

## Research article

## The Palaeolithic cave of Kalamakia (Mani Peninsula), Greece: new insights on the palaeoenvironment using microvertebrates and mesowear analysis of ruminant teeth

Maria Kolendrianou<sup>a</sup>, Stefanos Ligkovanlis<sup>a</sup>, Ioannis Maniakas<sup>a,b</sup>, Marianthi Tzortzi<sup>a</sup>, George Iliopoulos<sup>a,\*</sup><sup>a</sup> Department of Geology, University of Patras, GR- 26504, Rio, Patras, Greece<sup>b</sup> Natural History Museum of Crete, School of Sciences and Engineering, University of Crete, Knossos Avenue, GR-71409, Irakleio, Greece

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## ABSTRACT

In the present study, results from the examination of mammalian teeth from the cave of Kalamakia with modern techniques, as well as a qualitative overview of the microvertebrate and lithic material, are presented together with a revision of previous related work done for the site, in order to assess the palaeoenvironmental conditions in the area and the role they played in the Neanderthal's repeated occupation of the cave. Geometric morphometrics analyses performed on the first lower molars of *Microtus* spp. individuals revealed persistent populations of the subgenus *Terricola*, in which the presence of *Microtus thomasi* and *Microtus subterraneus* are continuous through the stratigraphic units. Mesowear analyses performed on ruminant teeth showed no significant variation in toothwear through time, except for relatively elevated levels of dietary abrasion for the more recent samples. The study of the lithics revealed that Neanderthals visited the cave in alternating short and more permanent episodes of occupation, with the human occupants exhibiting special concern for raw material economy, while exploiting poor raw materials for the construction of their tools. The overview of the microvertebrate remains showed a growing trend towards the upper stratigraphic units, where taxa typical of temperate climate, open woodland and shrubland become more dominant. These results, along with observations derived from previous studies, suggest that temperate climate and open environment were the factors that mainly contributed to making the cave of Kalamakia attractive as a habitation site to the humans of the area.

## 1. Introduction

During the last years, the importance of Greece as a locus of early-human activity has been acknowledged in several works (Darlas, 2007; Galanidou, 2004; Papagianni, 2000; Darlas and Psathi, 2016; Tourloukis et al., 2016; Tourloukis and Harvati, 2018). Research excavations, concerning the Middle and Upper Pleistocene, however, had been scarce or old (e.g.: Petralona (Poulianos, 1971), Asprochaliko and Kastritsa (Higgs and Vita-Finzi, 1966; Bailey et al., 1983), Franchthi (Perles, 1987), Klissoura (Koumouzelis et al., 2001; Kaczanowska et al., 2010 etc.) until very recently, when new interdisciplinary groups started examining new sites (e.g.: Marathousa (Panagopoulou et al., 2015), Mavri Spilia (Tourloukis et al., 2016; Garefalakis et al., 2018), Rodafnidia (Galanidou et al. 2013, 2016) or revising material from older excavations e.g.: Apidima

(Harvati et al., 2019), Kokkinopilos (Tourloukis, 2009), Kalamakia (present study) etc.

Although Greece exhibits a large number of caves, rock shelters and open-air sites (Bailey et al., 1999; Tourloukis, 2010; Tourloukis and Harvati, 2018) Mani peninsula, in particular, has a considerable number of well-known (Kalamakia (de Lumley and Darlas, 1994), Apidima (Pitsios and Liebhaber, 1995) and Lakonis (Panagopoulou et al., 2002) and lesser known or recently excavated Palaeolithic sites (Melitzia, Kolominitsa, Skoini 3, Skini 4, Tripsana, Kastanis (Darlas and Psathi, 2016), Mavri Spilia (Tourloukis et al., 2016; etc.). These sites keep highlighting the importance of Mani peninsula in paleoanthropology related studies, with inferences on palaeoenvironmental and archaeozoological research as well.

\* Corresponding author.

E-mail address: [iliopoulosg@upatras.gr](mailto:iliopoulosg@upatras.gr) (G. Iliopoulos).

### 1.1. Geological setting

Mani Peninsula constitutes the extension of Taygetos mountain range and is mainly composed of Upper Cretaceous – Lower Eocene white-grey to white, medium-bedded platy semi-crystalline limestones, which belong to the Mani geotectonic unit (Plattenkalk) (Papadopoulou – Vrynioti and Kampolis, 2011). The latter is tectonically overlaid by the Phyllite-Quartzite series (Sabatakakis et al., 2016). The metamorphic limestones have been fractured due to the strong influence of the Hellenic arc during the Late Miocene (de Lumley and Darlas, 1994). Tectonism is represented by NNW-SSE and minor E-W oriented faults formed during the Miocene (Mariolakos et al., 1985). The western part of the peninsula is characterized by a stepped geomorphology, with well-developed terraces and coastal cliffs formed in the limestone. The presence of terraces demonstrates the non-continuous uplift to the west and subsidence to the south (Figure 1). The Tyrrenian terrace must have been completely free of scree deposits at the beginning of the last glacial and the caves overlooking this plateau were most favorable for habitation at that time (Darlas and Psathi, 2016). Along the entire western steep coast, on a vertical cliff overhanging the sea, the tectonic uplift in conjunction with the eustatic sea level fluctuations of the Quaternary, were responsible for the formation of several inland and submerged caves belonging to an extended karstic system (Bassiakos, 1993). The karstic formations are often filled with Quaternary deposits which are mainly represented by talus cones and screes (Sabatakakis et al., 2016). Several of these caves had been originally eroded by the marine transgressions of Marine Isotope Stage (MIS) 5e and MIS 5c, were reoccupied during MIS 4 and were eroded for a second time from the transgressions of the Holocene, resulting in only a small number of caves preserving archeological remains (Darlas and Psathi, 2016).

### 1.2. Kalamakia cave

Kalamakia cave, is one of the numerous fossil-bearing caves at Mani peninsula, such as Apidima, Kolominitsa, Kastanis, Laconis and Melitzia, filled with Pleistocene deposits preserving cultural remains from the Middle Paleolithic (de Lumley and Darlas, 1994; Darlas and de Lumley, 1999, 2004). Throughout the entire height of the cave's walls, borings attributed to bivalve shells (*Lithophaga* sp.), indicate that the cave had been submerged for a significant part of the Pleistocene and was filled by more than 7 m thick clastic deposits which can be divided into distinct units (Darlas and Psathi, 2016; Harvati et al., 2013). The lowermost unit (Unit 0) represents a marine crusting attributed to marine transgression MIS 5e, followed by a second marine, beach rock deposit (Unit II) associated with the MIS 5c transgression, an age that has been confirmed by an U/Th radiometric dating of a marine shell (IPH Kal 9304: 109.000 + 14.000/-13.000 kBP) (de Lumley and Darlas, 1994). Unit I consists of a stalagmitic column that rests directly on the bedrock of the cave at the NW side of the entrance and its formation has been attributed to MIS 5, based on pollen analysis (de Lumley and Darlas, 1994). The overlying Unit III and IV consist continental deposits up to 4m that show a very strong anthropogenic component (Darlas and Psathi, 2016). Particularly, Unit III is composed by sandy continental deposits very rich in silts and clays and, considering its brecciated nature, only the top layers were excavated in an area of 8m<sup>2</sup> (de Lumley and Darlas, 1994; Darlas and de Lumley, 1999). Unit IV consists of angular gravel in a reddish silty-clay sand matrix, that was excavated vertically, covering an area of 4–10m<sup>2</sup> (de Lumley and Darlas, 1994; Darlas and de Lumley, 1999). Charcoal found at the topmost Unit VI gave a <sup>14</sup>C AMS dating of >39,000 years BP (GifA 94592) (Darlas and Psathi, 2016). The uppermost 2.5m, which compose Unit VI, are practically culturally barren. One coprolite

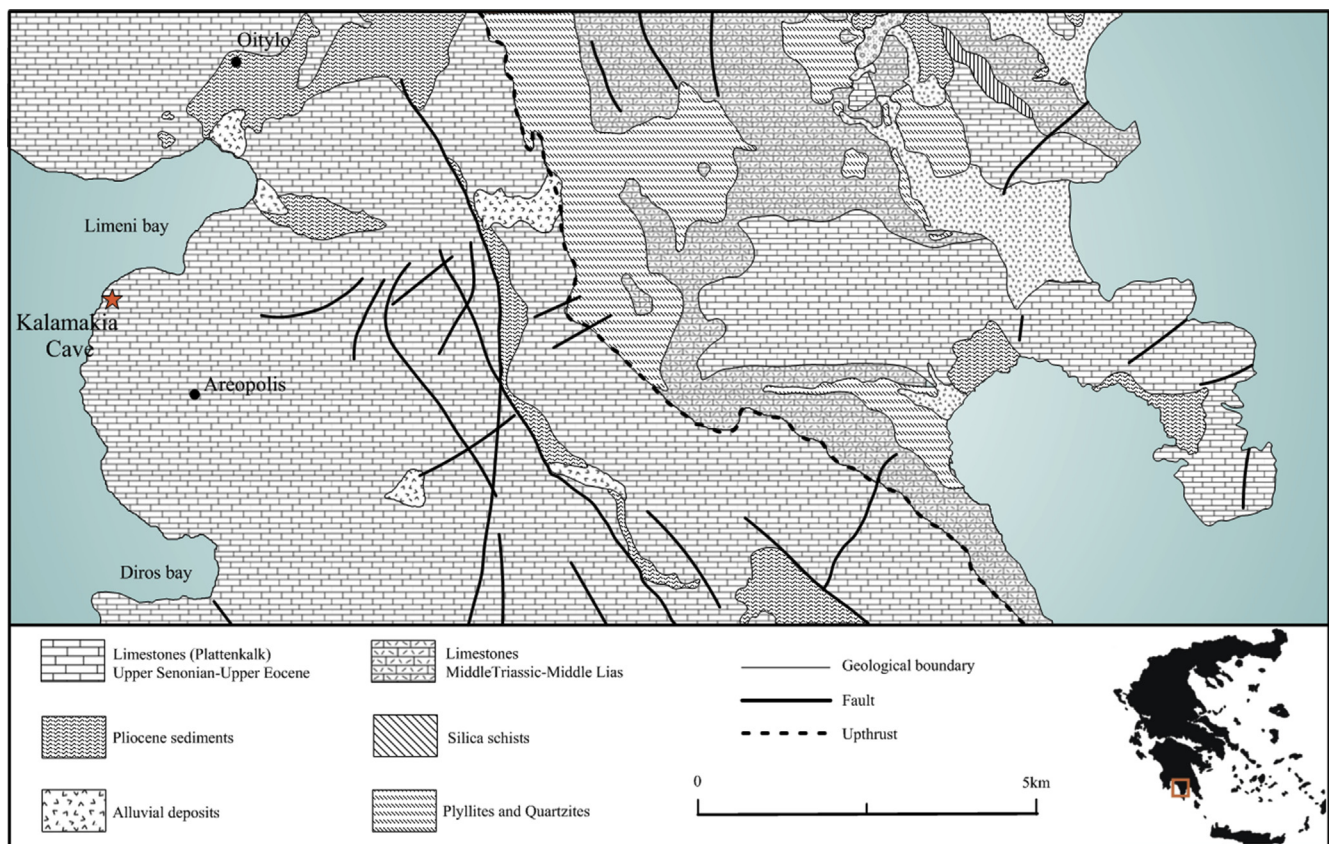


Figure 1. Simplified geological map presenting the geological and tectonic setting of the area surrounding the cave of Kalamakia.

provided a  $^{14}\text{C}$  AMS dating of  $22,410 \pm 120$  for the last unit (27,770–26,330 cal BP; Beta-245334) (Darlas and Psathi, 2016).

