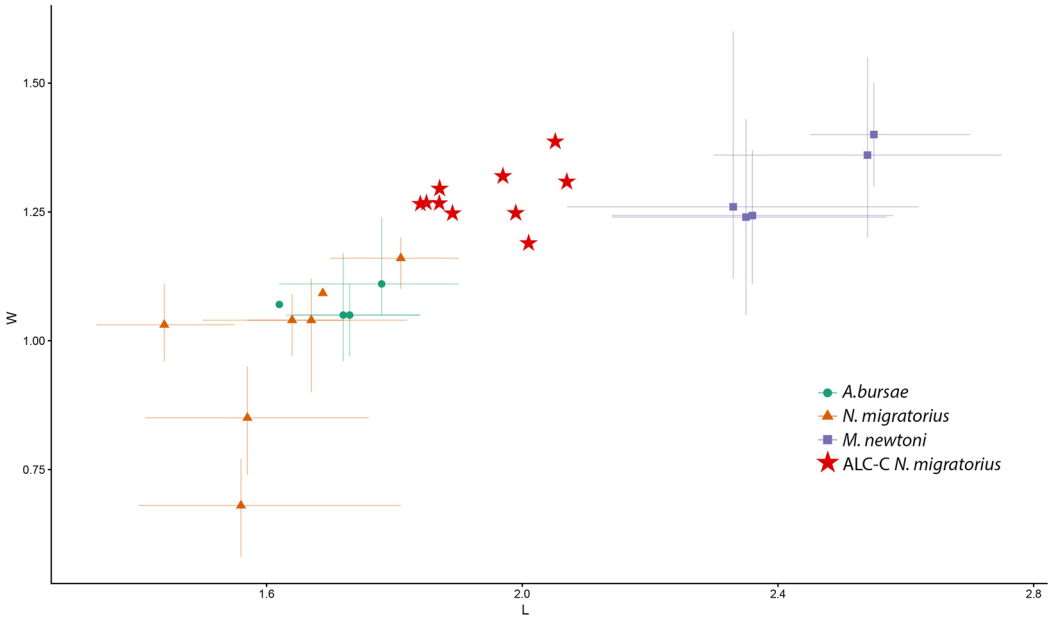

Figure 7. Metrical comparison of Cricetidae m1 from API.LC-C with Allocricetus bursae, Mesocricetus newtoni, *and* Nothocricetulus migratorius. *Data from Bogićević et al. (2011), Lozano-Fernández et al. (2019), Popov (1989, 2000), Pradel (1989), Rey-Rodríguez et al. (2022), Tsoukala and Chatzopoulou (2005), and van de Weerd (1973); see Supplementary Table 4. The lines indicate the min-max range taken by the literature.*

Genus *Microtus* Schrank, 1798

Microtus (Terricola)

Five extant species of the genus *Microtus*, living in Greece, have been reported by Thanou et al. (2012)—*M. levis*, *M. (T.) subterraneus*, *M. (T.) thomasi*, *M. guentheri*, and *M. (T.) felteni*. Kryštufek and Shenbrot (2022) report, in addition, *M. rossiaemeridionalis* and *M. hartingi*. During the Late Pleistocene, representatives of the *Microtus* (*Microtus*) *arvalis/agrestis* group were also present (Vasileiadou and Sylvestrou 2022). The study of Late Pleistocene voles from Greece is still ongoing and our current knowledge is limited. For example, *M. thomasi*, a species endemic to the Balkans, is rarely mentioned in the fossil record and its distinction from other *Terricola* species is currently based only on Geometric Morphometrics (Kolendrianou et al. 2023; Rey-Rodríguez et al. 2024).

The API.LC-C assemblage includes 131 *Microtus* m1, 38 of which are complete enough to take measurements and to observe the relevant morphological features, while the remaining are either broken or covered with breccia. The molars exhibit variation in size and morphology suggesting the presence of at least two different-sized *Microtus (Terricola)* species and a *Microtus* sp. (Figure 8).

Microtus (Terricola) Morphotype 1

Material

Left hemimandible with m1–m3; 3 left and right hemimandibles with m1–m2; 2 left and 1 right hemimandibles with m1; 4 left and 5 right m1.

Description

Characteristic features are: 1) T4 and T5 are confluent, and 2) the ACC (anteroconid complex) is symmetrical with BRA4 and LRA5 developed (Figure 9a-d).

Microtus (Terricola) Morphotype 2

Material

Two left and 1 right hemimandibles with m1–m2; left hemimandible with m1; 4 left and 5 right m1.

Description

Characteristic features are: 1) T4 and T5 are confluent, and 2) the ACC is asymmetrical with a weakly developed LRA5 and a better developed BRA4 (Figure 9e-h).The molars that are assigned to morphotype 2 tend to be larger in size than those of morphotype 1, and dimensionally similar to those of morphotype 3 (similar to *Microtus* sp.) (see below and Figure 8).

The m1 assigned to morphotypes 1 and 2 have a confluent T4 and T5 in common. However, they show variation in the (a)symmetry of the ACC and in dimensions. The number of specimens, however, is too limited to be sure that we are dealing with different species. The confluent T4 and T5 ('pitymyan rhombus') (Nadachowski 1982), present in the *Microtus* morphotypes 1 and 2, characterizes the subgenus *Terricola* (Brunet-Lecomte et al. 1992; 2001). This sub-genus includes the species *M. thomasi*, *M. felteni*, *M. liechtensteini*, and *M. subterraneus* (Brunet-Lecomte et al. 2001). The morphological similarities of the lower m1 and the lack of reference collection hamper species identification of the API.

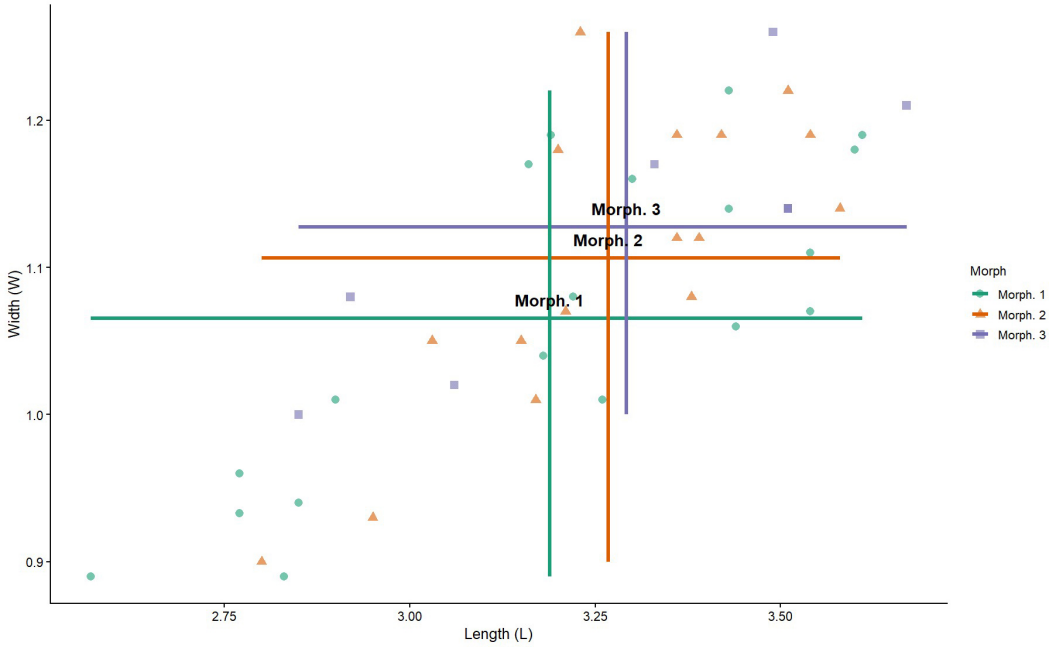

Figure 8. Scatter plot of Length (L) and Width (W) of the different morphotypes of Microtus *specimens of API.LC-C in mm. The lines indicate the min-max range.*

