

The small mammal fauna from the Palaeolithic site Marathousa 1 (Greece)

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Abstract

The lacustrine deposits exposed at the Lower Palaeolithic site Marathousa 1 (Megalopolis, S. Greece) and intercalated between lignite Seam II and III yielded a collection of small vertebrate remains. The assemblage includes fish and small mammals; the mammal assemblage encompasses a variety of species, dominated by voles (arvicolids) of the genera *Arvicola* and *Microtus*. Other rodents are represented by a dipod cf. *Alactaga* and a murid of the genus *Apodemus*. In addition, there is a number of insectivore remains that refer to the family Soricidae, and more specifically to the genus *Crocidura*.

The unrooted *Arvicola* molars show a positive '*Mimomys*' enamel differentiation with a mean SDQ value of 122, indicating a late Middle Pleistocene age (ca. 400 ka.) (MIS 12/11). The Marathousa 1 assemblage is clearly younger than the Choremi assemblages sampled ca. 20 years ago in the same basin. In the Choremi assemblage, *Mimomys*, the predecessor of the genus *Arvicola*, is the predominant arvicolid.

1. Introduction

Vertebrate fossils are a reliable source of information about the fauna that inhabited an area in the past and also, because of the habitat restrictions and/or preference of specific taxa, a source of information about the environmental and climatological conditions during the time of deposition of the sediments. For the reconstruction of the regional environmental conditions in the past, small mammals are useful, because the collected remains are in most cases the result of a natural accumulation, in the form of pellets, by birds of prey that scour a larger area surrounding the site to collect food.

In addition, small mammal fossils are often a useful proxy to date a site. Faunal changes through time due to the migration of species, the extinction as well as the evolution of species form the base for the establishment of a biostratigraphical framework and are used to put the fauna in a (bio)stratigraphically broader context. Vertebrate faunas can, therefore, be used to correlate deposits from a geographically larger area and indicate the relative age of the deposits. Often, some well-represented small mammal species (e.g., voles) show a relatively rapid evolution and are therefore biostratigraphically important. The potential of small mammals to give a relative date, within an archaeological context, is in particular relevant for the Lower and Middle Palaeolithic such as the Lower Palaeolithic site Marathousa 1 located in the Megalopolis Basin on the Peloponnese (Greece) (Panagopoulou et al., 2015; Harvati, 2016; Tourloukis and Harvati, 2018; Figure 1).

The intramontane Megalopolis Basin contains an alternation of lacustrine silts, clays and marls with regularly intercalated lignite seams. Papers and reports published in the 19th century and the first half of the 20th century mention the occurrence of mammalian fossils in the exposed deposits in the basin. Melentis studied the larger mammal remains collected at several localities near the village of Megalopolis. The fossil assemblages included a.o. Proboscidea, Equidae, Rhinocerotidae, Suidae, Cervidae and Bovidae (Melentis 1961, 1963a&b, 1965a - e). The stratigraphical position of the finds is, however, not clear (Vinken, 1965; Sickenberg, 1975); the age ranges from the Early to the Late Pleistocene (Melentis, 1961). Sickenberg (1975) described fossil mammalian remains collected by a team of German geologists from the Marathousa Beds in 1962 and 1963. The faunal assemblage includes *Vulpes* sp., *Panthera leo fossilis*?, *Mammuthus meridionalis*, *Equus* sp. ex aff. *aluticus*, *Stephanorhinus etruscus*, *Hippopotamus amphibious antiquus*, four different cervids including *Cervus* (s.l.) *peloponnesiacus* and *Praemegaceros verticornis*, and a water buffalo

Bubalus marathousae (Sickenberg, 1975). The Marathousa Member also yielded a remarkable specimen, an upper molar M3 of a hominid (Sickenberg, 1975; Marinos, 1975; Xirotiris et al., 1979; Harvati, 2016), the oldest evidence for the presence of hominids in Europe, according to Sickenberg (1975) (see also Harvati et al., 2009).

Sickenberg regarded the occurrence of *Praemegaceros verticornis*, a species that survived until late Cromerian time (Pfeiffer, 2002; for a discussion about the age of the Bilshausen record see: Van Kolfschoten and Turner (1996)), as a biostratigraphical marker that indicates that the fauna has a post-Villafranchian age and predates the late Middle Pleistocene Holsteinian (Sickenberg, 1975). He correlated the Marathousa Member fauna with the early Biharian. However, it is important to realise that the definition of the term Biharian sensu e.g. Kretzoi (1965), Kretzoi and Pécsi (1979) and Van der Meulen (1973) (arvicolid faunas dominated by the genus *Microtus*) changed since Sickenberg's publication. (for more details see Van Kolfschoten, 1990). Fejfar and Heinrich (1981) proposed a revised biostratigraphical subdivision of the Quaternary based on the Arvicolidae succession. They defined the Biharian, although presented as a chronostratigraphic unit, however, not valid as such (see Van Kolfschoten, 1990), on the basis of biostratigraphical data and in their proposal the Biharian is characterized by the co-occurrence of the genera *Mimomys* and *Microtus*. The transition from *Microtus (Allophaiomys)* to *Microtus (Microtus)* species marks the transition between the Early and the Late Biharian and the *Mimomys – Arvicola* transition during the early Middle Pleistocene marks the end of the Biharian and the beginning of the Toringian (e.g., Fejfar and Heinrich, 1981; Tesakov, 2004).

Benda et al. (1987) refuted Sickenberg's opinion and assumed a late Villanyian age for the lower lignite bed of the Marathousa Member exposed in the Thoknia open cast lignite mine based on a small collection of fossil vertebrates collected by De Bruijn and Van der Meulen in the early eighties. The presumed late Villanyian age is based on the absence of the genus *Microtus* from the small mammal assemblage.

In order to resolve the debate on the stratigraphical position of the Marathousa Member, Doukas and colleagues sampled the Marathousa Member in 1995 at a section exposed at Choremiou. The lowermost Lignite Seam I, the base of Lignite Seam II and Lignite Seam III yielded botanical as well as faunal remains; mammalian fossils are, however, not very abundant (Van Vugt, 2000; Doukas and Papayianni, 2016). De Bruijn and Van Kolfschoten studied the faunal remains and presented their results in Van Vugt (2000). They

concluded that the fauna from Seam I should be correlated with the late Early Biharian or the Late Biharian, whereas the faunas from Seam II and III have a Late Biharian age (sensu Fejfar and Heinrich, 1981).

New fossil material including small mammals has been collected in the Megalopolis Basin at the archaeological site named Marathousa 1. During the Marathousa 1 excavations in 2013 – 2017 a small assemblage of smaller mammal remains has been collected from deposits of the Marathousa Member intercalated between Lignite Seam II and III. The results of the investigations are presented in this paper and the stratigraphical position of the finds is discussed in the light of the previous debate on the age of the Marathousa Member deposits.

2. Geographical and Geological Setting

The Lower Palaeolithic site Marathousa 1 is located in the Megalopolis Basin (C. Peloponnesus, Greece) (Fig. 1) at the north-western margin of the open cast lignite mine and. A section of alternating lacustrine, fluvial and alluvial deposits is exposed (Panagopoulou et al., 2015). The geological sequence exposed in this quarry is the so-called Marathousa member in which four distinct lignite units are included (Seam I-IV). The depositional sequence represents full interglacial-glacial-interglacial cycles with alternating warm/wet-cold/arid climatic conditions (Karkanis et al., this issue). The Palaeolithic site and the layers that yielded the faunal remains are stratigraphically intercalated between lignite Seam II and III. Two areas, A and B, in close proximity were excavated (Panagopoulou et al., 2015, this issue). Both areas, A and B, have produced fossil mammal remains in spatial and stratigraphic association with lithic artefacts (Konidaris et al., 2017; Tourloukis et al., this issue b). Most of the archaeological and palaeontological remains were recovered in units UA3c and UA4 in Area A and UB4c and UB5a in Area B. The majority of the fossil small mammalian remains from Area A are from the units UA3b and UA3c, the level that also contains the lithic artefacts and the slaughtered proboscidean (Konidaris et al., 2017). In Area B, the majority of the small mammal remains comes from unit UB4c, the cultural horizon of that area.