### 1.3. Previous research

#### 1.3.1. Pollen analysis

Pollen analyses were performed on samples of calcitic laminae from the stalagmitic pillar (Unit I) formed during the deposition of units III and IV (Lebreton et al., 2008) at the entrance of the cave (de Lumley and Darlas, 1994). Samples of sandy-clay deposits along the stratigraphic sequence of units III, IV, V and VI were found to be barren. This was attributed to an intense post-depositional oxidation that seems to have destroyed all the original pollen material (Lebreton et al. 2007, 2008).

Nevertheless, the pollen material from the stalagmitic pillar itself, revealed two zones (Lebreton et al. 2007, 2008):

The first, expanding through the lowermost and almost up to the upper part of the pillar, was characterized by deciduous trees, with *Pinus* and mesophilic species (*Quercus t. pedunculata-pubescens*, *Fraxinus*, *Carpinus t. betulus*) having a strong presence in the assemblage and pointing towards a supra-Mediterranean forest with the addition of hydrophilic trees such as *Betula* and *Alnus* (Lebreton et al., 2008). The presence of a supra-Mediterranean forest so close to the sea level, along with high humidity conditions, pointed the researchers (Lebreton et al., 2008) towards either an interstadial stage (interglacial 5d, 5b or an interstadial from MIS4 or MIS3) or a locally induced factor that led to an increase in humidity (as testified by the high rates of *Betula* and *Alnus* in the pollen record of Kalamakia).

The second zone includes the uppermost part of the stalagmitic pillar and is characterised by a decrease in most of the previously mentioned arboreal taxa (except *Quercus t. pedunculata-pubescens* and *Fraxinus*) and an increase of a mainly Mediterranean pre-steppe vegetation (*Artemisia*, other Asteraceae representatives, *Quercus t. ilex-coccifera* and *Ephedra*). There is also a rise in the Mediterranean shrub forest, marked by an increase of the genera *Olea* and *Phyllirea* (Lebreton et al., 2008). A similar environment was observed from samples taken from a small stalagmite at the base of unit IV, allowing the correlation of the second zone of the pillar with this unit.

Unfortunately, the pollen zones of Kalamakia cannot be correlated accurately with the two stratigraphic Units III and IV, as there was no way of establishing successfully the boundary between the two units in the pillar (Lebreton et al., 2008). The two pollen zones cannot be placed also in a precise chronological context due to the absence of radiometric data (Voinchet and Darlas, 1998; Lebreton et al., 2008).

However, Lebreton et al. (2008) attempted to place the palaeoenvironmental events indicated by the pollen record of Kalamakia within a more specific chronological framework of the Upper Pleistocene: the first pollen zone could refer to a wet interstadial, followed by a severe climatic episode probably characterized by long and accentuated summer aridity as testified by Mediterranean forest spread (second pollen zone). This Mediterranean prestepic vegetation has adapted to long periods of drought, either during isotopic stage 4 in the lower Weichselian or during the isotopic stage 3 of the Pleniglacial. The presence of xerophilic species shows that the structure and evolution of Mediterranean vegetation during glacial periods depends more on aridity than on temperature.

#### 1.3.2. Fauna

**1.3.2.1. Molluscs.** Mollusc remains were mainly retrieved from Units II and III (de Lumley and Darlas, 1994) but, more interestingly, some valves (consisting exclusively of *Callista chione*) discovered in Unit IV were retouched as scappers (Darlas and de Lumley, 2004; Darlas, 2007; Douka and Spinapolic, 2012). Three *Spondylus gaederopus* shells were also recovered in the same unit. However, they did not exhibit any

evidence of retouching, leading to the hypothesis that they were probably manuports (Darlas and de Lumley, 2004).

These findings indicate probably a deliberate and thoughtful plan of the Neanderthals to exploit their available surroundings and natural resources, either these were raw lithic materials or seashells (Darlas, 2007; Douka and Spinapolic, 2012). Whether the retouching was performed on sea-shells brought to the cave for food consumption or not, this is a question that requires further examination before finally answered (Douka and Spinapolic, 2012).

**1.3.2.2. Microvertebrates.** The microvertebrate remains of Kalamakia have been examined in the past, but the only results published were just preliminary taxonomical lists (de Lumley and Darlas, 1994; Roger, 1997; Roger and Darlas, 1999), until Roger and Darlas (2008) published a list of taxa along with the respective number of remains and Minimum Number of Individuals (MNI) for each identified taxon and each layer. They identified 59 taxa to the species or genus level (where possible) and to the family level in the cases of unidentified remains such as Scincidae and Lacertidae. Among them, reptiles and birds were found to be the most diverse groups, including 21 taxa each, and rodents were found to be the most abundant (7051 remains), followed by reptiles (453 remains). No species typical of colder climates were identified in any of the stratigraphic units.

Unit IV was the richest with its lower part named “ensemble IV” and its upper part (mistakenly) called “ensemble V” bearing a total of 5870 remains. Unit VI on the other hand was the poorest with only 296 retrieved remains.

According to the species present in the assemblage at the time of deposition, the palaeoenvironment was probably open and relatively dry with some wet areas (Roger and Darlas, 1999, 2008) and the palaeoclimate could be characterized as temperate-Mediterranean (Desclaux in de Lumley and Darlas (1994); Roger and Darlas 2008). Interestingly, a shift towards drier conditions seems to have taken place between the deposition of the lower and upper layers of unit IV, with the lower part indicating a slightly more humid climate (as testified by the rodent, bird, reptile and amphibian remains) (Roger and Darlas, 2008). Finally, Roger and Darlas (2008) noted a slightly more abundant presence of temperate forest rodent species in unit VI. The possibility of predation bias in the assemblage, has been also considered as traces of digestion and remains from nocturnal raptors were retrieved (Roger, 2004; Roger and Darlas, 2008).

**1.3.2.3. Vertebrates.** Gardeisen and Trantalidou (1998) published the preliminary results on the study of the large vertebrates of Kalamakia from the initial excavations of the site. Later, Darlas and Psathi (2016) presented the full list of large vertebrates found in Kalamakia. Regarding the faunal representation, both published works (Gardeisen and Trantalidou, 1998; Darlas and Psathi, 2016) found that *Dama dama* and *Capra ibex* dominated, followed by *Sus scrofa*, and an occasional presence of Proboscidea and Bovidae. Concerning the carnivores retrieved from the site, both works agree that small sized representatives, although few in numbers, are mostly present, with the red fox (*Vulpes vulpes*) as the dominant carnivore of the assemblage (Darlas and Psathi, 2016). It is important though to note the strong presence of tortoises in the site (11.140 identified *Testudo* specimens, out of a total of 15.202 identified specimens in Units III and IV) with *Testudo marginata* remains dominating over *Testudo hermanni* (Darlas and Psathi, 2016).

Preliminary zooarchaeological and taphonomical analyses conducted by Gardeisen and Trantalidou (1998) revealed rather clearly the exploitation of the artiodactyls recovered in the site by the human occupants (large amount of long bone splinters, traces of bone cutting, large percentages of burned bones). Harvati et al. (2013) and Darlas and Psathi (2016) also conclude that the main accumulator of the site's mammalian and tortoise remains were the human occupants, but recognize some small contribution by the carnivores, as well.



**1.3.2.4. Human remains.** Lithic artifacts from Kalamakia have been discussed several times (see below). However, the fourteen human skeletal elements from the site have been mentioned or analytically examined only in a handful of published works (Darlas and de Lumley, 1998; Harvati et al., 2009; Harvati et al., 2013; McCarty et al., 2014; Bauer et al., 2018). The first report of human remains from Kalamakia, was a third left upper molar (named “KAL3” in Harvati et al., 2013) that was characterized by Darlas and de Lumley (1998) as “very robust” and severely worn.

All 14 human remains have been attributed to *Homo neanderthalensis*, originally because of the Mousterian lithic artifacts retrieved from the site (Darlas and de Lumley, 1998; Harvati et al., 2009). Later, determinations were confirmed from neanderthalian morphological

features identified on four diagnostic elements present in the assemblage: two permanent upper incisors (KAL 10, KAL11) and two lower fourth premolars (KAL 6, KAL9) from the lower part of unit IV (Harvati et al., 2013; Bauer et al., 2018). Apart from morphologically characteristic samples, two additional specimens from Kalamakia (KAL2 and KAL3) have been identified as Neanderthal remains, due to the metric values of their crown dimensions (Harvati et al., 2013). It has been estimated that the possible number of individuals present in the site ranges from 14 (reflecting the total amount of specimens retrieved) to 8 (Harvati et al., 2013). Based on occlusal fingerprint and microwear analyses (Harvati et al., 2013) on the aforementioned Unit III specimen, KAL3, a mixed habitat diet is reflected, consisting of both meat and plant food.



**Figure 2.** (i-ii) Recurrent centripetal Levallois cores, (iii) bifacial discoid core, (iv) exhausted core, (v) core on flake.

The preservation state of the hominin remains has been described as “highly fragmentary” by Harvati et al. (2013) with breakage, erosion, carnivore puncture marks and post-mortem anthropogenic modifications. Carnivore modifications seem to appear in the upper part of Unit IV sample KAL14, while anthropogenic modifications refer to wide grooves in the KAL5 upper premolar and KAL8 upper molar from the lower part of Unit IV (possibly reflecting toothpick grooves) (Harvati et al., 2013).

### 1.3.3. Stone industry

The published data on the Kalamakia Middle Palaeolithic stone industry (de Lumley and Darlas, 1994; Darlas and de Lumley, 1999, 2004; Darlas, 2007; Darlas and Psathi, 2016) offer a general framework concerning the major tendencies characterizing the site's lithic artefacts, enlightening at the same time aspects of the *Homo neanderthalensis* technological behavior and subsistence at Mani peninsula. The under discussion lithic assemblages have derived from 2 stratigraphic units (III and IV) and a series of occupational levels.