LC-C specimens listed under *Microtus* (*Terricola*) morphotype 1 and 2. Morphometric data have been previously employed to distinguish between species (e.g., Kolendrianou et al. 2023; Rey-Rodríguez et al. 2024), however, due to the limited sample size and the lack of published comparative values/raw comparative dataset, we did not conduct such an analysis. Future analysis using the tools of Geometric Morphometrics, might help identify them in species level (Rey-Rodríguez et al. 2024).

Microtus sp.

Material
Right hemimandible with m1–m2; 2 left and 4 right m1.

Description
Characteristic features are: 1) T4 and T5 are isolated, and 2) the ACC is about symmetrical with well-developed BRA4 and LRA5 (Figure 9i-l). The separated T4 and T5 and the overall symmetrical morphology of the lower m1s resemble the m1 of *Microtus* species such as *M. arvalis* and *M. rossiaemeridionalis*, species that are morphologically extremely similar (Markova et al. 2010). It is, therefore, not possible to assign the specimens to a specific *Microtus* species.

Family Muridae Gray, 1821
Genus *Apodemus* Kaup, 1829

Species *Apodemus epimelas* Nehring, 1902

Material
Three left and 1 right maxillae with M1–M3; 6 left and 5 right maxilla with M1–M2; 2 left and 2 right maxillae with M1; 1 M1 right; 5 left and 3 right hemimandibles with m1–m3; 14 left and 15 right hemimandibles with m1–m2; 8 left and 6 right hemimandibles with m1; 2 right hemimandibles with m1 and m3; right m1.

Description
Specimens exhibit variable states of preservation; some are partially (more or less) covered with breccia; and some have some reddish or brownish sediment adhered to them. Most of them have low to moderate tooth wear, with a few (n=4) exceptions: heavily worn molars of older individuals.

One hundred forty-one specimens are ascribed to *A. epimelas*. The M1 are robust and relatively large. Cusps t1 and t3 are symmetrical and aligned anteroposteriorly. The cusp t8 is connected to t12 and with t9, whereas t9 is not connected to t12. Cusp t4 is not connected to t7. In the M2, t1 is the same size as or larger than the t3, separated from t5. Cusp t9 is connected with t6 with a crest, and t12 is absent or very underdeveloped. In the M3, t1 is large, and t3 is very small. t4, t5 and t6 are united with t6 connected also to t8-t9 complex while t4 is not (see Figure 6f).

The m1 possesses a pronounced anterocentral cusp with numerous accessory cuspids. In the m2, the antero-labial cuspid is pronounced, with small accessory cusps in the labial cingulum and a reduced posterior heel. In the m3, the metaconid and protoconid are connected, without any c1 (posterior accessory cusp) present (Figure 6g).

Remarks
Apodemus mystacinus was historically divided into two subspecies, which were later elevated to distinct species based

Figure 9. The Microtus *remains (occlusal view) from API.LC-C, categorized in the three morphotypes.* Microtus (Terricola) *Morphotype 1, right (a, b) and left m1 (c, d);* Microtus (Terricola) *Morphotype 2, left m1-m2 (e-g) and left m1 (h);* Microtus *sp., left (i, l) and right m1 (j, k) (scale bar 1mm). The white lines highlight the differences between the morphotypes mentioned in the text.*

on molecular evidence—*A. epimelas*, distributed throughout the Balkan Peninsula, and *A. mystacinus*, occurring in Asia Minor and the Middle East (Filippucci et al. 2002; Michaux et al. 2005).

The distribution of the cusps in the M1 (symmetrical t1 and t3, the connection of t8 to t12 and t9, but not between t9 and t12) is a morphological trait that corresponds closely to *A. epimelas* as described by Storch (2004). Morphological distinction between *A. epimelas* and *A. mystacinus* is primarily evident in the M1, while comparative data on the other molars remain scarce in the literature. In the m1, the pronounced anterocentral cuspid and numerous accessory cuspids are characteristic of *A. mystacinus* (Storch 2004) but are also observed in *A. epimelas* (as *A. epimelas* was then considered a subspecies of *A. mystacinus*).

Species *Apodemus sylvaticus/flavicolis*

Material

One left and 2 right maxillae with M1–M3; 1 left and 5 right maxillae with M1–M2; 2 left and 1 right maxillae with M1; 1 left and 2 right hemimandibles with m1–m3; 10 left and 6 right hemimandibles with m1–m2; 4 left and 3 right hemimandibles with m1.

Description

Compared to the *A. epimelas* assemblage, the *A. sylvaticus/flavicollis* sample includes a larger number of molars with a higher degree of wear. Sixty-nine molars are assigned to *A. sylvaticus/flavicolis.* The molars, in general, display a simple overall morphology. The M1 are smaller and more oval in outline, with weak yet distinct accessory cusps, a well-developed t12, and symmetrical t1 and t3. In the M2, t1 is more developed than t3, with a more forward position with respect to t3; t9 is reduced, and t12 is absent. In the M3, the t1 is connected with the reduced t3. t4, t5 and t6 are also connected, forming a unified cusp, with t6 being in contact with anteriorly with the t3 and posteriorly with the united t8-t9 (Figure 6h).

The m1 also bears small but discernible accessory cuspids. Sometimes the anterocentral cuspid is more developed than the others. In the m2, the anterolabial cusp is present, the terminal heel is reduced, and the accessory cuspids are very underdeveloped in the labial cingulum or absent (Figure 6i-j).

Remarks

The molar morphology in *A. sylvaticus* and *A. flavicolis* is very similar, and they only have some metrical differences (Filippucci et al. 1996); therefore, we prefer to refrain from a specific attribution. The specimens show a combination of traits of *A. sylvaticus,* such as in M1 a symmetric location of t1 and t3 relative to t4-t6, the presence of t12, the developed anteroventral cuspid in the m1, but also characteristics of *A. flavicollis,* such as the well-developed t12 in M1, the absent or underdeveloped t9 in M2, the reduced anterocentral cuspid in m1, and the reduced labial cingulum in the m2 (Filippucci et al. 1996).

Apodemus sp.