3. Material & Methods

The small mammals were recovered through wet sieving of the sediments in the excavation premises in Megalopolis. The bulk of the sediment sample was screen washed on a 1mm mesh and subsequently sorted to categories of artefacts (lithics) and ecofacts (bones of large or small mammals, birds and fish, otoliths, insects, plant remains). The small mammal assemblage described in this paper includes the Insectivora and Rodentia remains collected at the areas of the Marathousa 1 site. Small mammal teeth were collected from both Areas A and B of the site (Fig. 2). The material from Area A comes from units UA3b, UA3c and UA4; numerous teeth were recovered from unit UA3c; the layer that yielded the lithics and the proboscidean. The material from Area B comes from units UB4a, UB4c, UB5a and UB6, with numerous teeth coming from Unit UB4c, the cultural horizon of the area. Table 1 and 2 present an overview of the identified remains per species and stratigraphical unit for the two areas A and B. Four out of the five identified taxa from area A were found in unit UA3c, the cultural horizon of the area; *Arvicola* is the best represented. Three genera were identified in Area B: *Crociodura*, *Arvicola* and *Microtus*; *Arvicola* is the best represented also in Unit UB4c, the unit with the palaeolithic finds.

The archaeological site yielded also remains of a beaver. The rodent species, although formally belonging to the Rodentia, is treated by the research team as a large mammal and therefore included in the larger mammal study (Konidaris et al., 2017). Two chiropteran bone fragments have been recorded: a distal humerus from UA3c and a proximal femur from UB4c. The humerus from area A is of the same dark brown coloration as the rest of the small mammal material; the femur of area B is of light coloration, possibly depicting an element of intrusion. A complete humerus with the usual brown coloration of the Marathousa small mammal assemblage was recovered from level UA3c. Based on its massive morphology that is characteristic for the humeri of a mole, the specimen is referred to the genus *Talpa*. The beaver, chiropteran and mole remains are not included in the present systematic description of the Marathousa 1 small mammal assemblage.

The identification of the fossil specimens described in this paper is based on their morphology and dimensions in comparison with modern and fossil (Pleistocene) comparative material as well as published data. The measurements and terminology of the Arvicolidae molars follow Van der Meulen (1973); the measurements of the Muridae follow Pasquier (1974) and Van de Weerd (1976); the measurements of the Soricidae follow Reumer (1984). Scatter plots as well as the overall statistics were performed in Excel (2007, Microsoft). The recording of the

breakage and digestion evidence on the molars follows Andrews (1990) and Fernandez-Jalvo et al. (2016).

Scanning Electron Microscope pictures were made at the University of Athens (Palaeontology) using JEOL JSM-6390; all samples were coated with Au-Pd.

4. Systematic description

4.1. Order: Eulipotyphla

Family: Soricidae, Fischer 1814

Genus: *Crocidura*, Wagler 1832

Material: UA3b: 2 I, 1 P4 dex.; UA3c: 1 mandible sin. with m1 and m2 (Fig. 3); UB4c: 1 mandible sin., 1 m2 sin.

Measurements are given in Table 3.

The absence of pigmentation at the Soricidae teeth from Marathousa 1 leads us to the genus *Crocidura*. The teeth depict the typical dental morphology of the European *Crocidura*. The following special characters have been noted: a) the upper incisors (I sup.) are not fissident, the buccal cingulum is well pronounced and the talon of these teeth has a double notch; b) the parastyle of the P4 is prominent and the posterior emargination is well-defined; c) the buccal cingulum of the m2 is evident (Fig. 3). The condyle and the angular process of the ascending ramus of the mandible betray all the *Crocidura* characteristics; the ascending ramus and the anterior part of the mandible are missing.

The Marathousa 1 *Crocidura* remains are too fragmented and too limited and the absence of complete mandibles makes a identification to species level problematic. The available measurements indicate that the Marathousa 1 remains are relatively large; larger than most of the dimensions of elements from comparative modern (*C. suaveolens*, *C. zimmermanni*), and Pleistocene reference specimens (*C. zimmermanni*, *C. kornfeldi*) (Table 3; Figure 4).

4.2. Order: Rodentia

Family: Cricetidae, Fischer 1817

Subfamily: Arvicolinae, Gray 1821

In the Marathousa 1 small mammal assemblage, the subfamily Arvicolinae is represented by two genera: *Arvicola* and *Microtus*. The molars of both genera are rootless. The *Arvicola* molars are characterized by a larger size and an occlusal surface of the m1 with only three closed triangles (Fig. 6). The *Microtus* molars are comparatively smaller; the occlusal surface of the lower m1 has five closed triangles.

4.2.1. Genus *Arvicola*, Lacépède 1799

Arvicola mosbachensis (Schmidtgen 1911)

Material: UA3b: 1 mandible with m1-m3; UA3c: 25 m1, 16 M3, 7 mandibles; UA4: 6 m1, 6 M3; UB4a: 1 m1, 1 M3; UB4c: 13 m1, 10 M3, 2 mandibles; UB5a: 2 m1, 1 M3; UB6: 1 M3. Measurements are given in Table 4. SDQ values are given in Table 5.

The genus is represented in the Marathousa 1 assemblage by the material listed above as well as a small number of isolated dental elements (M1, M2, m2, m3) which do not show any clear diagnostic features. In terms of morphology, the m1 is formed by a posterior lobe (PL), three closed triangles (T1-3) and the anterior cap (AC) (Fig. 6a). The AC of the *Arvicola* first lower molars from Marathousa 1 is formed by two opposite confluent triangles (T4-T5) and a single cap. Most of the first lower molars have a simple AC with a rounded anterior end; only twelve specimens have a more angular anterior margin of the AC.

The occlusal surface of the *Arvicola* third upper molars (M3) of Marathousa 1 (Fig. 6b-c) shows an elongated AL1 with concave sides of thinner enamel followed by one closed triangle (T2), two mostly confluent triangles (T3-4) and a more or less rounded PC. Only four molars show a fourth buccal salient and re-entrant angle (BSA4/BRA4).

Enamel thickness differentiation

The salient angles of the lower Arvicolinae molars have a concave anterior enamel edge (the leading edge in the mastication process) and a convex posterior enamel edge (the trailing edge) (Von Koenigswald, 1982). In many of the living Arvicolidae species of the genera *Arvicola* and *Microtus* the trailing edges are thinner than the leading edges; they have the so-called ‘*Microtus*’ or negative enamel thickness differentiation whereas the molars of most of the *Mimomys* species as well as the stratigraphically oldest and primitive *Arvicola* species, have the so-called ‘*Mimomys*’ or positive enamel differentiation. The main evolutionary trend in the *Arvicola* lineage is the change in the thickness of the enamel, from ‘*Mimomys*’ to ‘*Microtus*’ differentiation (Von Koenigswald, 1973; Heinrich, 1978, 1982; Sutcliffe and

Kowalski, 1976, van Kolfschoten, 1990, Maul et al., 1998; Ruddy, 2010). To quantify the differences in the enamel thicknesses Heinrich (1978) proposed to calculate the enamel thickness quotient (Schmelzband-Differenzierung-Quotient (SDQ) in the terminology of Heinrich 1982) and to measure the enamel thickness on both sides of the salient angles of the m1 (see Fig. 7), dividing the value of the trailing edge by the one of the leading edge and multiplying the quotient by 100.

The enamel band thickness differentiation (mean SDQ value) of the Marathousa 1 *Arvicola* assemblage based on the m1 salient angles was calculated following the method described by Heinrich (1978) is 122 (N=25; Range: 102-149).