**1.3.3.1. The raw materials.** Flint, andesite and quartz are referred as the main raw materials for the artefacts construction. Quartzite and limestone comprise secondary raw material choices (de Lumley and Darlas, 1994; Darlas and de Lumley, 1999, 2004; Darlas, 2007; Darlas and Psathi, 2016). Flint (Figure 2 i, iv, Figure 3 i, vi-vii, Figure 4 i-iii), mainly grey and black, has a semi-local origin coming from a distance of 12–20 km, northwest of the site (de Lumley and Darlas, 1994; Darlas and de Lumley, 1999, 2004; Darlas, 2007; Darlas and Psathi, 2016). It was probably collected from a secondary depositional context at the region of Trachila (Karkazi, 2018). Andesite (mostly ‘krokeatis’ type stone) (Figure 2, ii, Figure 3 iii, Figure 4 iv) has a more ‘exotic’ provenance. It can be found as a secondary deposition under the form of medium-sized nodules, at the banks of Evrotas river, 20–30 km north-east of the site (Darlas and de Lumley, 2004; Darlas and Psathi, 2016; Karkazi, 2018).

Quartz (Figure 2, iii, Figure 3 iv, Figure 4 v) can be found in various qualities at a maximum distance of a 10 km radius from the site. In many

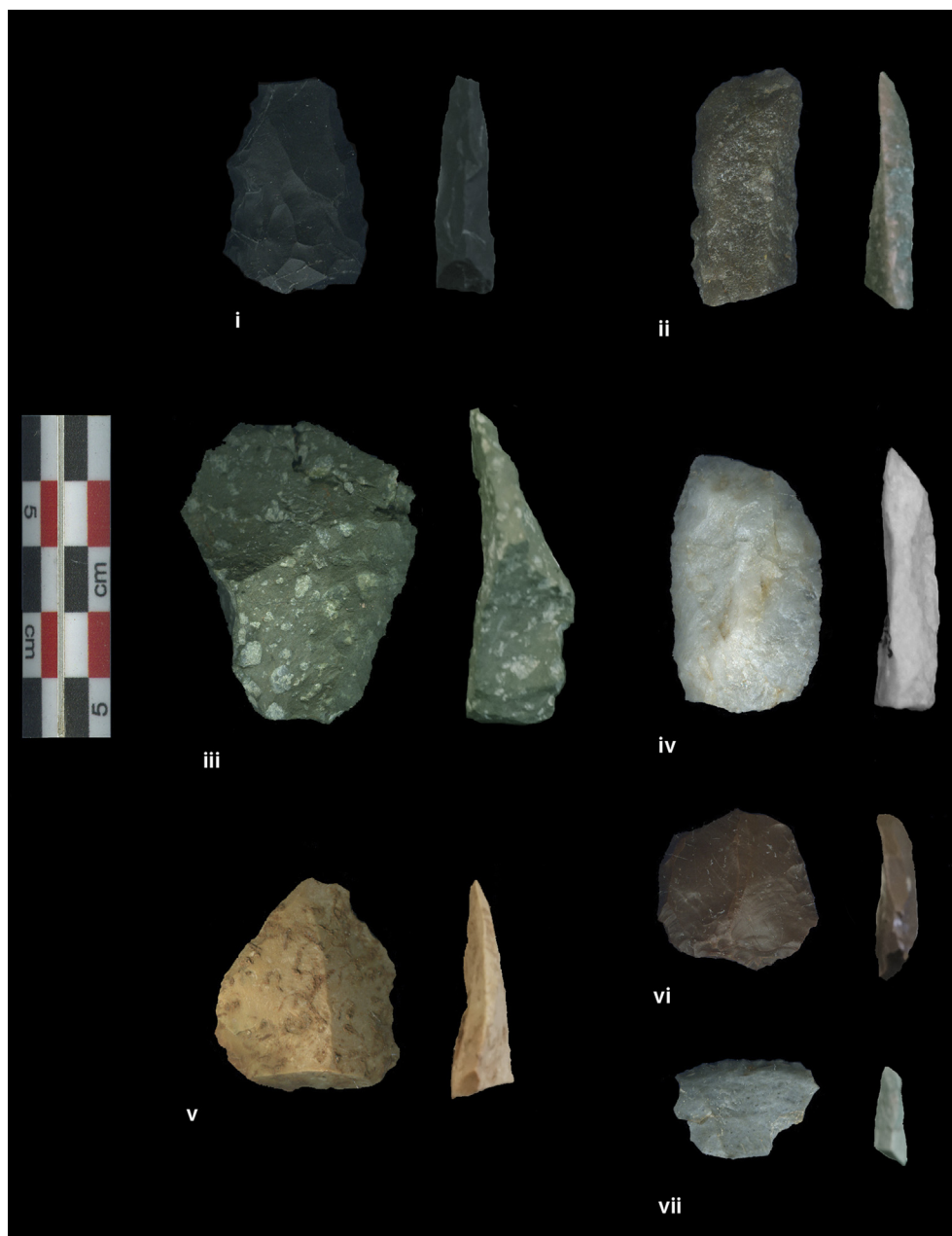
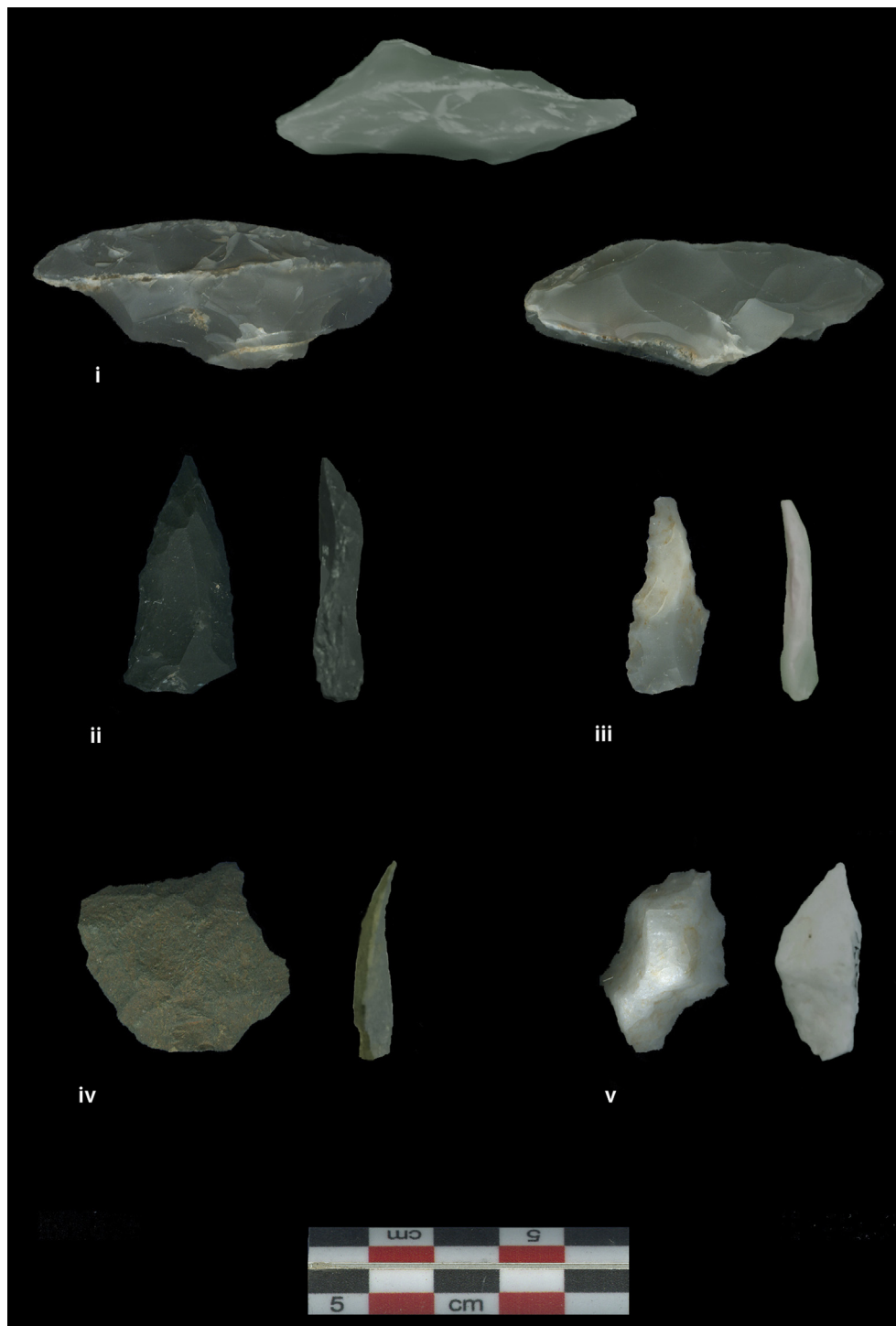


Figure 3. Side (i-vi) and transverse (vii) scrapers.

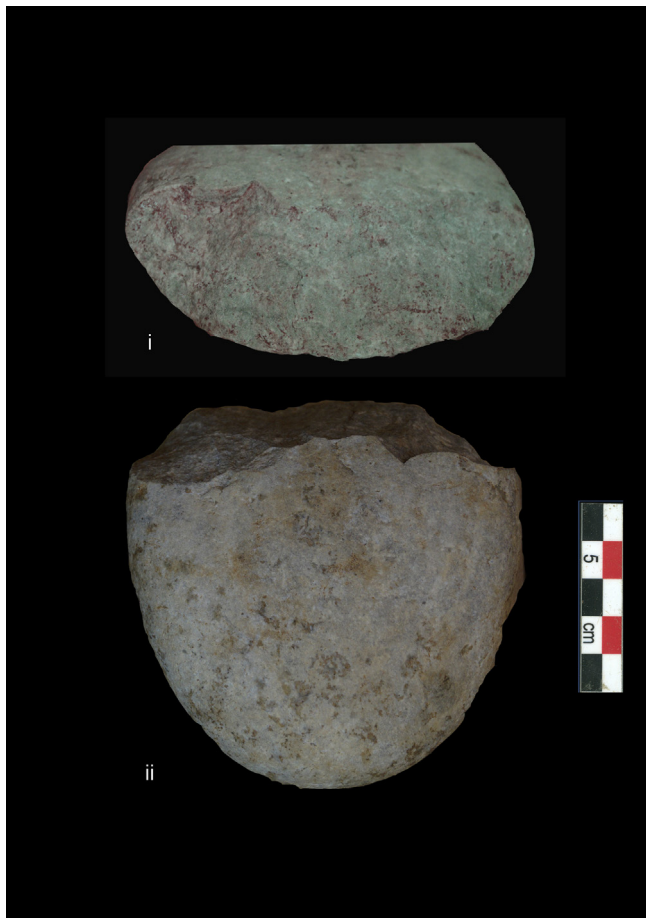


**Figure 4.** (i) Quina scraper (ii-iii) points, (iv) denticulate and borer, (v) double borer.

cases, it can be found within the cave stratigraphy under the form of regular flakes. Having the same provenance as quartz, quartzite is described as more homogeneous than the latter, resulting to the production of large blanks (Darlas and de Lumley, 2004; Darlas and Psathi, 2016) (Figure 2 v, Figure 3 ii). Local fine-grained, sublithographic, as well as coarse-grained (marble) limestones are also mentioned in small quantities. In the first case this stone type is regularly flakable, often

resulting to the production of large blanks (Figure 3 v), while marble reflects a rather opportunistic raw material choice for the construction of secondary tools (Darlas and de Lumley, 2004) (Figure 5).