Material

Two fragmented crania with all molars; 6 left and 4 right maxillae with M1–M3; 6 left and 9 right maxillae with M1–M2; 3 left and 2 right maxillae with M1; 1 right maxillae with M2; left M1; left M2; 12 left and 11 right hemimandibles with m1–m3; 6 left and 10 right hemimandibles with m1–m2; 5 left and 4 right hemimandibles with m1; 2 left hemimandibles with m1 and m3; 1 left and 1 right hemimandible with m2 and m3; 5 left and 5 right hemimandibles with m2; left hemimandible with m3; 1 left and 2 right m1.

The preservation of these specimens hampers their attribution to a species level. Several are covered with breccia, preventing metric or morphological description.

PALEOENVIRONMENTAL ANALYSIS

Previous studies on the fauna of API.LC-C provided only a brief mention of the small mammals and lagomorphs, reporting broadly 'Rodentia (including Microtinae and Cricetinae/Murinae)' and noting the presence of the lagomorphs *Oryctolagus cuniculus* and *Lepus* sp. (Lax 1995). The present study showed that the small mammal assemblage is diverse, including six families (Erinaceidae, Talpidae, Soricidae, Cricetidae, Muridae, and Leporidae) and at least 11 taxa, 9 of which were identified at species level (Table 1). The presence of *Oryctolagus* is not confirmed, as no cranial, dental, or postcranial material was distinctive enough to verify its presence. This updated faunal list allows for some preliminary paleoenvironmental results.

In terms of diversity, the API.LC-C assemblage includes three Eulipotyphla, at least six Rodentia, and two Lagomorpha taxa, with *Apodemus* (MNI=70), *Microtus* (MNI=53), and *Lepus* (MNI=35) being the most abundant in terms of MNI (see Table 1).

Lepus timidus is regarded as an arctic-boreal species (Hamill et al. 2006), usually inhabiting higher altitudes in cooler climates, in shrublands and grasslands (Bedson et al. 2021). Earlier literature, however, often regarded *L. timidus* as a species of mixed forest and linked it to the transition to open clearings (Angerbjörn and Flux 1995). As for the *L. europaeus,* it is considered to prefer more open habitats, but in currently agriculturally dominated landscapes (Sliwinski et al. 2019). The southernmost occurrence of the mountain hare was previously documented in Loutra Almopias Cave, Northern Greece, from the early part of the Late Glacial (Fladerer et al. 2023), and thus the API.LC-C record extends its geographic distribution even more to the south.

The THI analysis indicates that taxa preferring grassland (28%) and shrublands (28%) habitats dominate the assemblage, followed by those preferring rocky (22%) and forest (17%) environments. Taxa usually found near water bodies (wetlands) and those adapted to desert habitats appear to be represented by 3% each (Figure 10; Supplementary Table 5).

The HW analysis, which incorporates MNI values, shows a different pattern. Rocky areas comprise the largest proportion (50%), followed by grasslands (17%), shrublands (17%), and forests (12%). This distribution reflects the relative abundance of taxa contributing to each category (see Figure 10; Table 2).

Most species show broad ecological tolerances from forest to shrubland, and grassland habitats. The strong representation of rocky signal habitats, meaning an environment with rocky or stony substrates, results from the presence of *Chionomys nivalis* and *Apodemus epimelas*, which are also represented by a substantial number of individuals. This pattern-could also result from the inability to identify voles at species level. Nonetheless, the dominance of rocky habitats is consistent with the current environment and geomorphology of the area.

Species such as *C. nivalis*, *C. leucodon*, *L. europaeus*, and *N. migratorius* provide the strongest signal for the occurrence of grasslands and shrublands. Several taxa, including *A. sylvaticus/flavicollis* and *A. epimelas*, also show clear affinities with rocky habitats, consistent with their current ecological preferences. Forest habitats are mainly indicated by the presence of *Erinaceus* and by species occasionally associated with wooded environments such as *L. timidus*, *A. sylvaticus/flavicollis*, and *T. europaea.* Thus, while woodland elements were likely present, they were not the dominant component of the landscape. The prevalence of a rocky

TABLE 1. THE NISP AND MNI OF THE TAXA THAT COMPOSE THE SMALL MAMMAL FAUNA OF API.LC-C.

Taxa	NISP	MNI
Lepus sp.	395	27
Lepus europaeus	14	4
Lepus timidus	6	4
Erinaceus sp.	8	3
Talpa europaea	2	2
Crocidura leucodon	16	3
Cricetidae indet.	2	1
Soricidae indet.	1	1
Arvicolidae indet.	11	5
Microtus sp.	99	28
Chionomys nivalis	22	10
Microtus (Terricola) Morphotype 1	28	13
Microtus (Terricola) Morphotype 2	13	7
Microtus sp.	9	5
Nothocricetulus migratorius	42	11
Apodemus sp.	115	29
Apodemus sylvaticus/flavicollis	69	14
Apodemus epimelas	141	27
SUM	**993**	**192**

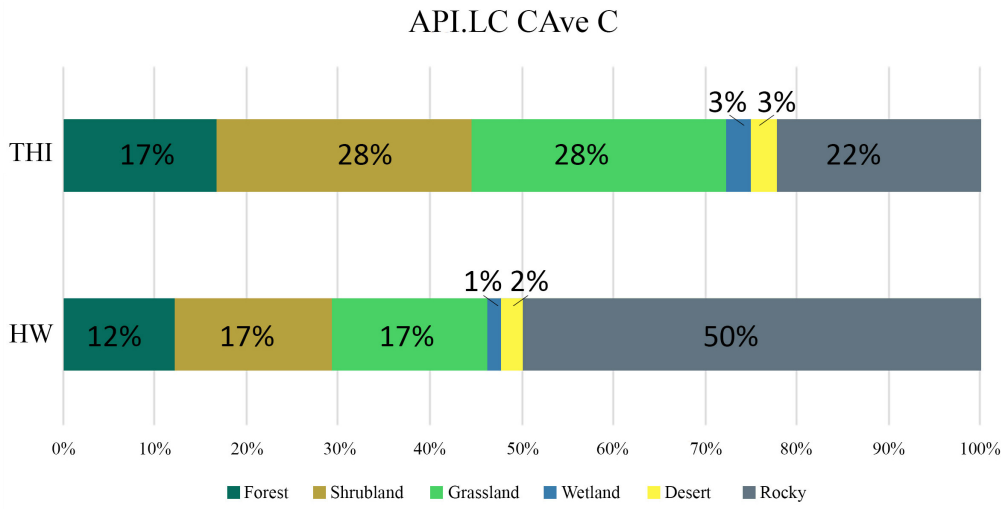

Figure 10. Paleoenvironmental reconstruction based on habitat suitability of rodents and insectivores. Values are expressed in percentages.