The size of the molars

According to Stuart (1982), there is, in addition to the changes in the enamel differentiation, a trend towards increased size in the m1 of *Arvicola*. The modern *Arvicola* molars from England are ca. 30 % larger than those of the Cromerian *Mimomys savini* (Van Kolfschoten, 1990). Carls (1986) also states that the fossils record indicates that there is an increase in size of the Water Voles during the Middle and Late Pleistocene. The Marathousa 1 Water Vole first lower molars have a mean length of 3.62 mm (see Table 5). A comparison of the length of the Marathousa *Arvicola* m1 with equivalent data of molars from other Pleistocene sites (see Table 5), indicates that the Marathousa *Arvicola* m1 is only slightly longer than the early Middle Pleistocene *Arvicola* m1 from Mosbach 2, Miesenheim I and Boxgrove. The dimensions correspond better with the *Arvicola* m1 of Barnham and Petersbuch with a late Middle Pleistocene age.

Taxonomic assignment

In the present-day European fauna the genus *Arvicola* is represented by four different species: *Arvicola amphibius*, *A. sapidus*, *A. italicus*, and *A. monticola* (Wilson et al., 2017). The Eurasian Water Vole *Arvicola amphibius* is widely distributed occurring in an area stretching from Great Britain in the west to east of Lake Baikal and Lena River in the east. Molecular markers indicate that *Arvicola amphibius* is a polytypic species with a large number of subspecies. *Arvicola terrestris* and *A. scherman*, taxonomic names that are often used in the (archaeo)zoological literature, are nowadays regarded as synonyms of *Arvicola amphibius*. The South-western water vole *Arvicola sapidus* occurs in France, Spain and Portugal. The

Montane Water Vole *Arvicola monticola* lives in mountainous areas in the Pyrenees and the Alps and the Italian Water Vole is mainly endemic to Italy (Wilson et al., 2017).

Water Voles are well represented in the Pleistocene fossil record of Eurasia and the fossil remains have been studied in detail by a large number of researchers including Hinton (1910, 1926), Heinrich (1978, 1982), Markova (1982, 2006) and Maul et al. (1998). The Water Voles with high crowned, rooted molars, dated to the late Early Pleistocene and the early Middle Pleistocene are often referred to as *Mimomys savini*. Fossil adult water voles with rootless molars are assigned to the genus *Arvicola* and based on (minor) differences in the occlusal pattern of an often restricted number of first lower and third upper molars as well as differences in the SDQ values are assigned to a number of species. The most common names used in the literature are *Arvicola terrestris*, *Arvicola cantianus* (= *Arvicola cantiana*) and *Arvicola mosbachensis*. Heinrich (1982) proposed to use the name *A. cantiana* for molars with a ‘*Mimomys*’ enamel differentiation (SDQ >100) and to assign molars with a ‘*Microtus*’ differentiation (SDQ <100) to *A. terrestris*. Many authors follow Heinrich’s proposal. Radulesco and Samson (1977) suggested to use *cantianus* instead of *cantiana* based on the fact that Hinton (1910) used *cantianus* in his description of the unrooted molars from Ingress Vale that he referred to ‘*Mimomys*’ *cantianus*. However, Maul et al. (2000) presented convincing arguments to use the name *Arvicola mosbachensis* instead of *Arvicola cantianus* for the Middle Pleistocene Water Voles with unrooted molars and a positive or ‘*Mimomys*’ enamel differentiation. This recommendation is followed in this paper.

The Marathousa 1 Water Vole molars are all high crowned and not a single molar shows indications for the formation of roots. The molars with a mean SDQ value of 122, having the so-called ‘*Mimomys*’ enamel differentiation i.e. the enamel of the trailing edges is markedly thicker than that of the leading edges. These features indicate an identification as *Arvicola mosbachensis*.

4.2.2. Genus *Microtus* Schrank 1798

Microtus sp. (cf. *M. arvalis*)

Material: UA3c: 6 m1, 3 M3; UB4a: 2 M3; UB4c: 4 m1; UB5a: 1 M3.
Measurements are given in Table 6.

The first lower molars (m1) show an elongated PC1, five closed triangles (T1-5), an AC3 formed by two confluent triangles (T6-7) and a rounded AC. The AC3 is of the ‘arvalid’ type, as defined by Van der Meulen (1973) (Fig. 8). In two specimens, the T4-5 are semi-confluent.

The occlusal surface of the upper third molars (M3) show an AL1 and three closed triangles (T2-3-4); T5 is confluent with PC1. An LSA 5 is well developed in lingual direction.

The morphological characteristics as well as the dimensions of the dental elements resemble those of the molars of the Common Vole *Microtus arvalis* (Fig. 9), a species that is recorded in the majority of the fossil Eurasian Middle and Late Pleistocene assemblages. However, the description of the morphological pattern applies also to other *Microtus* species such as *M. agrestis*. The upper M1 and occasionally the upper M2 of *M. agrestis* show the development of an extra salient angle at the posterior side of the molars; a feature that can be used to distinguish both species (e.g. Van Kolfshoten, 2013). Upper molars of the genus *Microtus* are unfortunately missing in the Marathousa 1 assemblage. Furthermore, the dental morphology of the sibling species *M. arvalis* and *M. rossiaemeridionalis* show extreme similarities (Markova et al., 2010). Hence, a firm species identification based on the available material is not possible. Due to the aforementioned congruent arguments on distinction between different *Microtus* species, a restriction of the identification to *Microtus* sp. (cf. *M. arvalis*) is preferred.

4.2.3. Family Muridae, Gray 1821

Subfamily Murinae, Murray 1866

Genus: *Apodemus sylvaticus* vel *A. flavicollis*, Kaup 1829

Material: UA3c: 1 m1 sin.

Measurements are given in Table 7.

The morphology of the *Apodemus* m1 (Fig. 10) is typical of the genus: there are two accessory cusps on the buccal side, the posterior one being better developed than the anterior one. All the main cusps are well-defined except for the anterocentral cuspid, which is confluent with the anterolingual and the anterobuccal cuspids; there is a well-defined posterocentral cuspid (nomenclature after Van de Weerd, 1976).

In terms of morphometry, we compared the Marathousa 1 m1 with modern *A. mystacinus*, *A. sylvaticus* and *A. flavicollis* as well as Pleistocene specimens from various localities: early Pleistocene (Tourkobounia 1 and Biçakci), Middle Pleistocene (Emirkaya), Late Pleistocene Arnissa (De Bruijn and Van der Meulen, 1975; Mayhew, 1977; Montuire et al., 1994; Van den Hoek Ostende et al., 2015). The measurements of the occlusal surface of the m1 from Marathousa 1 fall in the broad group of modern and Pleistocene *A. sylvaticus* and *A.*

flavicollis; these two species are caryotypically differentiated clades of the *Sylvaemus* group, but their phylogenetic relationship is still unclear (Michaux et al., 2002); their Holocene populations are also inseparable in terms of mandible morphology and shape (Kerr et al. 2017) (Figure 11). Other than a *A. sylvaticus* vel *A. flavicollis* identification, the occlusal measurements of *A. dominans* from Early Pleistocene Tourkobounia 1 and those of *A. atavus* from Middle Pleistocene Biçakci in Turkey are also close to the ones from Marathousa 1 (Van den Hoek Ostende et al., 2015) (Figure 11). However, the morphology of *A. dominans* from Tourkobounia 1 falls in the general *Apodemus* morphology, whereas that of the Biçakci *A. atavus* is more complex than the m1 from Marathousa 1. In conclusion, we can exclude the presence of *A. mystacinus* in the Marathousa 1 fauna and propose an *A. sylvaticus* vel *A. flavicollis* identification for the molar in question.

4.2.4. Family Dipodidae, Fischer 1817

Genus *Alactaga*, Cuvier 1836

?*Alactaga* indet.

Material: UA3c: 1 broken molar

A broken molar from UA3c can be associated with the genus *Alactaga*, although its fragmentary state does not allow us an accurate identification. No measurements could be taken due to damage.

