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USING GEOMETRIC MORPHOMETRICS ON THE STUDY OF LOWER FIRST MOLARS OF ARVICOLINAE (MAMMALIA, RODENTIA) FROM THE LATE PLEISTOCENE DEPOSITS OF KALAMAKIA CAVE (LACONIA) AND KLISSOURA CAVE 1 (ARGOLIS).

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ABSTRACT

The systematic rank and evolutionary trends of arvicolines have been a subject of debate for decades. Arvicolines have often been referred to family rank (Arvicolidae) given their high species variation and adaptive level. Nevertheless, many authors consider them to be of subfamily rank (Arvicolinae), an opinion shared by the author of this thesis as well. Rapid rates of reproduction in extant arvicolines, short lifespan and generation time, highly differentiated and abruptly evolving dentition and clear ecological distinctive features among certain species facilitate the use of members of this group as paleoenvironmental and paleoecological indicators. Additionally, arvicolines can provide various information associated with local biotopic characteristics, types of vegetation at regional or continental scale and climatic conditions. Furthermore, certain arvicoline species can be used as biostratigraphic markers providing the age of fossiliferous assemblages and the surrounding formations. Accurately identifying species in fossil assemblages is an important step in answering questions concerning paleoecology and evolution, but also a very complex and challenging task. In this thesis, a classification model was constructed based on geometric morphometrics of the first lower molars of the five extant arvicoline species of Greece (*Microtus felteni*, *Microtus guentheri*, *Microtus levis*, *Microtus subterraneus* and *Microtus thomasi)*. Subsequently, specimens from the Klissoura Cave 1 (Argolis, Greece) and Kalamakia Cave (Laconia, Greece) fossil assemblages were added to the constructed data base, in an effort to determine possible differentiations in the shape and size of the molars related with climatic changes in the studied areas and the phylogenetic relationships of fossil species compared to the extant ones.

ΠΕΡΙΛΗΨΗ

Η συστηματική ταξινόμηση και οι εξελικτικές τάσεις των μικρωτών αποτελούν θέμα συζήτησης επί σειρά δεκαετιών. Τα τρωκτικά αυτά συχνά κατατάσσονται στο επίπεδο της οικογένειας (Arvicolidae) λόγω της μεγάλης ποικιλίας ειδών και του βαθμού προσαρμογής τους. Πολλοί συγγραφείς τα κατατάσσουν στο βαθμό της υποοικογένειας (Arvicolinae), μια άποψη που αποδέχεται και ο συγγραφέας της παρούσας μεταπτυχιακής διατριβής. Οι ταχείς ρυθμοί αναπαραγωγής, η μικρή διάρκεια ζωής και γενεών, η μεγάλο εύρος ποικιλομορφίας και οι εξελικτικές τάσεις των οδοντικών χαρακτηριστικών, καθώς και πολυάριθμα ιδιαίτερα οικολογικά χαρακτηριστικά, καθιστούν τα τρωκτικά αυτά σημαντικούς παλαιοπεριβαλλοντικούς και παλαιοοικολογικούς δείκτες. Επίσης, τα τρωκτικά αυτά παρέχουν πληθώρα πληροφοριών αναφορικά με χαρακτηριστικά βιοτόπων, τύπους βλάστησης, σε τοπικό ή παγκόσμιο επίπεδο, και κλιματικές συνθήκες. Επιπλέον, συγκεκριμένα απολιθωμένα είδη χρησιμοποιούνται ως βιοστρωματογραφικοί δείκτες, παρέχοντας πληροφορίες για την ηλικία απολιθωματοφόρων θέσεων. Η αναγνώριση των ειδών σε απολιθωματοφόρες συναθροίσεις είναι εξαιρετικά σημαντική για την ερμηνεία των συνθηκών του παλαιοπεριβάλλοντος και των εξελικτικών τάσεων και προσαρμογών. Ωστόσο, είναι μια πολύ περίπλοκη και δύσκολη διαδικασία. Στην παρούσα διατριβή, σχεδιάστηκε ένα μοντέλο ταξινόμησης με βάση στοιχεία γεωμετρικής μορφομετρίας από τους κάτω πρώτους γομφίους των πέντε αρτίγονων ειδών (*Microtus felteni*, *Microtus guentheri*, *Microtus levis*, *Microtus subterraneus* και *Microtus thomasi)* που εντοπίζονται αυτή τη στιγμή στην Ελλάδα. Στη συνέχεια, απολιθωμένα δείγματα από τα σπήλαια Καλαμάκια (Λακωνία) και Κλεισούρα 1 (Αργολίδα) εξετάστηκαν με την ίδια μεθοδολογία προκειμένου να διερευνηθούν μεταβολές στο σχήμα και στο μέγεθος των γομφίων, η πιθανή συσχέτιση με τις κλιματικές μεταβολές στην υπό μελέτη περιοχή και οι φυλογενετικές σχέσεις μεταξύ απολιθωμένων και σύγχρονων ειδών.

1. INTRODUCTION

Arvicolines are herbivorous rodents of the family Cricetidae (Fisher, 1817) (superfamily Muroidea; Illiger, 1811) characterized by a robust body and a rounded, short head. The ears and eyes are small and the tail in the majority of the species is shorter than the accumulative length of body and head (Kryštufek and Vohralík, 2005). The first representatives appeared in Eurasia and North America during the Late Miocene, following environmental changes in the Northern Hemisphere (Repenning 1987; Repenning et al. 1990; Fejfar et al. 1997). Since that time, they have spread widely in the Northern Hemisphere, becoming one of the most successful groups of rodents during Late Cenozoic. Currently, the subfamily Arvicolinae is of Holarctic distribution and consists of twenty-six genera and approximately 130 species, divided in ten tribes, seven of which are classified as voles, two as muskrats and one as lemmings (Fejfar et al. 2011).

Owing to their success and wide distribution, numerous sites with diverse arvicoline fossilized accumulations have been discovered across Eurasia and North America. Arvicoline teeth and postcranial skeletal remains can be efficiently collected through simple wet sieving techniques, thus valuable data can be obtained with minimal cost and low effort.

As a result, the fossil record is overwhelmingly rich and there is a constantly increasing amount of information about the biostratigraphy, taxonomy, evolution, distribution and phylogeny of this group. However, the data about arvicoline origin and early history are inadequate (e.g., Repenning 1968; Fejfar et al. 1997; Agadjanian 2009) and a widely approved model about the origin of lemmings and voles has yet to be constructed.

Today, many researchers tend to agree that arvicolines derived from an adapted branch of cricetid rodents, known by the informal name “microtoid cricetids” (Schaub, 1934). The term “microtoid cricetids” is used to describe arvicoline-like brachyodont-bunodont cricetids. Highly specialized microtoid cricetids first appeared in Eurasia with *Microtocricetus* (Fahlbusch and Mayr, 1975) during the Early Vallesian (MN 9), deriving from a possible *Megacricetodon* (Fahlbusch, 1964) or *Democricetodon*(Fahlbusch, 1964) ancestry (Fejfar et al. 2011).

Microtus (Schrank, 1798) is a highly widespread and differentiated mammalian genus. Its morphological features designate it as an index for evolutionary studies among related taxa, species divergence estimations and interspecific/intraspecific geographical variability.

1.1. ARVICOLINES IN GREECE

Morphological and ecological adaptations are more commonly observed in populations living at habitats at the borders of a species distributional range, like the Mediterranean Peninsulas. During the climatic cycles of Pleistocene, several of the species inhabiting these peninsulas, have underwent numerous events such as isolation and population size reduction; such events can be detected in the intraspecific phylogenies of these species. Apart from said events, these phylogenies provide valuable information about the existence of numerous refugia in the Mediterranean area (Hewitt, 2001).

The isolation of the Mediterranean Peninsulas led to a plethora of endemic species and intraspecific differentiation. The Balkan Peninsula acted both as a natural border for the isolation of European populations and as a biogeographical route enabling species migration from Europe to Asia and vice versa (Thanou et al. 2012); furthermore, the paleogeographical and paleoclimatic features of the peninsula bear significant importance for the evolution of species. Throughout Pleistocene, the Balkan Peninsula has experienced numerous geomorphological alterations due to eustatic movements of the sea, caused by climatic change and shifts from cold and dry to warm and humid conditions, as a result of the glacial-interglacial alterations (Perissoratis and Conispoliatis, 2003). Currently, throughout the peninsula, the populations of several rodents, such as *Spermophilus citellus* (Linnaeus, 1766) (Fraguedakis-Tsolis and Ondrias 1985) and *Mus spicilegus* (Petényi, 1882) (Mitsainas et al. 2009) display high genetic and morphological variation in comparison with populations of the same species from Northern Europe (Thanou et al., 2012).

There are five extant representatives of *Microtus* in Greece; two members of the European subgenus *Microtus*: *Microtus guentheri* (Danford and Alston, 1880) and *M. levis* (Miller, 1908) and three members of the subgenus *Terricola*: *M. subterraneus* (de Sélys-Longchamps, 1836), *M. felteni* (Malec and Storch, 1963) and *M. thomasi* (Barrett-Hamilton, 1908). *M. felteni* and *M. thomasi* are endemic to the southwestern Balkans (Thanou et al., 2012).

It is worth mentioning that the southernmost distributional borders of these species are found in Greece (Niethammer 1982c, d; Mitchell-Jones et al. 1999; Fraguedakis-Tsolis et al. 2009). These species are spread across the mainland of Greece, however the only islands known to be populated by members of this genus are Euboia, inhabited by *M. thomasi* (Mitchell-Jones 1999) and Lesvos, where the occurrence of *M. guentheri* has been observed (Stamatopoulos and Ondrias 1995; Mitchell-Jones et al. 1999) (Fig. 1). More specifically:

Microtus levis

M. levis, the distribution of which is shown in Figure 1a, is a member of the European subgenus *Microtus* and the only member of the “arvalis” group found in Greece and European Turkey

Greek populations of *M. levis* are smaller from their northern and eastern conspecifics; significant differences are observed in cranial measurements, as well (Thanou et al., 2012). The phylogenetic relationships between these populations are still unclear as the genetic distances between the lineages are relatively similar. The lineage of Greek arvicolines displays certain distinctive features that may imply the existence of a refugium in the southeast Balkan Peninsula, functioning as a gene pool for the populations of Greece and possibly of surrounding areas (Thanou et al. 2012).

Microtus guentheri

M. guentheri is a species of social voles occupying temperate grasslands, sub-tropical high-altitude grasslands and cultivated lowlands. They are distributed widely from the southeast Balkan Peninsula to West Turkey and areas of the Middle East (Fig. 1b). Kryštufek et al. (2009b) have discovered two separate lineages, dividing the species in a western and a southern clade, genetically distant enough to be independent species. The populations from Greece are significantly smaller and are characterized by different skull measurements, in comparison with their northern conspecifics (Thanou et al. 2012).

Microtus subterraneus

M. subterraneus is a member of the subgenus *Terricola* and its distribution includes the majority of eastern and central Europe (Fig. 1c). Many studies (Niethammer 1982b; Kryštufek et al. 1994; Fraguedakis-Tsolis et al. 2009) have reported numerous variations in size and morphological features in populations of this species from Greece when compared to other European populations. Morphological disparities are observed when comparing Greek populations of this species, as well (Thanou et al. 2012). The current *M. subterraneus* populations of Greece were probably sheltered in a Balkan refugium during the Pleistocene, as molecular analyses presented by Thanou et al. (2012) indicate. The same authors (Thanou et al. 2012) have shown that Greek *M. subterraneus* are more closely related to central European populations, than populations from Turkey, despite the latter is located significantly closer than the former.

Microtus felteni and Microtus thomasi

These two species are members of the *Microtus (Terricola)* group and endemics to the Balkans; *M. felteni* occurs only in Albania, Greece, North Macedonia and Serbia, while *M. thomasi* is found in Albania, Greece, Serbia, North Macedonia, Bosnia and Herzegovina, and Montenegro. Owing to some primitive characteristics they are considered as archaic in the *Microtus* group. *M. thomasi* populations from Greece are highly divergent from their conspecific of northern Balkans; significant disparities are observed between Greek *M. thomasi* populations, as well (Thanou et al. 2012). Jaarola et al. (2004) considers *M. felteni* and *M. thomasi*, as sister-species indicating common phylogenetic histories. Thanou et al. (2012) opposed this hypothesis, supporting the influence of Balkan refugia on the speciation of these endemics found in the peninsula and suggested that these two species shared a common refugium in the Balkan Peninsula to persevere through the ice ages, before expanding.

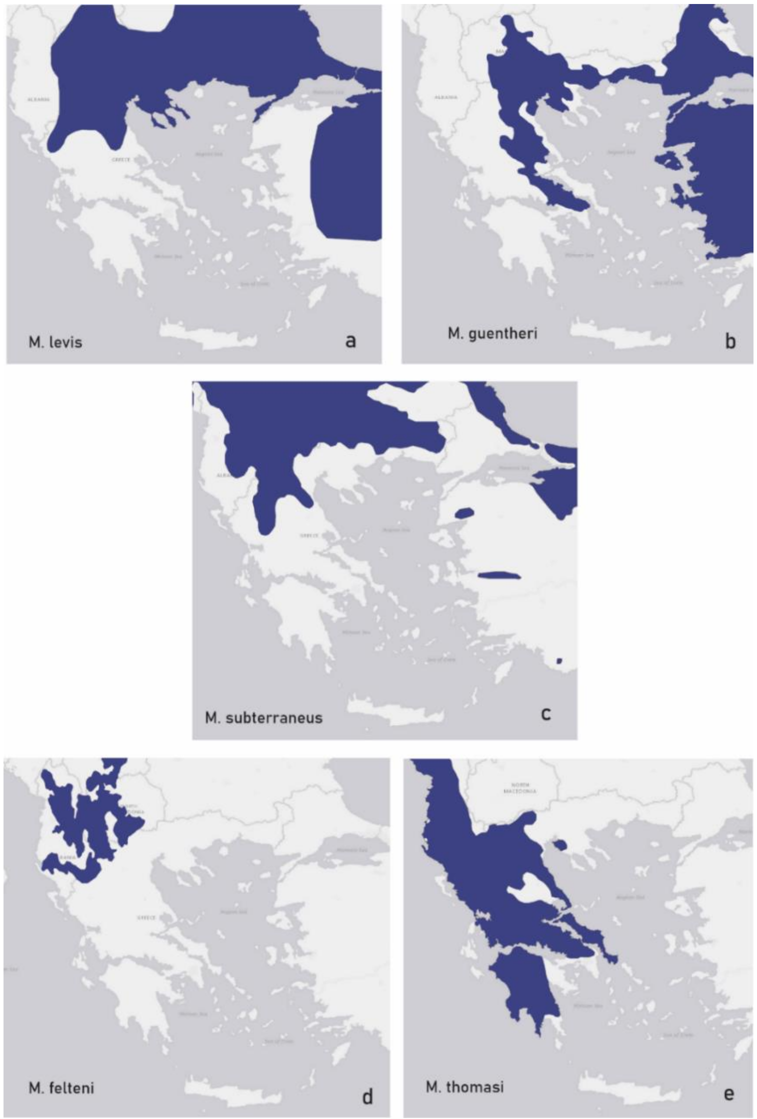


Figure 1: Map displaying the distribution of *M. levis* (1a), *M. guentheri* (1b), *M. subterraneus* (1c), *M. felteni* (1d) and *M. thomasi* (1e) in Greece (IUCN, 2020, modified).

Currently *M. thomasi* is the most widespread of the five vole species of Greece, occupying almost any grassland and crop field of continental Greece, from Western

Macedonia to the north to Peloponnese in the south (Mitsainas et al. 2010 and references therein) (Fig. 1e), contrary to *M. felteni*, restricted to alpine areas of the north-central mainland of Greece (Ondrias 1966; Vohralík and Sofianidou 1992; Mitchell-Jones 1999) (Fig. 1d).

Interestingly molecular analyses have shown that *M. thomasi* can be divided into two subgroups as the populations from the island of Euboia and southeast Sterea Ellada are distinctly differentiated from the voles of the remaining populations of Greece and other Balkan sites (Thanou et al. 2012). These observations support the legitimacy of the *atticus* clade as a separate taxon attributed to subspecific level (Tryfonopoulos et al. 2008) or even specific level (Rovatsos and Giagia Athanasopoulou 2011).

1.2. MORPHOLOGICAL ADAPTATIONS AND DENTAL CHARACTERISTICS OF ARVICOLINES

During Late Miocene, a series of dental features have developed simultaneously in several lineages of cricetids in different areas of Eurasia and North America, including the development of a more complex crown pattern and the acquisition of hypsodont molars. Hypsodonty was a critical advantage, because high-crowned teeth were more efficient for a diet consisted of silica-rich abrasive grasses (e.g. Poaceae), which were abundant throughout the Northern Hemisphere during that period (Fortelius et al. 2003).

Arvicolinae molars are, or in some cases tend to become, hypsodont, unlike cricetid molars which are typically brachyodont or bunodont and are characterized by cutting edges at the tubercles and absence of planar occlusal surface. While the enamel band is undifferentiated in primitive forms, it is mainly diversified in derived forms (Fejfar et al. 2011). The development of a more complex crown pattern in some cricetids, which happened progressively and started probably shortly before the transition to hypsodonty was completed, added to the same advantage. Increased amounts of enamel available for chewing ensured that the cutting edges of the molars would persevere throughout the lifespan of the rodent. Complexity of molar crown pattern was a result of a horizontal encasement of enamel walls on the margins of the teeth, forming parallel ridges (lophs)

This type of molars was optimized for chewing by using horizontal movements (Fejfar et al. 2011 and references therein). Arvicolines, among other mammals, evolved towards propalinal chewing (longitudinal movement of teeth), which increased enamel-to-enamel collision, thus reducing the effort of chewing to almost half by maximizing the effect of masticatory muscle movements.

The rodents of the subfamily Arvicolinae are defined by the following dental formula:

$$\frac{I = 1, C = 0, P = 0, M = 3}{i = 1, c = 0, p = 0, m = 3}$$

- Incisors: Two upper (I1, I2) and lower (i1, i2) rootless incisors (one on each side of the mandible and dentary) characterized by perpetual growth;
- Diastema: a short interval correlated with the absence of canines and premolars;
- Molars: Six upper (M1, M2, M3) and lower (m1, m2, m3) prismatic molars (three on each side of the mandible and dentary).

Although incisors can be used for taxonomic distinction, in most cases diagnoses are based on the highly differentiated molars. More specifically, regarding the diagnostic value of the occlusal surface, the teeth providing the most information are the first lower molars (m1) and the third upper molars (M3) (Borodin and Markova 2015; Rekovets and Kovalchuk 2017).

The first lower molars (m1) of the Arvicolinae are highly differentiated among the different forms. They are mostly rootless and prismatic, however in some primitive forms rooted molars are characteristic. Regardless of the taxon, arvicoline molars have a posterior loop, a series of enamel-bound triangles and an anterior cap; the spaces between the triangles are called re-entrant angles (Fig. 2).

In several cases, structural and histological features of molars can be used instead of the morphological characteristics of the occlusal surface, to identify arvicoline molars up to the genus or, in some cases, the species level. This method is particularly useful in cases when the material is fragmented (e.g. in pellets of birds of prey, carnivore excrements, material from alluvial type localities) and identification via other methods is impossible (Borodin and Markova 2015).

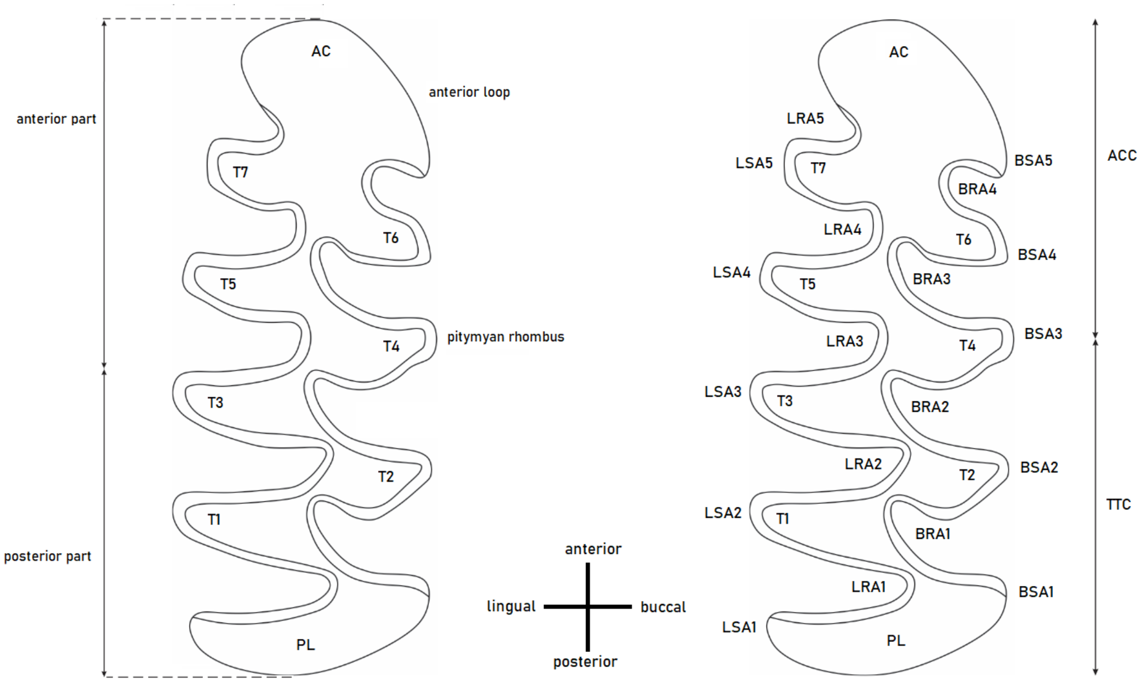


Figure 2: Occlusal surface of the lower first molar of a Microtus vole. Left: Nomenclature of the first lower molar of *Microtus* with the key elements of the occlusal surface (Brunet-Lecomte and Chaline 1991). Right: Cusps and triangles: AC – anterior cup; ACC – anteroconid complex; PL – posterior lobe; T – triangle; TTC – trigonid – talonid complex. Angles: BRA – buccal (labial) re-entrant angle (= syncline); BSA – buccal (labial) salient angle (= anticline); LRA – lingual re-entrant angle (syncline); LSA – lingual salient angle (anticline) (Kryštufek and Vohralík 2005).