**1.3.3.2. Synthesis and the toolkit.** The great majority of the industry artefacts (over 90%) consists of blanks with a maximum size less than 20mm (Darlas and de Lumley, 2004). Cores are few and in most cases are



**Figure 5.** Chopper on coarse grained limestone (marble). (i) Section of the distal end, (ii) Upper surface.

small. Considering debitage, the blanks with flake proportions (between 20–30mm) outnumber by far the elongated artefacts (Darlas and de Lumley, 2004; Darlas and Psathi, 2016). Apart from the limited productive flaking procedures, the main technical actions taking place in the cave regard tool manufacture or resharpening. Retouched implements (flint blanks) index is relatively high (22%–26,9%), while many waste-flakes/chips have been also recognized (Darlas and de Lumley, 2004; Darlas and Psathi, 2016). Retouched blanks, limited in numbers, altogether are of small dimensions (Darlas and de Lumley, 2004; Darlas and Psathi, 2016) and have been mostly formatted through scalar detachments with Quina type retouch (e.g. Figure 4 i).

Regarding typology, side-scrapers of good quality and typical form-in some cases of very small dimensions-are referred as the main tool type. They are mainly simple, lateral or transverse, and less often double (e.g. Figure 3 i–vi, Figure 4 i).

The few recovered points are very well shaped (e.g. Figure 4 ii–iii). Notches and denticulates are founded in small proportions along with pointed implements, such as borers and small piercers (e.g. Figure 4 iv–v).

## 2. Materials and methods

### 2.1. Materials

Material from the excavations conducted in Kalamakia by the Ephorate of Paleanthropology and Speleology of Greece (Greek Ministry of Culture) in collaboration with the University of Athens and the Muséum National d'Histoire Naturelle (Paris) during 1996–2003, was re-examined by the authors in the Laboratory of Palaeontology and Stratigraphy (LPS, Dept. of Geology, University of Patras), regarding the

microfaunal remains and the mesowear analysis of ruminant teeth, and in the laboratory of the Ephorate of Paleanthropology and Speleology of Greece, regarding the stone industry (qualitative overview of the lithic material).

### 2.2. Methods

#### 2.2.1. Microfauna identification

Microfaunal remains were examined stereomicroscopically, to a greater arithmetical extent (32.319 remains) compared to previous work (qualitative assessment of the microvertebrates species conducted by Desclaux and presented in de Lumley and Darlas (1994); 7.611 remains examined by Roger and Bailon and presented in Roger and Darlas (2008)). In the present study, bird and tortoise remains were not examined (and the respective specimens presented in Roger and Darlas (2008) have not been commented herein). The microfaunal remains in this study were identified taxonomically based on literature (Peshev et al., 2004; Hilson, 2005; Kryštufek and Vohralík, 2005 for micromammals; Venczel, 2000 for snakes; Rauscher, 1992 for lizards; Bailon, 1999 for amphibians and de Buffrenil et al., 2011; Blain et al., 2014 for osteoderms) and the LPS's comparative skeleton collection.

Additionally, 70 Arvicolinae (identified as *Microtus* sp. from their morphology) lower first molars (m1) were selected equally and randomly from units III, IV and VI in order to be examined applying geometric morphometrics (as described in Zelditch et al. (2012) and in Killick (2012) with a deeper focus in *Microtus* specimens). Fossil samples were compared with 121 lower first molars from different individuals belonging to the five extant *Microtus* species found in Greece (*M. levis*, *M. subterraneus*, *M. thomasi*, *M. guentheri* and *M. felteni*) using the same methodology. The samples from the five extant *Microtus* species were not collected from a protected area.

The m1s from Kalamakia were chosen based on their preservation state (only whole molars were examined) and photographed with a Canon G12 Powershot camera under a SZM1 Optika stereomicroscope. The m1s from the extant specimens were photographed under a Zeiss stereomicroscope with an attached Zeiss AxioCam Erc 5s camera by members of the Laboratory of Zoology (Section of Animal Biology, Dept. of Biology, University of Patras) from whom they were identified to the species level.

The landmarks used in the analysis were adopted from Wallace (2006) (solid black circles in Figure 6) with the addition of five extra landmarks in the anterior part of m1 (Table 1, black outlined circles in Figure 6). The addition of these landmarks lead to more definitive results in the segregation of the extant specimens (upon which the landmarks were originally tested) and, consequently, the complete set of all 26 landmarks was applied on the dataset of both fossilized and modern m1s. The programs used in the analysis were tpsDig2 2.17 (Rohlf, 2013), MorphoJ (Klingenberg, 2011) and PAST 3.25 (Hammer et al., 2001). A Relative Warp Analysis, similar to the standard Principal Component Analysis, but preferred for 2D landmark configurations (Hammer et al., 2001), was conducted for the shape of the molars and, an one-way Analysis Of Variance (ANOVA similarity test) was executed 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).

#### 2.2.2. Mesowear analysis of ruminant teeth

Apart from microfaunal systematics, ruminant teeth have been examined to provide information about these animals' feeding ecology, with the employment of the *mesowear method*, originally introduced by Fortelius and Solounias (2000), by evaluating the relative relief and sharpness of the upper and lower molars cusp apices (M1–M3, m1–m3) through digital photography with the aid of the software tpsDig2 2.17 (Rohlf, 2013). From the available dental material, only the adult isolated teeth and tooth rows bearing molars were sampled, whereas those in very





**Figure 6.** Landmarks used in the analysis of lower first molars (m1s) from Kalamakia. Landmarks pointed with solid red circles were adopted by Wallace (2006) and landmarks pointed with red outlined circles were added by the authors (Table 1).

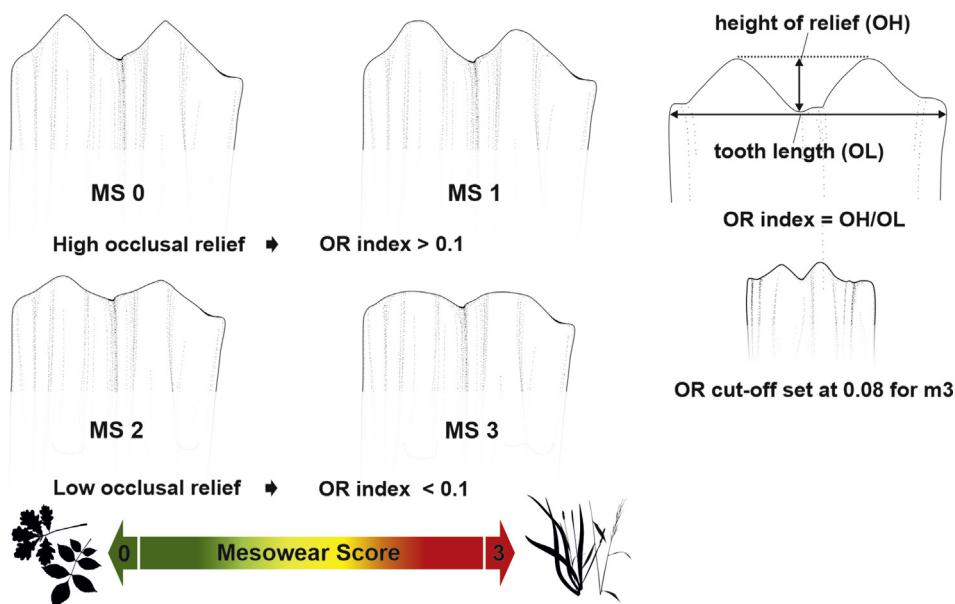
**Table 1.** Location descriptions of the five additional landmarks used by the authors (landmarks 1–5 in Figure 2). Nomenclature of the molar pattern adopted from Kryštufek and Vohralík (2005).

Landmark	Location
1	Point of maximum curvature of buccal re-entrant angle 4
2	Point of maximum curvature of lingual re-entrant angle 5
3	Point of maximum curvature of the buccal tip of the anterior cup
4	Midpoint of the anterior loop of the anterior cup
5	Point of maximum curvature of the lingual tip of the anterior cup

early wear stages (juvenile individuals), or extremely worn or even taphonomically altered were discarded from the analysis. Nevertheless, the inclusion of M1, M3 and m1, m3 fulfil the need of a larger dataset, based on the “expanded” model proposed by (Kaiser and Solounias, 2003), but also the demand of consistency with the primary application of the method as all selected specimens were preferably at an

intermediate stage of wear. Overall, 134 teeth of 5 different ruminant taxa (*Dama dama*, *Cervus elaphus*, *Capreolus* sp., *Capra ibex*, *Bos primigenius*) were taken into account in two separate analyses of the combined samples of maxillar (n = 66) and mandibular (n = 68) specimens respectively.

Serving as a proxy for the average long-term (life-time) dietary habits of the studied populations, the mesowear method can relate the macroscopic molar facet shape to abrasion levels of the consumed plant material (Figure 7). In general, less abrasive food items (e.g., soft dicotyledonous leaves) should allow attrition (tooth-to-tooth wear) to dominate, maintaining high and sharpened molar cusps, whereas more abrasive components, associated with an increased soil or dust particle ingestion in a grass-dominated environment, result in rounder and lower cusp apices as the tooth wears (Figure 7). The occlusal relief can be classified quantitatively as high or low, depending on the distance of the cutting edges on the buccal side for maxillar or on the lingual side for mandibular teeth from the bottom of the valley between them (Figure 7).



**Figure 7.** Illustration of the mesowear categorical scoring system and the parameters employed for the analysis, following Fortelius and Solounias (2000). Cusp shape was classified subjectively as sharp: with no rounded area between the mesial and distal facets cusps; rounded: with a smooth tip between the mesial and distal facets on the lower slope or blunt: more flattened and lacking distinct facets.



**Table 2.** Tukey's pairwise post-hoc test, The Studentized Range Statistic Q is given in the lower left triangle of the array, and the probabilities p (equal means for null hypothesis) in the upper right.