5. Taphonomical aspects

The preservation state of the Marathousa 1 small mammal assemblage indicates waterlogged desiccated conditions, as the majority of the bones are affected by the lignite formation and are therefore dark brown or black. In terms of fragmentation and preservation, we noticed a better preservation of molars and incisors than of jaws and post-cranial elements; this is probably due to the enamel endurance of the teeth versus the collagen component of the skeleton. A few of the Arvicolinae molars depict slight enamel loss due to digestion activity of an avian predator.

In terms of evidence for avian digestion, the distinction criteria set by Fernandez-Jalvo et al. (2016) have been used; all observations were done only on the occlusal surface of mounted molars. Heavy digestion was noted on three specimens: one *Apodemus* m1, one *Microtus* m1 and the molar fragment assigned to cf. *Alactaga*; moderate digestion was noted on two m1, one *Arvicola* and one *Microtus*; light digestion was noted on four *Arvicola* molars (two m1

and two M3). These features indicate that predators played a role in the accumulation of (at least part of) the small mammal remains. However, it is important to take into account that there are also predators that leave minimal or no traces of digestion on the occlusal surface (Fernandez-Jalvo et al., 2016). Hence, we cannot exclude the possibility that predators played a role in the accumulation of the majority of the small mammal assemblage.

The observations made by Fernandez-Jalvo et al. (2016) on modern pellet contents have formed a key for the identification of the predator, since the digestion system of each predator affects the dental remains in a different way. Heavily digested (etched) molars could have been regurgitated by an owl, for example *Bubo bubo* or *Strix aluco*; moderately digested molars by e.g. *Bubo africanus* and *Strix nebulosa*; lightly digested molars by *Tyto alba* and/or *Nyctea scandiaca*. The modern avian biodiversity of the Peloponnesus includes *Bubo bubo*, *Tyto alba* and *Strix aluco*; all generalists in terms of their diet. Nevertheless, in the rich avifauna of Marathousa 1, no owl remains have as yet been reported (Michailidis et al., this issue). Since the available digested material is limited and the excavated avifauna does not include any raptor or owl, we can only hypothesize about the identity and the habits of the predator, that could also be a carnivorous mammal. The available material is too scanty to support the identification of the predator.

6. Palaeoecological conclusions

The palaeoecological conclusions drawn on the Marathousa 1 small mammal assemblage are limited because of the small number of species represented in the fauna. The composition of the smaller mammal assemblage is biased by the way the material is collected. Using a 1 mm mesh size (see 3. Material and methods) resulted most probably in the loss of dental material of the smaller insectivores and rodents. The Marathousa 1 fauna is dominated by *Arvicola*, the Water Vole, a species that mainly prefers a semi-aquatic habitat staying within 2 meters of the water's edge in marshes around e.g. ponds and lakes (Wilson et al., 2017). The Common Vole *Microtus arvalis* prefers to inhabit well-drained open landscapes (Wilson et al., 2017). Representatives of the genera *Crocidura* and *Apodemus* inhabit a variety of terrestrial habitats and their occurrence is not very informative. The occurrence of the jerboa of the genus *Alactaga* is not sure. A confirmation of its occurrence would imply the presence of a steppe dweller indicating areas with steppe vegetation in the vicinity of the lake.

7. Biostratigraphical conclusions

Biostratigraphical data such as the (co-)occurrence of specific botanical and/or zoological species are often used to put the deposits of a site in a broader stratigraphical context and determine the (relative) age of, e.g., archaeological finds. The Marathousa 1 section did not yield species that have a restricted stratigraphical range or a combination of species with a limited stratigraphical overlap. The fossil record indicates that most taxa occur in Europe during most of the Middle and Late Pleistocene or even longer and they are not part of a lineage with clear evolutionary changes in time. However, the water vole is an exception and offers the opportunity to trace its evolutionary stages during the Middle and Late Pleistocene by comparing the evidence from different dated localities in Eurasia. The Pleistocene water vole record shows an evolutionary lineage, the *Mimomys savini* – *Arvicola* lineage, with marked changes in the height of the crown, the formation of roots and the differentiation of the enamel that covers the salient angles of the upper and lower molars. The Early Pleistocene Water Voles show an increase in crown height; the early Middle Pleistocene Eurasian fossil record (e.g., West Runton, Voigtstedt, Choremi 1-4) is marked by the occurrence of high crowned rooted molars known as *Mimomys savini* (Van Kolfschoten, 1990; Van Vugt, 2000). The formation of roots disappears during the early Middle Pleistocene. There are a number of faunal assemblages that mark the transition from rooted to unrooted molars for example Isernia (Italy), Mosbach 2 (Germany), Prezletice (Czech Republic) (Von Koenigswald and Van Kolfschoten, 1996) and Chui- Atasova I (Danukalova et al., 2016) (see Table 5). The so-called transitional assemblages, assigned to *Arvicola mosbachensis*, are characterized by the co-occurrence of rooted and unrooted molars; root formation only occurs in adult individuals and predominantly in the M3. Their SDQ values are high.

A sequence of mammalian assemblages dated to the early and late Middle Pleistocene is known from the Kärlich section (Neuwied Basin, Germany) (Von Koenigswald and Van Kolfschoten, 1996; Van Kolfschoten and Turner, 1996; Van Kolfschoten in prep.). Unit Kärlich F, loess deposits that are correlated with the Don-Glaciation and with MIS 16, just as the underlying Unit E, yielded *Mimomys savini* molars whereas deposits of the overlying Unit G correlated with MIS 15, yielded unrooted water vole molars assigned to *Arvicola mosbachensis*. These observations indicate that the *Mimomys* – *Arvicola* transition took place in Western and Central Europe during the MIS 16/MIS 15 transition. However, the transition in Eastern Europe appears to be later (Maul and Markova, 2007; *Mimomys* survives in that

region until the latest early Middle Pleistocene (Muchkap Stage) whereas the earliest *Arvicola* faunas have a Likhvin (=Holsteinian (MIS 11) age.

The early Middle Pleistocene fossil record includes also a number of water vole assemblages with high SDQ values and unrooted molars; even the adult M3 molars are unrooted.

Examples are the Water Vole assemblages from Miesenheim I, Boxgrove that are regarded as slightly younger than the previous ones and are correlated with MIS 13 (Maul and Parfitt, 2010). In the Middle and Late Pleistocene period postdating the transitional phase, one can observe the reduction of the trailing edges in the succession of faunal assemblages, which is based on criteria other than the *Arvicola* evolution (Von Koenigswald, 1973). The evolution of *Arvicola*, as is indicated by Von Koenigswald (1973) for fossils of Central European faunas, can also be traced in the British faunas (Sutcliffe and Kowalski, 1976) and in the Hungarian faunas (Jánossy, 1976).

Geographical gradient

The Eurasian fossil record indicates variation in SDQ values through time. However, the living Water Voles indicate that there is, at least in the present, a geographical gradient in the SDQ values. Röttger (1986, 1987) studied the extant *Arvicola* populations from Europe, Turkey and Iran to investigate the interspecific variation in the molars. Her results show that there is a large variation in the differentiation of the enamel thickness in the extant *Arvicola* subspecies. The Western European populations show the so-called 'Microtus' differentiation, whereas the populations from Iran show the 'Mimomys' enamel differentiation. The values for Hungary and Italy are intermediate (see Table 5). Röttger's results indicate the occurrence of "advanced" populations in N.W. Europe and "primitive" populations in S. E. Europe; a geographical gradient in the SDQ values of the living *Arvicola* populations. It is so far unknown if a similar gradient existed in the past.

The biostratigraphical age of the Marathousa 1 fauna

Based on the occurrence of *Arvicola mosbachensis* we can conclude that the Marathousa 1 fauna has a post Biharian, Toringian age. Hence, the fauna is younger than the *Mimomys* faunas collected from the Choremi deposits presented by Van Vugt (2000). The SDQ values of the Marathousa 1 Water Voles with a mean of 122 are lower than the values of the stratigraphically older *Arvicola* assemblages from localities such as Isernia, Mosbach 2,

Miesenheim I and Boxgrove, correlated with resp. MIS 15 and MIS 13 (see Table 5). Hence, based on the SDQ values of the Marathousa 1 Water Vole, assuming that the rate of the evolutionary changes in the enamel differentiation is comparable with that observed in e.g. Central Europe, one can conclude that a late Middle Pleistocene age (MIS 12/11) is most plausible. If a geographical gradient has to be taken into account, it would imply a younger age. Additionally, the results of the comparison of the Marathousa *Arvicola* m1 length with other Pleistocene *Arvicola* m1 length also support the assumption that a MIS 12/11 age for the Marathousa 1 fauna is most plausible (see Table 5).