1.3. GEOLOGICAL SETTING

Kalamakia Cave

Mani Peninsula is the middle of the three peninsulas formed in the southern part of Peloponnese. It is part of the Taygetos mountain range, mostly comprised of semi-crystalline, grey to white metamorphic limestones of Late Cretaceous to Early Eocene age; these limestones are part of the Mani geotectonic unit (Plattenkalk) (Papadopoulou-Vrynioti and Kampolis 2011; Thiebault 1982). Above the limestones lies the Phylite-Quartzite series (Sabatakakis et al. 2016).

Figure 3: Geographic position of Kalamakia Cave (source: maps google).

Kalamakia Cave is located on the western coast of Mani Peninsula, approximately 2.5 km northwest of the town of Areopolis, at the entrance of Itylo bay (Fig. 3) and is one of the several fossil-bearing caves of Mani Peninsula. The systematic excavations of the cave began in 1993 and were concluded in 2006, yielding several lithic and animal remains from the Middle Paleolithic (De Lumley and Darlas 1994; Darlas and De Lumley 1999, 2004).

The cave is 20 m deep and its entrance, lying approximately 10 m from the current seashore, 7 m wide and 8 m high. At the bottom of the cave there are two marine layers (Unit 0 and Unit II), the deposition of which are correlated with the marine transgressions of MIS 5e and 5c respectively. On top of these layers lie approximately 7 m of accumulated continental deposits, divided in three units (Units III, IV and VI). Units III and IV, combining for more than 4 of the total 7 m, are rich in Middle Palaeolithic remains, contrary to Unit VI which is almost culturally sterile (De Lumley and Darlas 1994; Darlas and De Lumley 1999, 2004).

The walls of the cave bear marks of *Lithophaga* sp. activity, a strong indication that the cave was submerged during the Pleistocene for a long period of time, probably until MIS 5e (Fig. 4a). During MIS 5d a marine regression reveals the cave, the floor of which is comprised by algae and limestone (Unit 0, marine layer), while sometime between 109-100 k BP (MIS 5c) the sea rises again to cover parts of the cave, depositing the beach rock layer (Unit II) (Fig. 4b). Remains discovered on both of these layers indicate that the cave was inhabited during those stages (Darlas and Psathi 2016).

Between 84,000-77,000 years BP, a regression of the sea removes the lower debris from the interior of the chamber, creating a solid erosional surface inclining towards the back of the cave, while limestone boulders detaching from the cave roof and exterior accumulate at the entrance of the cave (Fig. 4c). During the transition from MIS 4 to MIS 3 a new wave of debris accumulation at the entrance and the deposition of loose sediment in the interior of the cave (Unit IV; 39,000 years BP) took place (Fig. 4d) (Darlas and Psathi 2016).

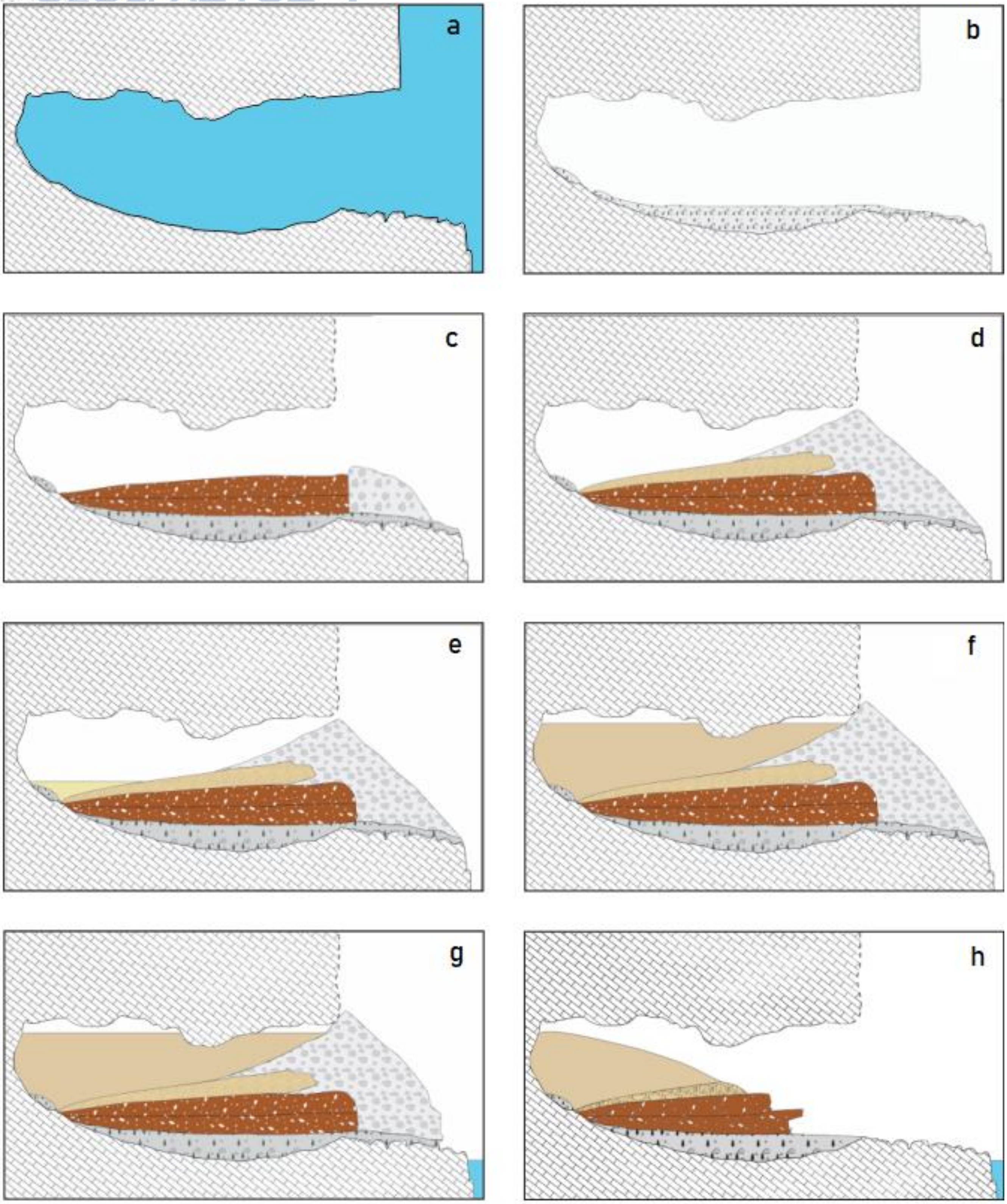


Figure 4: The evolution of Kalamakia Cave from MIS 5e (4a) to present (4h) (Darlas pers. comm., modified).

This stage marks the last presence of hominids in the interior of the cave, as the falling debris gradually blocked the entrance. The chamber of the cave, consisted of sediments and silt, is only accessible to small and larger mammals through smaller lateral caverns and tunnels (Darlas and Psathi 2016) (Fig. 4e).

During MIS 3 (45,000-40,000 years BP) the entrance of the cave is sealed and the interior is filled with silt rich sediments. Carnivore coprolites have been found in the sediments comprising Unit VI, indicating the presence of mammals in the cave during that period. The cave entrance is still blocked, suggesting lateral routes of entrance to the cave and possibly explaining the absence of hominid remains (Darlas and Psathi 2016) (Fig. 4f).

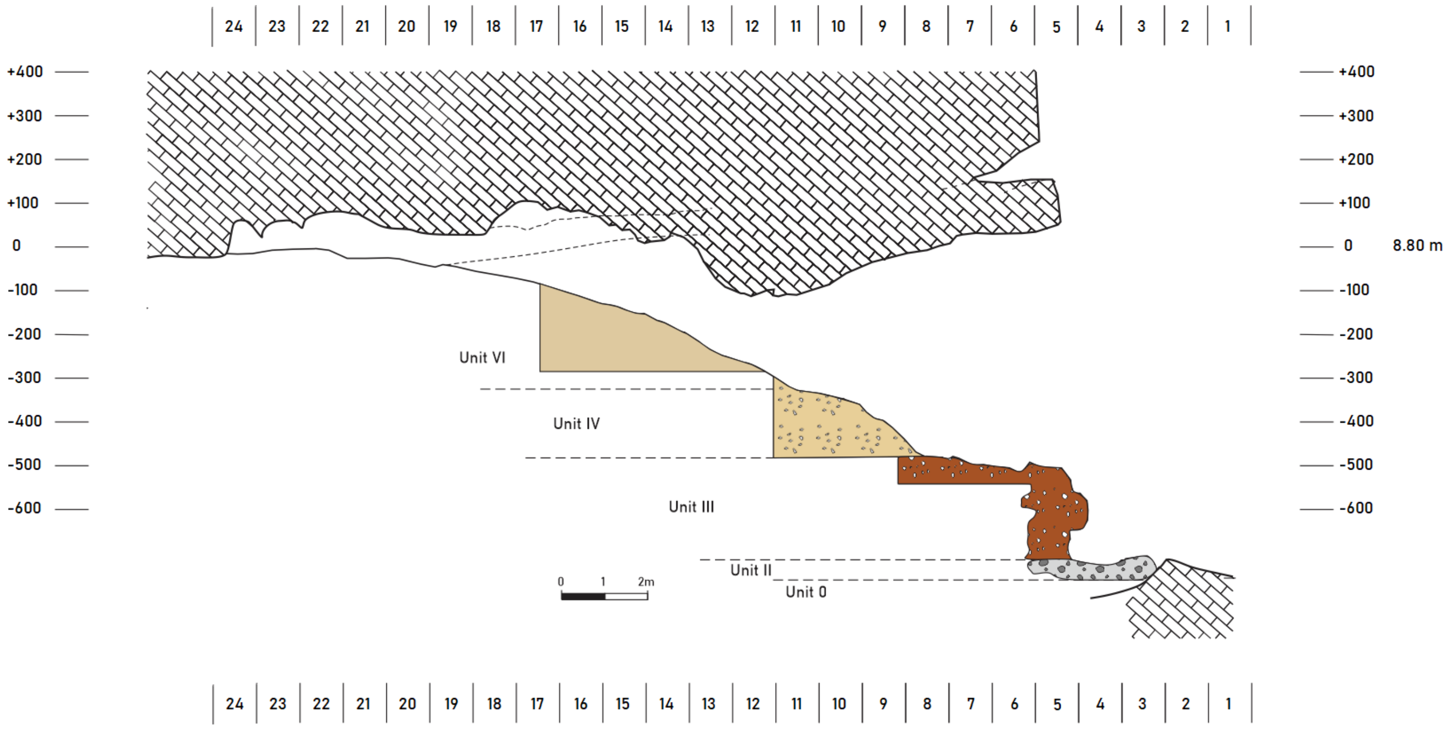


Figure 5: Excavation layers of Kalamakia cave (Units 0, II, III, IV and VI) (Darlas and Psathi 2016, modified).

The debris in the entrance are gradually being drifted by a new transgression of the sea (Fig. 4g), slowly removing the sealing of the cave entrance. Unit V is consisted of leftover debris and sterile sediments and thus it was not further investigated. Eventually, the boulders and the debris at the entrance of the cave are removed, revealing a series of layers in the chamber of the cave (Darlas and Psathi 2016) (Fig. 4h).

The excavation of the interior of the cave was conducted horizontally and all layers were examined thoroughly (Fig. 5). Unit VI has been dated to >39,000 years BP (^{14}C AMS dating on charcoal). The sediments of Unit IV were examined throughout their whole extent in an area of 4–10 m^2. Unit III is comprised of extremely hard, lithified sediments; thus, it was partly excavated on the top layers in an expanse of approximately 8 m^2. The palaeontological/archaeological deposits of the cave are probably dated between 100,000 and >39,000 years BP. Furthermore, a single specimen (coprolite) from Unit VI has been attributed to 22,410±120 years BP, by ^{14}C AMS dating (Darlas and Psathi 2016).

The fossil material discovered during the excavations indicate the existence of multiple taxa of large and small mammals, amphibians, reptiles and birds (Tab. 1), as well as hominids. More specifically, the large mammal fauna of the cave is consisted of 17 taxa with fallow deer (*Dama dama*) being the most common, followed by wild boar (*Sus scrofa*) and ibex (*Capra ibex*). A few fossils belonging to elephants and rhinoceros were also discovered in the assemblage. Carnivore remains have also been found throughout the stratigraphic sequence in low numbers, with the red fox (*Vulpes vulpes*) being the most abundant. Numerous land tortoise fossils have been collected from the lower half of Unit IV. These remains belong mainly to the marginated tortoise (*Testudo marginata*) and, to a lesser extent, to Hermann's tortoise (*Testudo hermanni*) (Darlas and Psathi 2016).

Several studies of large mammals (Gardeisen and Trantalidou 1998; Darlas and Psathi 2016) and analyses based on micro-vertebrate remains and pollen (Lebreton et al. 1998; Lebreton et al. 2008; Roger and Darlas 2008; Kolendrianou et al. 2020) have shown a relatively temperate climate characterized by open woodlands for Kalamakia Cave and the surrounding areas. More specifically, two pollen zones were identified by Lebreton et al. (2008) based on samples from a stalagmitic pillar: a zone of increased humidity indicating a supra-Mediterranean forest, and a zone indicating the presence of presteppic Mediterranean vegetation and an increase in Mediterranean shrublands. Though a correlation between the two zones and the units of Kalamakia Cave would not be entirely accurate, data from several studies (Roger and Darlas 2008; Darlas and Psathi 2016; Kolendrianou et al. 2020) suggest that the climate in Kalamakia Cave and the adjacent areas was mostly dry and warm, with the presence of wet periods. Analyses performed on remains of birds revealed a similar trend (a shift towards drier conditions) (Roger and Darlas 2008).

A total of 14 isolated human remains (mainly teeth) attributed to Neanderthals, have been discovered throughout the excavation site (Harvati et al. 2013, Harvati 2016). Hominids have systematically occupied the cave and are probably responsible for the structure and modification of the major part of the mammal and land tortoise remains accumulations. Taphonomic analyses, (emphasizing on the condition, fragmentation and body part representation) indicate methodical processing of ungulates (mostly fallow deer and ibex) and tortoises. Carnivore scavenging and predation activity has been observed on both mammal and tortoise remains in all layers of the excavation site, as well. Some short-term layers in Units IV and VI have been formed by carnivores. The majority of the observed carnivore marks are correlated with canid activity (Darlas and Psathi 2016).

Table 1: Faunal list from Kalamakia Cave and the surrounding areas (Darlas and Psathi 2016; Kolendrianou et al. 2020).

Artiodactyla
Sus scrofa
Cervus elaphus
Dama dama
Capreolus capreolus
Bos primigenius
Capra ibex

Carnivora
Ursus arctos
Panthera pardus
Lynx lynx
Felis silvestris
Canis lupus
Vulpes vulpes
Martes sp.
Mustela sp.

Chiroptera
Myotis cf. *blythii*
Pipistrellus sp.
Rhinolophus sp.

Lagomorpha
Lepus europaeus

Reptilia
Lacerta sp.
Pseudopus apodus
Ablepharus sp.
Anguis sp.
cf. Podarcis sp.
Gekkonidae
Scincidae
Coronella austriaca
Dolicophis caspius
Elaphe quatuorlineata
Eryx jaculus
Malpolon insignitus
Natrix natrix
Natrix sp.
Telescopus fallax
Vipera ammodytes
Zamenis longissimus
Zamenis situla
Colubridae indet.
Testudo marginata
Testudo hermanni

Proboscidea
Palaeoloxodon antiquus

Rodentia
Apodemus epimelas
Apodemus sp.
Chionomys nivalis
Glis glis
Sciurus vulgaris
Microtus arvalis
Microtus subterraneus
Microtus thomasi
Leporidae
Muridae

Insectivora
Erinaceus sp.
Talpa sp.
Crocidura suaveolens

Perissodactyla
Stephanorhinus sp.

Amphibia
Bufo bufo
Rana sp.

Aves
Puffinus puffinus
Accipiter nisus
Falco cf. *vespertinus*
Alectoris graeca
Coturnix coturnix
Eudromias morinellus
Chlidonias sp.
Columba livia/oenas
Otus scops
Athene noctua
Strix aluco
Apus apus
Apus cf. *pallidus*
Hirundo rustica
Certhia sp.
Turdus cf. *philomenos*
Corvus corone
cf. *Corvus monedula*
cf. *Pica pica*
Pyrrhocorax pyrrhocorax
Emberiza citrinella

Primates
Homo neanderthalensis

Klissoura Cave 1

Klissoura Cave 1 is located in the northeastern border of Argive Plain, at the entrance of Berbadiotis river gorge called Klissoura (narrow in Greek), at a distance of 7 km from the ancient city of Mycenae and 4 km from the nearest modern-day village of Prosymna (Fig. 6).

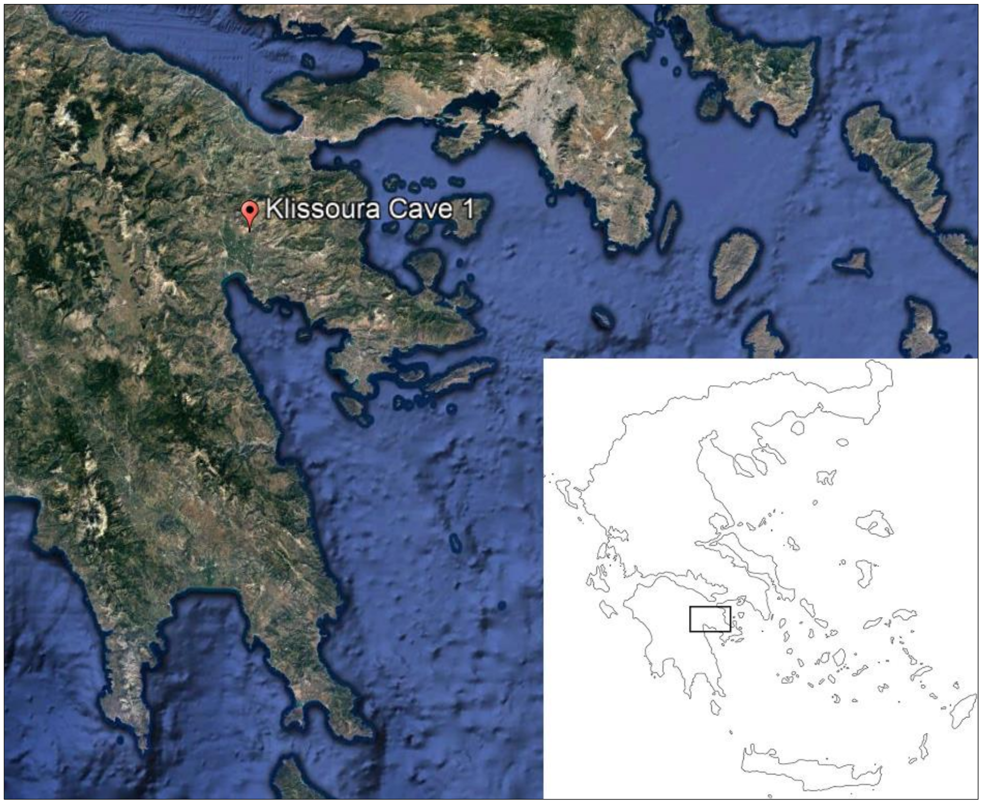


Figure 6: Geographic position of Klissoura Cave 1 (source: maps google).

The Argive Plain is a graben formed during the Neogene, filled with fluvial, alluvial and lacustrine deposits. The area around the cave consists of Triassic to Jurassic, medium to thick bedded gray and white limestones, which switch laterally to thin bedded limestones with intercalations of cherts (radiolarites) and nodules (Karkanas 2010).

The gorge is more than 2 km long and 500 m wide, connecting the Argive Plain with the Limnes plateau through Berbati valley. Lying at an elevation of 114 m above sea level and ca. 12 m above the ephemeral Berbadiotis riverbed, Klissoura Cave 1 faces southeast, towards the Argive Plain. The cave is formed in highly karstified gray Triassic limestones and its entrance is blocked by limestone boulders, probably due to a nearby chimney collapse (Karkanas 2010).

The excavation, a project conducted by the Ephoreia of Paleoanthropology and Speleology of the Ministry of Culture of Greece and the Institute of Archaeology of the Jagiellonian University of Kraków, started 1992, in an effort to determine the neolithization of NW Peloponnese. The gorge was initially mentioned as a potential location of interest by Giannopoulos and Koumouzelis in 1992, during a brief survey around the slopes to north of the Argive Plain. Subsequent excavations revealed the presence of hominids in the valley and gorge from the Paleolithic to the Byzantine Era (Well and Runnels 1996). To ensure that the findings were limited to the gorge, several excavations were organized in the slopes of the mountains east and west of the gorge. Only six among a total of 35 caves and rock shelters contained paleontological/archaeological remains, with Klissoura Cave 1 being the richest (Koumouzelis et al. 1996; Koumouzelis et al. 2004).