	KAL- III	KAL-IV	KAL- VI	<i>M. felteni</i>	<i>M. guentheri</i>	<i>M. levis</i>	<i>M. subterraneus</i>	<i>M. thomasi</i>
KAL- III		0.43	0.02	$6.91 \times 10^{-13}$	0.53	$7.03 \times 10^{-7}$	0	$1.11 \times 10^{-10}$
KAL-IV	2.94		0.96	$4.59 \times 10^{-8}$	1	0.01	0	$1.18 \times 10^{-5}$
KAL-VI	4.69	1.55		$1.40 \times 10^{-6}$	0.82	0.17	0	0
<i>M. felteni</i>	11.68	8.98	8.04		$1.79 \times 10^{-9}$	0.01	0.05	0.62
<i>M. guentheri</i>	2.74	0.04	2.1	9.82		0	0	$4.41 \times 10^{-7}$
<i>M. levis</i>	8.24	4.98	3.64	5.20	5.83		$9.65 \times 10^{-13}$	0.42
<i>M. subterraneus</i>	18.72	15.43	14.84	4.31	17.05	11.61		$1.63 \times 10^{-6}$
<i>M. thomasi</i>	10.51	7.42	6.30	2.54	8.37	2.97	8	

The latter (OR index, Figure 7) was metrically evaluated based on the ratio expressed as the intercuspal valley height (OH, Figure 7) divided by the total tooth occlusal surface length (OL, Figure 7), setting the limit between high and low cusps at 0.1, following the methodology of Fortelius and Solounias (2000), for M1-M3, m1-m2 teeth and 0.08 for specifically m3 after the suggestion of Louys et al. (2011) (Figure 7). In each case, the sharpest cusp (either the paracone/metaconid or metacone/endoconid) was scored. Four mesowear categories, were implemented in accordance to the simplified traditional scoring system of Fortelius and Solounias (2000): 0 for high relief/sharp cusps, 1 for high relief/round cusps, 2 for low relief/round cusps, and 3 for low relief/blunt cusps, with lowest and highest values exposing the extremities of the attrition-abrasion wear gradient and the browsing-grazing herbivore dietary continuum (Figure 7).

### 3. Results

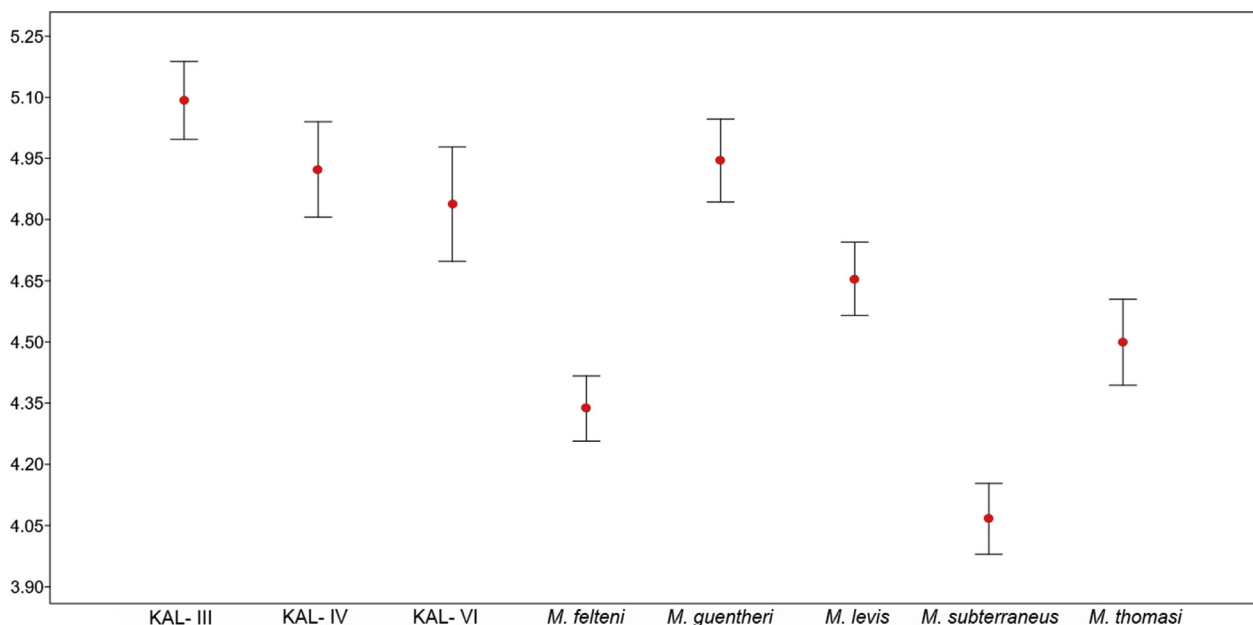
#### 3.1. Geometric morphometrics analyses on *Microtus* sp. lower first molars

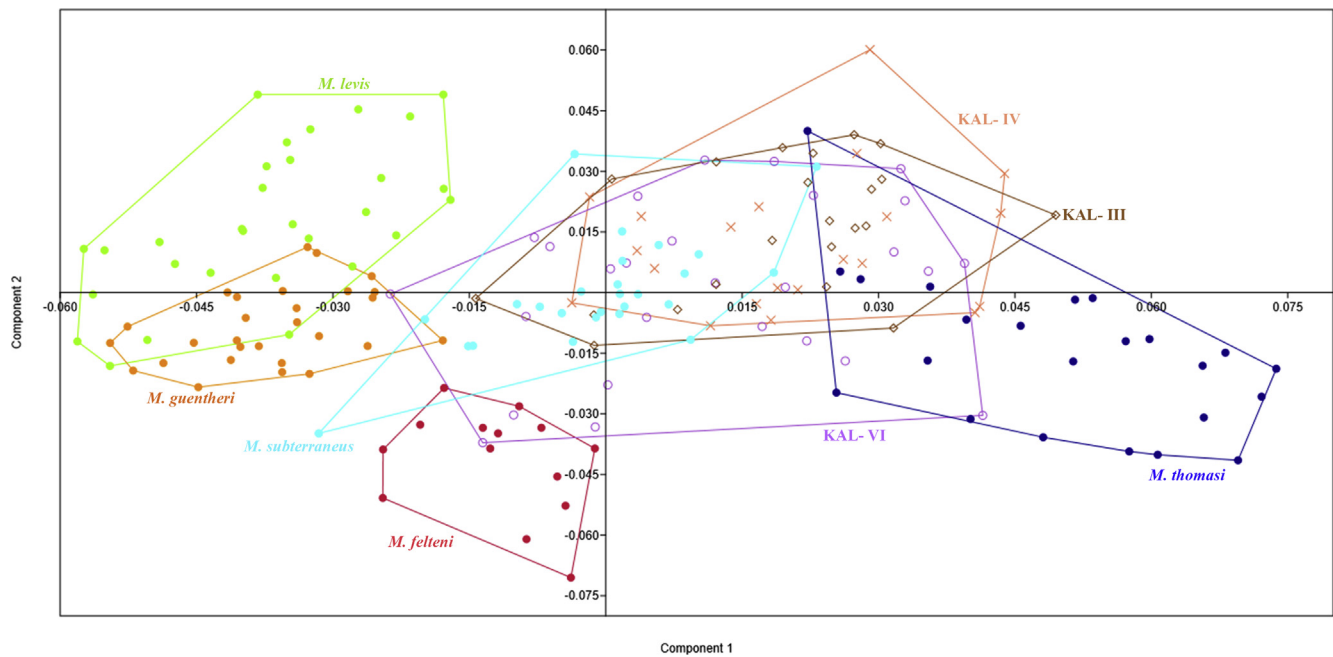
The results for the analyses of the centroid size and the shape of the *Microtus* molars are presented separately.

#### 3.1.1. Centroid size analyses

The performed ANOVA on the centroid size of the studied molars showed a high F value ( $F = 39.57$ ) and a  $p < 0.05$  ( $p = 1.709 \times 10^{-33}$ ), indicating that at least one group mean was significantly different from the others. To examine this significant inequality with appropriate adjustment for the multiple pairs testing, a Tukey's pairwise post-hoc test (Tukey, 1949) was performed, with its significance estimated according to Copenhaver and Holland (1988) (Table 2) to figure out which groups in the sample differ.

According to Table 2, the biggest similarities between pairs, appear primarily between the fossil material from unit IV and *M. guentheri*, and subsequently between the groups from unit IV and VI, *M. guentheri* and unit VI and *M. guentheri* and unit III. Every other tested pair has obviously lower values of p and higher values of Q, indicating no similarities between their means. This is in accordance with the mean and whiskers plot shown below (Figure 8) where the mean values of the Kalamakia samples from every stratigraphic unit coincide with the mean value of the *M. guentheri* specimens, while there are also some minor differences between the mean centroid sizes of the three units (unit III- corresponding to the warmer MIS 5a-presents the highest and unit VI - deposited during the coolest MIS 2- the lowest value).

**Figure 8.** Mean and whiskers plot of the mean value of each group presented as a point (red), the whisker's type corresponding to its standard error and its length the 95% interval.



**Figure 9.** Relative Warp Analysis of shape of the fossilized lower first molars of *Microtus* sp. from Kalamakia, according to the stratigraphic unit from which they were retrieved (brown diamond for unit III “KAL-III”, coral x for unit IV “KAL-IV” and purple circle for unit VI “KAL-VI”) and of the five extant *Microtus* species of Greece (*Microtus felteni* (red), *Microtus guentheri* (orange), *Microtus levis* (green), *Microtus subterraneus* (light blue) and *Microtus thomasi* (dark blue)). The values used in the analysis were the residuals computed by the regression.

**3.1.2. Shape analyses**

Before the listing of the results concerning shape, it should be mentioned that a regression analysis was initially performed with Procrustes coordinates as the dependent variables and log-transformed centroid size as an independent variable, in order to check for and remove the possible influence of size on shape analyses (Klingerberg, 2016). The regression predicted only a 2.11% of influence of size on shape and the residuals computed were used for the Relative Warp Analysis that followed (Figure 9, Table 3).

There is a clear distinction between the modern *Microtus* species (Figure 9), while the fossilized samples fit well within the *Microtus* (*Terricola*) group (*M. felteni*, *M. subterraneus* and *M. thomasi*) and seem to lean towards the *M. subterraneus* cluster according to the Relative Warp axis 1 (Component 1), which is the most informative (unfortunately describing only 47.01% of the shape variance, but still considered indicative of the trend appearing in the analyses). According to the second Relative Warp axis (Component 2, raising the description of the shape variance to 67.18%), the fossilized material seems to differ between the three stratigraphic layers from which the molars were retrieved, with specimens from unit VI (corresponding to MIS 2) slightly diverging from the ones from units IV (MIS 3) and III (MIS 5a).

Procrustes distances among the different groups (Table 3) were chosen over Mahalanobis distances, to illustrate the absolute magnitude of the deviation of shape in the sample (Klingerberg and Monteiro,

2005). The smallest distances appear between the different units of the fossilized material (values between 0.0236- 0.0320) followed by the distances between the fossilized material and the extant species *M. subterraneus* (0.0475 for unit III, 0.0500 for unit IV and 0.0547 for unit VI), with the distance between the species *M. levis* and *M. guentheri* also presenting a low value (0.0494).

**3.2. Microfauna identification**

A total of 32.319 microvertebrate specimens were examined and the results of their identification (Table 4) are presented as taxon presence/absence per stratigraphic unit (identification to the species level was not always possible because of the fragmentation of some of the specimens). Characteristic remains from rodents and reptiles that will be discussed below, are also presented (Figure 10).