A comparison with the other Megalopolis Basin faunas

The conclusion that the Marathousa 1 fauna most probably dates to MIS 12/11, implies that Marathousa Lignite Seam III, which is overlying the deposits that yielded the small mammal assemblage, must be late Middle Pleistocene in age or younger. Lignite Seam III in the Choremi section, presented by Van Vugt (2000) and Van Vugt et al. (2001), is based on the occurrence of *Mimomys* correlated to the late Biharian, with an early Middle Pleistocene age. Hence, the Marathousa 1 Seam III and the Choremi Seam III are not identical and must differ in age.

8. Summarizing conclusions

The Marathousa 1 small mammal assemblage is, although relatively small in number of identifiable remains and with a very limited number of species, very important in the determination of the (bio)stratigraphical age of the finds and the associated Palaeolithic artefacts. The water vole *Arvicola mosbachensis* is the most important species for this purpose and fortunately it is by far the most dominant species. More than 80 molars have been collected so far; these molars form a rather solid base for our biostratigraphical conclusions that we are dealing with an evolutionary advanced, but still rather primitive *Arvicola*, that is known from Central and Northwestern European faunas with a late Middle Pleistocene age. A MIS 12/11 age which seems much plausible based on the SDQ values and the size of the *Arvicola* molars is in broad agreement with the age indication provided by ESR (Blackwell et

al., this issue) and post-IR IRSL (Jacobs et al., this issue) dating, as well as the results of the magnetostratigraphy of the Megalopolis basin (Tourloukis et al., this issue a).

The Marathousa 1 small mammal fauna is an important fauna because of its age in combination with the geographical position of the locality. The region is poorly known and is lacking (bio)stratigraphically well-documented reference points with a rich fauna. In order to increase the importance of the locality, more fossil remains should be collected to enlarge the mammalian assemblages and hence, amplify the number of species. However, more important is to sample the entire Marathousa section to look for mammal fossils. The Marathousa Member appears to be rather rich in mammalian remains and test samples have shown that the preservation conditions are promising. The validity of our (bio)stratigraphical conclusions for the Palaeolithic Marathousa 1 horizon would increase with the placement of the fauna in the local context of a well-dated faunal sequence.

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Figure captions

Fig. 1. Map of the Megalopolis basin showing the Marathousa 1 Lower Palaeolithic site as well as the Choremi locality mentioned in the text (modified after Giusti et al., this issue).

Fig. 2. Section drawing of the Marathousa 1 stratigraphy depicting the Units that contain the small mammal remains. The dashed parts marks the Units without any small mammal fossils (modified after Karkanas et al., this issue).

Fig. 3. SEM image of a *Crocidura* left mandible with m1 and m2.

Fig. 4. Scatter diagram showing the dimensions (Talonid Width and Length) of the m2 of fossil and living *Crocidura* species. The data of the Pleistocene Cretan *Crocidura* are from Reumer (1986); the data of the Pleistocene Spanish *C. kornfeldi* are from Rofes and Bescos (2011); and the dimensions of the Pleistocene *Crocidura* from Emirkaya are from Montuire et al. (1994). The data of the modern *C. suaveolens* and *C. zimmermanni* are based on the reference collection of the Museum of Natural History of Crete (courtesy P. Lymberakis).

Fig. 5. The Arvicolidae m1, nomenclature of the occlusal surface and measurement protocol (modified after Van der Meulen, 1973). a) Terminology of the occlusal surface of the m1: AL, anterior lobe; PL, posterior lobe; BSA1–4 buccal salient angles; LSA1–5, lingual salient angles; T1–7, crown triangles. b) Occlusal surface of the left first lower molar of *Microtus*, illustrating the parameters that were measured. L-L'=L; W-W'=W; a-L=a; b-b'=b; c-c'=c; d-d'=d.

Fig. 6. SEM image of *Arvicola* sp. m1 (a) and M3 (b, c).

Fig. 7. *Arvicola* m1 with SDQ measurement protocol. Locations of enamel thickness measurements following Heinrich (1982).

Fig. 8. SEM image of *Microtus* sp. (cf. *M. arvalis*) m1.

Fig. 9. Scatter diagram showing the dimensions (Length and Width) of the m1 of fossil *Microtus* species. The dimensions of the Pleistocene *Microtus* from Emirkaya are from Montuire et al. (1994).

Fig. 10. Image of the *Apodemus* sp. m1.

Fig. 11. Scatter diagram showing the dimensions (Length and Width) of the m1 of fossil and extant *Apodemus* species. The data of the Pleistocene *Apodemus microps* and *dominans* are from Tourkobounia 1 (De Bruijn and van der Meulen, 1975); the dimensions of *Apodemus* from Biçakci, Emirkaya and Arnissa are from; Mayhew (1977); Montuire et al. (1994); Hoek Ostende et al. (2015). The data of the modern *A. sylvaticus*, *flavicollis* and *mystacinus* are based on the reference collection of the Naturalis Centre of Biodiversity, the Netherlands (courtesy L. van den Hoek Ostende).

Table captions

Table 1: Identified small mammal finds per stratigraphical Unit at Marathousa 1-Area A.

Table 2: Identified small mammal finds per stratigraphical Unit at Marathousa 1-Area B.