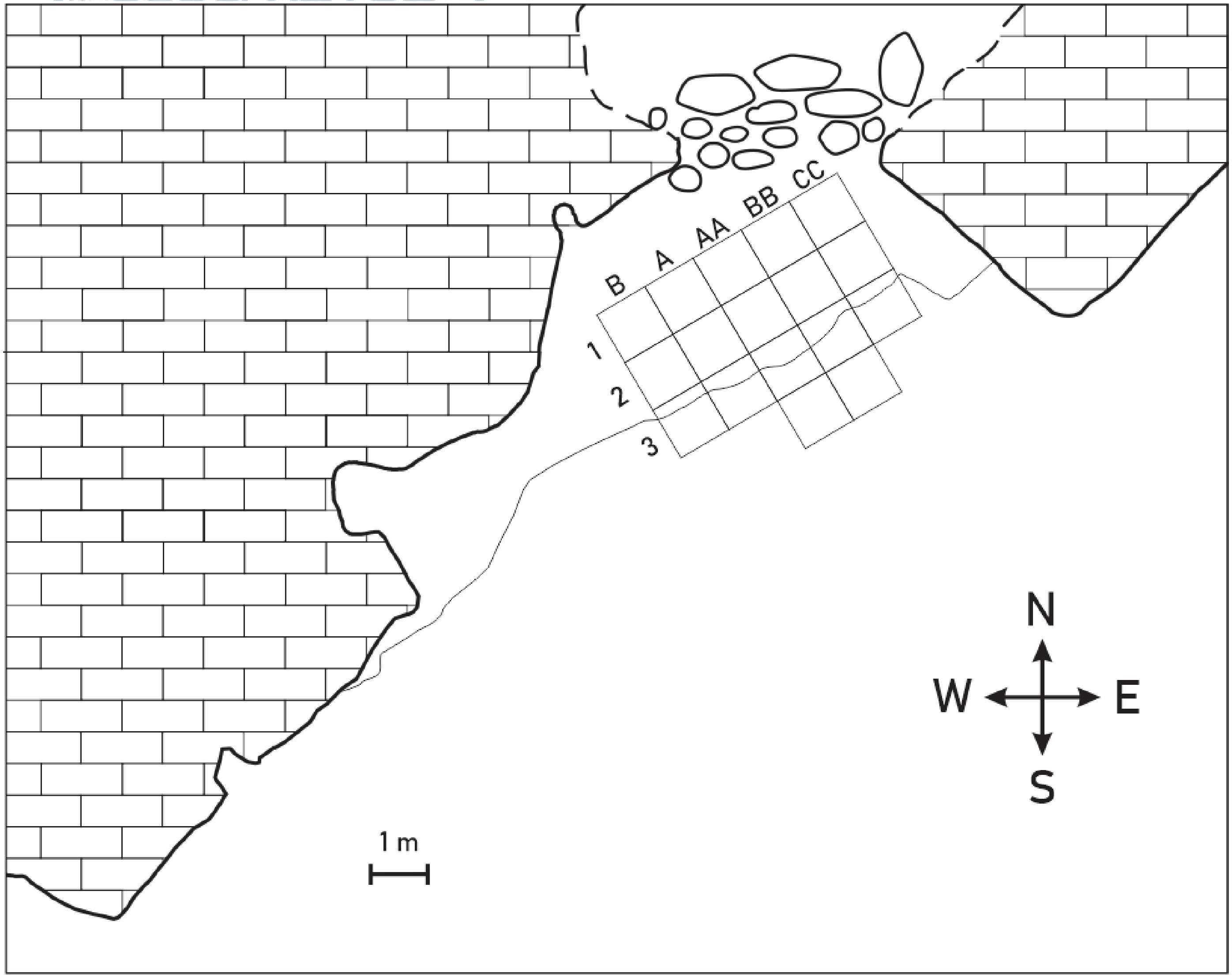


Figure 7: Excavation grid of Klissoura Cave 1. The dripping line is marked by the dotted line; the dashed line marks the cave chamber (Karkanas 2010, modified).

The excavation, conducted at the entrance of Klissoura Cave 1, started in 1993 and was completed in 2006. The sampling area was divided into several 1X1 squares (Fig. 7). Each square was subsequently excavated as successive horizons of 5 cm thick sediment. The total depth of the excavation was 6 m, divided into 21 layers and several sublayers. The correlation between ages, Klissoura Cave 1 layers and Marine Isotopic Stages (MIS) is given in Table 2.

Table 2: Table displaying the correlation between cultural periods and layers of Klissoura Cave 1 (Kolendrianou, 2015).

Cultural content	Layer	Marine Isotopic Stage (MIS)	Estimated Age (BP)
Mesolithic	3	1	-
Mesolithic	3a	1	-
Epigravettian	IIb	2	-
Epigravettian	IId	2	-
Aurignacian - Gravettian	6	2-3	-
Aurignacian - Gravettian	6a	2-3	-
Upper Palaeolithic	III'	3	-
Upper Palaeolithic	III'a	3	-
Upper Palaeolithic	III''	3	-
Upper Palaeolithic	III''/IIIc	3	-
Middle Aurignacian	IIIe	3	-
Middle Aurignacian	IIIg/IIIg carb	3	-
Middle Aurignacian	III''' bottom	3	-
Lower Aurignacian	IV/VI	3	-
Uluzzian (Early Upper Palaeolithic)	V	3	-
Middle Palaeolithic	VI	3	-
Middle Palaeolithic	VII	3	-
Middle Palaeolithic	VIII	4-3	55000-57000
Middle Palaeolithic	X	4-3	-
Middle Palaeolithic	XI/XI carb	-	-
Middle Palaeolithic	XII	-	-
Middle Palaeolithic	XIII	4	-
Middle Palaeolithic	XIV	4	-
Middle Palaeolithic	XV	4-5	-
Middle Palaeolithic	XVa	4-5	77000-79000
Middle Palaeolithic	XVa/XVI	4-5	-
Middle Palaeolithic	XVI	5a	-
Middle Palaeolithic	XVII	5b	-
Middle Palaeolithic	XVIII	5b	90000
Middle Palaeolithic	XIX	5c	95000-98000
Middle Palaeolithic	XXa	5c	-
Middle Palaeolithic	XXc	5d-e	-
Middle Palaeolithic	XXe	5e	-
Middle Palaeolithic	XXI	6	150000-200000

Apart from micro-vertebrate remains, Klissoura Cave 1 contained remains of large mammals, birds and reptiles (Tab. 3).

Table 3: Faunal list from Klissoura Cave 1 and the surrounding areas (Kolendrianou, 2015).

Artiodactyla	***Reptilia***	***Rodentia***	***Aves***
Dama dama	*Testudo marginata*	*Arvicola* sp.	*Otis tarda*
Capra ibex	*Testudo hermanni*	*Microtus* sp.	*Alectoris graeca*
Bos primigenius	*Testudo graeca*	*Apodemus flavicolis*	
Sus scrofa	*Dolichophis caspius*	*Apodemus sylvaticus*	***Insectivora***
Cervus elaphus	*Malpolon monspessulanus*	*Apodemus epimelas*	*Erinaceus* sp.
Capreolus capreolus	*Telescopus fallax*	*Mus musculus*	*Crocidura suaveolens*
Rupicapra rupicapra		*Mus macedonicus*	*Crocidura leucodon*
	Amphibia	*Sciurus* sp.	*Suncus* sp.
Perissodactyla	*Bufo* sp.		*Neomys* sp.
Equus hydruntius	*Rana* sp.	***Chiroptera***	*Sorex* sp.
	Pelophylax kurtmuelleri	Rhinolophidae sp.	*Talpa* sp.
Lagomorpha	*Hyla* sp.		
Lepus europaeus	Salamandridae sp.	***Carnivora***	***Primates***
Oryctolagus cuniculus		*Meles meles*	*Homo neanderthalensis*

Layer XXI is characterized by the presence of remains belonging to small rodents (*Microtus* sp., *Apodemus* sp.) and, occasional remains of insectivores, lizards, snakes and hedgehogs. No large vertebrates were discovered in this layer of Klissoura Cave 1.

A significant increase in the number and abundance of taxa is observed, in layer XIX. Remains of various taxa such as *Crocidura* spp., Bufonidae, Muridae, land tortoises and taxa that were not present in the previous layer assemblages (*Erinaceus* sp., lizards, snakes) indicate the presence of humid woodlands; this indication confirms previous estimations of the deposition of this layer during the warm episode of MIS 5c.

Layer XVIII is the richest layer of the cave, in terms of micro-vertebrate remains, contrary to significantly less fossils of large mammals. The new taxa discovered (Salamandridae, *Talpa* sp., *Neomys* sp.) are correlated with open humid meadows, something that is uncharacteristic during the cold episode of MIS 5b. The considerable increase of micro-vertebrate remains in this layer is correlated with an increase in the populations of birds of prey in Klissoura Cave 1 and the surrounding area, or with the slow rate of sediment deposition (lag deposit) at that period (Starkovich 2011).

In layers X-XVII large taxa are significantly more common compared to micro-vertebrates, suggesting that ungulates were the most dominant group in the faunal assemblages of Klissoura Cave 1 and the surrounding areas. Considering that the vegetation and the climatic conditions of Peloponnese during that period correspond to MIS 4 (or to a transition towards MIS 4), it is safe to assume that grazers were inhabiting dry and open fields, while browsers occupied the humid woodlands that appeared during warm intervals (Starkovich 2011).

Layers XV-XVII, XIV-XIII (layers XII and XI were considered as secondary depositions and therefore were not included in the analyses) and X were deposited during the late stages of MIS 5 and MIS 4, during which the vegetation varied from humid forest, to mixed forests and steppes, respectively. These habitats were occupied by wild boars, red deer and roe deer (to a lesser degree) and bovids, equids, ibex and great bustards, respectively. Brown hare, land tortoises and fallow deer were also present in all of the mentioned biotopes. The presence of micro-vertebrate remains in these layers is probably circumstantial (Starkovich 2011).

The distribution of species in the previously mentioned layers is rather typical. However, a deficiency in great bustard and other bird remains was observed in layer VIII (overlying the previously mentioned layers and formed during similar conditions). Small quantities of micro-vertebrate remains were also discovered in this layer. These observations are probably related to a reduction of dry open habitats in the valley or a possible change of the predatory activity in the area (Starkovich 2011).

2. MATERIALS AND METHODS

Fossil material

The studied fossil material for this study comprised of a total of 124 lower first arvicoline molars (identified as *Microtus* sp. based on their morphology and referred to as “fossil” in the following analyses) from two palaeontological sites. These samples were selected and processed in order to examine morphological adaptations, detect evolutionary trends and, in the case of Kalamakia Cave, to test the validity of already published taxonomic identification. For both excavation sites, identification was performed to the level of subgenus using geometric morphometric criteria on the first lower molars.

More specifically, regarding the Kalamakia Cave site, 89 molars were selected equally and randomly from three different layers (Unit III, Unit IV and Unit VI) which correlate with Marine Isotopic Stages 5a, 3 and 2, respectively. Unit III and VI levels are represented by 30 molars, whereas level IV is represented by 29 molars.

In the case of the Klissoura Cave 1, the samples were collected from six levels (VIII, XII, XVa, XVIII, XIX and XXI) which correlate with Marine Isotopic Stages 3, 3, 4-5, 5b, 5c and 6, respectively. However, due to shortage of well-preserved teeth from this site, several levels (VIII, XII, XVa and XVIII) are represented by a single molar; levels XIX and XXI are represented by 25 and 6 samples respectively.

All fossil samples were selected based on their state of preservation and only molars with undamaged occlusal surfaces were used in the analyses. The occlusal surface of specimens was photographed with a Canon G12 Powershot camera under a SZM1 Optika stereoscope.

Modern samples

A total of 147 lower first molars were collected for the extant arvicoline reference dataset. The species used for the creation of the extant database are the five extant *Microtus* species found in Greece. More specifically, *M. guentheri* and *M. levis* were represented by a sample size of 30 each?, *M. subterraneus* by 23, *M. felteni* by 14 samples and *M. thomasi* was represented by a total of 50 samples: 20 samples from individuals from the mainland of Greece (Epirus) and 30 samples from individuals from Peloponnese. The molars from the extant specimens were identified to the species level by members of the Laboratory of Zoology (Section of Animal Biology, Dept. of Biology, University of Patras) based on the individuals' external morphology criteria and DNA data. Subsequently, they were photographed under a Zeiss stereoscope with an attached Zeiss AxioCam Erc 5s camera by a member of the Museum of Zoology (Section of Animal Biology, Dept. of Biology, University of Patras) and were provided to the author of the present study as reference material.

The brightness and contrast of all photographs (both from the extant and fossil specimen database) were adjusted with GIMP 2.10 to highlight the features for digitization, as suggested by Zelditch et al. (2012).

Landmark schemes and digitization

The selection of landmarks used for the analyses of shape in this thesis was based on the work of Wallace (2006) with five additional landmarks in the anterior part of the molar (Tab. 4 and Fig. 8). The use of landmarks 22 to 26 (Kolendrianou et al. 2020) provided more accurate results in the identification and discrimination of the extant specimens (upon which the landmarks were originally tested). The landmarks were digitized directly on the photographs.

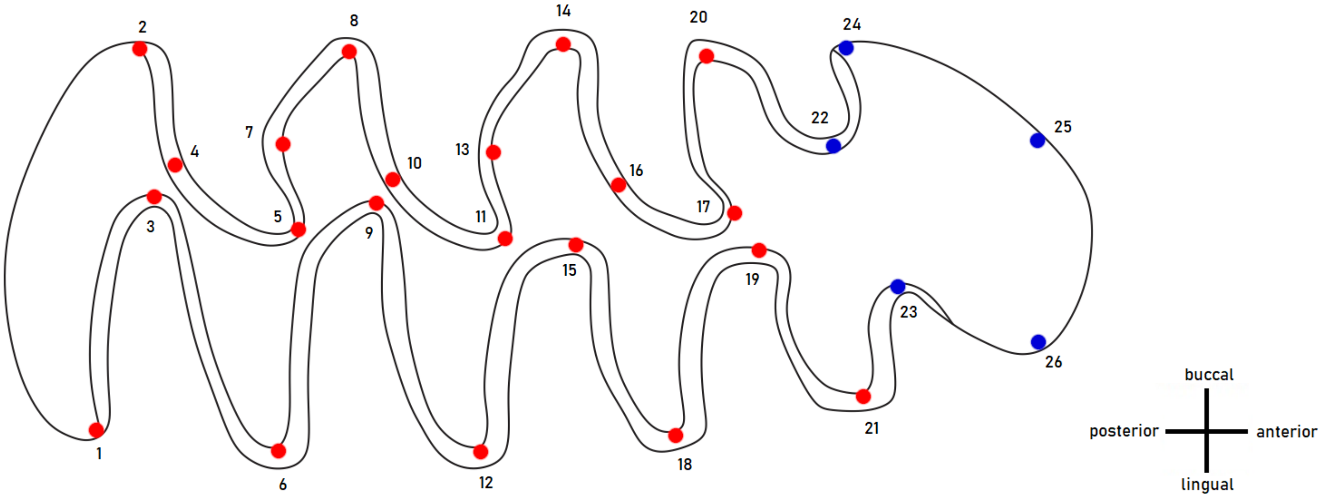


Figure 8: Landmarks used in the analyses of lower first molars from Kalamakia Cave and Klissoura Cave 1 sites. Landmarks pointed with red dots (1-21) were adopted by Wallace (2006) and landmarks pointed with blue dots (22-26) were added by Kolendrianou et al. (2020) (Tab. 4).

Table 4: Position description of the landmarks based on Wallace (2006) (landmarks 1-21, marked with red dots in Figure 8) and the five additional landmarks added by Kolendrianou et al. (2020) (landmarks 22-26, marked with blue dots in Fig. 8).

Landmark	Position
1	Terminal end of enamel band on the lingual side of the posterior loop (LSA1)
2	Terminal end of enamel band on the buccal side of the posterior loop (BSA1)
3	Most medial point of lingual re-entrant angle 1 (LRA1), at the boundary between enamel and cement
4	External edge of the enamel band at point of maximum curvature along the leading edge of the posterior loop
5	Most medial point of buccal re-entrant angle 1 (BRA1), at the boundary between enamel and cement
6	Intersection of leading and trailing edges of enamel on triangle 1 (T1)
7	Most posterior position along the boundary of dentine and enamel of triangle 2 (T2)
8	Intersection of the leading and trailing edges of enamel on triangle 2 (T2)
9	Most medial point of lingual re-entrant angle 2 (LRA2), at the boundary between enamel and cement
10	Outside edge of the enamel band at point of maximum curvature along the leading edge of triangle 2 (T2)
11	Most medial point of buccal re-entrant angle 2 (BRA2), at the boundary between enamel and cement
12	Intersection of leading and trailing edges of enamel on triangle 3 (T3)
13	Most posterior position along the boundary of dentine and enamel of triangle 4 (T4)
14	Intersection of the leading and trailing edges of enamel on triangle 4 (T4)
15	Most medial point of lingual re-entrant angle 3 (LRA3), at the boundary between enamel and cement
16	Outside edge of the enamel band at point of maximum curvature along the leading edge of triangle 4 (T4)
17	Most medial point of buccal re-entrant angle 3 (BRA3), at the boundary between enamel and cement
18	Intersection of leading and trailing edges of enamel on triangle 5 (T5)
19	Most medial point of lingual re-entrant angle 4 (LRA4), at the boundary between enamel and cement
20	Intersection of the leading and trailing edges of enamel on triangle 6 (T6)
21	Intersection of leading and trailing edges of enamel on triangle 7 (T7)
22	Point of maximum curvature of buccal re-entrant angle 4 (BRA4)
23	Point of maximum curvature of lingual re-entrant angle 5 (LRA5)
24	Point of maximum curvature of the buccal tip of the anterior cup
25	Midpoint of the anterior loop of the anterior cup
26	Point of maximum curvature of the lingual tip of the anterior cup

Based on the results of the present-day specimen database, the complete set of all 26 landmarks was applied on the dataset of both fossilized and modern molars. The programs used in the analysis were tpsDig2 2.17 (Rohlf 2013), MorphoJ (Klingerberg 2011) and PAST 3.25 (Hammer et al. 2001). A Canonical Variance Analysis (CVA) was conducted for the shape of the molars and, a one-way Analysis of Variance (ANOVA similarity test) was performed based on the centroid size values exported from MorphoJ, in order to check the null hypothesis that several univariate samples (centroid size values for each specimen) were taken from populations with the same mean (species).

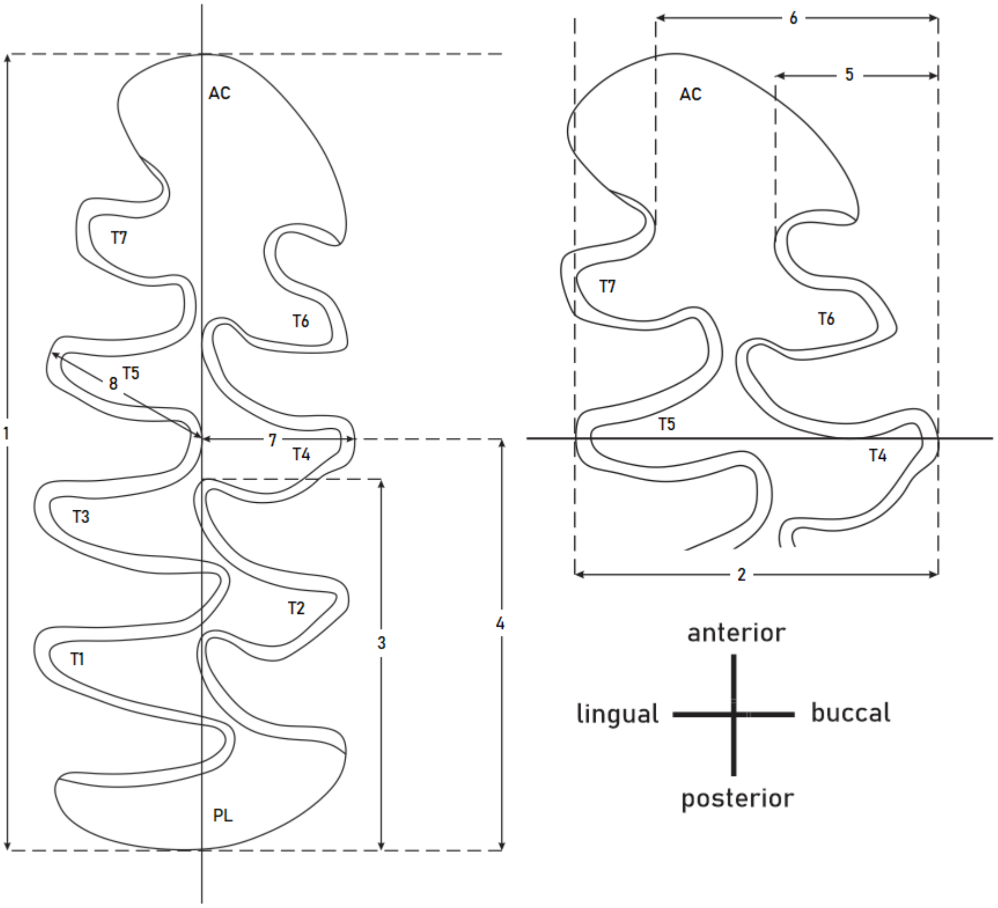


Figure 9: Occlusal view of the first lower molar of *Microtus* with the 8 measurements used in this study. Measurements 1-6 were selected based on the works of Montuire and Brunet-Lecomte (2004) and Brunet-Lecomte (2010) and measurements 7-8 were adopted from Navarro et al. (2018). Each measure is markev by the prefix V (V1-V8).

In addition to landmark analysis, the general morphology of the specimens was analyzed by a series of measurements of the occlusal surface of the molar (Fig. 9). These variables were selected to observe the quantification of the morphological differentiations in certain parts of the molar. The analyses were based on a total of 8 measurements: the 6 most informative among a total of 23 measurements from the work of Montuire and Brunet-Lecomte (2004) and 2 measurements adopted from the work of Navarro et al., 2018 (Fig. 9) and a series of indices.

The analyses were conducted on the following six parameters: Overall length = V1, Development of the anterior part = (V1-V3)/V1 x 100, Tilt of the pitymyan rhombus = V4-V3, Closure of the anterior loop = (V6-V5)/V2 x 100, Length/width ratio = V1/V2 (Montuire and Brunet-Lecomte, 2004; Brunet-Lecomte, 2010) and T5/T4 ratio = V8/V7 (Navarro et al., 2018) (Fig. 9). Centroid size, the square root of the sum of the squared distances between each point and the centroid of the configuration, was also used to measure size.

The T5/T4 length ratio index (V8/V7) (Fig. 9) is a useful tool in fossil species determination, especially in the absence of other diagnostic features (Nadachowski 1984; Navarro et al. 2018), since the degree of asymmetry between Triangle 4 and Triangle 5 varies among species.

The overall size of the molar is correlated with environmental changes as molars tend to be larger in individuals living in warm conditions (Montuire and Brunet-Lecomte 2004; Piras et al. 2009).

The tilt of the pitymyan rhombus (V4-V3) is one of the most significant indices, frequently used to distinguish the various vole species (Fig. 9). When used as a parameter at an intraspecific level this index yields information about climatic conditions, since according to studies the pitymyan rhombus is generally more tilted in voles living in cold conditions, and habitat adaptations, as tilt is correlated with fluctuations in altitude and terrain (Montuire and Brunet-Lecomte 2004; Brunet-Lecomte et al. 2010).

The closure of the anterior loop is an important criterion, used to distinguish extant and Pleistocene representatives of the subgenus *Terricola* (Brunet-Lecomte 1990) and certain geographical populations of arvicolines (Brunet-Lecomte 2004). However, when used for intraspecific level it is of lesser significance (Brunet-Lecomte et al. 2010).