TABLE 2. THE SCORE OF EACH TAXON ON API.LC-C OF THE HABITAT IT OCCUPIES TODAY, BASED ON THE IUCN RED LIST AND THE MNI.

taxa/divided equally	MNI	Forest	Shrubland	Grassland	Wetland	Dessert	Rocky
Lepus europaeus	4		0.5	0.5			
Lepus timidus	4	0.25	0.25	0.25	0.25		
Erinaceus sp.	3	0.33	0.33	0.34			
Talpa europaea	2	0.34	0.33	0.33			
Crocidura leucodon	3		0.5	0.5			
Chionomys nivalis	10						1
Nothocricetulus migratorius	7	0.25	0.25	0.25		0.25	
Apodemus sylvaticus/flavicollis	14	0.33	0.34	0.33			
Apodemus epimelas	27						1
sum	**74**						

area is consistent with the site's geomorphological context, as the Apidima caves occur within a limestone coastal cliff. Overall, the THI results suggest that the broader area around Apidima Cave C was a mosaic environment, dominated by shrublands and grasslands, with rocky zones and limited patches of woodland.

The ecological preferences of the small mammals offer valuable insights into the paleoenvironment surrounding Apidima Cave C. Previous paleoenvironmental inferences for this context relied exclusively on large mammals. Those works described the region as a mixed steppe landscape with patches of forested areas. This interpretation is partly based on the presence of *Martes foina*, a species associated with mixed forests and rocky hillsides (Tsoukala 1999). The presence of cervids, particularly red deer, was interpreted as indicative of forested ecotonal habitats between forests and grasslands (open woodland; Lax 1995). In addition to previous suggestions of a prevalence of forest or open-woodland environments, our study indicates that although forest patches were present around the site, they were not the primary habitat. Grassland and shrubland components are equally evident, and rocky environments are strongly represented. These data suggest a more heterogeneous landscape than previously proposed.

The strong rocky signal observed in the HW results is largely driven by the high MNI values of *C. nivalis* and *A. epimelas.* Differences between the THI and HW reconstructions highlight the influence of taxonomic abundance on inferred habitats. THI produces a more balanced representation of forest, shrubland, and grassland environments. This mixed signal of open and closed environments is consistent with a mosaic landscape of forest patches, grasslands, and shrublands, but could also indicate a time-averaged assemblage. In the absence of a detailed taphonomic analysis and considering the nature of the assemblage, with limited contextual information, the environmental reconstruction derived from the THI and HW must be interpreted with caution.

DISCUSSION AND CONCLUSIONS

In the Mani Peninsula, paleoenvironmental data from the study of small mammals are available for the Upper Paleolithic Melitzia cave and the Middle Paleolithic Kalamakia cave (Kolendrianou 2021; Kolendrianou et al. 2023). Several species are shared across all three sites, including *Erinaceus* sp., *Talpa* sp., and *Apodemus epimelas,* indicating rocky (*A. epimelas*) and temperate (*Erinaceus*) environments in the area.

Similarities between the small mammal fauna of all three sites are also in the voles, with representatives of the subgenus *Terricola, M.* cf. *subterraneus*, and *M.* cf. *thomasi* (similar to Morphotype 1 and 2), being present in both Melitzia and Kalamakia cave, as well as *M. arvalis* (similar to *Microtus* sp.), which is recorded in the Kalamakia cave (Kolendrianou 2021; Kolendrianou et al. 2020).

Nothocricetulus migratorius and *A. sylvaticus/flavicollis* also occur at Apidima, Melitzia, and Kalamakia. *Glis glis and Dryomys nitedula* are present in Melitzia and Kalamakia but are absent from the Apidima Cave C assemblage; thus, forests were likely not a major element of the local vegetation communities around the Apidima caves, but their absence may also be due to recovery biases (see Materials and Methods). Among lagomorphs, *Lepus europaeus* is known from both Melitzia and Apidima, whereas *L. timidus* is not recorded at any of these sites (Kolendrianou 2021; Kolendrianou et al. 2023). Differences also arise within the Soricidae—Melitzia and Kalamakia contain *C. leucodon*, *C. suaveolens*, and *Sorex minutus*, whereas Apidima yields only

C. leucodon. Overall, Apidima Cave C shares several microfaunal components with the neighboring sites. Notably, the main difference, apart from the absence of *L. timidus*, is the presence of forest dwellers such as *Glis glis*, *Dryomys nitedula*, and *Sciurus vulgaris*, whose presence in the other sites aligns with a more pronounced woodland signal compared to API.LC-C. Nonetheless their absence in API-LC-C is most likely related to recovery biases.

Comparable data also exist from Panthera Cave (Kythros islet, Ionian Sea, Greece), where Middle Paleolithic lithic artifacts have been recovered alongside large- and small-sized vertebrate remains (Kolendrianou 2021). *Apodemus epimelas* and representatives of the subgenus *Terricola* (*M.* cf. *subterraneus* and *M.* cf. *thomasi*) have been identified in both sites; however, *Sciurus vulgaris*, a typically forest-dwelling taxon, is recorded only in the Panthera cave.

Compared to the locality Loutra Almopias Cave (Northern Greece, including Ia and LAC), the fauna shows similarities with API.LC-C in the presence of *T. europaea*, *C. leucodon*, *Apodemus species*, and *N. migratorius*; however, the fauna of Loutra Almopias Cave is much more diverse and includes additionally specimens of *T. minor* (only in LAC), *Spalax leucodon*, *A. uralensis*, *Mesocricetus newtoni*, *A. amphibius*, and the forest dwellers *Dryomys nitedula*, *Glis glis*, *Spermophilus citellus*, and *Muscardinus avellanarius* (Chatzopoulou 2014), which are not present in API.LC-C. *Lepus europaeus* and *L. timidus* are common faunal elements in all three sites, while *Ochotona pusilla* is absent from API.LC-C (Fladerer et al. 2023). *Microtus arvalis* (similar to *Microtus* sp.) and *M. subterraneus* (only in LAC, similar to the morphotypes 1 and 2) are the voles present in both Loutra Almopias Cave and APL.LC-C; the species *M. agrestis* is only present in Loutra Almopias Cave (Fladerer et al. 2023).

Nothocricetulus migratorius, *Microtus* sp., and *L. europaeus*, which is reported from the Late Pleistocene locality of Agios Georgios Cave (Kilkis, Northern Greece; Piskoulis et al. 2024) are also present in API.LC-C and Loutra Almopias Cave. However, *O. pusilla*, *Spalax leucodon*, *M. newtoni*, *Spermophylus citellus*, and *A. amphibius* are absent in API.LC-C, but present in Loutra Almopias Cave (Piskoulis et al. 2024).

From the identified taxa, the only species currently absent from Greece are *Lepus timidus* and *N. migratorius*. However, the absence of the latter is believed to be due to insufficient research effort (Nedyalkov 2016).

The two leporids of Apidima Cave C might have inhabited similar environments, though *L. timidus* tends to move into higher altitudes (Thulin 2003). Their co-occurrence in the API.LC-C assemblage could indicate a wider range of landscapes available around the site or stratigraphic mixing/time averaging.