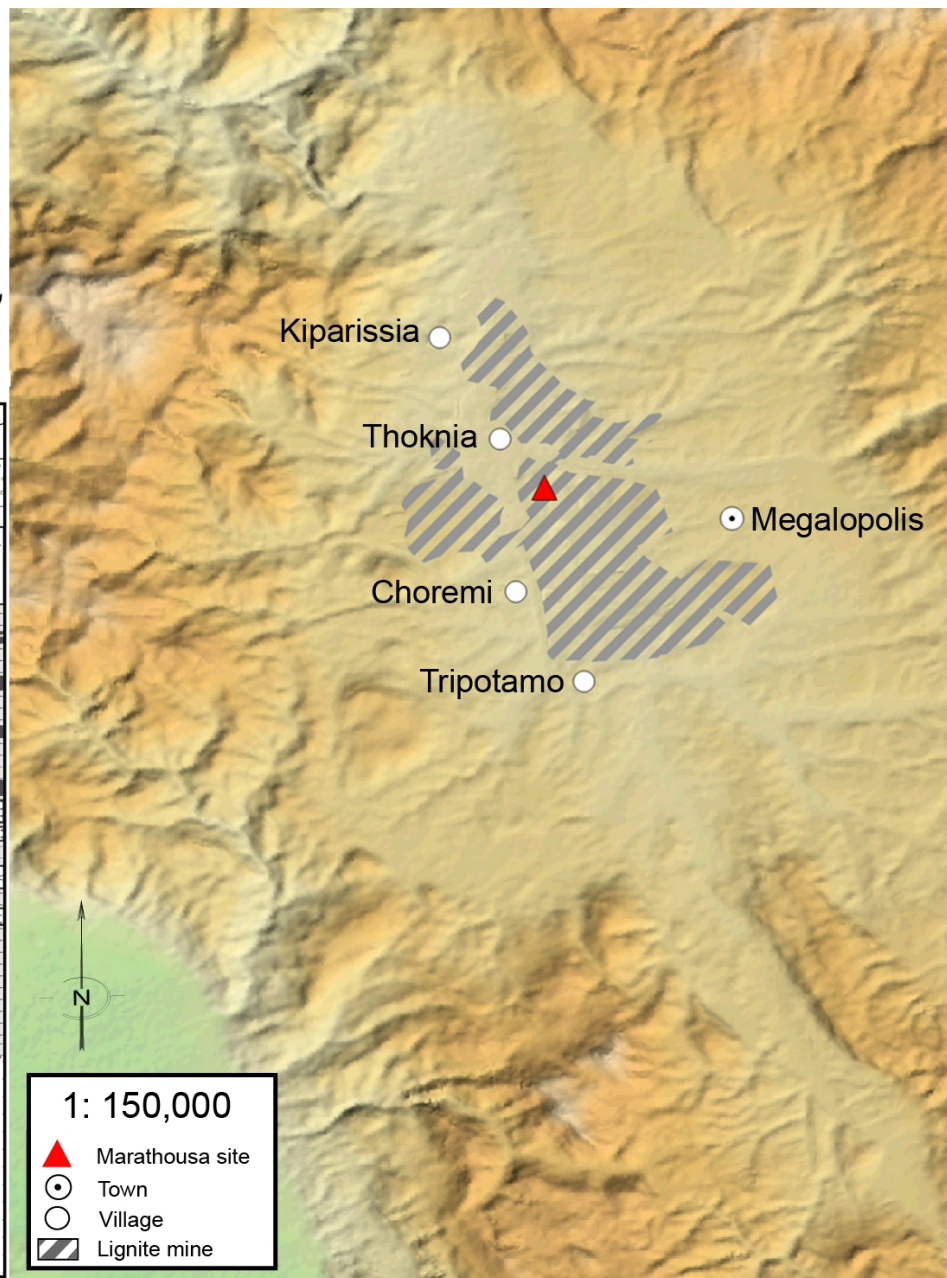
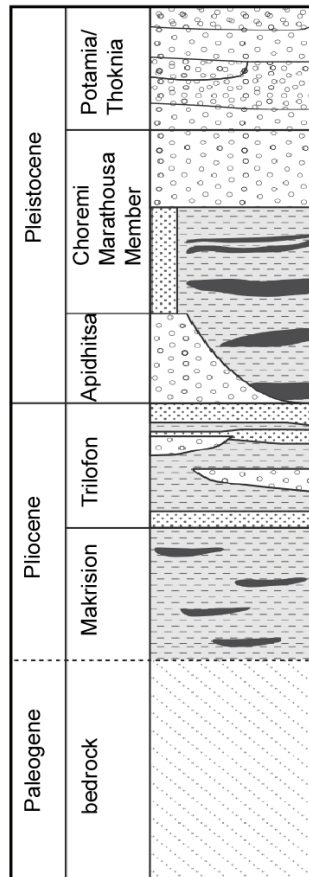
Table 3: Dimensions of the *Crocidura* remains from Marathousa 1.

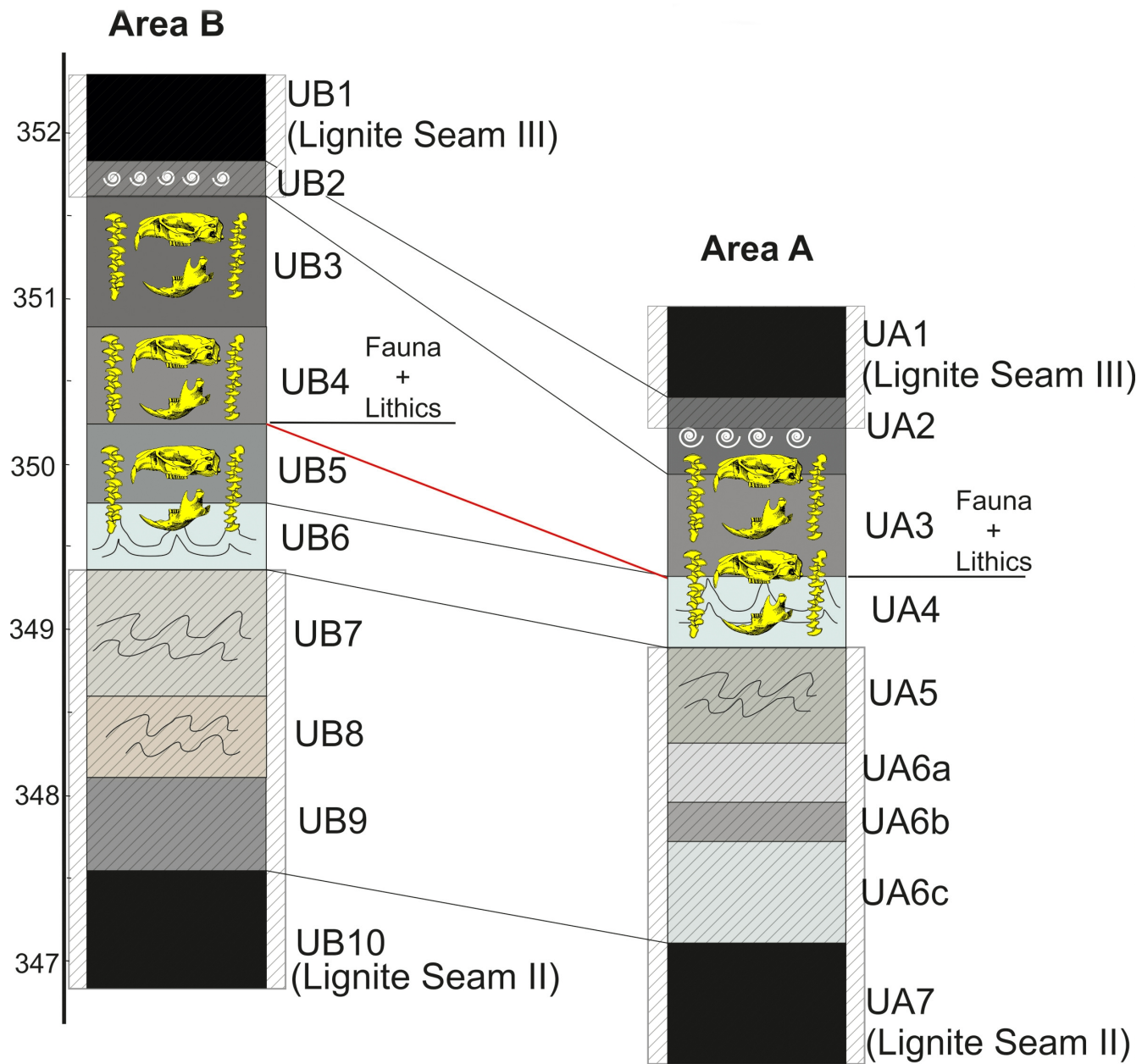
Table 4: Occlusal dimensions from the *Arvicola* molars from Marathousa 1.