3. RESULTS

Geometric morphometrics

Initially, the landmark scheme proposed by Wallace (2006) was applied to the extant arvicoline dataset. Landmarks 1 to 21 (Tab. 4 and Fig. 8) provided information about the divergence of the shape of the molar; however, the discrimination of the present-day vole species in the analyses performed was not adequately distinct (Fig. 10). As a result, the addition of further landmarks in the anterior cup (AC) of the molar was considered essential.

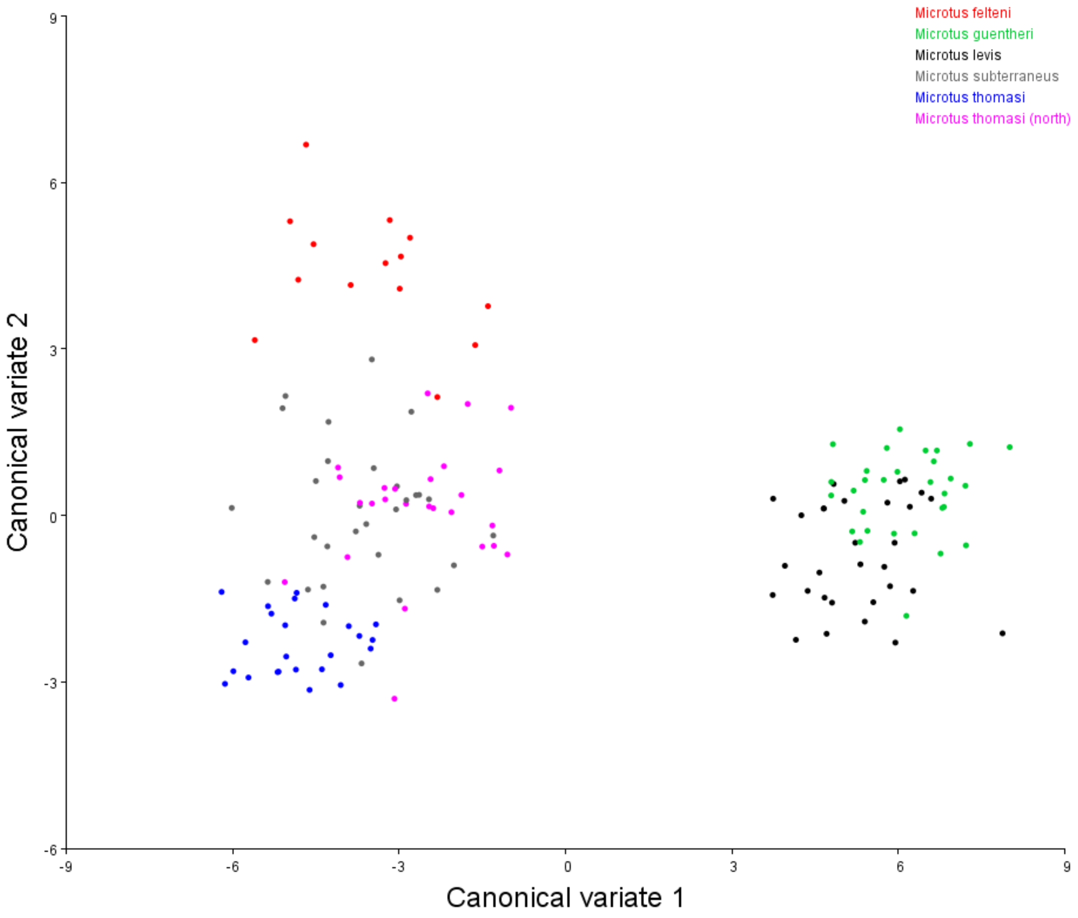


Figure 10: Canonical Variate Analysis (CVA) based on molar shape of present-day arvicoline populations from Greece with landmarks proposed by Wallace (2006).

The distinction between the subgenera *Microtus* and *Terricola* and their representatives is clearly demonstrated in the Canonical Variate Analyses (CVA) chart (Fig. 11), based on the adopted landmark scheme of 26 landmarks (Kolendrianou et al. 2020). *M. guentheri and M. levis*, members of the subgenus *Microtus*, are grouped on the left side of the chart, isolated from the *Terricola* populations (*M. felteni*, *M. subterraneus* and *M. thomasi*) that clustered on the right part of the chart. A slight overlap in the clusters of *M. felteni* and *M. thomasi* individuals is observed.

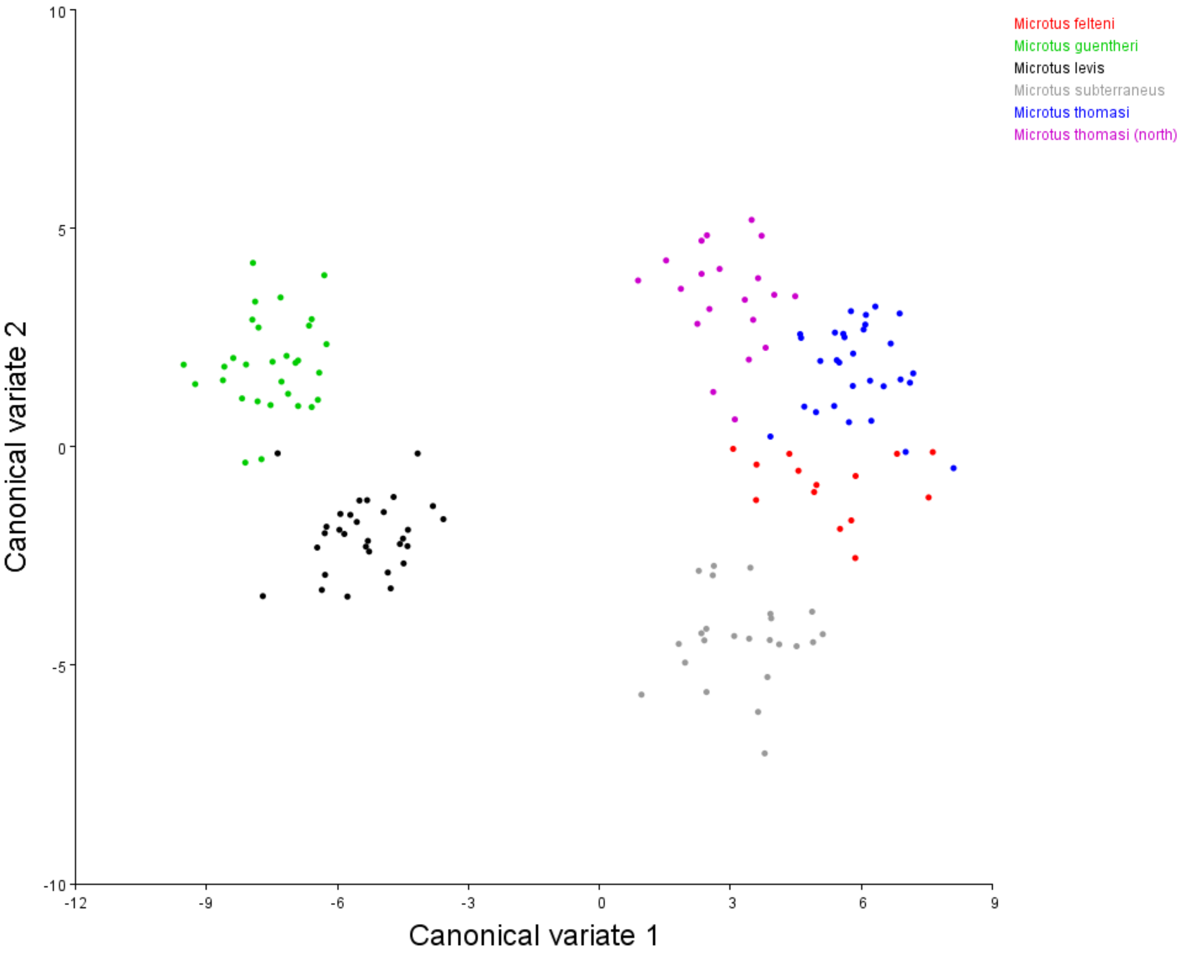


Figure 11: Canonical variate analysis based on molar shape of *M. felteni* (red), *M. guentheri* (green), *M. levis* (black), *M. subterraneus* (grey), *M. thomasi* (blue and pink) populations from Greece.

The most significant differentiation in the molar shape of extant arvicolines is observed at the third lingual re-entrant angle (LRA3), followed by lesser but still notable changes in the second, third and fourth buccal re-entrant angles (BRA2, BRA3 and BRA4), represented in the analyses by landmarks 15, 11, 17 and 22, respectively. Changes observed in the posterior loop (PL), the anterior cup (AC), the buccal salient angles (BSA) and lingual salient angles (LSA) are trivial (Fig. 12).

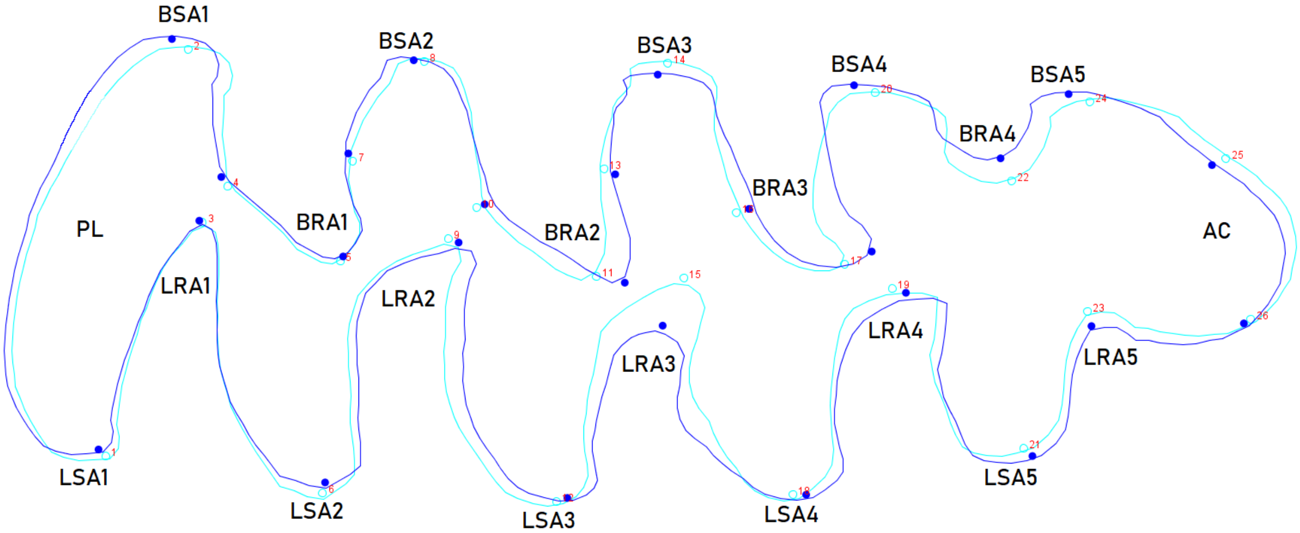


Figure 12: Visual representation of the changes in the occlusal surface of the molars of the extant arvicoline species of Greece. The light blue line marks the mean shape and the blue line marks the landmark displacement.

Fossil specimens

A Canonical Variate Analysis (CVA) was conducted, to examine the fossil specimens from Kalamakia Cave and Klissoura Cave 1. The analysis displayed significant divergence in the shape of the molars of the individuals from these sites, despite a small overlapping area in the chart (Fig. 13).

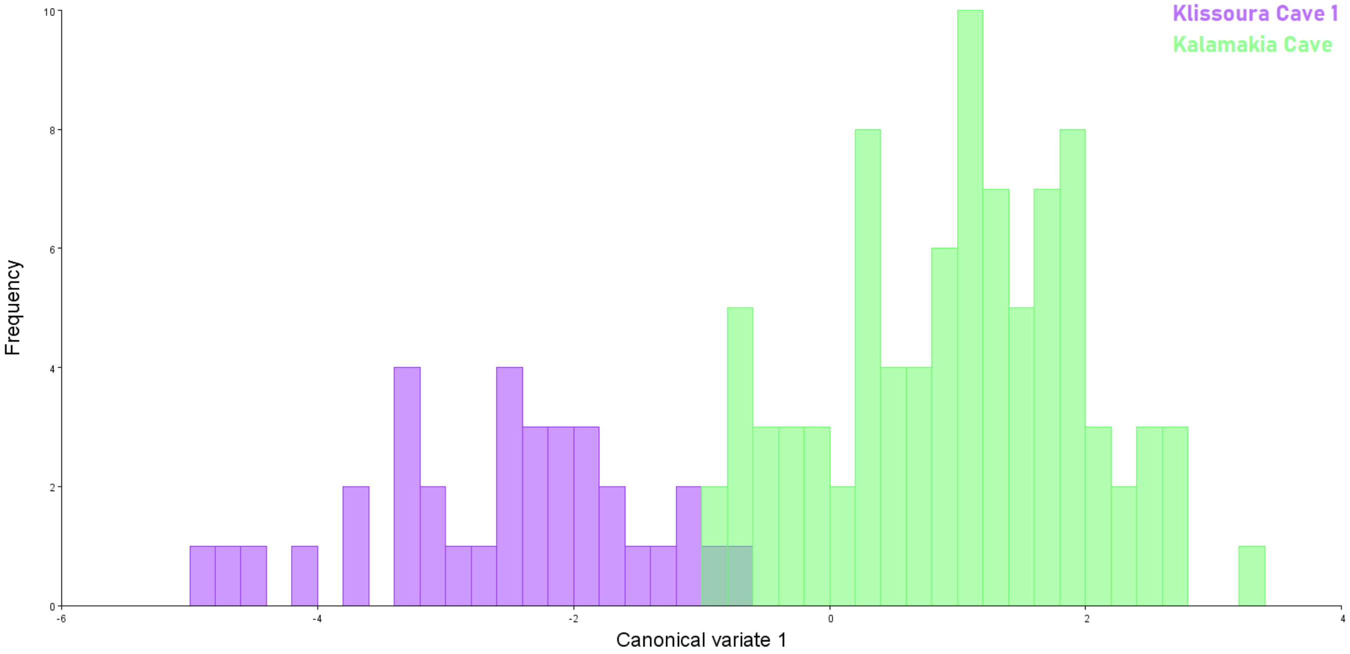


Figure 13: Canonical variate analysis based on molar shape of fossil arvicoline populations from Kalamakia Cave (green) and Klissoura Cave 1 (purple).

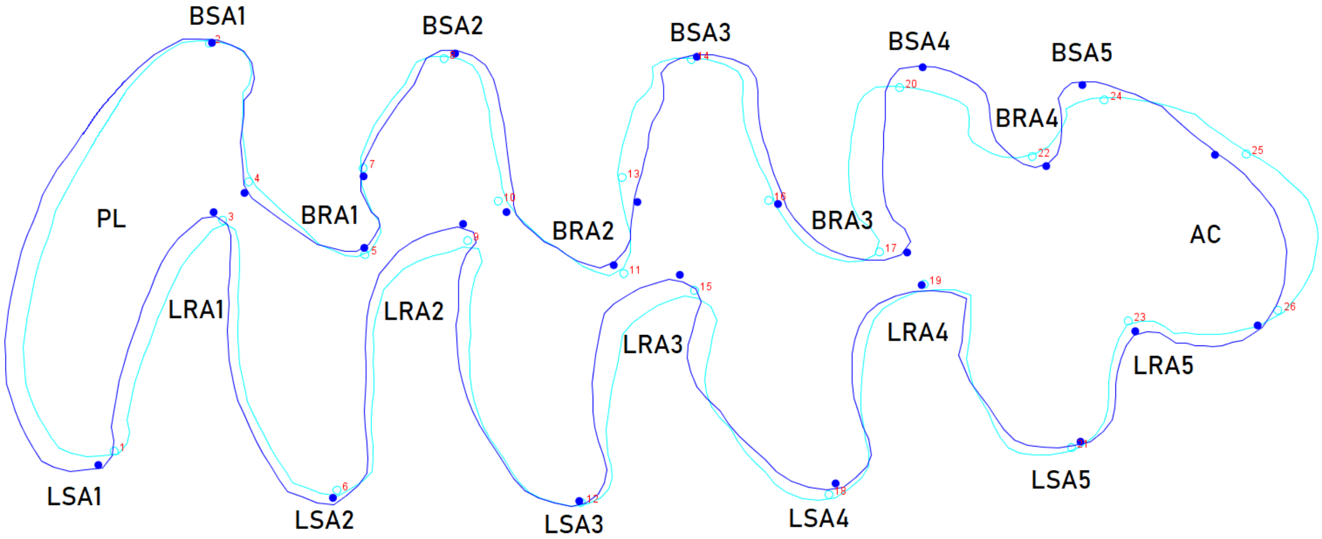


Figure 14: Visual representation of the variations of shape in the occlusal surface of the molars of the fossil specimens from Kalamakia Cave and Klissoura Cave 1.

The examination of the occlusal surface of the molars from these sites revealed several differences, the most significant of which was observed at the most posterior position of triangle 4 (T4), the intersection of leading and trailing edges of the enamel on triangle 6 (T6), several points along the anterior cup (AC) and the third buccal re-entrant angle (BRA3). Less and not as significant changes were observed in the posterior part of the molar (Fig. 14).

The specimens were separated into two categories: those collected from layers deposited during warm MIS and those collected from layers deposited during cold MIS. Subsequently, a Canonical Variate Analysis was performed on the specimens, which revealed differences between molars from individuals living in cold and warm conditions in both sites, despite an overlap observed in the chart (Fig. 15).

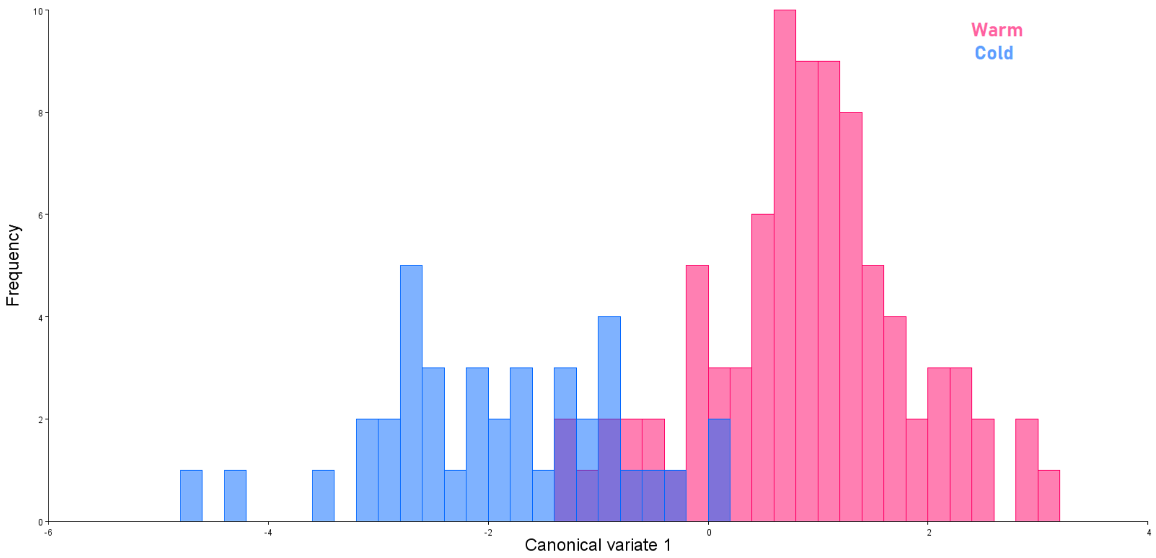


Figure 15: Canonical variate analysis based on changes of the molar shape during cold periods (blue) and warm periods (red).

Significant disparities were observed in the middle and anterior part of the molars (triangles 4 to 7 and anterior cup). The most essential changes were detected at the third lingual re-entrant angle (LRA3), the third buccal re-entrant angle (BRA3) and the anterior cap (AC). Alterations in the posterior part of the tooth were insignificant (Fig. 16).

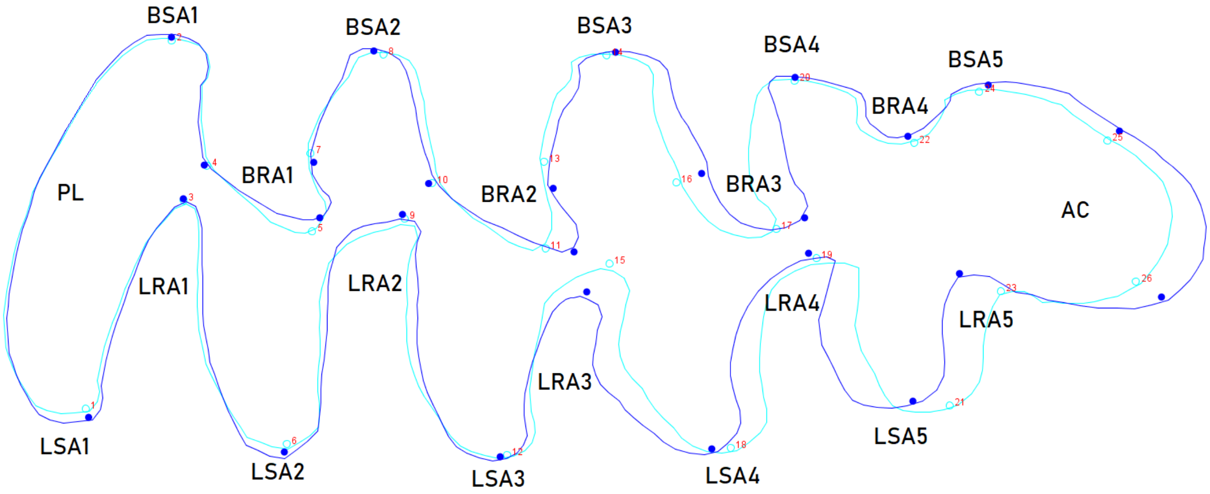


Figure 16: Visual representation of the changes in the occlusal surface of the molars of the fossil specimens from Kalamakia Cave and Klissoura Cave 1.Light blue marks the mean shape during cold conditions, while dark blue marks the mean shape during warm conditions.

All specimens

Subsequently, all specimens were added in the analyses to examine similarities with the extant populations, based on the overall shape of the molar (Fig. 17).