The presence of *L. timidus* in API.LC-C marks the current southernmost presence known of the species, which until now was in the Loutra Almopias Cave LAC, a middle Würm site (Late Pleistocene) (Fladerer et al. 2023). The species is described as a cold-adapted taxon whose distribution in Europe expanded southward during glacial or stadial conditions (Smith 2017). Its occurrence, along with that of the snow vole (*C. nivalis)*, suggests a phase with colder climatic conditions in the Apidima Cave C sequence. Considering that the most recent radiocarbon dates obtained from perforated shell beads from the legacy collection of Apidima Cave C range between 21,120 cal ka and 31,940 cal ka (Harvati et al. 2026 [this issue]) and that in Peloponnese mountains, glaciers reached their maximum before 30 ka, earlier than the global Last Glacial Maximum (LGM, Pope et al. 2017), the extended distribution of these taxa might associate with the LGM (Allard et al. 2020).

Noteworthy are also the dimensions of the API.LC-C *Crocidura leucodon*, *L. timidus*, and *T. europaea* specimens, which fall within the ranges indicated in the existing literature and tend towards those reported for larger individuals. In addition, measured dimensions of *C. nivalis*, *N. migratorius*, *A. epimelas*, and *A. sylvaticus/flavicollis* in the API.LC-C sample frequently exceed those of the comparative material, even though the specimens are morphologically similar. Body size variations in small mammalian taxa, especially rodents, have been associated with climatic factors (Alhajeri and Steppan 2018; Chen et al. 2025; Kart Gur et al. 2025; Westover and Smith 2020), environmental productivity (Zhan and Wang 2025), intra-specific competition (Martin et al. 2025), and predation pressure (Li et al. 2021). More specifically, larger body sized rodents and lagomorphs have been observed in relation to higher latitudes and/or lower temperatures, especially on an intra specific level (Alhajeri and Steppan 2018; Bergman 1847; Kart Gur et al. 2025) although other abiotic factors such as precipitation, have also been proposed to influence body size (Westover and Smith 2020), mostly when higher taxonomic levels are considered; other studies propose a stronger effect of resource abundance on body size variation (Yom-Tov and Yom-Tov 2004).

Dental metrics can be used to estimate body size (Renaud and Michaux 2007). The larger dimensions of fossil rodents in the API.LC-C assemblage could thus be the result of lower temperatures compared to the comparative material assemblage. The pattern of increasing body size within arvicolid species has already been reported (Horáček and Sánchez Marco 1984). Habitat fragmentation and subsequent population isolation would result in speciation and would be consistent with the aforementioned inference of a colder period in the studied context. Nonetheless, it should be kept in mind that the API.LC-C collection has been subjected to recovery bias against smaller-sized specimens, which could have skewed the dental metric analyses as well. The complete study of the faunal taphonomic signal is still ongoing; therefore, the influence of predator trophic preferences and possible presence of an avian predator.

Another interesting fact about this accumulation is the mixed nature of the species present, e.g., the coexistence of more cold-adapted species, such as *C. nivalis* and *L. timidus* (arctic-subarctic, Thulin 2003), and temperate species, such as *Erinaceus* and *L. europaeus* (Furió et al. 2015). The taxonomic composition of the assemblage could be indicative of a cold climate, while cold-adapted taxa expanded their ranges.

Multiple molecular studies indicate that several taxa

persisted in Balkan and Greek refugia during adverse glacial or stadial conditions. Such studies include the two leporids (*L. europaeus* and *L. timidus* [Kasapidis et al. 2005; Minoudi et al. 2018; Stamatis et al. 2009]) *Erinaceus* sp. (Seddon et al. 2001), and the various voles extant in Greece (Thanou et al. 2012). Within *the Apodemus* species, *A. flavicollis* appears to have survived in a southern Italo-Balkan glacial refugium (Michaux et al. 2005), whereas *A. sylvaticus* persisted in northern refugia (Herman et al. 2016). Genetic bottlenecks and population fragmentation during the Quaternary glaciations have been identified in several taxa, such as *Lepus europaeus* (Minoudi et al. 2018) and *A. sylvaticus* (Michaux et al. 2005).

However, the evidence is insufficient to support such a conclusion at present. More importantly, we have observed variation in specimen preservation, with some showing compact calcareous encrustations and others covered in looser sediment. These observations are also consistent with excavation archives indicating that at least three stratigraphic horizons were excavated during the Pitsios investigations in Apidima Cave C (Lombardo et al. 2026a [this issue]). Hence, given the nature of the assemblage, which lacks stratigraphic information for the origin of the specimens, an ecological palimpsest affected by time-averaging (Lyman 2017) is a more plausible explanation. Consequently, paleoenvironmental interpretations must be approached with appropriate caution until broader spatial and temporal patterns are investigated further.

Overall, the present study identified 979 specimens of small mammals attributed to 11 taxa at the genus level, providing the first taxonomic overview of the Apidima C legacy-small mammal assemblage and contributing to the baseline for Late Pleistocene small mammal communities in the area. The occurrence of *L. timidus* and *C. nivalis* indicate cold conditions, possibly corresponding to the Last Glacial Maximum, consistent with the recent dating results (Harvati et al. 2026 [this issue]). At the same time, the reconstructed paleoenvironment using HW and THI suggests a heterogeneous landscape comprising forest areas, shrublands, grasslands, and rocky habitats in the vicinity of the site. These findings demonstrate the importance of the study of legacy collections, which provides a valuable contribution for the reconstruction of past environments and forms the foundation for future investigations. Nevertheless, the study should be considered in light of the inherent limitations of the legacy assemblage, including itme-averaging and material collection biases, which may have affected paleoecological interpretations. Ongoing fieldwork at the site and upcoming research efforts on newly excavated, stratigraphically controlled materials will refine the interpretations and may elucidate whether the area had a refugium role during colder phases.

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DATA AVAILABILITY STATEMENT

Data are contained within the article and the Supplementary Materials.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

KC: writing-original draft, review and editing; formal analysis; investigation; visualisation; data curation; validation; **ER**: writing-review and editing; validation; **GEK**: writing-review and editing; validation; **TvK**: writing-review and editing; validation; **KE**: resources; **VGG**: resources; **KH**: writing-review and editing; validation; funding acquisition. All authors have read and agreed to the published version of the manuscript.

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Special Issue: The Apidima Legacy Collections: New Analyses and Interpretations

Supplement 1 to New Insights Into the Small Mammal Assemblage (Eulipotyphla, Rodentia, Lagomorpha) from the Apidima Cave C Legacy Collection: Taxonomy and Preliminary Paleoenvironmental Interpretations

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SUPPLEMENT 1
This supplement contains: Supplementary Tables 1–5 and Supplementary Figure 1.