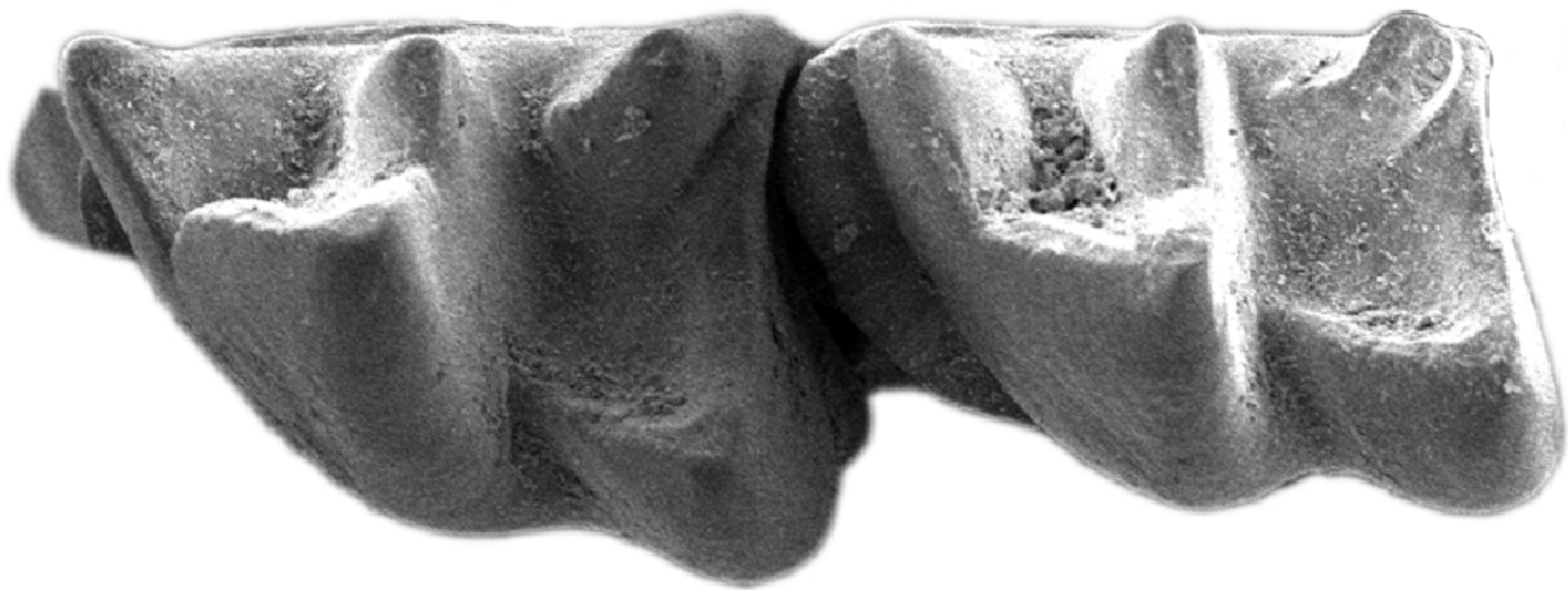
Table 5. The SDQ values and dimensions of the first lower molars of *Arvicola mosbachensis* from Marathousa 1 compared with data of Middle Pleistocene and extant Water Voles.

Table 6: Occlusal dimensions of the *Microtus* remains from Marathousa 1.

Table 7: Occlusal measurements of the *Apodemus* molar from Marathousa 1.

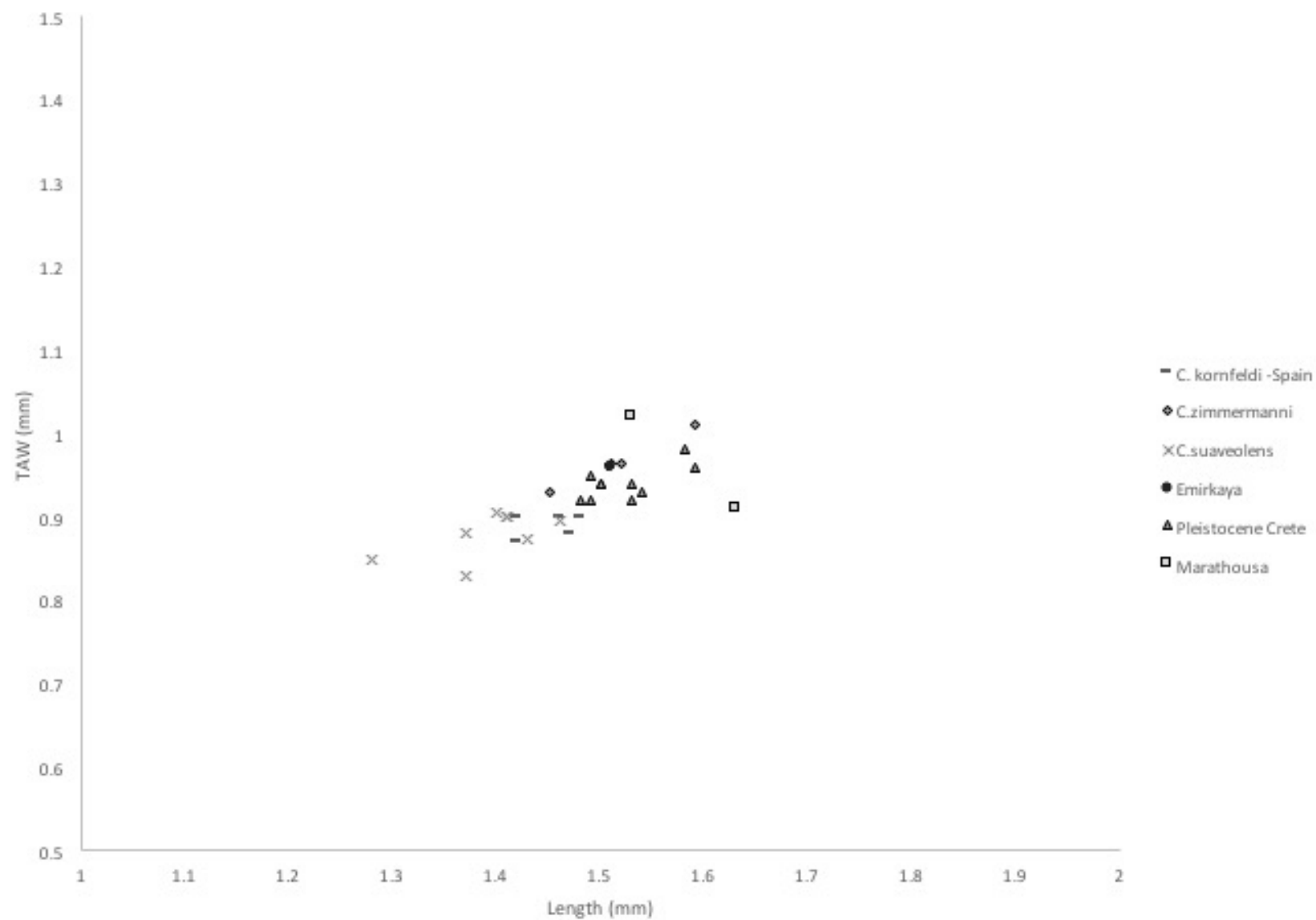


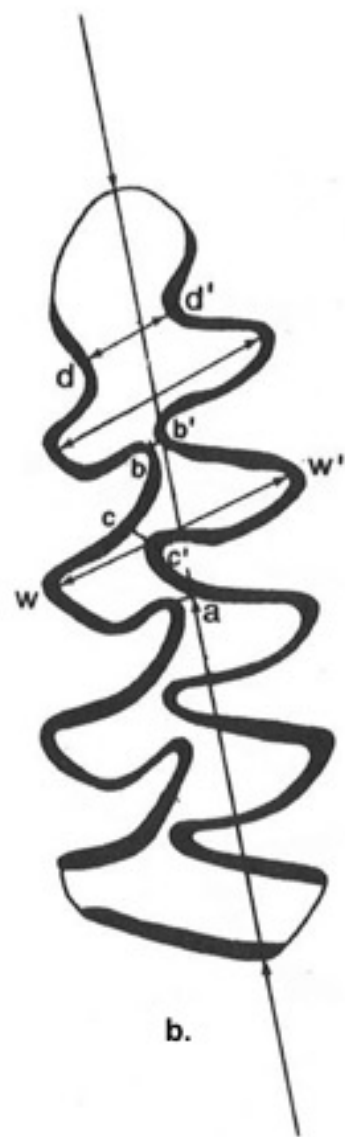
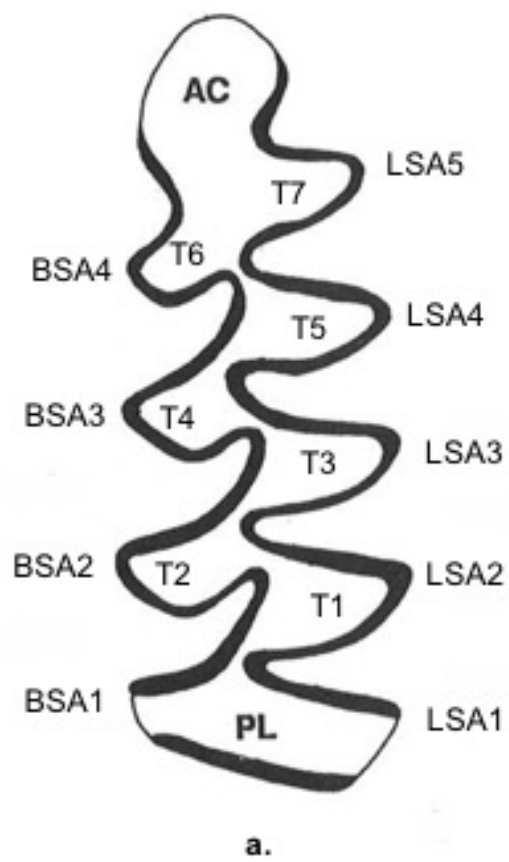