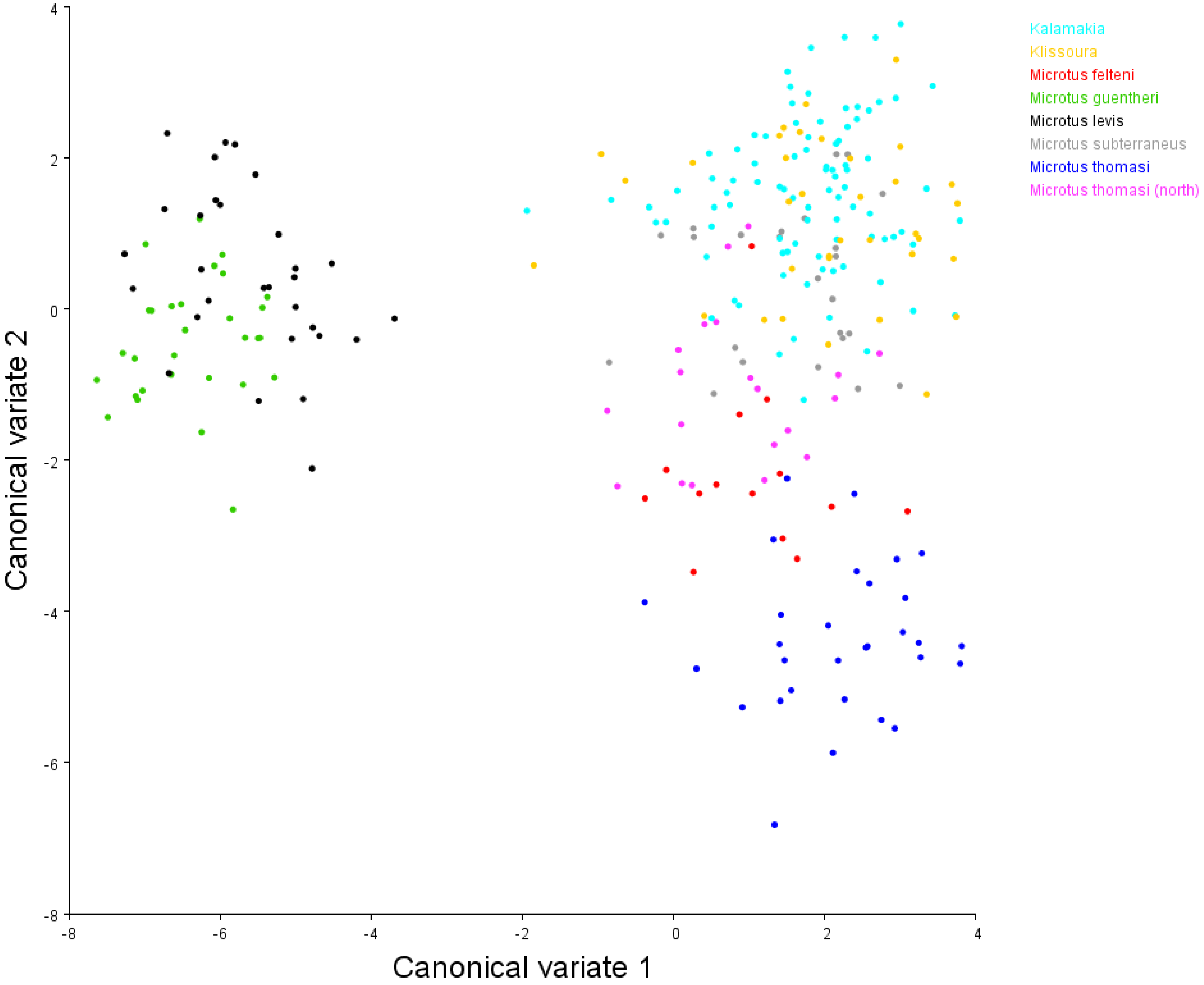
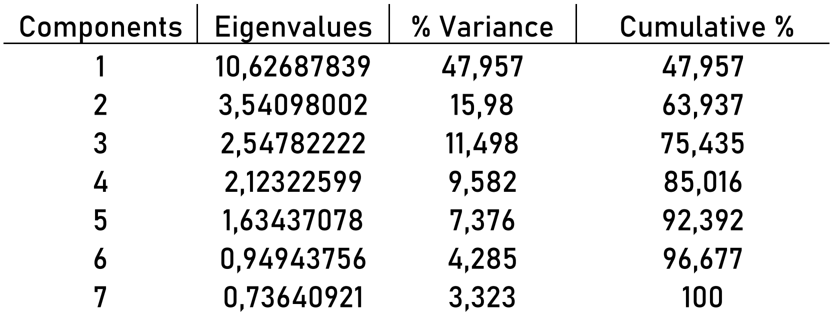


Figure 17: Canonical variate analyses chart based on molar shape of extant and fossil specimens.

Component 1 explicates 47.96% of the variance and Component 2 describes an additional 15.98% of the variance, raising the cumulative percentage to 63.94%. These values are relatively low; however, they are demonstrative of the trend observed in the divergence of molar shape (Tab. 5).

Table 5: Eigenvalues, variance and cumulative percentage of each component.



Components	Eigenvalues	% Variance	Cumulative %
1	10,62687839	47,957	47,957
2	3,54098002	15,98	63,937
3	2,54782222	11,498	75,435
4	2,12322599	9,582	85,016
5	1,63437078	7,376	92,392
6	0,94943756	4,285	96,677
7	0,73640921	3,323	100

.

As demonstrated in the Canonical Variate Chart (Fig. 17), the fossil arvicolines from Kalamakia Cave and Klissoura Cave 1, fall within the ranges of present-day representatives of the *Microtus* (*Terricola*) group and, more specifically, towards the *M. subterraneus* and *M. thomasi* from northern Greece; a small number of individuals from both sites fall within the range of *M. felteni* as well. None of the fossil specimens seem to bear resemblance to the extant species *M. levis* and *M. guentheri*.

Procrustes distances (Tab. 6) were selected to demonstrate the degree of shape divergence between the different groups of the accumulative dataset of present-day and fossil arvicolines (Klingenberg and Monteiro 2005).

The smallest Procrustes distance is observed between the fossil material from Kalamakia Cave and material from Klissoura Cave 1 (0.0173), followed by values detected between fossil material from Kalamakia Cave and Klissoura Cave 1 and the extant species *M. thomasi* from northern Greece (values 0.0281 and 0.0356 respectively). The distances between the fossil specimens and *M. subterraneus* (0.0461 and 0.042

respectively) were also small, contrary to the distances between the fossil specimens and species of *Microtus (Microtus)* group, *M. levis* (0.062 and 0.0592) and *M. guentheri* (0.0627 and 0.062) (Tab. 6).

Table 6: Procrustes distances among the fossil specimens from Kalamakia Cave and Klissoura Cave 1 and the present-day arvicolines of Greece.

	Kalamakia	Klissoura	*M. felteni*	*M. guentheri*	*M. levis*	*M. subterraneus*	*M. thomasi*
Klissoura	0,0173						
M. felteni	0,0489	0,043					
M. guentheri	0,0627	0,062	0,065				
M. levis	0,062	0,0592	0,0682	0,0431			
M. subterraneus	0,0461	0,042	0,0446	0,0579	0,0568		
M. thomasi	0,0369	0,0393	0,0557	0,0766	0,0796	0,061	
M. thomasi (north)	0,0281	0,0356	0,0545	0,0666	0,0703	0,0589	0,0359

Regarding changes in the occlusal surface of the molar, the third lingual re-entrant angle (LRA3) is the most divergent part of the tooth, similar to the extant arvicoline dataset. Variation is also observed at the buccal re-entrant angles 3 and 4 (BRA3 and BRA4, respectively) and the lingual re-entrant angle 5 (LRA5). No significant changes are observed in the posterior loop (PL), the anterior cup (AC), the buccal salient angles (BSA), and lingual salient angles (LSA) (Fig. 18).

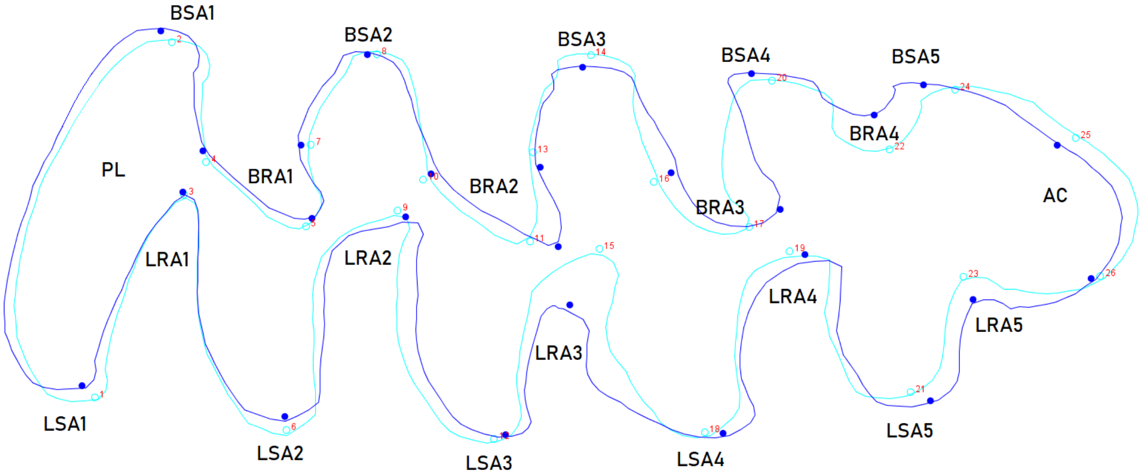


Figure 18: Visual representation of the variation of changes in the occlusal surface of the molars of the fossil and extant arvicoline specimens. Mean shape and maximum landmark displacement are displayed with light blue and blue outlines, respectively.

Centroid size

Centroid size is an essential tool in geometric morphometrics, mainly because it is uncorrelated with every shape variable when landmarks are positioned around mean positions (REFS). Analyses were performed on the accumulative dataset of present-day and fossil arvicolines to examine possible relations between extant and fossil specimens.

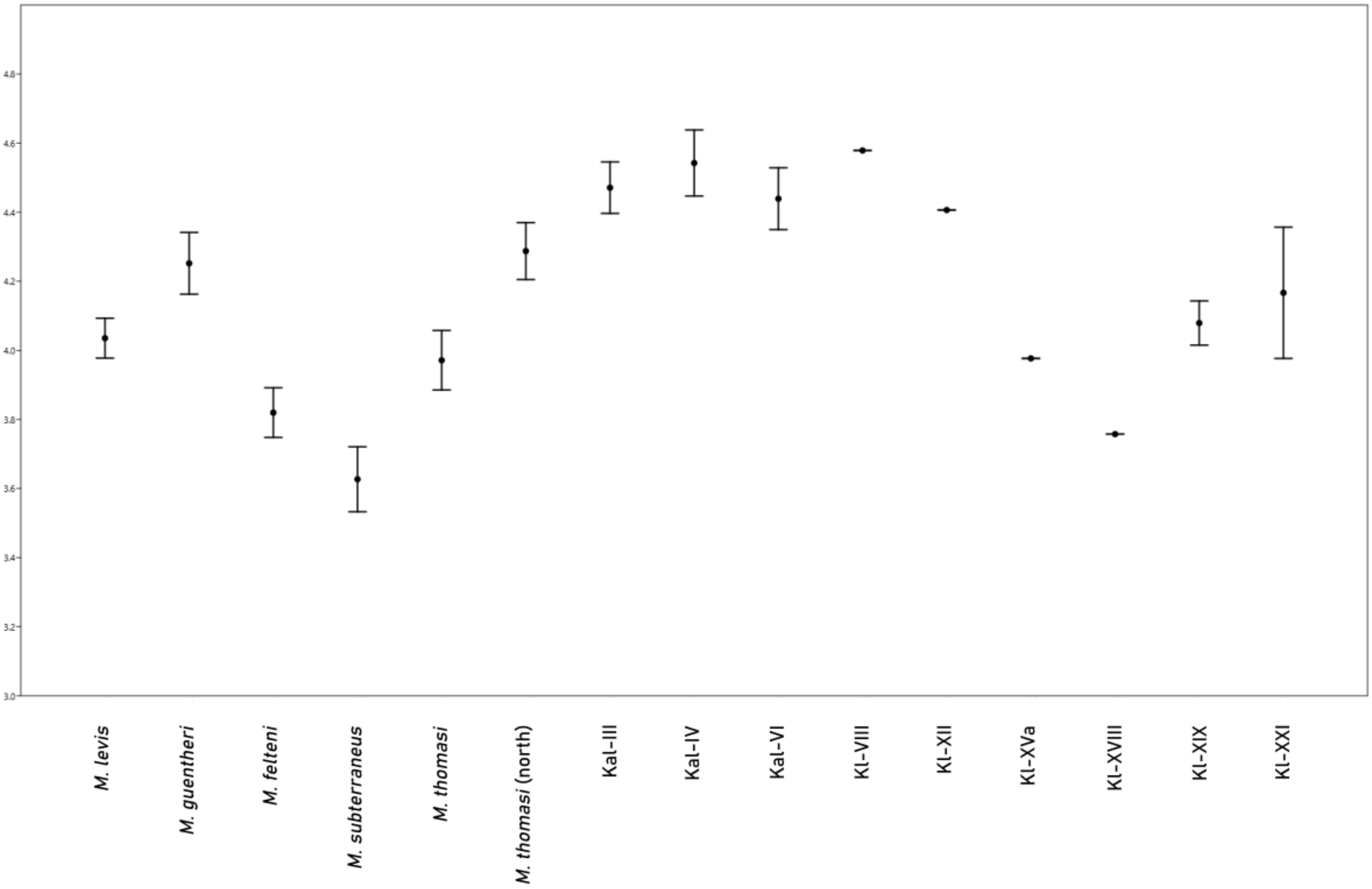


Figure 19: Mean and whisker plot for the centroid size of extant and fossil arvicolines (Standard error - 95% interval).

The representatives of the subgenus *Microtus (Microtus)* are characterized by higher values of centroid size than the majority of the *Microtus* (*Terricola)* populations from southern Greece, with the exception of *M. thomasi* populations from northern Greece.

The range between minimum and maximum values of the present-day arvicolines suggest wide fluctuations of centroid size intraspecific level. A significant overlap in minimum and maximum values is observed between the species (Tab. 10).

Table 7: Description of the centroid size of the molar in extant arvicoline and fossil populations from Kalamakia Cave and Klissoura Cave 1. N = sample size, SD = standard deviation, SEM = standard error of the mean, Min = minimum, Max = maximum.

Population	N	Mean	SD	SEM	Median	Min	Max
Microtus levis	30	4,04	0,16	0,03	4,07	3,77	4,41
Microtus guentheri	30	4,25	0,25	0,05	4,26	3,82	4,78
Microtus felteni	14	3,82	0,14	0,04	3,80	3,60	4,06
Microtus subterraneus	23	3,63	0,23	0,05	3,62	3,16	4,05
Microtus thomasi	30	3,97	0,24	0,04	3,94	3,55	4,41
Microtus thomasi (north)	20	4,29	0,19	0,04	4,26	4,06	4,61
Kal-III	30	4,47	0,21	0,04	4,49	4,00	4,87
Kal-IV	29	4,54	0,26	0,05	4,52	4,05	5,15
Kal-VI	30	4,44	0,25	0,05	4,45	3,88	4,94
Kl-XIX	25	4,08	0,16	0,03	4,08	3,83	4,54
Kl-XXI	6	4,17	0,24	0,10	4,15	3,87	4,53

The average values of centroid size belonging to rodents from Kalamakia Cave rank as the highest in the dataset (4.54) of both extant and fossil specimens and correspond with the present-day populations of *M. thomasi* (4.29) from northern Greece and *M. guentheri*, as displayed in Figure 19. Samples from Units III and VI of Kalamakia Cave display similarities in centroid size values (average, minimum and maximum scores), while samples from Unit IV are larger (Tab. 7).

The mean values of specimens from Kl-XIX and Kl-XXI appear to be relatively similar. The populations from these layers, correspond to present-day *M. guentheri* and *M. thomasi* from northern Greece. Slight variations are observed at the minimum, maximum and mean values of the centroid size between these layers, possibly attributed to the inadequate representation of Kl-XXI (Tab. 12). The remaining layers were not included in the analyses performed, since they yielded no statistical information.

Overall, an increase in centroid size is observed in specimens originating from units deposited during warm MIS 3 and 5a in Kalamakia Cave (Unit III and IV). The opposite trend is detected in the examined layers of Klissoura Cave 1, however due to the small number of samples no accurate assumptions can be made (Tab. 7).

Length – Length/Width ratio

Overall length (Fig. 20a) and index V1/V2 (Length/ Width ratio) (Fig. 20b) display variation in tooth size, between specimens collected from layers deposited during warm and cold MIS. Analyses conducted on 124 lower first molars (m1) (87 from arvicolines living in warm MIS and 37 from arvicolines living in cold MIS), indicate a slight increase of molar size in individuals living in warm MIS.

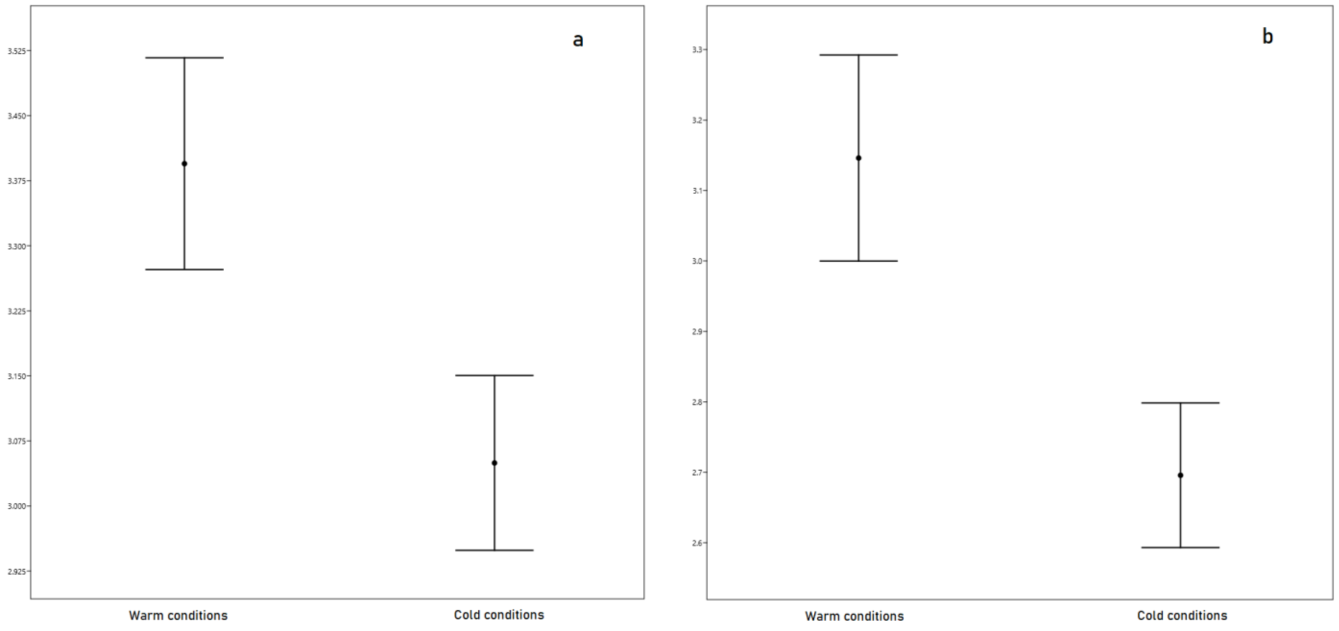


Figure 20: Mean and whisker plot for Overall length (a) and Length/Width ratio (b) from specimens of warm and cold conditions (Standard error - 95% interval).

More specifically, as shown in Tables 8 and 9, the molars belonging to specimens from Kalamakia Cave are significantly larger than their conspecifics from Klissoura Cave 1. There is no distinct differentiation in the size of samples from the same excavation site. Arvicoline molars collected from layers deposited during warm MIS were somewhat larger than those collected from layers deposited during cold MIS.

Concerning Kalamakia Cave, the mean length of molars from Units III (3.08) and IV (3.14) (warm MIS 3 and 5a, respectively) are marginally larger than the samples collected from Unit VI (3.07) (cold MIS 2) (Tab. 8). The same tendency is observed in the length/width ratio (Tab. 9).

The opposite was observed in the specimens from Klissoura Cave 1; the mean length of the specimens collected from Layer XIX (2.82) (corresponding to warm MIS 5c) is marginally lower than the mean length of specimens collected from Layer XXI (2.87) (corresponding to cold MIS 6) (Tab. 8); the same trend is detected in the length/width ratio (Tab. 9). However, no accurate comment could be made about these changes, owing to inconsistencies in the sample sizes of the two categories (28 and 8 samples from warm and cold conditions, respectively).

Table 8: Description of the overall length of the first lower molars in fossil populations from Kalamakia Cave and Klissoura Cave 1. N = sample size, SD = standard deviation, SEM = standard error of the mean, Min = minimum, Max = maximum.

Population	N	Mean	SD	SEM	Median	Min	Max	Conditions
Kal-III	30	3,08	0,16	0,03	3,09	2,68	3,38	Warm
Kal-IV	29	3,14	0,21	0,04	3,11	2,78	3,67	Warm
Kal-VI	30	3,07	0,21	0,04	3,08	2,63	3,49	Cold
Kl-XIX	25	2,82	0,15	0,03	2,82	2,57	3,11	Warm
Kl-XXI	6	2,87	0,19	0,08	2,86	2,59	3,17	Cold
Kl-VIII	1	-	-	-	-	-	3,12	Warm
Kl-XII	1	-	-	-	-	-	3,02	Warm
Kl-XVa	1	-	-	-	-	-	2,66	Cold
Kl-XVIII	1	-	-	-	-	-	2,56	Warm

Table 9: Description of the length/width ratio of the first lower molars in fossil populations from Kalamakia Cave and Klissoura Cave 1. N = sample size, SD = standard deviation, SEM = standard error of the mean, Min = minimum, Max = maximum.

Population	N	Mean	SD	SEM	Median	Min	Max	Conditions
Kal-III	30	2,72	0,16	0,03	2,73	2,39	3,09	Warm
Kal-IV	29	2,66	0,15	0,03	2,66	2,37	2,96	Warm
Kal-VI	30	2,65	0,16	0,03	2,65	2,36	3,12	Cold
Kl-XIX	25	2,66	0,13	0,03	2,64	2,44	3,10	Warm
Kl-XXI	6	2,71	0,12	0,05	2,67	2,58	2,87	Cold
Kl-VIII	1	-	-	-	-	-	2,62	Warm
Kl-XII	1	-	-	-	-	-	2,63	Warm
Kl-XVa	1	-	-	-	-	-	2,69	Cold
Kl-XVIII	1	-	-	-	-	-	2,42	Warm

T5/T4 length ratio

Analyses conducted on the extant and fossil datasets revealed differences and similarities between the extant and fossil vole species (Fig. 21).