Supplementary material

New insights into the small mammal assemblage (Eulipotyphla, Rodentia, Lagomorpha) from the Apidima Cave C legacy collection: Taxonomy and preliminary paleoenvironmental interpretations

Lepus								
upper incisor	L mean	Lmin	Lmax	N	Breadth mean	Wmin	Wmax	N
	(mesial-distal)				(Buccal lingual)			
L. europaeus	2.41	1.85	2.77	6	3.52	2.87	4.48	6
L. timidus	2.29			1	2.98			1
Lepus sp.	2.4	2.25	2.55	5	3.34	4.27	3.42	5
p3	N	Lmin	Lmean	Lmax	N	Wmin	Wmean	Wmax
L. europaeus	7	3.95	4.3	4.67	8	3.14	4.09	4.87
L. timidus	4	3.58	4.46	5.01	4	3.09	3.94	4.71
Lepus sp.	2	4.58	4.63	4.69	2	3.43	4.09	4.76
lower incisor	N	Llmin	Lmax	Bmin	Bmax			
L. europaeus	2	3.12	3.44	2.34	2.54			
Erinaceus sp.	P3	P4	canine	p2	m1	m1	m2	
L	3.14	5.11	ca. 3.07	4.12	7.58	7.07	6.43	
W	3.01	5.87	1.82	3.33	4.81	5.05	4.12	
Talpa europaea	Humerus							
DE	8.46							
D	4.45							
Crocidura leucodon	p4	m1	m2	m3				
N	2	3	2	2				
L	0.91-1.09	1.46-1.7	1.59-1.76	1.26-1.36				
TRW	0.79-0.8	1.05-1.09	1.01-1.1	0.76-0.77				
TAW		1.18-1.24	1.06-1.12					
Nothocricetulus migratorius	M1	M2	m1	m2				
N	1	2	14	12				
L	2,04	1,45-1,63	1,62-2,21	1,36-1,65				
W	1,35	1,32-1,38	0,93-1,38	1,19-1,39				
Microtus m1	N	Lmin	Lmax	Lmean	N	Wmin	Wmax	Wmean
Microtus (Terricola) Morphotype 1	19	2.57	3.61	3.17	19	0.89	1.22	1.06
Microtus (Terricola) Morphotype 2	14	2.95	3.58	3.31	16	0.9	1.26	1.11
Microtus sp.	6	2.85	3.67	3.22	6	1	1.26	1.12
Chionomys nivalis	20	2.79	3.73	3.55	20	1.04	1.33	1.2

Muridae m1	N	Lmin	Lmax	Lmean	Wmin	Wmax	Wmean	
A. epimelas	*55*	1.95	2.91	2.67	1.22	1.74	1.6	
A. sylvaticus/flavicolis	26	2.09	2.7	2.47	1.26	1.64	1.48	

Table 1. Measurements of different dental and postcranial (in *Talpa*) elements of the small mammals from Apidima legacy collection from Cave C. Measurements in mm.

Reference	Locality	*Genus*	*species*	nDE	minDE	meanDE	maxDE	nD	minD	meanD	maxD
This study	Apidima API.L.C.-C	*Talpa*	*europaea*			8,46				4,45	
Niethammer (1990)	Europe	*Talpa*	*europaea*	63	6,7		6,9	63	3,3		4,7
Koenigswald (1970)	Petersbuch	*Talpa*	*europaea*	90	7,4	8,32	9,3	90	3,5	3,85	4,25
Parfitt (1999)	Boxgrove	*Talpa*	*europaea*	29	7,3	8,28	9,2	38	3,59	3,87	4,3
Stuart (1982), Maul (1990)	Voigstedt	*Talpa*	*europaea*	2	7,8	7,81	7,82	2	3,66	3,68	3,7
Maul and Parfitt (2010)	West Runton	*Talpa*	*europaea*	1		8,17		1		3,71	
Stuart (1981)	West Runton	*Talpa*	*europaea*	2	8,8	8,9	9	3	3,64	3,73	3,78
Malec in Storc et al. (1973)	Hohensülzen	*Talpa*	*fosilis*	2	9	9,1	9,2	2	4,3	4,35	4,4
Maul (2001)	Untermaßfeld	*Talpa*	*europaea*	2	8,43	8,78	9,14	3	4,14	4,43	4,64
Koenigswald (1970)	Petersbuch	*Talpa*	*minor*	46	5,4	5,96	6,5	46	2,7	2,96	3,35
Parfitt (1999)	Boxgrove	*Talpa*	*minor*	29	5,88	6,73	7,85	40	2,73	3,18	3,52
stuart (1991, Maul (1990)	Voigstedt	*Talpa*	*minor*	13	6,21	6,58	7	18	3,06	3,19	3,43
Koenigswald (1973)	Husarenhof 4	*Talpa*	*minor*	2	6,25	6,82	7,4	2	3,04	3,28	3,45
Stuart (1981)	West Runton	*Talpa*	*minor*	36	6,6	7,27	7,8				
Malec in Storc et al. (1973)	Hohensülzen	*Talpa*	*minor*	4	6,6	6,75	6,9	5	3,3	3,36	3,5
Cleef-Roders and Hoek Ostende (2001)	Bergen op Zoom (NL)	*Talpa*	*europaea*	10	7,7		9,1	10	3,6		4,5
Cleef-Roders and Hoek Ostende (2001)	Oude Mirrum (NL)	*Talpa*	*europaea*	34	8,3		9,6	36	4		4,8
Niethammer (1990) from Cleef-Roders and Hoek Ostende (2001)	Kleinalm/Niede r Tauern (D)	*Talpa*	*europaea*	15	6,7		7,8	15	3,3		3,9
Niethammer (1990) from Cleef-Roders and Hoek Ostende (2001)	Ramsau Dachstein (D)	*Talpa*	*europaea*	18	7,1		8,6	18	3,4		4,2
Niethammer (1990) from Cleef-Roders and Hoek Ostende (2001)	Rheinland (D)	*Talpa*	*europaea*	14	7,8		9,3	14	4,8		4,2
Niethammer (1990) from Cleef-Roders and Hoek Ostende (2001)	Spain	*Talpa*	*europaea*	16	8,1		9,9	16	4,3		4,7

Niethammer (1990) from Cleef-Roders and Hoek Ostende (2001)	Greece	*Talpa*	*stankovici*	3	8,6		8,7	3	4		4,3
Niethammer (1990) from Cleef-Roders and Hoek Ostende (2001)	Italy	*Talpa*	*romana*	1		9		1		4,6	
Niethammer (1990) from Cleef-Roders and Hoek Ostende (2001)	Tessin (I)	*Talpa*	*caeca*	38				38	3,2		3,8
Niethammer (1990) from Cleef-Roders and Hoek Ostende (2001)	alpi di Benedetti (I)	*Talpa*	*caeca*	17				17	2,9		3,5
Niethammer (1990) from Cleef-Roders and Hoek Ostende (2001)	Pelister (former Yogoslavia)	*Talpa*	*caeca*	30				30	2,8		3,4
Niethammer (1990) from Cleef-Roders and Hoek Ostende (2001)	Spain	*Talpa*	*occidentalis*	20	0,65		7,8	20	3		4,1

Table 2 Measurements (in mm) of the humerus in samples of various *Talpa* species.