**3.3. Mesowear analysis of ruminant teeth**

Summary statistics for corresponding mesowear data and the relative proportions of species falling in the % high, % low, % sharp, % round and % blunt categories for each taxon and among different strata have revealed a dietary range from slight browsing to a mixed feeding strategy (Tables 5, 6, Figures. 11, 12). The vast majority of the analyzed sample belongs to *Capra ibex* and *Dama dama*, mainly deriving from remains of

**Table 3.** Procrustes distances among the fossilized lower first molars of *Microtus* sp. from Kalamakia according to the stratigraphic unit from which they were retrieved (“KAL-III” for unit III, “KAL-IV” for unit IV and “KAL-VI” for unit VI) and the five extant *Microtus* species of Greece: *Microtus felteni*, *Microtus guentheri*, *Microtus levis*, *Microtus subterraneus* and *Microtus thomasi*. The values used in the analysis were the residuals computed by the regression.

	KAL- III	KAL-IV	KAL- VI	<i>M. felteni</i>	<i>M. guentheri</i>	<i>M. levis</i>	<i>M. subterraneus</i>
KAL-IV	0.0236						
KALVI	0.0320	0.0257					
<i>M. felteni</i>	0.0645	0.0643	0.0556				
<i>M. guentheri</i>	0.0687	0.0689	0.0612	0.0665			
<i>M. levis</i>	0.0616	0.0632	0.0590	0.0714	0.0494		
<i>M. subterraneus</i>	0.0475	0.0500	0.0547	0.0592	0.0762	0.0649	
<i>M. thomasi</i>	0.0580	0.0538	0.0573	0.0778	0.0955	0.0963	0.0707

**Table 4.** Presence/Absence of the identified taxa of Kalamakia per stratigraphic unit.

	Unit VI	Unit IV	Unit III
<b>Amphibia</b>			
<i>Bufo bufo</i>	+	+	
<i>Bufotes viridis</i>	+	+	
Ranidae	+		+
<b>Reptilia</b>			
<i>Lacerta</i> sp.	+	+	+
<i>Pseudopus apodus</i>		+	+
<i>Ablepharus</i> sp.		+	
<i>Anguis</i> sp.	+	+	+
cf. <i>Podarcis</i> sp.	+	+	
Gekkonidae		+	
Scincidae		+	
<i>Coronella austriaca</i>	+		
<i>Dolichophis caspius</i>		+	
<i>Elaphe quatuorlineata</i>	+	+	+
<i>Eryx jaculus</i>		+	+
<i>Malpolon insignitus</i>	+	+	
<i>Natrix natrix</i>	+	+	
<i>Natrix</i> sp.		+	
<i>Telescopus fallax</i>	+	+	
<i>Vipera ammodytes</i>	+	+	
<i>Zamenis longissimus</i>	+		
<i>Zamenis situla</i>	+	+	
Colubridae indet.	+	+	+
<b>Chiroptera</b>			
<i>Myotis cf. blythii</i>	+		
<i>Pipistrellus</i> sp.		+	
<i>Rhinolophus</i> sp.		+	
<b>Insectivora</b>			
<i>Crociodura suaveolens</i>	+	+	+
<i>Erinaceus</i> sp.		+	+
<i>Talpa</i> sp.		+	
<b>Rodentia</b>			
<i>A. epimelas</i>	+	+	+
<i>Apodemus</i> sp.	+	+	+
<i>Chionomys nivalis</i>	+	+	
<i>Glis glis</i>	+	+	+
<i>Sciurus vulgaris</i>	+		
<i>Microtus arvalis</i>	+	+	
<i>Microtus subterraneus</i>	+	+	+
<i>Microtus thomasi</i>	+	+	+
Leporidae	+	+	+
Muridae		+	+

Generally, the microfaunal assemblage is quite diverse with reptiles being the most abundant group and rodents following (in accordance with Roger and Darlas (2008)). Concerning taxa richness, Unit IV with 30 taxa (identified to the species, genus or family level) presents the highest richness, whereas unit VI with 23 taxa and unit III with only 11 taxa are following (similar to Roger and Darlas (2008)).

stratum IV, dated to approximately MIS4-MIS3. The predominant mesowear pattern among fossil samples is high cusp relief combined with rounded cusp apices, showing surprisingly no incidence of blunt cusps. Overall mesowear scores were ranging from 0.94 to 0.90 for the upper and lower molars in *Capra ibex* (Tables 5, 6). Lower values, ranging from 0.71 to 0.78, were recorded in *Dama dama* reflecting a tendency to leaf browsing for the mid-sized cervids in comparison to the other taxa (Tables 5, 6) and the adoption of a flexible attritional diet as yet reported from other European fallow deer fossil populations in Central and Northern Europe (Rivals and Lister, 2016; Saarinen et al., 2016).

Moreover, the tooth wear of the small number of specimens of other taxa studied here, *Bos primigenius* (n = 3), *Capreolus* sp (n = 1), *Cervus elaphus* (n = 9), uncovers a similar feeding behavior with the small bovid (MS = 1.00) (Table 6).

#### 4. Discussion

An evaluation of the published data reviewed in the Introduction, as well as the new (mesowear analysis) and revisited (microfauna, lithics) data concerning Kalamakia, leads to a series of suggestions which refer to the palaeoenvironmental conditions and human subsistence at the site and its surroundings during the Middle Palaeolithic.

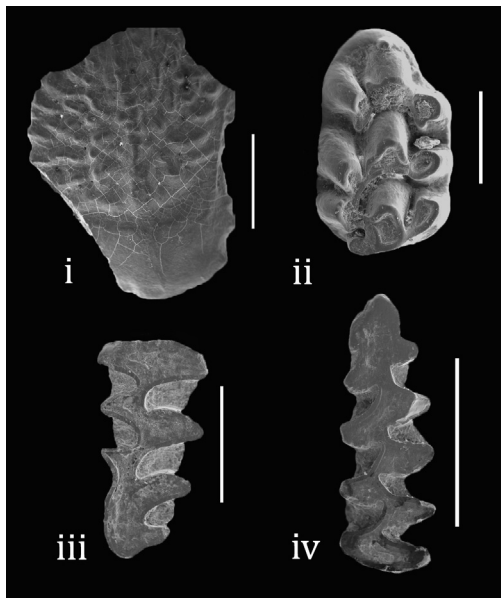
##### 4.1. Geometric morphometrics analyses on *Microtus* sp. lower first molars

Concerning the centroid size analysis (*Tukey pairwise* post-hoc test –Table 2 and mean and whiskers plot- Figure 8), it is rather clear that the mean centroid size of the specimens collected from Kalamakia seems to fit best with those corresponding to extant *M. guentheri* individuals. However, this tendency should not be interpreted as taxonomic similarity with *M. guentheri*, but as a population of slightly more robust individuals (with regard to *M. guentheri* being “a moderately large but robust vole”, according to Kryštufek and Vohralík (2005)). No other comments could be expressed towards the rodents’ body size, since no other skeletal element was examined in the same logic (e.g. complete mandibles), other than the first lower molars. Based on the observation that the centroid size from the specimens collected from unit III (corresponding to the warmest MIS 5a) have the highest mean and that the specimens from unit VI (corresponding to the coolest MIS 2) have the lowest mean value (Figure 8), a correlation trend between centroid size and climate seems to be plausible.

Concerning the shape of the *Microtus* first lower molars from Kalamakia, it seems that it is independent from size with only a 2.11% prediction of size influence on shape (regression). Having in mind the differences in the centroid size between the molars from the different stratigraphic units (Figure 8) and the slight divergence between the clusters of the fossilised molars corresponding to warmer (MIS 3 and MIS 5a) and the ones corresponding to colder climate conditions (MIS 2) regarding their shape (Figure 9), a possible relationship between molar morphology should be considered in relation to a climate effect or some kind of effect regarding geological time itself on the molars’ morphology through diversification and evolution during the glacials (Bilton et al., 1998; Kryštufek and Griffiths, 2002; Kryštufek et al., 2009). Possibly, the divergence time of the extant vole species, used here as reference material, could be the critical factor controlling the observed diversification. For example, the divergence time for the *M. subterraneus* populations of central Europe- northern Balkans is estimated to a hundred thousand years earlier than the deposition of the lower unit III (Macholan et al., 2001) or even the earlier appearance of the Italian endemic vole *M. savii* (Kotsakis et al., 2003).

Whatever the case, the shape of the Kalamakia lower first molars seems to fit better with the *Terricola* subgenus and, specifically, the *M. subterraneus* and the *M. thomasi* morphotypes (Figure 9, Table 3), with *M. subterraneus* probably being the dominant *Microtus* species at Kalamakia. Both species, however, seem to have had persisting populations throughout the Kalamakia deposits. This is verified by the distribution of the samples tested with geometric morphometrics in all three units and by the stereoscopic observations of the morphology of the lower first and upper third molars’ morphology.

The presence of *M. thomasi* in southern Peloponnese is not surprising since it is the only extant *Microtus* species in Greece with a geographical range extending beyond the northern/northwestern part of the country and reaching Peloponnese (Kryštufek, 1999a; Thanou et al., 2012; IUCN, 2019). The presence of *M. subterraneus*, though, needs to be discussed further as its current geographical range covers most of Greece’s northern borderline, with two branches extending only north of mount Ossa in



**Figure 10.** Scanning Electron Microscope (SEM) photographs of microvertebrate specimens from Kalamakia. (i) Osteoderm from *Pseudopus apodus*, scale bar is 2 mm (note the vertical carina- Blain et al., 2014). The white lines that can be seen on the specimen, correspond to secondary cracks made on the surface of the osteoderm and do not affect its natural morphology., (ii) upper first molar from *Apodemus epimelas*, scale bar is 1 mm (note the connections between the cusps t8-t9-t12, indicating the prevalence of *A. epimelas* rather than the *A. mystacinus* morphology-nomenclature and morphological character description by Storch, 2004), (iii) upper third molar of *Microtus subterraneus*, scale bar is 1 mm (iv) lower first molar of *Microtus thomasi*, scale bar is 2 mm (note the broadly confluent dental fields of T4- T5, known as the “pitymoid condition” typical of the pine voles-nomenclature and morphological character descriptions by Kryštufek and Vohralík (2005)).

Thessaly to the east and north of Amvrakikos Gulf to the west of the country (Kryštufek, 1999b; Thanou et al., 2012; IUCN, 2019).