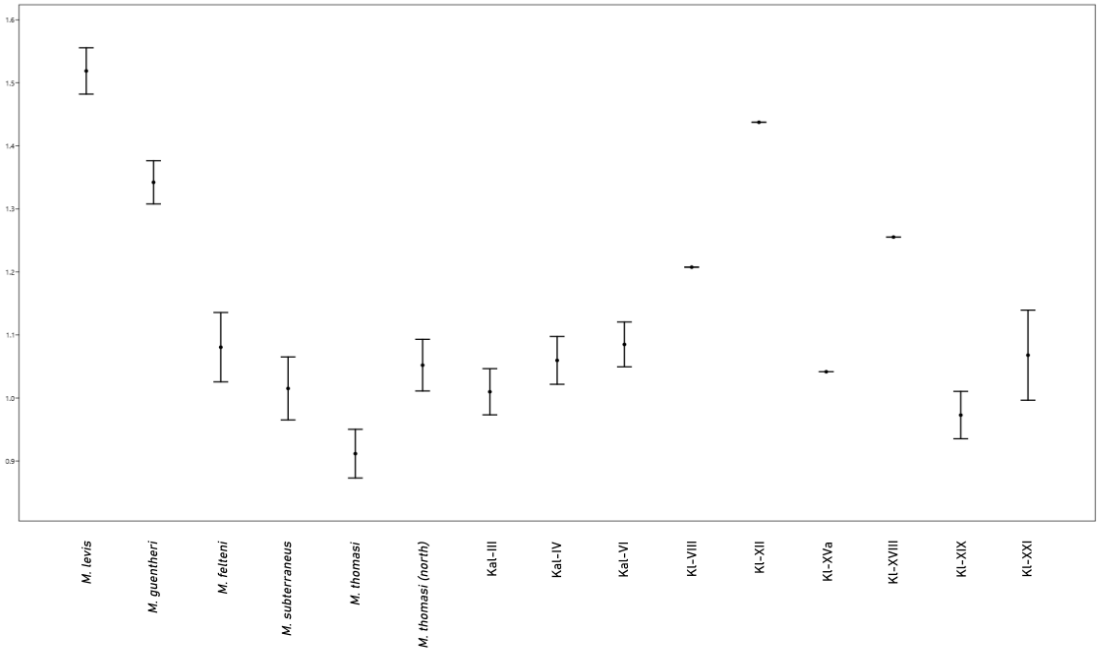


Figure 21: Mean and whisker plot for the T5/T4 length ratio of extant and fossil arvicolines (Standard error - 95% interval).

As shown in Figure 21, extant populations *M. levis* and *M. guentheri*, both members of the *Microtus (Microtus)* group, are separated from the rest of the populations of the dataset. This is correlated with the significantly higher average scores observed in these species (Tab. 5). This observation suggests that triangle 5 (T5 - lingual side of the molar) is distinctly larger than triangle 4 (T4 - buccal side of the molar) in present-day representatives of the *Microtus (Microtus)* group, compared to members of *Microtus (Terricola)* group.

The minimum and maximum measurements of T5/T4 ratio of the *M. levis* populations are unmistakably larger than those observed at the rest of the taxa. *M. guentheri* is also differentiated from the rest of the specimens regarding the minimum values, however virtually same values of maximum ratio are shared by *M. guentheri*, *M.*

felteni and *M. subterraneus*. Triangle 5 (T5) is consistently larger than triangle 4 (T4) in all present-day species from continental Greece, while *M. thomasi* from southern Greece (Peloponnese) is the only extant population in which triangle 4 (T4) is generally larger than triangle 5 (T5) (mean value of this index is < 1).

Table 10: Description of the T5/T4 length ratio in extant arvicoline and fossil populations from Kalamakia Cave and Klissoura Cave 1. N = sample size, SD = standard deviation, SEM = standard error of the mean, Min = minimum, Max = maximum.

Population	N	Mean	SD	SEM	Median	Min	Max
Microtus levis	30	1,52	0,10	0,02	1,53	1,32	1,81
Microtus guentheri	30	1,34	0,10	0,02	1,35	1,15	1,53
Microtus felteni	14	1,08	0,11	0,03	1,08	0,89	1,20
Microtus subterraneus	23	1,02	0,12	0,03	1,02	0,85	1,24
Microtus thomasi	30	0,91	0,11	0,02	0,89	0,72	1,12
Microtus thomasi (north)	20	1,05	0,09	0,02	1,07	0,89	1,24
Kal-III	30	1,01	0,10	0,02	1,01	0,75	1,31
Kal-IV	29	1,06	0,10	0,02	1,05	0,92	1,30
Kal-VI	30	1,08	0,10	0,02	1,12	0,85	1,34
Kl-XIX	25	0,97	0,10	0,02	1,00	0,80	1,16
Kl-XXI	6	1,07	0,09	0,04	1,05	0,95	1,17

The measurements of specimens from Kalamakia Cave and Klissoura Cave 1 correspond to extant *M. subterraneus* and *M. thomasi* from northern Greece (Tab. 10). An increase of the average T5/T4 ratio is observed through time; specimens from the most recent layer (Unit VI – mean value 1.08) have a higher ratio of T5/T4 compared to older layers from the two sites (Unit III – 1.01 / Unit IV – 1.06 / Layer XIX – 0.97), Specimens from layer Kl-XXI have slightly high scores in the average of this index; however, these results may not be indicative, owing to the relatively small amount of samples from this layer.

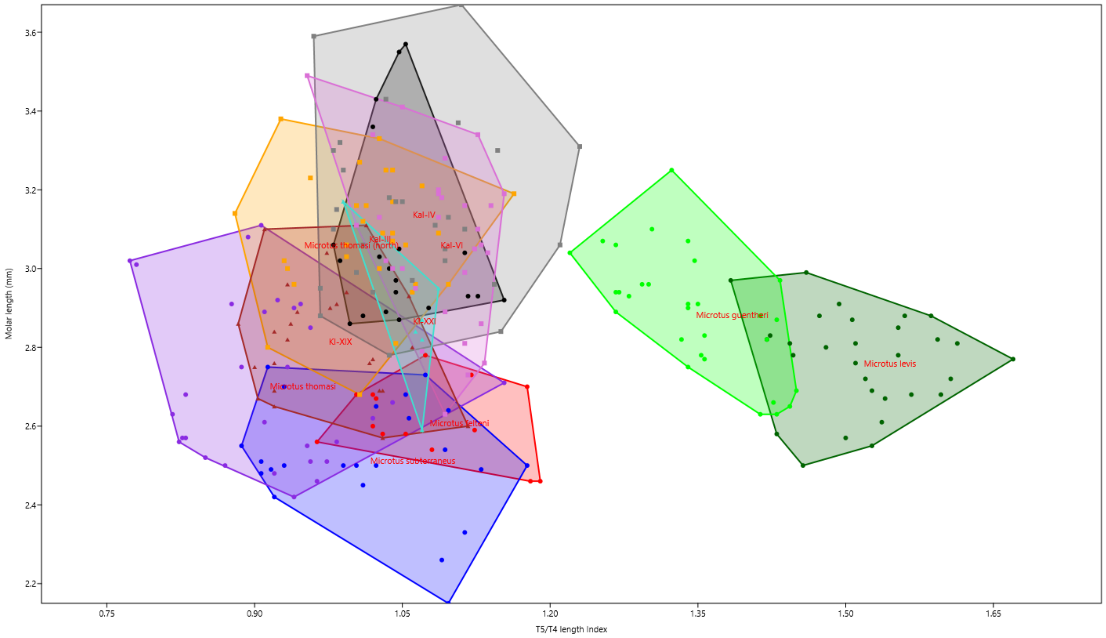


Figure 22: Molar length and T5/T4 length index correlation between present-day arvicolines (*M. levis* - dark green, *M. guentheri* – lime, *M. felteni* – red, *M. subterraneus* – blue, *M. thomasi* from Peloponnese – purple, M. thomasi from northern Greece – black) and fossil specimens from Kalamakia Cave (Unit III – orange, Unit IV – grey, Unit VI – pink) and Klissoura Cave 1 (Layer XIX – brown, Layer XXI – turqoise).

The overall data of Kalamakia Cave and Klissoura Cave 1 (Layers Kl-XIX and Kl-XXI) demonstrate resemblance of the vole species of the two sites, considering the average T5/T4 length ratio (Tab. 5). The fossil specimens from both sites fall within the range of the modern-day representatives of the subgenus *Terricola*, *M. subterraneus* and *M. thomasi*. The molars could not be accurately attributed to certain species; however, it is safe to assume that they are correlated with extant representatives of the subgenus *Terricola* (Figs 21 and 22).

As displayed in Figure 22, the discrimination between the subgenera *Microtus (Microtus)* (right side of the chart) and *Microtus (Terricola)* (left side of the chart) is distinct. Fossil specimen from Kalamakia Cave (Units III, IV and VI) and Klissoura Cave 1 (Layers XIX and XXI) coherently correspond with the *Terricola* group and more specifically with *M. thomasi* and *M. subterraneus*. A slight correlation with *M. felteni* is observed as well.

Tilt of the pitymyan rhombus

Based on analyses of the tilt of the pitymyan rhombus the fossil specimens from both excavation sites display similarities and correlate with present-day *M. subterraneus* and *M. thomasi*, both representatives of the subgenus *Terricola* (Fig. 23). *M. levis* and *M. guentheri*, members of the subgenus *Microtus* are grouped together, isolated from the rest of the specimen.

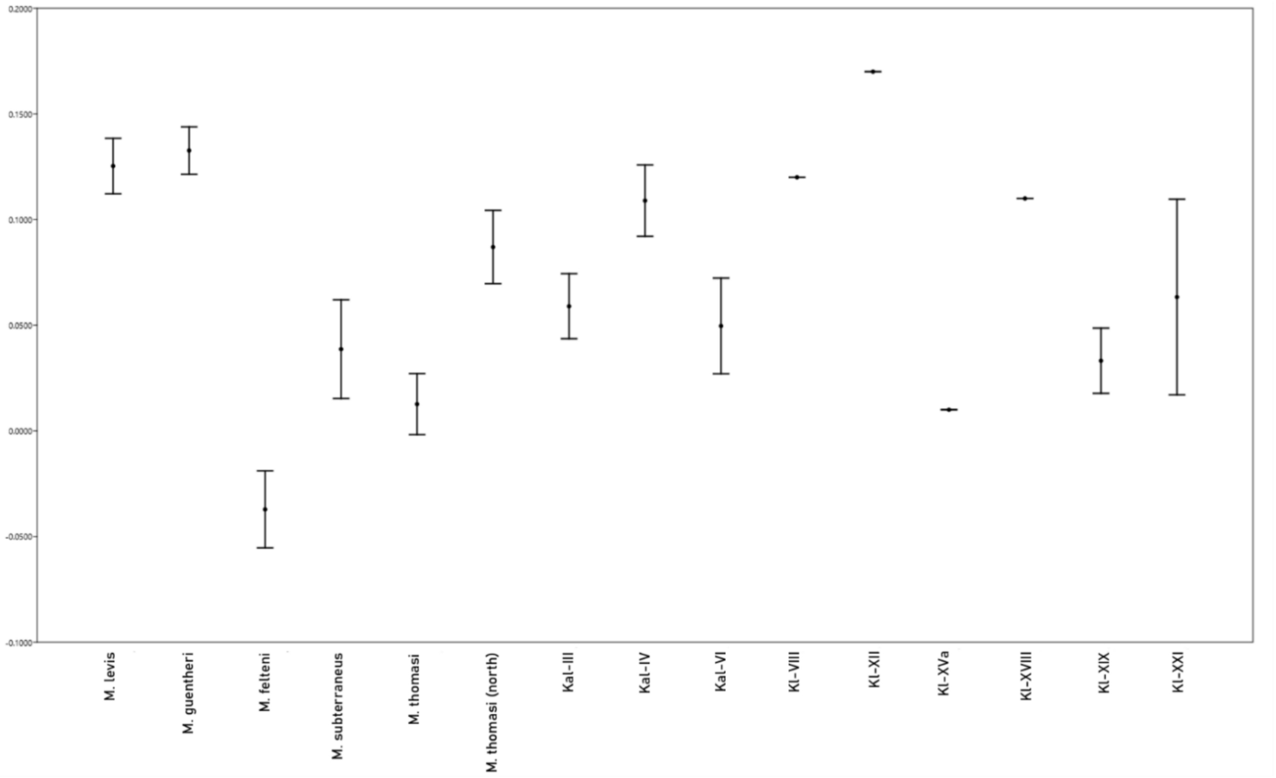


Figure 23: Mean and whisker plot for the tilt of the pitymyan rhombus of extant and fossil arvicolines (Standard error - 95% interval).

Table 11: Description of the tilt of the pitymyan rhombus in extant arvicoline and fossil populations from Kalamakia Cave and Klissoura Cave 1. N = sample size, SD = standard deviation, SEM = standard error of the mean, Min = minimum, Max = maximum.

Population	N	Mean	SD	SEM	Median	Min	Max

Microtus levis	30	0,13	0,04	0,01	0,14	0,05	0,21
Microtus guentheri	30	0,13	0,03	0,01	0,13	0,08	0,22
Microtus felteni	14	-0,04	0,03	0,01	-0,04	-0,09	0,06
Microtus subterraneus	23	0,04	0,06	0,01	0,04	-0,10	0,16
Microtus thomasi	30	0,01	0,04	0,01	0,02	-0,09	0,08
Microtus thomasi (north)	20	0,09	0,04	0,01	0,08	0,01	0,16
Kal-III	30	0,06	0,04	0,01	0,07	-0,05	0,13
Kal-IV	29	0,11	0,05	0,01	0,11	-0,05	0,23
Kal-VI	30	0,05	0,06	0,01	0,06	-0,17	0,15
Kl-XIX	25	0,03	0,04	0,01	0,03	-0,05	0,11
Kl-XXI	6	0,06	0,06	0,02	0,04	0,01	0,15

Significant differences are observed in members of the two extant subgenera of the genus *Microtus.* The average and median values of this index for *M. levis* and *M. guentheri* are almost identical, while for all representatives of the *Microtus (Terricola)* group the same values are significantly lower (with the exception of *M. thomasi* northern populations). The pitymyan rhombus is tilted towards the anterior part of the tooth in *M. levis, M. guentheri* and *M. thomasi* from northern Greece, as indicated by the minimum values of this index for these species. The minimum and maximum measurements reveal that the pitymyan rhombus is tilted towards both the anterior and the posterior part of the molar and the range is generally larger in extant *Terricola* species. *M. felteni* is the only case in which the rhombus is mainly tilted towards the posterior part of the tooth (Tab. 11).

The average and median values of specimens from all units of Kalamakia Cave correspond to modern-day *M. thomasi* individuals from northern Greece, while specimens from Unit VI bear resemblance to *M. subterraneus* as well(Tab. 11). Though the maximum tilt observed in Unit IV corresponds with *M. felteni* or *M. guentheri*, this measurement represents a single molar and can, therefore, be considered as an outlier. The minimum measurement observed in Unit VI is significantly lower than any other measurement in the dataset; however, as in the case of maximum measurement of tilt in

Unit IV, this measurement corresponds to a single specimen and can, therefore, be considered as an outlier.

Additionally, the average and median values of layer Kl-XIX correlate with *M. subterraneus* extant populations, however the minimum and maximum scores of these populations are distinctly differentiated (Tab. 11). Arvicolines from layer Kl-XXI seem to correspond to present-day *M. subterraneus*, as well. It is worth mentioning that the range of tilt of the specimens from layer XXI is considerably wide; this could be attributed to the relatively small sample size of this layer. Layers Kl-VIII, Kl-XII, Kl-XVa and Kl-XVIII provide no information when examined individually, thus they were not used in the analyses of Klissoura Cave 1.

The accumulative data of the two sites indicate significant resemblance of the species in the two faunal assemblages, as shown by the average tilt of the pitymyan rhombus (Tab. 11).

Closure of the anterior loop

Based on analyses conducted on measurements of the occlusal surface of the molars, the closure of the anterior loop yielded important information. A clear distinction between *Microtus* and *Terricola* can be readily detected by examining values of this index, in the representatives of the two subgenera (Tab. 12). As shown in Figure 24, the majority of the fossil specimens and samples bear strong resemblance to present-day *M. thomasi*. Specimens from layers VIII, XII and XVIII from Klissoura Cave 1, seem to correspond with present *M. subterraneus*; however, as aforementioned, since these layers are represented by a single specimen, no statistical information was provided.

More specifically, the maximum and average percentage of closure is significantly lower in *M. levis* and *M. guentheri* compared to the rest of the specimens. A significant amount of range overlap regarding the minimum values of these species and individuals from *M. felteni* and *M. subterraneus* populations is observed. However, the higher average and median values of these species indicate that this overlap is created by a wider range of values observed in the mentioned species. The range of the anterior loop closure is distinctly narrower in the extant populations of *M. guentheri* and *M. levis* (18.14 and 17, respectively) contrary to the much wider ranges of *M. felteni* (33.16), *M. subterraneus* (37.82) and *M. thomasi* (48.39); the same ranges of closure of the anterior loop are observed in populations of *M. thomasi* from northern and southern Greece (Tab. 12).

Table 12: Description of the closure of the anterior loop in extant arvicoline and fossil populations from Kalamakia Cave and Klissoura Cave 1. N = sample size, SD = standard deviation, SEM = standard error of the mean, Min = minimum, Max = maximum.

Population	N	Mean	SD	SEM	Median	Min	Max
Microtus levis	30	16,24	4,09	0,75	15,83	8,74	25,74
Microtus guentheri	30	18,08	4,89	0,89	18,80	8,47	26,61
Microtus felteni	14	25,39	9,40	2,51	22,69	13,73	41,90
Microtus subterraneus	23	18,92	7,81	1,63	17,71	4,08	32,67
Microtus thomasi	30	36,07	11,43	2,09	34,23	14,61	63,00
Microtus thomasi (north)	20	33,48	9,54	2,13	28,58	22,76	53,15
Kal-III	30	35,19	6,28	1,15	34,95	24,30	44,04
Kal-IV	29	32,41	7,59	1,41	31,45	18,80	53,70
Kal-VI	30	36,09	9,57	1,75	37,18	15,38	55,56
Kl-XIX	25	35,63	8,45	1,69	34,19	18,37	59,05
Kl-XXI	6	36,98	5,45	2,22	37,46	29,29	43,00

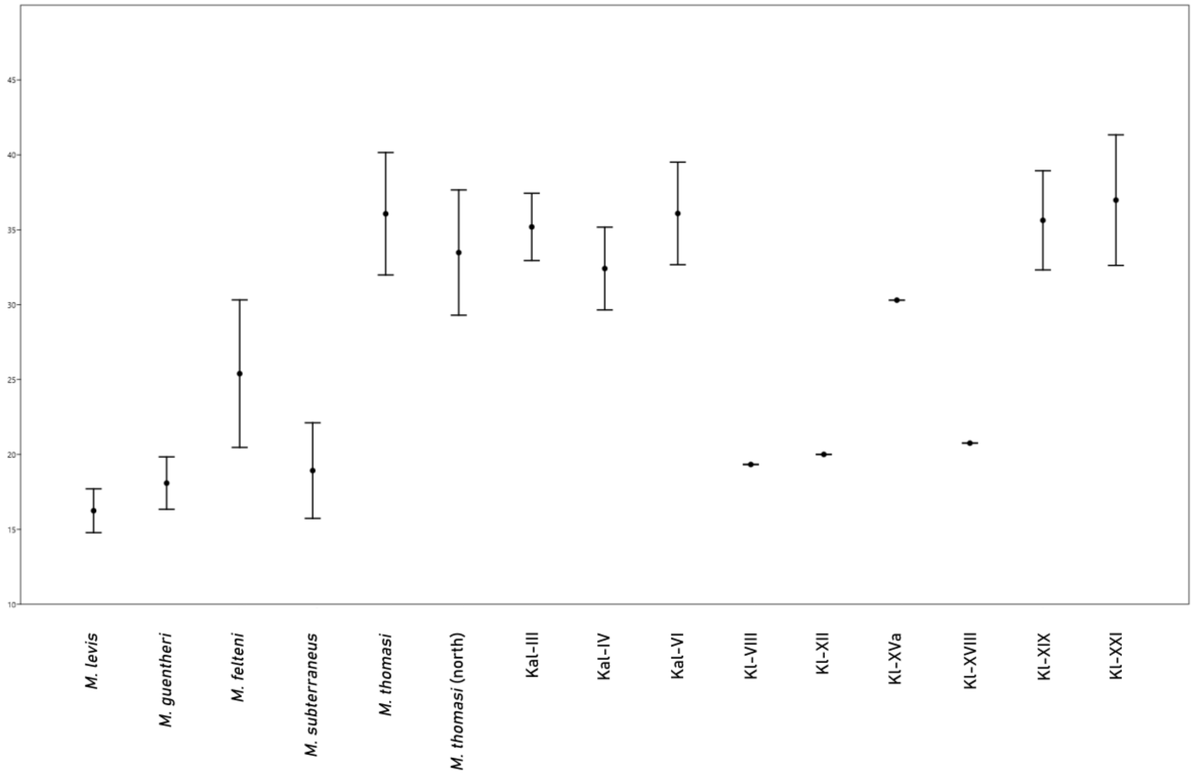


Figure 24: Mean and whisker plot for the closure of the anterior loop of extant and fossil arvicolines (Standard error - 95% interval).

Specimens from Kalamakia Cave are characterized by significantly high values in all variables, indicating unmistakable resemblance to the present-day *M. thomasi*. Individuals from Unit III displayed the highest percentage of minimum closure and the lowest percentage of maximum closure in the assemblage, suggesting a narrow range of variation. The distinctly higher maximum and lower minimum percentages of closure observed in Units IV and VI display a wide range of anterior loop close (Tab. 12).