Reference	Locality	Genus	species	L N	Lmin	Lmean	Lmax	TRW N	TRW min	TRW mean	TRW max	TAW N	TAW min	TAW mean	TAW max
This study	Apidima Cave C (Legacy Collection)	*Crocidura*	*leucodon*	1		1.59				1.1				1.12	
This study	Apidima Cave C (Legacy Collection)	*Crocidura*	*leucodon*	1		1.76				1.01				1.06	
Koufos et al. (2001)	Marathousa	*Crocidura*	*kornfeldi*	3	1.452	1.474	1.5	4	0.84	0.865	0.906	4	0.889	0.934	0.995
Reumer (1986)	Kommo (Crete)	*Crocidura*	*suaveolens caneae*	9		1.54		9		0.9		9		0.95	
Reumer (1986)	Kommo (Crete)	*Crocidura*	*suaveolens caneae*	39		1.5		39		0.91		39		0.95	
Reumer (1986)	Kommo (Crete)	*Crocidura*	*zimmermanni*	3		1.5		3		0.92		3		0.94	
Reumer (1986)	Kommo (Crete)	*Crocidura*	*zimmermanni*	6		1.54		6		0.95		6		1	
Rofes and Cuenca-Bescós (2010)	Sima del Elefante TE8	*Crocidura*	*kornfeldi*	14	1.39	1.48	1.55	14	0.86	0.92	0.97	14	0.84	0.9	0.94
Rofes and Cuenca-Bescós (2010)	Sima del Elefante TE9	*Crocidura*	*kornfeldi*	52	1.35	1.46	1.58	52	0.83	0.91	0.97	52	0.79	0.9	0.98
Rofes and Cuenca-Bescós (2010)	Sima del Elefante TE10	*Crocidura*	*kornfeldi*	18	1.29	1.42	1.55	18	0.85	0.87	1.03	18	0.72	0.87	0.96
Rofes and Cuenca-Bescós (2010)	Sima del Elefante TE12	*Crocidura*	*kornfeldi*	8	1.33	1.42	1.53	8	0.86	0.9	0.92	8	0.88	0.9	0.94
Rofes and Cuenca-Bescós (2010)	Sima del Elefante TE13	*Crocidura*	*kornfeldi*	5	1.42	1.47	1.52	5	0.87	0.9	0.94	5	0.87	0.88	0.9
Rofes and Cuenca-Bescós (2010)	Sima del Elefante TE14	*Crocidura*	*kornfeldi*	7	1.39	1.47	1.61	7	0.84	0.88	0.93	7	0.87	0.88	0.93
Reumer (1984)	Villany 3	*Crocidura*	*kornfeldi*	92	1.31	1.43	1.58	93	0.73	0.87	0.96	92	0.75	0.89	1.01

Reumer (1984)	Osztramos 3/2	*Crocidura*	*kornfeldi*	2	1.4	1.49	1.57	2	0.88	0.9	0.91	2	0.91	0.92	0.93
Chatzopoulou (2014)	Loutra Almopias LAC	*Crocidura*	*leucodon*	5	1.597	1.699	1.767	5	0.972	1.045	1.116	5	0.999	1.071	1.141
Berto et al. (2024)	Pirro Nord 13	*Crocidura*	*kornfeldi*	1		1.4				0.94				1	
Rzebik-Kowalska (2007)	Poland (recent)	*Crocidura*	*leucodon*	12	1.41		1.53					12	0.95		1.04
Fanfani (1999)	Valdemino	*Crocidura*	*leucodon*		1.37	1.55	1.76		0.9	1	1.19		0.95	1.05	1.22
Fanfani (1999)	Centro Italia	*Crocidura*	*leucodon*		1.43	1.59	1.7		0.95	1.02	1.16		0.98	1.07	1.27

Table 3 Measurements (in mm) of the m2 in samples of various *Crocidura* species.

Literature	Site	*Genus*	*Species*	n L	LMin.	LMax.	LMean	n W	Wmin	Wmax	Wmean
This study	Apidima Cave C (Legacy Collection)	*Nothocricetulus*	*migratorius*				2.07				1.31
This study	Apidima Cave C (Legacy Collection)	*Nothocricetulus*	*migratorius*				2.01				1.19
This study	Apidima Cave C (Legacy Collection)	*Nothocricetulus*	*migratorius*				2.05				1.39
This study	Apidima Cave C (Legacy Collection)	*Nothocricetulus*	*migratorius*				1.89				1.25
This study	Apidima Cave C (Legacy Collection)	*Nothocricetulus*	*migratorius*				2.21				
This study	Apidima Cave C (Legacy Collection)	*Nothocricetulus*	*migratorius*				1.87				1.3
This study	Apidima Cave C (Legacy Collection)	*Nothocricetulus*	*migratorius*				1.97				1.32
This study	Apidima Cave C (Legacy Collection)	*Nothocricetulus*	*migratorius*				1.85				1.27
This study	Apidima Cave C (Legacy Collection)	*Nothocricetulus*	*migratorius*				1.62				
This study	Apidima Cave C (Legacy Collection)	*Nothocricetulus*	*migratorius*				1.84				1.27
This study	Apidima Cave C (Legacy Collection)	*Nothocricetulus*	*migratorius*				1.89				
This study	Apidima Cave C (Legacy Collection)	*Nothocricetulus*	*migratorius*				1.87				1.27
This study	Apidima Cave C (Legacy Collection)	*Nothocricetulus*	*migratorius*				1.89				
This study	Apidima Cave C (Legacy Collection)	*Nothocricetulus*	*migratorius*				1.99				1.25
Lozano-Fernandez et al. (2019)	Bois-de-Riquet (US2A)	*Allocricetus*	*bursae*	3	1,63	1,84	1,73	3	0,97	1,11	1,05
Lozano-Fernandez et al. (2019)	Bois-de-Riquet(US2B)	*Allocricetus*	*bursae*	15	1,64	1,84	1,72	15	0,96	1,17	1,05
Lozano-Fernandez et al. (2019)	Bois-de-Riquet (US2C)	*Allocricetus*	*bursae*	1			1,62	1			1,07
Popov (1989)	Morovitsa cave	*Allocricetus*	*bursae*	21	1,62	1,9	1,78	21	1,05	1,24	1,11

Popov (1989)	Morovitsa cave	*Mesocricetus*	*newtoni*	25	2,14	2,57	2,35	25	1,05	1,43	1,24
Popov (2000)	Cave 16	*Nothocricetulus*	*migratorius*	19	1,57	1,82	1,67	19	0,9	1,12	1,04
Popov (2000)	Cave 16	*Mesocricetus*	*newtoni*	55	2,07	2,62	2,33	55	1,12	1,6	1,26
Van der Weerd (1973)	Varkiza 2	*Nothocricetulus*	*migratorius*	3	1,5	1,72	1,64	a3	0,97	1,09	1,04
Tsoukala and Chatzopoulou (2005)	Kitselis Pothole	*Nothocricetulus*	*migratorius*	1			1,688	1			1,092
Pradel (1989)	Bacho Kiro Cave	*Nothocricetulus*	*migratorius*	20	1,55	1,44	1,334	20	0,96	1,11	1,031
Pradel (1989)	Bacho Kiro Cave	*Mesocricetus*	*newtoni*	22	2,14	2,58	2,36	22	1,11	1,37	1,243
Bogićević et al. (2011)	Baraniva Cave	*Nothocricetulus*	*migratorius*	7	1,7	1,9	1,81	7	1,1	1,2	1,16
Bogićević et al. (2011)	Baraniva Cave Layer 2	*Mesocricetus*	*newtoni*	8	2,45	2,7	2,55	8	1,3	1,5	1,4
Bogićević et al. (2011)	Baraniva Cave Layer 4	*Mesocricetus*	*newtoni*	28	2,3	2,75	2,54	28	1,2	1,55	1,36
Rey-Rodríguez et al. (2022)	Azokh Cave	*Nothocricetulus*	*migratorius*	4	1,4	1,81	1,56	4	0,58	0,77	0,68
Rey-Rodríguez et al. (2022)	Natural history museum of London (NHM)	*Nothocricetulus*	*migratorius*	16	1,41	1,76	1,57	16	0,74	0,95	0,85