The authors believe that the species' descent southwards, followed the plains west of Pindos (Figure 13), which acted as a barrier to the animals' dispersal, as has been observed in several other animal groups already (Psonis et al., 2018 and references therein). An individual of the species, by account of an upper left and upper right third molar, has been identified by Tsoukala et al. (2006) as *Microtus subterraneus/multiplex* in the material from Kitseli pothole (Nemea, NE Peloponnese). This could fit with our hypothesis, since Nemea is located close to the main mountain ranges of Peloponnese and could be easily accessible by the individuals descending from the west, following the southern waterfront of the

Corinth lake that existed during the penultimate (Figure 13ii) and last (Figure 13i) glacial periods, not being blocked by the mountain ranges of north and central Peloponnese. In the same work (Tsoukala et al., 2006), another *Microtus* species, *M. arvalis*, has been identified from a mandible fragment (preserving all molars) and three upper molars. The presence of *M. arvalis* in Nemea and in Kalamakia (although in relatively small numbers), suggests a migration route similar to the one proposed for *M. subterraneus*.

#### 4.2. Microfauna identification

The microfaunal list presented herein (Table 4), has comparatively minor differences with the last work on microvertebrates from Kalamakia (Roger and Darlas, 2008). Small differences in the occurrences of taxa in the different stratigraphic units can be attributed to differences regarding each contributor's methodology of identifying/presenting the taxa (e.g. in units IV and III *Pseudopus apodus* herein, but *Pseudopus* sp. in Roger and Darlas (2008) or in unit IV *Rhinolophus* sp. herein but *Rhinolophus hipposideros* for Roger and Darlas (2008)).

Nevertheless, a critical difference from the work of Roger and Darlas (2008), is the attribution of *Apodemus* remains in the species of *Apodemus mystacinus* (currently found in Turkey, Georgia, the coast of Middle East and on the Greek islands of Rhodes and Crete) (Wilson and Reeder, 2005), instead of *Apodemus epimelas* (currently found in the Republic of Macedonia, mainland Greece and the eastern coast of the Adriatic Sea) (Storch, 1999; Wilson and Reeder, 2005). The differentiation resides neither in the modern geographical distribution of the two species, nor in the relatively recent taxonomic split of the two species based on allozymes (Filippucci et al., 2002) and skull morphometrics analysis (Vohralík et al., 2002), but on the distinctive morphology of the first upper molar as it had been documented as early as the 1960s (Mirić, 1966; Spitzenberger, 1973; Storch, 1977), which is present in every single specimen of the Kalamakia assemblage (Figure 10 ii).

The *A. epimelas* individuals found in Kalamakia are, to our knowledge, the first mentioned occurrences of the species in Pleistocene deposits from Peloponnese. They also appear to have formed a strong and persistent population, found in the site from ca 100 kya BP in unit III to the most recent unit VI and until today. However, the phylogeographic distribution of *A. mystacinus* vs. *A. epimelas* in Greece (mainland and insular) has been already discussed in Storch, 2004 with the identification (Storch, 2004) of *A. epimelas* in Arnissa (N. Greece- Mayhew, 1978) and Varkiza (central Greece-van de Weerd, 1973) from specimens corresponding to MIS6 deposits, and thus, Kalamakia population contributes further to his distribution hypothesis. Nevertheless, there is a need to reexamine the individuals identified as *A. mystacinus* in the same region in previous micromammal studies of sites from mainland Greece under the light of *A. epimelas* presence (summarized in Doukas and Papagianni (2016)).

**Table 5.** Summary statistics of the mesowear data for the maxillar molars examined in this study (n: number of specimens; m: score mean; S.D: standard deviation).

Species	N	m	S.D.	% high	% low	% sharp	% round	% blunt
<b>Taxa averaged over all strata</b>								
<i>Capra ibex</i>	17	0.94	0.43	94.1	5.9	11.77	88.23	0
<i>Capreolus</i> sp. (unit IV only)	1	1.00	-	100	0	0	100	0
<i>Cervus elaphus</i> (unit IV only)	4	1.00	0.00	100	0	0	100	0
<i>Dama dama</i>	44	0.71	0.46	100	0	29.54	70.46	0
<b><i>Capra ibex</i> by strata</b>								
III	3	1.00	-	100	0	0	100	0
IV	11	0.91	0.54	100	0	36.36	63.63	0
<b><i>Dama dama</i> by strata</b>								
III	4	0.75	0.50	100	0	25	75	0
IV	39	0.69	0.47	100	0	30.77	69.23	0
VI	1	1.00	-	100	0	0	100	0



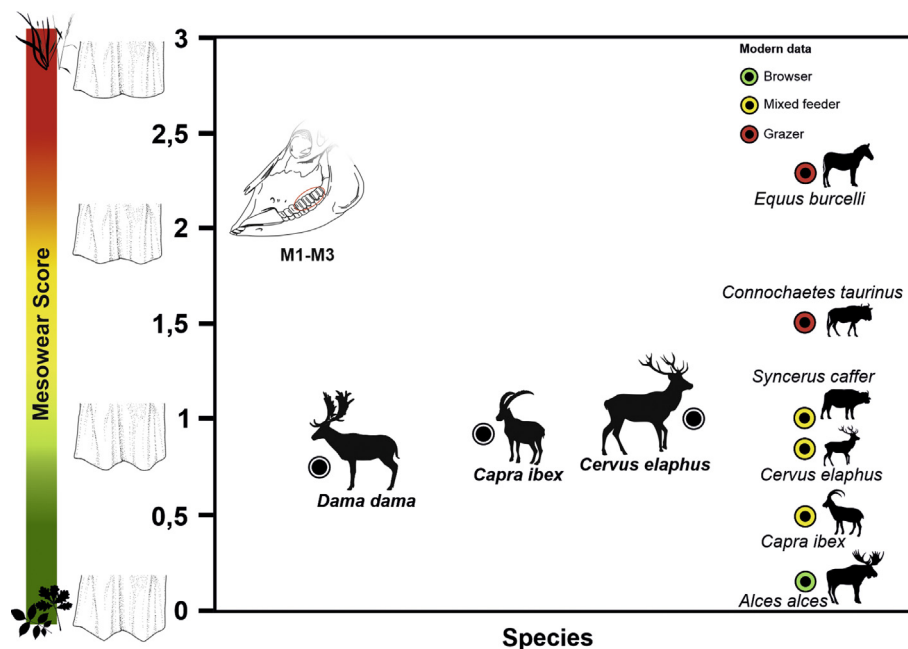
**Table 6.** Summary statistics of the mesowear data for the mandibular molars examined in this study (n: number of specimens; m: score mean; S.D: standard deviation).

Species	N	m	S.D.	% high	Percent low	% sharp	% round	% blunt
<b>Taxa averaged over all strata</b>								
<i>Bos primigenius</i> (unit III and IV)	3	1.00	0.00	100	0	0	100	0
<i>Capra ibex</i>	10	0.90	0.32	100	0	10	90	0
<i>Cervus elaphus</i> (unit IV only)	5	1.00	0.00	100	0	0	100	0
<i>Dama dama</i>	50	0.78	0.42	100	0	22	78	0
<b>Capra ibex by strata</b>								
III	1	1.00	-	100	0	100	0	0
IV	8	0.88	0,36	100	0	12.5	87.5	0
VI	1	1.00	-	100	0	100	0	0
<b>Dama dama by strata</b>								
III	5	0.60	0.55	100	0	40	60	0
IV	42	0.79	0.42	100	0	19	81	0
VI	3	1.00	0.00	100	0	0	100	0

Based on the ecological preferences (IUCN, 2019) of the recorded taxa (Table 4) estimates can be inferred regarding the palaeoenvironment and palaeoclimate of Kalamakia and its surrounding area. Most of the microvertebrates identified in Kalamakia, both in Roger and Darlas (2008) and in the present study, prefer open and temperate habitats and are found in Mediterranean ecosystems. The most common types of habitats that have been identified, and which dominated the assemblages throughout all three units are shrubland and forest habitats (*Lacerta* sp., *Anguis* sp., *Apodemus* sp., *Microtus subterraneus*, *Glis glis*, *Elaphe quatuorlineata*). In addition, the shrubland habitat signal becomes gradually more intense from the lowermost unit III to the upper unit VI (with the addition of taxa such as *M. arvalis*, *Zamenis situla*, *Vipera ammodytes*, *Coronella austriaca* and *Dolicophis caspius* in the upper units). The presence of saxicolous taxa is continuous in Kalamakia (*A. epimelas*, *M. subterraneus*, *C. nivalis*, *C. austriaca*, *D. caspius*, *V. ammodytes*, *C. suaveolens*) attesting to a rocky terrain surrounding the cave. The presence of water bodies in the close proximity is also marked by the identification of taxa such as *Bufo bufo* and *Bufo viridis* in units IV and VI and *Anguis* sp. and *Natrix natrix* in every unit.

### 4.3. Mesowear analysis

The mesowear analytical method is not fully informative of the degree of grazing vs. browsing preference in an intermediate diet. Even though, we could expect that these stand on the low end for grazers, showing a slight reliance on short grasses, the higher proportion of rounded cusps found in this work in contrast to the analysis conducted by Fortelius and Solounias (2000) should be considered on its extant counterpart (>60% against <40%), whose diet is sustained by a relatively large amount of herbaceous dicots (Parrini et al., 2009). In terms of average wear signal comparisons of *Capra ibex* and *Dama dama* among different strata populations, it is rather reasonable to conclude that there is no significant variation through time. However, despite our limited data from stratum III, relatively elevated levels of dietary abrasion were indicated for the more recent sample (stratum IV) of the fallow deer mandibular molar teeth. In a broad sense, our findings (Figures 11 and 12), mainly on the most robust samples derived from stratum IV, seem to suggest general mixed feeding traits of the fossil and modern representatives of ibex and fallow deer (and to some extent, of red deer) and the dwelling of open shrublands or often somewhat forested biomes in



**Figure 11.** Mean mesowear scores on the combined maxillary molar samples of *Capra ibex*, *Cervus elaphus* and *Dama dama*. Comparative reference data on M2 of extant forms were taken from Fortelius and Solounias (2000), Rivals et al. (2010).

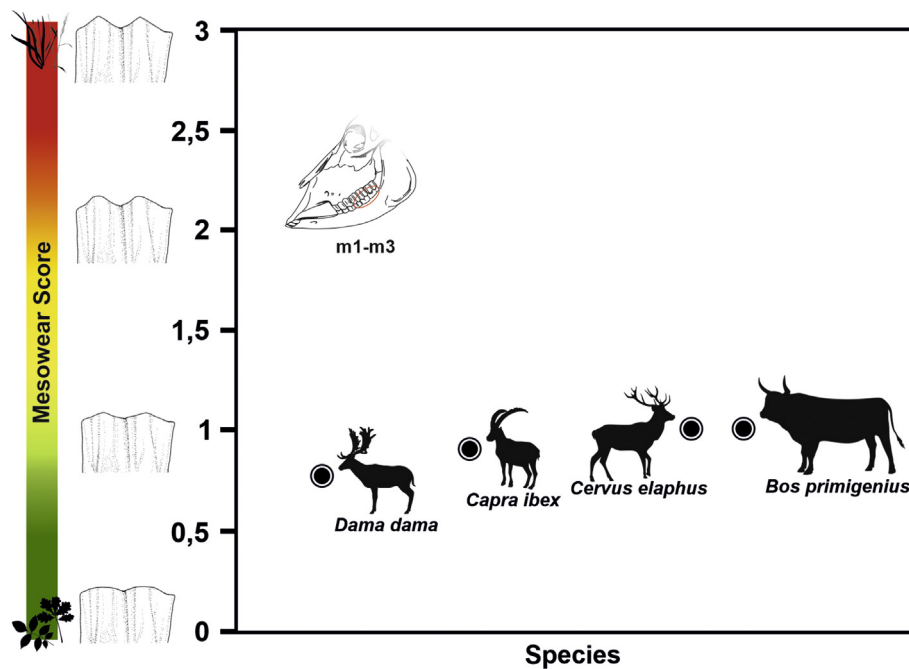


Figure 12. Mean mesowear scores on the m1-m3 fossil samples examined in this study.