Regarding Klissoura Cave 1, it is worth mentioning that only layers Kl-XIX and Kl-XXI provide statistical information; the remaining layers were represented by single specimens and therefore were not used in the analyses. Specimens from both statistically informative layers correlate with extant *M. thomasi*, considering the high scores of average percentage of anterior loop closure. A wider morphological variety of the closure of the anterior loop can be observed in layer Kl-XIX (Tab. 12).

Development of the anterior part of the molar

Several similarities and differences and significant overlapping of measurements were observed throughout the dataset in both present-day and fossil arvicolines in the analyses of the development of the anterior part of the first lower molar.

Table 13: Description of the development (%) of the anterior part of the molar in extant arvicoline and fossil populations from Kalamakia Cave and Klissoura Cave 1. N = sample size, SD = standard deviation, SEM = standard error of the mean, Min = minimum, Max = maximum.

Population	N	Mean	SD	SEM	Median	Min	Max
Microtus levis	30	53,77	1,50	0,27	53,82	51,25	56,62
Microtus guentheri	30	53,35	0,98	0,18	53,41	51,85	55,26
Microtus felteni	14	48,77	1,49	0,40	48,84	45,15	51,56
Microtus subterraneus	23	52,77	2,45	0,51	53,09	47,41	59,44
Microtus thomasi	30	49,00	1,77	0,32	49,61	44,80	51,37
Microtus thomasi (north)	20	50,40	1,89	0,42	50,94	47,24	53,44
Kal-III	30	50,94	1,54	0,28	51,13	47,65	53,63
Kal-IV	29	51,93	1,74	0,32	52,52	47,47	54,52
Kal-VI	30	51,08	2,32	0,42	51,37	44,41	54,55
Kl-XIX	25	50,82	1,83	0,37	51,19	46,47	55,16
Kl-XXI	6	46,54	3,62	1,48	46,23	41,70	51,53

The most remarkable observation was the range between the minimum and maximum values among the examined specimens. The widest range of development was detected in the *M. subterraneus* and specimens from Kl-XXI layers, from the extant and the fossil dataset respectively. The anterior part of the molar was larger than the posterior part in the majority of groups, excluding the extant *M. felteni* and *M. thomasi* populations and the specimens from Kl-XXI layer (average value was below 50%). The present-day representatives of the subgenus *Microtus*, *M. levis* and *M. guentheri*, were the only populations in which the anterior part of the first lower molar was larger than the posterior part in all specimens; the minimum values of development of the anterior part of the molar were exceeding 50% in both species (Tab. 13).

The fossil molars bear resemblance to extant member of the subgenus *Terricola*, as the minimum values of development from both Kalamakia Cave and Klissoura Cave 1 do not fall within the range of either *M. levis* or *M. guentheri* (Tab. 13).

A slight increase in the maximum percentages of development is observed in Kalamakia Cave through time, however the average values are fluctuated. Specimens from all units fall within the ranges of present-day *M. subterraneus* and *M. thomasi* from northern Greece (Tab. 13).

Regarding Klissoura Cave 1, individuals from layer Kl-XIX fall within the ranges of extant *M. subterraneus* and *M. thomasi* from northern Greece, while specimens discovered in layer Kl-XXI do not resemble any of the examined populations (Tab. 13). Samples collected from layers VIII, XII, XVa and XVIII were not included in the analyses.

As shown in Figure 25, *M. levis* and *M. guentheri* are plotted higher than the rest of the populations. Specimens from Units III, IV and VI (Kalamakia Cave) and layer Kl-XIX (Klissoura Cave 1) seem to bear resemblance to present-day *M. subterraneus* and *M. thomasi* from northern Greece. The values and range of the development of the anterior part of specimens from layer XXI were not observed in any of the extant of fossil specimens.

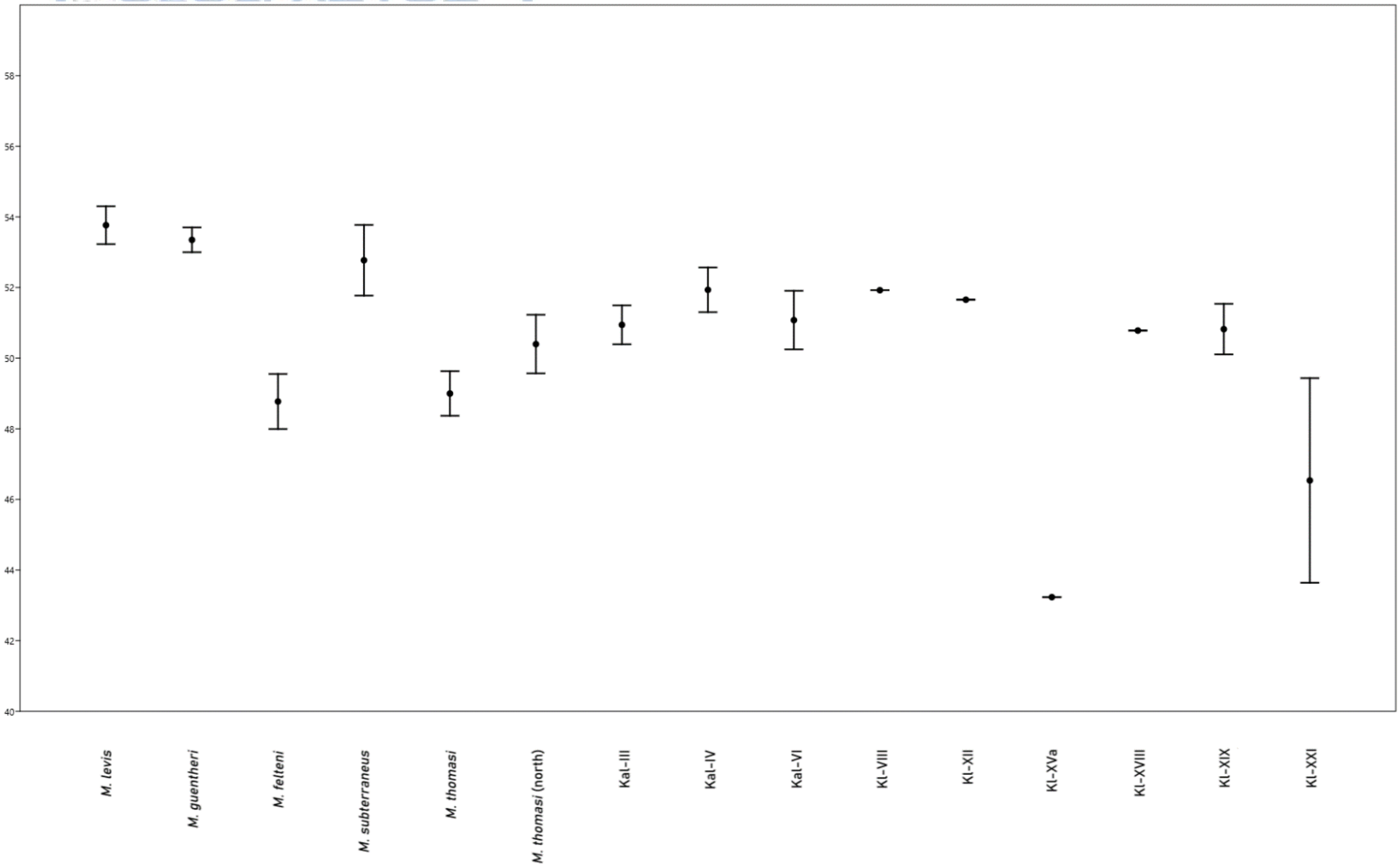


Figure 25: Mean and whisker plot for the development of the anterior part of extant and fossil arvicolines (Standard error - 95% interval).

Principal Components Analysis

A Principal Components Analysis (PCA) was conducted to determine which indices could be considered more informative about the divergence in the shape of the molars, of both present-day and fossil arvicolines (Tab 14, Figs 26-28).

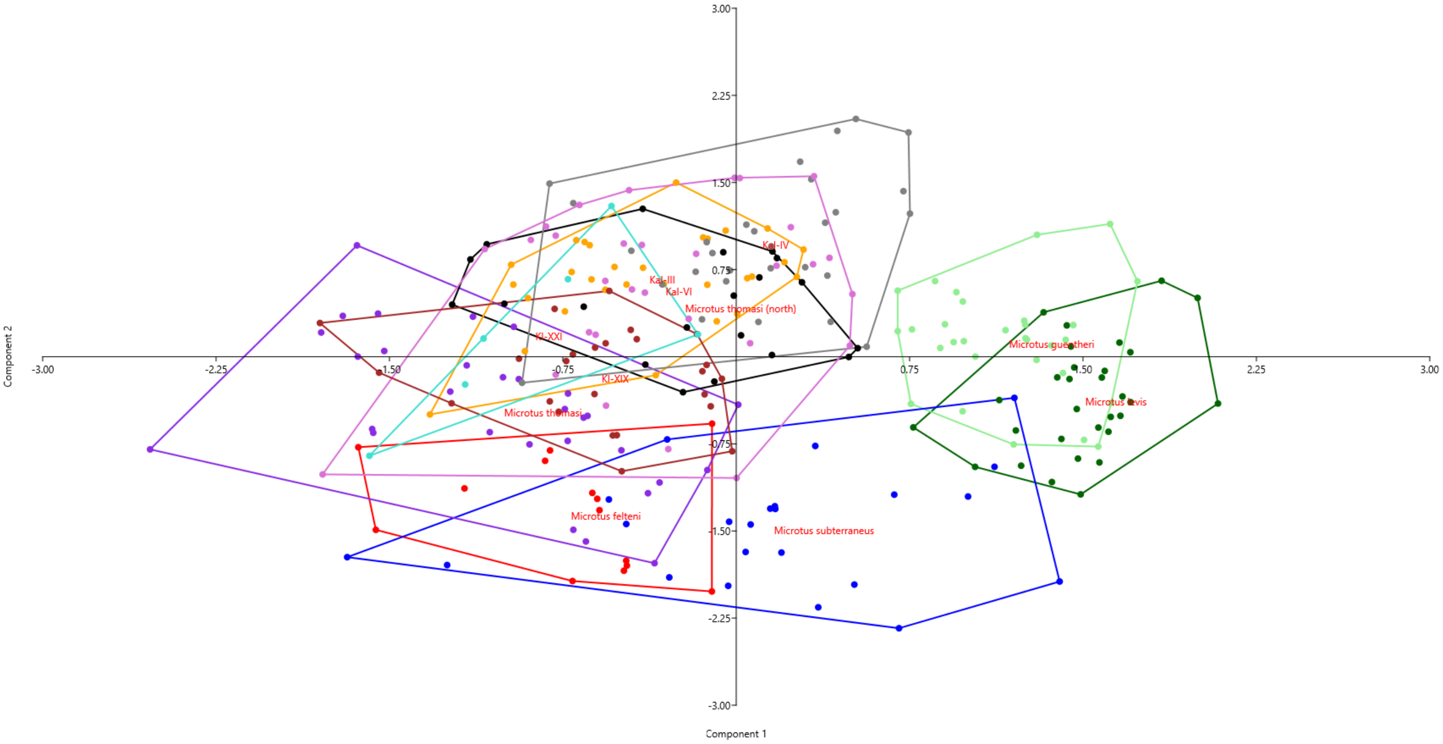


Figure 26: Principal Component Analysis scatter plot displaying the correlation between present-day arvicolines (*M. levis* - dark green, *M. guentheri* – lime, *M. felteni* – red, *M. subterraneus* – blue, *M. thomasi* from Peloponnese – purple, M. thomasi from northern Greece – black) and fossil specimens from Kalamakia Cave (Unit III – orange, Unit IV – grey, Unit VI – pink) and Klissoura Cave 1 (Layer XIX – brown, Layer XXI – turqoise).

The PCA chart (Fig. 26) demonstrates the distinct differentiation of the two subgenera of *Microtus*; *Microtus (Terricola)* species clustered on the left side of the chart, while *Microtus (Microtus)* species are grouped on the right side of the chart. The resemblance of the fossilized specimens with the present-day *Microtus (Terricola)* group is coherently displayed as well.

Table 14: Table showing the Eigenvalues and variance percentage of each Principal Component.

PC	Eigenvalue	% variance
1	2,78956	55,79100
2	1,55773	31,15500
3	0,43077	8,61530
4	0,16809	3,36170
5	0,05386	1,07720

Based on the loadings plot of the PCA, component 1 is positively correlated with indices T5/T4 length ratio, Tilt of the pitymyan rhombus and Development of the anterior part, while Closure of the anterior loop has a negative correlation in PC1. These four indices have approximately equal importance. Centroid size seems to have a trivial effect in component 1 (Fig. 27).

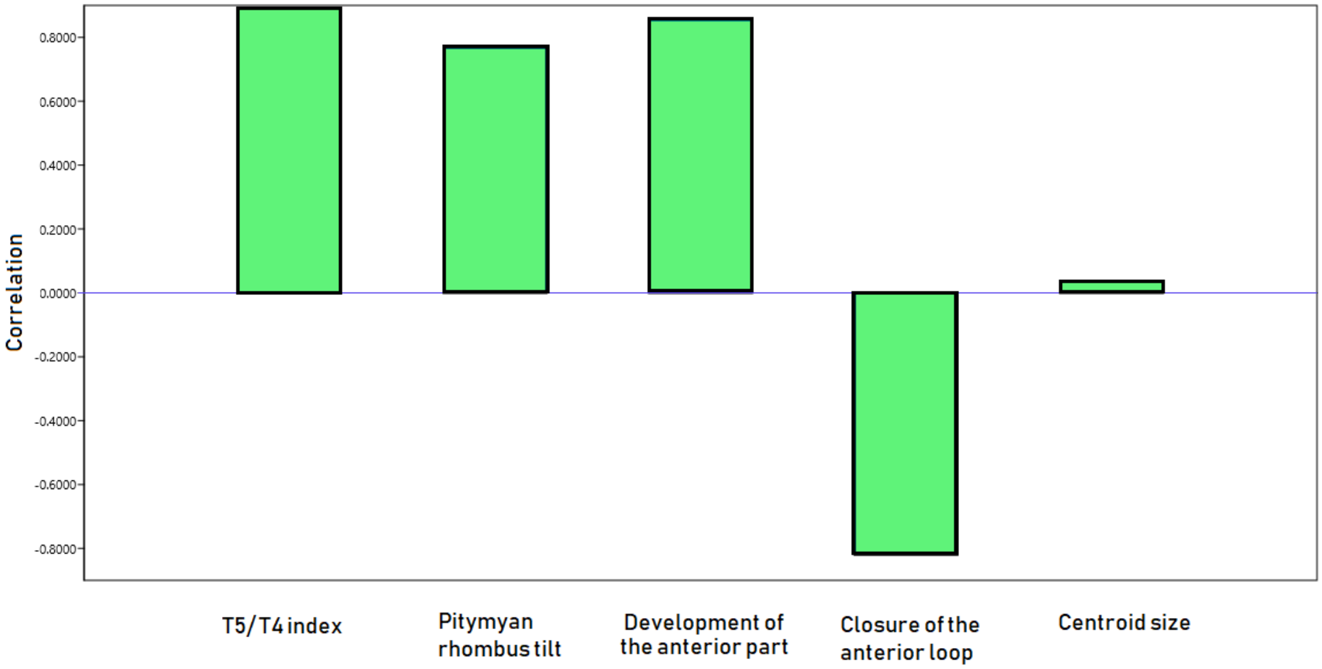


Figure 27: Principal Component Analysis correlation loadings plot for Principal Component 1 (PC1).

As shown in Table 14, the first two components accumulate for 87% of the variance generated by the five indices used in the analyses. More specifically PC1 explicates 56% of the generated variance, while PC2 corresponds to 31% of the variability. PC3 is not as significant, while PC4 and PC5 could be characterized as trivial.

Component 2 is positively correlated with indices Tilt of the pitymyan rhombus, Closure of the anterior loop and Centroid size. As displayed in Figure 3, Centroid size seems to be the most significant, while Tilt of the pitymyan rhombus and Closure of the anterior loop are of equal importance. Indices T5/T4 length ratio and Development of the anterior part are of minor significance for component 2.

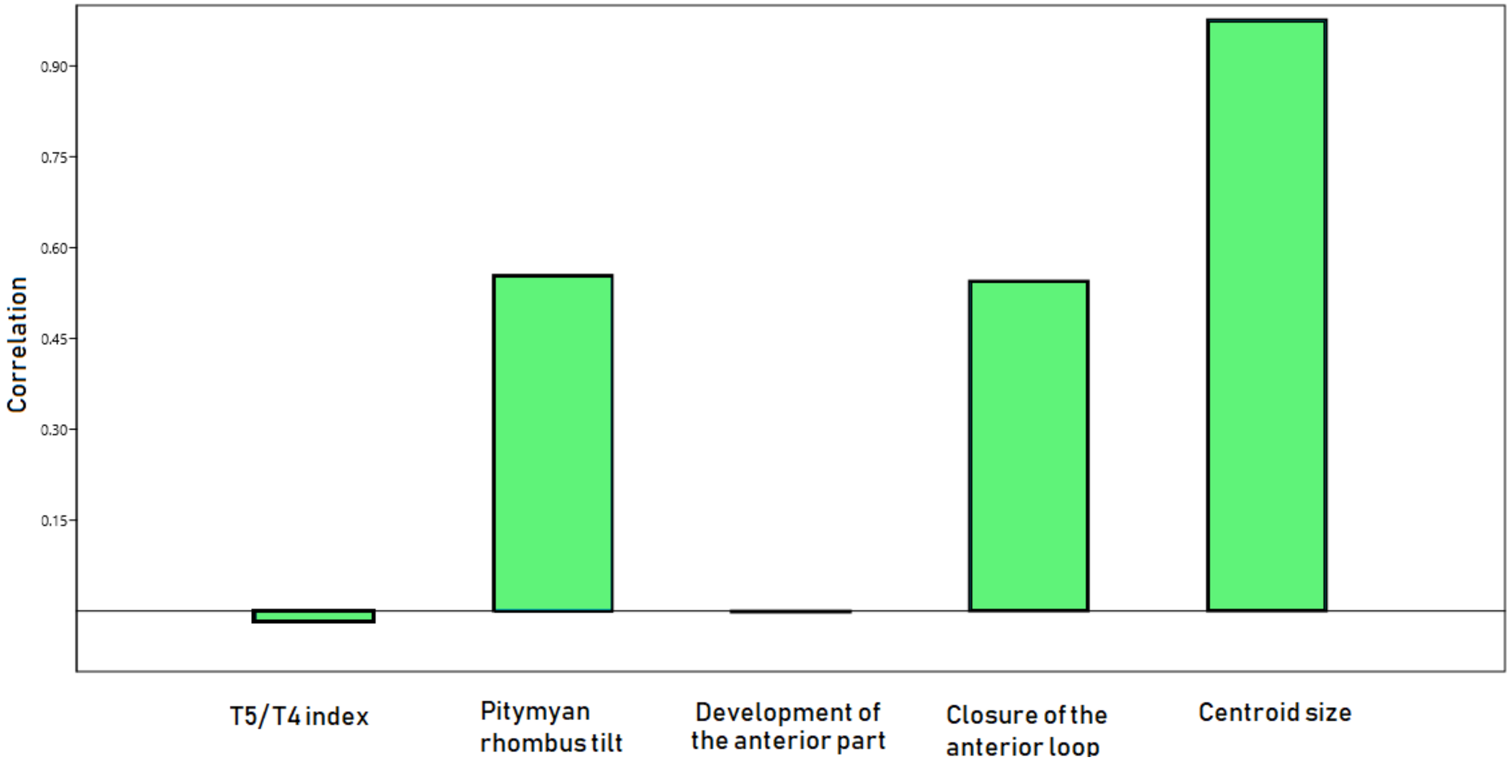


Figure 28: Principal Component Analysis correlation loadings plot for Principal Component 2 (PC2).

4. DISCUSSION

As aforementioned, the landmarks proposed by Wallace (2006) were tested in the initial analyses of the extant arvicoline dataset. Though the landmark scheme provided a solid discrimination of the subgenera *Microtus (Microtus)* and *Microtus (Terricola)*, it provided limited discrimination of the species within these groups (Fig. 28). As seen in the Canonical Variate chart (Fig. 28) the two subgenera are distinctly discriminated; however, the discrimination and grouping of species in clusters were less accurate.

To enhance the discrimination of the present-day species five additional landmarks were placed at critical points of the anterior cup (AC) of the molar (Fig. 8). These landmarks provided more definitive results in the discrimination of the extant species (Fig. 11); subsequently the improved landmark scheme was applied to the cumulative dataset (Fig. 17).

Concerning the extant arvicoline dataset, the analyses performed on the shape of the molars displayed significant divergence between the two present-day subgenera of *Microtus*; the extant arvicoline species of these groups were efficiently discriminated, as well (Fig. 11). Remarkably, a noteworthy divergence of the molar shape was observed within the different populations of *M. thomasi* from Peloponnese and northern Greece (Epirus) (Fraguedakis-Tsolis et al., 2009). However, this observation is not related to the topic of this thesis and will not be discussed presently.

A relatively distinct divergence was observed between the shape of the molars of the fossil samples from the two sites, despite a small overlap (Fig. 13). The majority of alterations was observed in the middle and anterior part of the molar, while the posterior part was the least divergent (Fig. 14). Divergence in the shape of the molar was observed, when individuals collected from warm MIS were compared to specimens from cold MIS (Fig. 15). Again, the middle and anterior part of the tooth were the most divergent, while changes in the posterior part of the tooth were insignificant (Fig. 16).

The fossil samples from Kalamakia Cave and Klissoura Cave 1 fit within the *Microtus (Terricola)* group and more specifically with *M. subterraneus* and *M. thomasi*, as shown by Component 1 (CV1) of the canonical variate analysis, describing 47.96% of the total variation of the shape of the molar and Component 2 (CV2) describing 15.98% of the total variation (Fig. 17). These two components, though not exceptionally high, combine for 63.94% of the cumulative percentage of variation, demonstrating the tendency of alterations in molar shape (Tab. 5). Procrustes distances among the specimens (Tab. 6) verify the resemblance between the fossilized specimens with the *M. thomasi* and *M. subterraneus* morphotypes. It is worth mentioning that despite the relatively distinct differentiation between the fossil specimens from Kalamakia Cave and Klissoura Cave 1 (Fig. 13), the smallest Procrustes Distances were detected between the specimens from these sites. This reveals closer relationships between the fossil arvicolines of the two sites, in comparison with the present-day arvicolines of Greece.