Table 4 Measurements (in mm) of the m1 in samples of *Nothocricetulus, Allocricetus, and Mesocricetus* species.

References and abbreviations mentioned in the main text.

taxa/divided equally	Forest	Shrubland	Grassland	Wetland	Dessert	Rocky
Lepus europaeus	0	2	2	0	0	0
Lepus timidus	1	1	1	1	0	0
Erinaceus sp.	0.99	0.99	1.02	0	0	0
Talpa europaea	0.68	0.66	0.66	0	0	0
Crocidura leucodon	0	1.5	1.5	0	0	0
Chionomys nivalis	0	0	0	0	0	10
Nothocricetulus migratorius	1.75	1.75	1.75	0	1.75	0
Apodemus sylvaticus/flavicollis	4.62	4.76	4.62	0	0	0
Apodemus epimelas	0	0	0	0	0	27
SUM	9.04	12.66	12.55	1	1.75	37
Habitat Weight (HW)	0.1221622	0.171081	0.1695946	0.013513514	0.023649	0.5
taxa/divided equally	Forest	Shrubland	Grassland	Wetland	Dessert	Rocky
Lepus europaeus		0.5	0.5			
Lepus timidus	0.25	0.25	0.25	0.25		
Erinaceus sp.	0.33	0.33	0.34			
Talpa europaea	0.34	0.33	0.33			
Crocidura leucodon		0.5	0.5			
Chionomys nivalis						1
Nothocricetulus migratorius	0.25	0.25	0.25		0.25	
Apodemus sylvaticus/flavicollis	0.33	0.34	0.33			
Apodemus epimelas						1
SUM	1.5	2.5	2.5	0.25	0.25	2
Taxonomic Habitat Index (THI)	0.1666667	0.277778	0.2777778	0.027777778	0.027778	0.222222

Table 5. The score of each taxon of Apidima legacy collection from Cave C, of the habitat it occupies today, based on the IUCN Red List

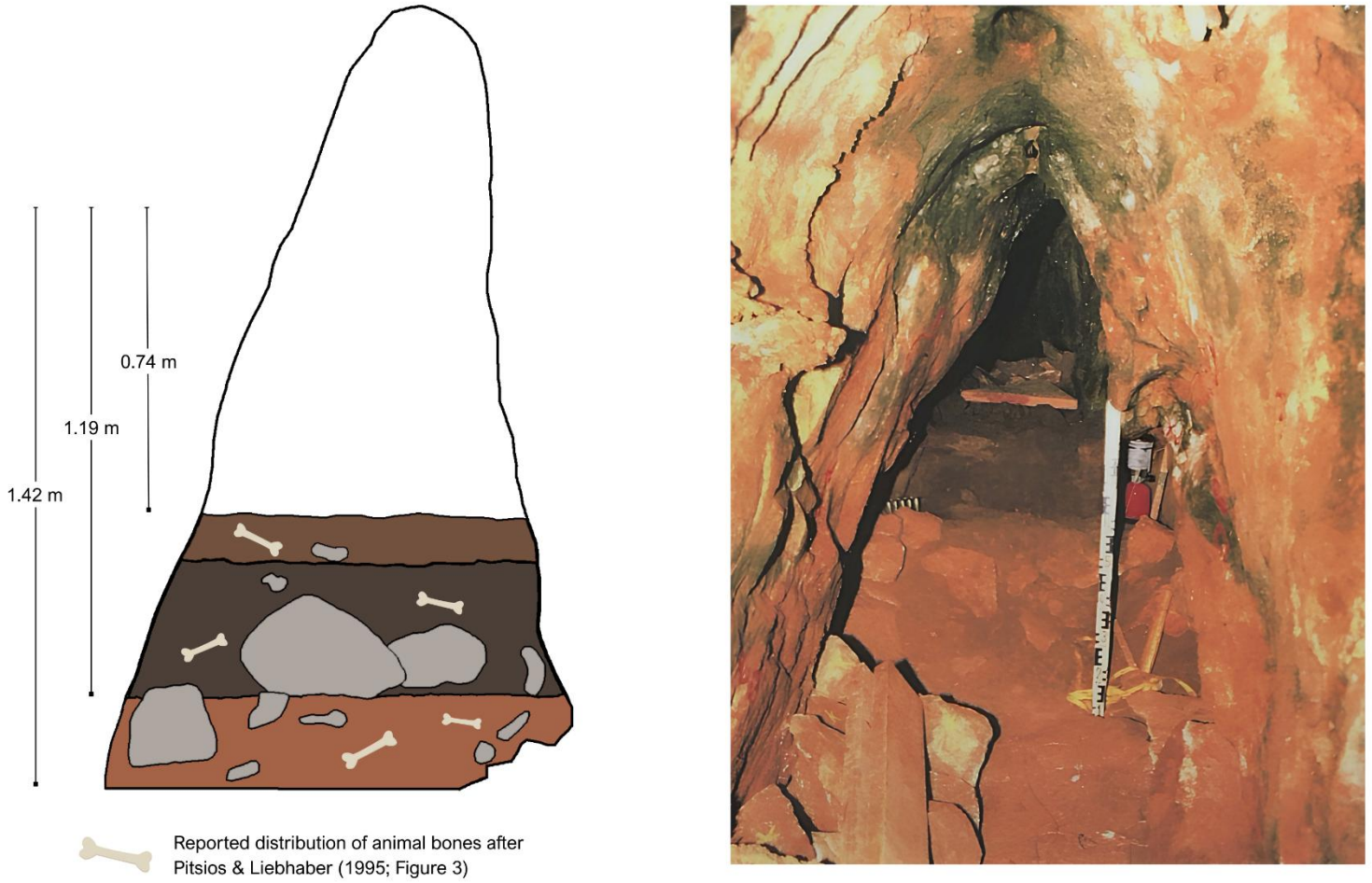

Figure 1. Left: Reconstruction of the reported stratigraphic column and animal bones distribution after Pitsios and Liebhaber (1995). Right: Archival photograph from Pitsios' excavation (Museum of Anthropology, National and Kapodistrian University of Athens).