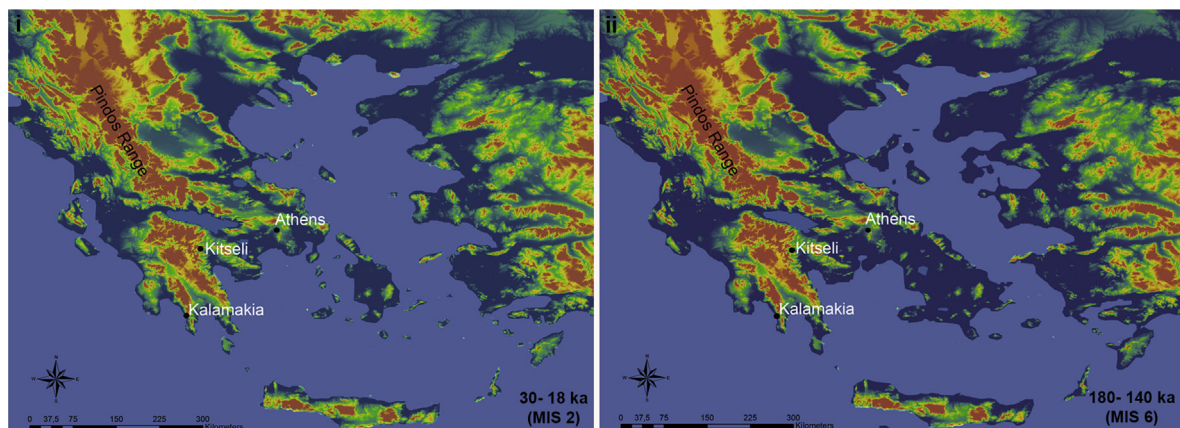


Figure 13. Palaeogeographic maps of Greece: (i) 30-18 ka, Marine Isotopic Stage 2, (ii) 180-140 kya, Marine Isotopic Stage 6 (sea levels after Lykousis, 2009). The darker blue areas indicate the lowlands formed by the palaeocoast.

mountainous areas (e.g. Jackson 1977; Apollonio et al., 1998; Fortelius and Solounias (2000; Parrini et al., 2009; Rivals and Lister, 2016; Saarinen et al., 2016). The mesowear pattern implies a landscape with vegetational heterogeneity and possibly a variety of occupied habitats across the surrounding area of the cave. Moreover, as neither of the overrepresented fallow deer and ibex seem specialized to grazing or adapted strictly to soft woodland forage, the absence of a developed grassy cover is clearly supported, in relation to the general composition of the mammal faunal assemblage of the site (see Lebreton et al. (2008)). The mesowear signal of the examined populations can be primarily attributed to the exploitation of a rather wide spectrum of relatively nutritional feeding items at a least partly wooded environment during the mild glacial episode of that time.

#### 4.4. Palaeoenvironmental interpretation

The assemblages of larger vertebrates from Kalamakia indicate a relatively temperate climate with open woodland surroundings (Gardeisen and Trantalidou, 1998; Darlas and Psathi, 2016) which agrees

with the evidence from the pollen and microvertebrate analyses (Lebreton et al., 1998; Lebreton et al., 2008; Roger and Darlas, 2008 and this study). Lebreton et al. (2008) were able to distinguish two pollen zones, with the first one being characterized by increased humidity suggesting a supra-Mediterranean forest and the second one denoting a Mediterranean presteppic vegetation and an increase in the Mediterranean shrub forest. Mesowear analysis and the re-examination of microvertebrates, performed in this study, intensify the existence of a shrub forest and a relatively wooded environment. A similar trend (a change towards drier conditions) is mentioned in the analysis of bird remains performed by Roger and Darlas (2008).

Evidence derived from the study of taxa and the population of vertebrate species (Roger and Darlas, 2008; Darlas and Psathi, 2016; this study), as well as from the palynological analysis of the stalagmitic pillar of unit I (Lebreton et al., 1998) suggest that the palaeoenvironment around Kalamakia was generally dry and relatively warm, although some wet areas were also present. Despite the fact that the lower sequences of Kalamakia cave (lower part of unit IV) indicate a more humid climate, the uppermost is composed by a Mediterranean forest with shrubs.

#### 4.5. Stone industry

Findings density at these living floors demonstrates that the cave served mostly as a short-term and sometimes as a longer term camp site. Though, despite this alternation, the lithic assemblages, except for the heterogeneity of raw materials, seem to show little differentiation regarding their main techno-typological features within the various occupational levels.

As noticed, the proportion of the main raw materials which varies through the levels revealing differences in raw material procurement strategies as well as in human groups mobility over time (Darlas and Psathi, 2016).

The small amount of cores, which in most cases are exhausted, do not allow a complete reconstruction of the in situ flaking procedures. In addition, given that primary flakes and technical pieces are almost absent, it can be considered that usually cores are pre-shaped outside the cave and they are imported afterwards for the production of a small series of artefacts. Moreover, it is mentioned that the site blanks repertory seems to be complemented by a large number of imported artefacts in the form of final products (Darlas and de Lumley, 2004).

On site core reduction is described as often opportunistic, due to the raw materials' properties (presence of cleavages) which prohibit predictable and organized reduction, mainly during the last phases of the cores exploitation (e.g. Figure 2 iv.). However, it seems that core flaking, under the technical principles of well-organized methods, was being applied during the first stages of blanks production (e.g. Figure 2, i-iii).

Observation on final products reveals that for many of them a centripetal or unipolar levallois reduction sequence has been probably followed (e.g. Figure 3 i, vi, Figure 4 iv). More precisely, typologically levallois implements count around 18% of the total flake component, increasing more with reference to flint and andesitic flakes (Darlas and de Lumley, 2004). According to published data, a discoid component seems to be also present within the industry as it is pronounced from a series of pseudolevallois points and some cores as well (e.g. Figure 2 iii, Figure 3 iii) (Darlas, 2007).

As it has also been mentioned in previous works (Darlas and Psathi, 2016; Darlas, 2007) the distant provenance of the main exploitable lithic resources alongside their properties, affect raw material economy and subsequently the stone industry features. Thus, a special effort of the human groups was observed to take advantage of the productive and usable dynamic of the lithic material as far as possible, a situation often creating particular technological adaptations (e.g. exploitation of non-usual raw materials for tool construction such as marble or shells). Such practices were probably also followed by special strategies of useful lithic implements management (e.g. tools, plain blanks and cores import and export in and from the site), assuming a more cost-conscious planning, in order for the human group's needs in tool equipment to be fulfilled during their movements in the area.

#### 4.6. Cave occupation

Kalamakia cave has been intermittently inhabited by both humans and carnivores, where the carnivore activity is more intensified in the upper units. The zooarchaeological analyses (Gardeisen and Trantalidou, 1998; Harvati et al., 2013; Darlas and Psathi, 2016) indicates that hominins were responsible for most of the macrofaunal accumulation. Specifically, Gardeisen and Trantalidou (1998) introduced the hypothesis that larger animals, such as the proboscideans retrieved from the site, were not hunted or scavenged by the humans, rather that they have been transported inside it. They also interpreted the large portion of burned bone splinters as part of the hominins effort to preserve the hearth's intensity in the cave (either by tossing them into the fire or by keeping

them in the hearth area after their disposal) and the breakage of long bones and phalanges as a way to procure higher amounts of animal fat by accessing bone marrow (Gardeisen and Trantalidou, 1998). Darlas and Psathi (2016) agree that the main accumulator of mammalian and tortoise remains were the human occupants but recognize a smaller contribution by the carnivores, mainly in Units IV and VI. In the taphonomic analysis performed by Harvati et al., 2013 and Darlas and Psathi 2016, "a systematic and complete processing of medium-sized ungulates at the site" is noted, while carnivores seemed to have scavenged the remains accumulated by humans.

In unit IV, both human occupation and carnivore denning are alternating. A consistent human presence has been identified for the lower part of unit IV (with anthropogenic evidenced by KAL5 and KAL3 samples (Harvati et al., 2013)). Alternating occupation episodes between humans and carnivores were taking place during the deposition of the upper part of Unit IV, with carnivores mostly scavenging the animal bone remains collected by humans (carnivore marks on KAL14 (Harvati et al., 2013)), until the formation of unit VI, during which the sole occupants of the cave were carnivores (Darlas and Psathi, 2016).

## 5. Conclusions

In the context of all the works mentioned in this study, Kalamakia seems to comprise a rather stable point of an extended Neanderthal occupational network, as testified by the numerous sites with Middle Palaeolithic habitation at the broader area. Within this network, the enrichment of the available data is expected to reveal its particularities in the future. However, the reasons why Neanderthals occupied periodically but in such a persistent and stable way the cave of Kalamakia should not be attributed to the raw material procurement and exploitation. The factor that made Kalamakia attractive for repetitive occupation should be attributed to the palaeoenvironmental parameters that were favorable for the human activity, such as the relatively temperate climate and the rather preferable environmental conditions (open woodland, Mediterranean shrub forests), giving the human occupants of Kalamakia favorable habitation grounds and plentiful hunting opportunities.

Apart from describing Kalamakia cave as a human occupation site, the present study contributes to its nature as a site of palaeogeographic research for rodent palaeozoogeography as well, with the documentation of species such as *Microtus subterraneus* for the first time so far south in southern Greece and *Apodemus epimelas* in the Peloponnese. The present study also constitutes the first study of *Microtus* lower first molars with geometric morphometrics. These results, however, only raised more questions that demand further research on the Arvicolinae routes of dispersal in the southern Balkans during the Pleistocene and the possible correlation of their dental morphology with climate.

## Declarations

### Author contribution statement

Maria Kolendrianou: Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Stefanos Ligkovanlis: Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Ioannis Maniakas: Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Marianthi Tzortzi: Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

G. Iliopoulos: Conceived and designed the experiments; Analyzed and interpreted the data; Wrote the paper.

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### Competing interest statement

The authors declare no conflict of interest.

### Additional information

No additional information is available for this paper.

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