Overall throughout the analyses of the shape of the molars, in both the fossil and the extant arvicoline dataset, it is clear that the most divergent and informative part of the molar is the anterior part with the vast majority of the changes occurring from triangle 4 (T4) to anterior cup (AC), contrary to few and insignificant changes observed in triangles 1 to 3 (T1, T2 and T3) and the posterior loop (PL), a tendency observed by Kryštufek and Vohralík (2005).

Regarding the centroid size (mean and whisker plot – Fig. 19, summary statistics – Tab.7) of the present-day arvicolines of Greece, the high mean values observed in the two members of *Microtus (Microtus)* group indicate that these rodents are considerably more robust than the rest of the extant arvicoline populations of the dataset, with the exception of *M. thomasi* individuals from northern Greece. Remarkably, the mean centroid size of *M. thomasi* individuals from northern Greece is substantially higher than the one observed in populations of the same species from Peloponnese (Fraguedakis-Tsolis et al. 2009).

The mean centroid size of individuals from the three units of Kalamakia Cave (Units III, IV and VI) and the two statistically informative layers of Klissoura Cave 1 (Layers XIX and XXI) seem to correspond with the mean centroid size of *M. guentheri* and *M. thomasi* individuals from northern Greece, an observation made for the case of Kalamakia Cave by Kolendrianou et al. (2020) as well. The resemblance should be interpreted as similarities in the size of the molars, rather than as taxonomic relevance between these species and the fossil specimens. On the grounds that no other skeletal parts were examined, no accurate assumption about the overall size of the fossilized rodents could be made (Kolendrianou et al. 2020).

The mean centroid size of specimens from Units III and IV (corresponding to warm MIS 5a and 3, respectively) is slightly higher than the mean value of specimens from Unit VI (corresponding to cold MIS 2) (Tab. 7). The opposite tendency was observed in the specimens of Klissoura Cave 1. It should be mentioned that layers represented by a single specimen (Layers VIII, XII, XVa and XVIII) were included in the cumulative analyses of size. The mean centroid size of the specimens collected from Layer XIX (corresponding to warm MIS 5c) is marginally lower than the mean centroid size of specimens collected from Layer XXI (corresponding to cold MIS 6). However, since the age of this layer cannot be accurately estimated, it is possible that this observation is correlated with a warm episode that transpired during MIS 6. Whatever the case, no accurate comment could be made, owing to inconsistencies in the sample sizes of the two categories (28 and 8 samples from warm and cold conditions, respectively).

Analyses of the length and length/width ratio (summary statistics - Tabs 8 and 9), have shown that specimens from Kalamakia Cave were slightly larger than specimens from Klissoura Cave 1.

Several authors have argued that climate has an indirect effect on the size and robusticity of mammalian herbivore teeth (Janis 1988; Martin 1993; Renaud et al. 2005; Fortelius et al. 2006, Piras et al. 2009). These authors have stated that decreases in temperature and the dominance of dry conditions (usually correlated with high values of $\delta^{18}O$), are related with the expansion of silica rich grasses; this type of abrasive vegetation forces herbivores to develop more robust teeth. During periods with decreased $\delta^{18}O$, the plants are not as abrasive, thus there is no need for robust teeth. Therefore, elongated molars and increases in the L/W ratio are correlated with warm conditions (less abrasive plants), while lower L/W ratio values and increases in robusticity are correlated with cold conditions (silica rich, more abrasive vegetation) (Piras et al. 2009). This tendency is detected in the fossil specimens from Kalamakia Cave, as well. The mean values of length from Units III and IV (warm MIS 5a and 3, respectively) are slightly higher than the mean value of length observed in Unit VI (cold MIS 2). Likewise, the value of L/W ratio are slightly lower in Unit VI, suggesting more symmetrical and robust molars.

Regarding Klissoura Cave 1, the mean molar size seems to be slightly higher in layer XXI (deposit during the cold MIS 6) (Tabs 8 and 9); however, since the age of this layer cannot be accurately estimated, it is possible that this observation is correlated with a warm episode that transpired during MIS 6. Whatever the case, no accurate comment could be made, owing to inconsistencies in the sample sizes of the two categories (28 and 8 samples from warm and cold conditions, respectively).

The asymmetry between triangles 4 (buccal side) and 5 (lingual side) of the anteroconid (expressed as T5/T4 length ratio in this thesis) has been used as a taxonomic criterion between arvicoline species by several authors (Chaline 1972; Navarro et al. 2018). Nadachowski (1984) argued that this index provides little taxonomic information as an independent measurement, however when combined with the overall length of the molar, it can distinguish vole species with “high probability”.

In the present thesis, analyses of this index, both as an independent measurement (Fig. 21) and correlated with molar length (Fig. 22), have displayed a clear discrimination between the two subgenera of the genus *Microtus*. The mean values of individuals from *M. levis* and *M. guentheri* (both members of the *Microtus (Microtus)* group) coherently indicate that triangle 5 (T5 – lingual side) is larger than triangle 4 (T4 – buccal side) in the first lower molars of these voles, an observation made by Kryštufek and Vohralík (2005) as well. The mean values of the members of the *Microtus (Terricola)* group from the mainland of Greece show that T5 is generally slightly larger than T4. Remarkably, in individuals of *M. thomasi* from Peloponnese T4 is larger than T5 (mean T5/T4 ratio < 1). This observation is probably correlated with morphological variations among *M. thomasi* populations from Greece (Fraguedakis-Tsolis et al. 2009).

The means of specimens from Kalamakia Cave and Klissoura Cave 1 correspond with the means of specimens of present-day *Terricola*, and more specifically, *M. subterraneus* and *M. thomasi* from northern Greece (Fig. 21). The correlation of this index with the total length of the lower first molars yielded similar results (Fig. 22). A slight gradual increase of the average values of T5/T4 length was observed through the consecutive units of Kalamakia Cave (Unit III – 1.01 / Unit IV – 1.06, Unit VI – 1.08). This observation can be further supported by an even lower average value of this index in layer XIX (0.97) of Klissoura Cave 1, corresponding to the older MIS 5c.

The tilt of the pitymyan rhombus, a commonly used taxonomic criterion between the vole species (Brunet-Lecomte et al. 2010; Montuire and Brunet-Lecomte 2004; Spitzenberger et al. 2000), provided a distinct discrimination of the extant species in two groups (mean and whisker plot - Fig.23, summary statistics - Tab. 11). This clear discrimination can be explained by the range of tilt observed in the pitymyan rhombus of each species. *M. levis* and *M. guentheri*, present-day members of the *Microtus (Microtus)* group, are characterized by exclusively positive values in this index, indicating that the pitymyan rhombus was tilted towards the anterior part of the tooth in all individuals. The range of tilt is wider in present-day *Microtus (Terricola)* species and the pitymyan rhombus seems to be tilted both towards the anterior and the posterior part of the molar. *M. felteni* is the only species in which the pitymyan rhombus is generally tilted towards the posterior part of the tooth; *M. subterraneus* displayed the widest intraspecific range of tilt. Remarkably, the divergence between *M. thomasi* populations from Peloponnese and northern Greece was once again sizeable, with populations from northern Greece displaying a significant resemblance towards *M. subterraneus*, on the grounds of maximum values of tilt, and the *Microtus (Microtus)* group by displaying a tilt exclusively towards the anterior part of the molar.

The mean values of specimens collected from Kalamakia Cave and Klissoura Cave 1 appear to fit best with the mean values observed in *Microtus (Terricola)* and more specifically, *M. subterraneus* and *M. thomasi* populations from northern Greece, once again (Fig. 23). It is worth mentioning that a single molar from Unit IV of Kalamakia Cave falls within the range of *M. levis* or *M. guentheri*; however, since this measurement represents a single specimen, no further comments could be made on this resemblance (Tab. 11).

Intraspecific analyses on *Microtus (Terricola) grafi* from the Upper Pleistocene of Bacho Kiro (Bulgaria) by Montuire and Brunet-Lecomte (2004), have shown that the pitymyan rhombus is less tilted in individuals living in warm conditions, an observation confirmed in the case of Kalamakia Cave; the range between the minimum and maximum values of tilt in individuals living in Units III and IV (warm MIS 5a and 3, respectively) is significantly lower than the same values of Unit VI (cold MIS 2) (Tab. 11). Inconsistencies between the sample sizes of the different layers of Klissoura Cave 1 do not permit accurate comments to be made.

According to Brunet-Lecomte et al. (2010) the degree of tilt of the pitymyan rhombus can provide geographical information, as the authors of this work observed that the pitymyan rhombi of *Terricola* individuals living in mountain habitats were less tilted (towards the posterior part of the molar) in comparison with individuals from lowlands. However, this tendency was not detected in the present-day *Terricola* species examined in this study; this could be related with the wider range of habitats and altitudes examined by Brunet-Lecomte et al. (2010) or the fact that South-Eastern *Terricola* species have a generally less tilted pitymyan rhombus (Brunet-Lecomte and Nadachowski 1994). Additionally, it should be mentioned that the observation of Brunet-Lecomte et al. (2010) could only be applied to the extant vole database (Tab 15), since the altitude of both fossil sites remained virtually unaltered during the last 200Ky; Kalamakia Cave was either submerged or close to sea level (Darlas and Psathi 2016) and the area around Klissoura Cave 1 was stable (Lykousis 2009).

Table 15: Minimum and maximum altitudes of the present-day arvicoline specimens.

Species	Minimum Altitude (m)	Maximum Altitude (m)
Microtus levis	15	90
Microtus guentheri	130	1400
Microtus felteni	1400	1420
Microtus subterraneus	408	1550
Microtus thomasi	0	25
Microtus thomasi (north)	490	630

The closure of the anterior loop and some variations of this index have been used as a criterion for both intraspecific and interspecific discrimination of vole species (Brunet-Lecomte et al. 2010; Montuire and Brunet-Lecomte 2004; Spitzenberger et al. 2000; Brunet-Lecomte 1990; Brunet-Lecomte and Chaline 1991; Nappi et al. 2006). In the present analyses, this index provided a distinct discrimination of the two subgenera of the genus *Microtus* (mean and whisker plot – Fig. 24, summary statistics – Tab. 12). Despite a relatively sizeable overlap in the observations, *M. levis* and *M. guentheri* displayed a narrow connection between the anterior cup and triangles 6 and 7, a morphology observed by Kryštufek and Vohralík (2005), in individuals of these species from Turkey and Cyprus, as well. The mean values of members of the *Microtus (Terricola)* group are distinctly higher, with the exception of *M. subterraneus* specimens, which seem to resemble the mean values observed in *M. guentheri*. The highest mean values were detected in *M. thomasi* populations from both Peloponnese and northern Greece; however, the former appear to have a wider range.

Specimens from all units of Kalamakia Cave seem to correspond with the means of present-day *M. thomasi* individuals. The means of specimens from Klissoura Cave 1 seem to fit the means of *M. thomasi* individuals, as well. A tendency towards decrease in the homogeneity of specimens is observed through time; the most homogenous layer is Unit III (oldest layer in Kalamakia Cave), in which the highest minimum and the lowest maximum values are observed, contrary to Unit VI (most recent layer), in which the lowest minimum and the highest maximum values are observed.

Intraspecific analyses of *M. (T.) savii* between north-central and southern Italian populations (Nappi et al., 2006), as well as analyses at interspecific level in the *Microtus (Terricola)* group of northern and southern species of western Europe (Brunet-Lecomte, 1988; 1990), have shown that southern populations tend to have a more open anterior loop compared to central and northern populations; an observation which, according to the authors, seems to be correlated with geography. This tendency was observed in this thesis as well; regarding the present-day arvicolines, populations of *M. thomasi* from Peloponnese have slightly more open anterior loops in comparison with their conspecifics from northern Greece. *M. subterraneus* displayed a closed anterior loop, an observation made by Brunet-Lecomte (1990) as well. The fossil specimens from Kalamakia Cave and Klissoura Cave 1 (both located in Peloponnese), have a relatively open anterior loop as well.

The discrimination of the subgenera *Microtus (Microtus)* and *Microtus (Terricola)* provided by the development of the anterior part of the molar was quite distinct (mean and whisker plot – Fig. 25, summary statistics – Tab. 13). In *M. levis* and *M. guentheri* the values of the development of the anterior part of the molars are distinctly consistent; in all specimens, the anterior part was developed and the range between the minimum and maximum percentage of development is very narrow. Unlike the members of the *Microtus (Microtus)* group, the voles of the *Microtus (Terricola)* subgenus are characterized by a wide range of between the minimum and maximum percentage of development. *M. felteni* and *M. thomasi* display a generally slightly smaller anterior part compared to the posterior part of their molars; *M. subterraneus* individuals have a slightly more developed anterior part, an observation made initially by Brunet-Lecomte (1990).

The means of specimens collected from the three units of Kalamakia Cave and layer XIX of Klissoura Cave 1 seem to best fit the means of *Microtus (Terricola)* group and more specifically, *M. subterraneus* and *M. thomasi* from northern Greece, while the mean of specimens from layer XXI of Klissoura Cave 1 appears to correspond to *M. thomasi* individuals from Peloponnese. Brunet-Lecomte et al. (2010) observed a tendency towards an increase in the development of the anterior part of *M. (T.) multiplex* from mountain areas, in comparison with populations from lowlands. This tendency was not observed in the data of this thesis, as fossil populations from lowlands (Kalamakia Cave and Klissoura Cave 1) displayed developed anterior parts; however, as aforementioned, this could be related with distinct differences in the examined altitudes between the work of Brunet-Lecomte et al. (2010) and the present thesis.

A Principal Components Analysis (PCA) (Figs 26, 27 and 28) was conducted to demonstrate the importance of the examined indices. The discrimination of the two subgenera was based mainly on Component 2, positively correlated with the tilt of the pitymyan rhombus, the degree of closure of the anterior loop and centroid size. The discrimination between the species within these groups was based on Component 1, positively correlated with the asymmetry of triangles 4 and 5, the tilt of pitymyan rhombus and the development of the anteroconid complex; closure of the anterior loop had a negative correlation and the importance centroid size was trivial.

Several studies have shown that numerous species of the Iberian, Italian and Balkan Peninsulas, such as the common vole (*Microtus arvalis*) (Bužan et al. 2010), the lesser-white toothed shrew (*Crocidura suaveolens*) (Dubey et al. 2007a) and the European ground squirrel (*Spermophilus citellus*) (Kryštufek et al. 2009), are characterized by significant intraspecific divergence in comparison to their conspecifics from other parts of continental Europe and Asia. According to these authors, this divergence is a result of isolation in refugial areas during the glacial-interglacial cycles. Thanou et al. (2012) suggested that the Mediterranean peninsulas concentrated numerous endemic species and promoted intraspecific variations. In the same work (Thanou et al. 2012) the authors proved the existence of multiple sub-refugia within the Mediterranean Peninsulas. Fraguedakis-Tsolis et al. (2009) have found that *M. levis, M. guentheri* and *M. thomasi* populations from Greece are smaller than their conspecifics from other areas; they also observed significant intraspecific divergence between populations of *M. subterraneus* and *M. thomasi* from Greece, an observation made for populations of *M. thomasi* in the current thesis, as well. These observations support the claims of Thanou et al. (2012) for the existence of sub-refugia in the Balkan Peninsula.

Concerning the fossil samples, the shape analyses and the majority of indices demonstrate resemblance of the fossil arvicoline lower first molars from Kalamakia Cave and Klissoura Cave 1 with the *Microtus (Terricola)* subgenus and, more specifically, with *M. subterraneus* and *M. thomasi* individuals from northern Greece. The distribution of similar morphotypes throughout the three units of Kalamakia Cave (Units III, IV and VI) and the statistically informative layers of Klissoura Cave 1 (Layers XIX and XXI) suggests that these species persevered throughout the various layers of both sites.

M. thomasi is the only species of the genus *Microtus* currently not confined to the mainland of Greece and inhabiting Peloponnese (Kryštufek 1999a; Thanou et al. 2012; IUCN 2019), therefore its presence in these sites comes as no surprise.

Unlike *M. thomasi*, *M. subterraneus* is currently confined to northern parts of the country, with populations reaching Thessaly to the east (north of mount Ossa) and Epirus to the west (Amvrakikos Gulf) (Kryštufek 1999a; Thanou et al. 2012; IUCN 2019); not extending to Peloponnese and Sterea Ellada, mainly due to the obstacle posed by Pindos mountain range (Psonis et al. 2018).

This study constitutes the first documentation of *M. subterraneus* in Klissoura Cave 1; however, Kolendrianou et al. (2020) identified *M. subterraneus* remains in layers of Kalamakia Cave. This observation led the authors to a hypothesis concerning the presence of this species in Peloponnese. They suggested that the descent of species towards Peloponnese “followed the plains west of Pindos”. Tsoukala et al. (2006) have also identified a single individual from Kitseli pothole (Alea, Nemea, NE Peloponnese) as *Microtus subterraneus/multiplex* based on an upper left and upper right third molar (M3), further supporting the presence of a *M. subterraneus* in Peloponnese.

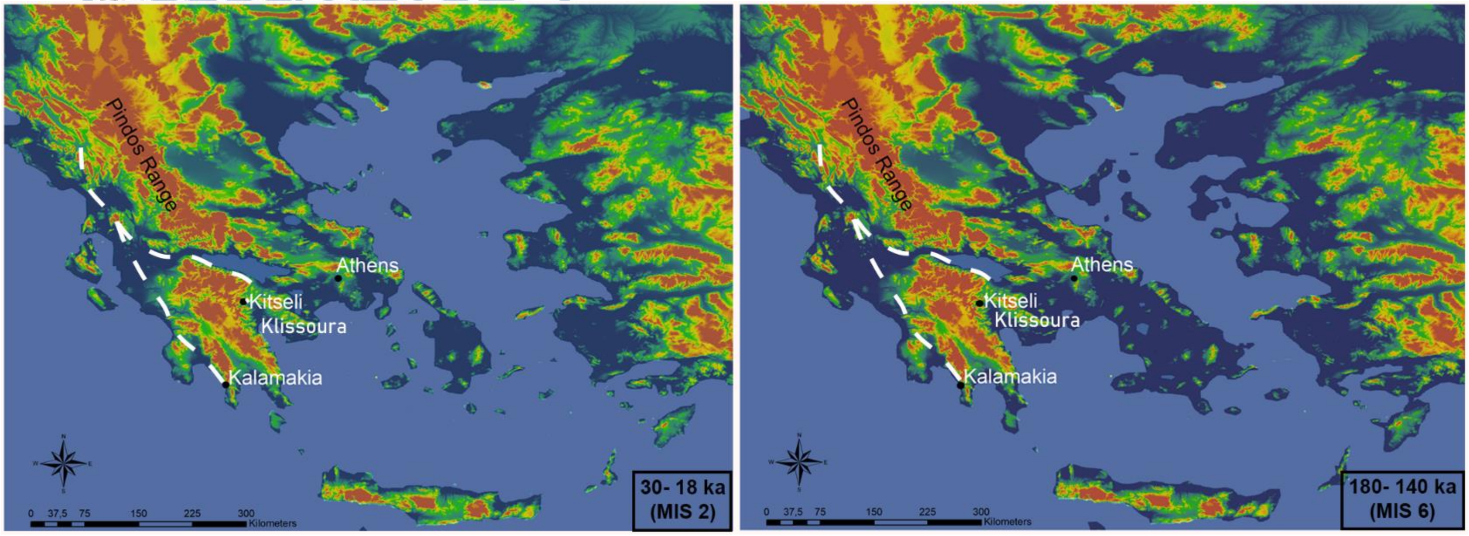


Figure 29: Possible dispersal scenario to Peloponnese during MIS 2 (left) and 6 (right) (Kolendrianou et al. 2020, modified).

Though the hypothetical dispersal scenario suggested by Kolendrianou et al. (2020) (Fig. 29) is entirely plausible, analyses in this thesis, which included *M. thomasi* individuals from northern Greece, have displayed similarities between present day *M. subterraneus* and *M. thomasi* populations from northern Greece. This resemblance indicates a common morphotype of *M. thomasi-subterraneus* in the northern parts of the country. Therefore, the similarities observed between these present-day populations and the fossil specimens from both sites, could be attributed to a similar morphotype. These phenotypic similarities may be interpreted to affinities in habitat and landscape in the mentioned areas.

5. CONCLUSIONS

The geometric morphometrics analyses performed on extant and fossil *Microtus* lower first molars in the context of this thesis, yielded a series of results that can be summarized within the following major points.

Firstly, concerning the methodology that was followed in the landmark analyses, the five additional landmarks located in the anterior cup of the lower first molar, proposed by Kolendrianou et al. (2020) in addition to the landmarks proposed by Wallace (2006), seemed to provide more precise results in the distinction of species according to molar shape, as was indicated by such analyses performed on a set of already identified extant *Microtus* individuals. The results of geometric morphometrics analyses were further supported by analyses performed on a series of measurements on the occlusal surface of the molar. These indices provided a relatively clear distinction between fossil and present-day species, even when they were examined independently. However, the combination of these indices with information from the geometric morphometrics analyses provided more definite results.

Analyses conducted on these measurements and indices and the morphotypes of the molars of fossilized specimens from Kalamakia Cave and Klissoura Cave 1, demonstrate resemblance of the fossil samples with the *Terricola* subgenus and, more specifically, with *M. subterraneus* and *M. thomasi* individuals from northern Greece. Previous studies from Peloponnese indicate the existence of *Microtus subterraneus* in Kalamakia Cave (Kolendrianou et al. 2020) and Kitseli, Nemea (Tsoukala et al. 2006). However, significant resemblance in the shape of the molar between the two extant species from northern areas of Greece, suggest the existence of a common morphotype between these species. Thus, further research is needed before accurate assumptions can be made.

Regarding the extant vole database, significant intraspecific divergence in the shape and size of the molar was observed between present-day *M. thomasi* populations from Epirus and Peloponnese, as individuals from northern Greece were not only significantly larger but also displayed slight divergence in the overall shape of the molar, in comparison with their conspecific from Peloponnese.

Both geometric morphometrics and analyses of the measurements of the occlusal surface of the molar, indicate that the middle and anterior part of the molar is the most divergent, while changes in the posterior part are rather insignificant. A correlation between climate and alterations in the shape and size was detected in several indices; the pitymyan rhombus appeared to be less tilted and the molars appeared to be longer in individuals collected from layers deposited during warm Marine Isotope Stages (MIS).

However, further research is needed as the aforementioned findings only raised more questions regarding the phylogeny and dispersal routes of the voles in the southern Balkans during the Pleistocene, and the possible effect of climate on the morphology and size of the molars.

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