1 mm

Marathousa Crocidura







a



b



c

1 mm



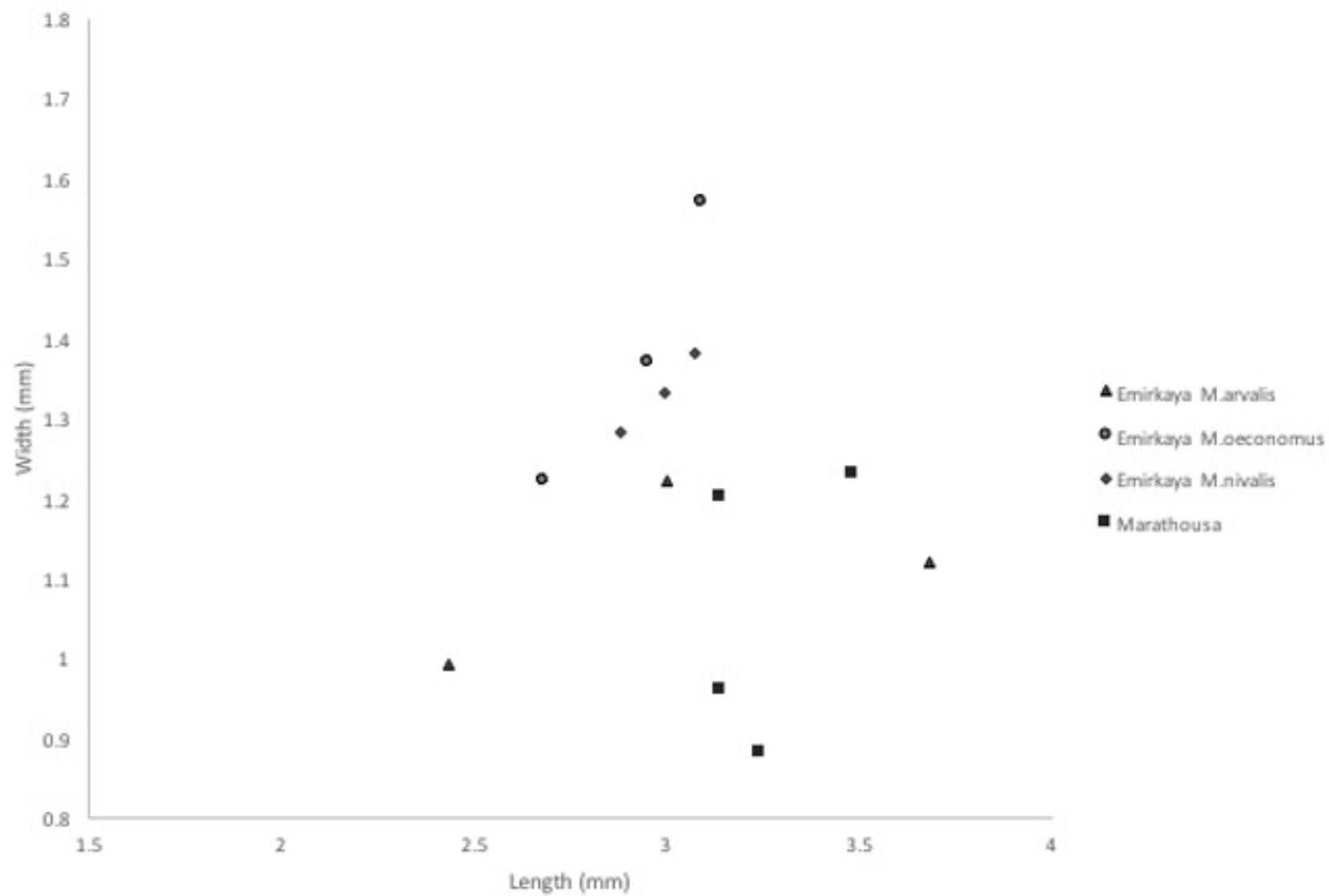




1 mm



Marathousa Microtus m1





1 mm

Area A	<i>Crocidura sp.</i>	<i>Arvicola mosbachensis</i>	<i>Microtus cf. arvalis</i>	<i>Apodemus sp.</i>	<i>?Alactaga indet.</i>
Units					
UA3b	2 upper incisors, 1 P4	1 mand. with m1, m2, m3;			
UA3c	1 mand. with m1, m2	3 mand. with m1, m2, m3; 3 mand. with m1,m2; 1 mand. with m1; 25 m1; 16 M3	6 m1; 3 M3	1 m1	1
UA4		6 m1; 6 M3			

Area B	<i>Crocidura sp.</i>	<i>Arvicola mosbachensis</i>	<i>Microtus cf arvalis</i>
Units			
UB4a	1 mandible, 1 m2	1 m1; 1 M3	2 M3
UB4c		1 mand. with m1, m2; 1 mand. with m1; 13 m1; 10 M3	4 m1
UB5a		2 m1; 1 M3	1 M3
UB6		1 M3	

Crocidura sp.		N	Mean	Range
m1	L	1	1.57	
m1	TAW	1	1.14	
m1	TRW	1	1.09	
m2	L	2	1.58	1.53-1.63
m2	TAW	2	0.965	0.91-1.02
m2	TRW	2	0.935	0.9-0.97
upper incisor	L	2	2.09	2.08-2.09
upper incisor	LT	2	0.78	0.75-0.81
upper incisor	H	2	1.34	1.31-1.36

<i>Arvicola mosbachensis</i>		Mean	Range	N	St Dev
m1	L	3.62	3.18-3.96	40	0.19
m1	W	1.33	1.15-1.48	46	0.06
m1	A	0.76	0.02-1.57	47	0.68
m1	b	0.47	0.16-1.59	46	0.21
m1	c	0.31	0.19-0.56	46	0.06
M3	L	2.4	1.88-2.79	33	0.18
M3	W	1.17	0.89-1.89	27	0.18

Site		rooted molars	MIS	mean SDQ	N	SDQ range	mean Length	N	Lenght range	publication
Hungary (Fehetro)	<i>Arvicola</i>	no	recent	93.8	13					Röttger, 1987
Turkey (Tatvan)	<i>Arvicola</i>	no	recent	124.6	5					Röttger, 1987
Iran	<i>Arvicola</i>	no	recent	134.4	3					Röttger, 1987
Maastricht-Belvédère 4 (Netherlands)	<i>Arvicola</i>	no	7	102.0	25	86 - 113	3.74	5	3.60 - 3.90	van Kolfschoten, 1990
Weimar-Ehringsdorf UT (Germany)	<i>Arvicola</i>	no	7	112.3	9	103 - 126	3.70	8	3.52 - 3.86	Maul et al., 1998
Schöningen - Reinsdorf Igl (Germany)	<i>Arvicola</i>	no	9	115.2	135	100 - 137	3.63	37	3.15 - 4.14	van Kolfschoten, 2014
Petersbuch 1 (Germany)	<i>Arvicola</i>	no	11	126.2	11	107 - 146	3.65	10	3.48 - 4.00	Maul et al. 1998
Barnham (UK)	<i>Arvicola</i>	no	11	ca. 142	14		3.57	77	3.14 - 4.01	Maul & Parfitt, 2010
Visogliano/A-1 (Italy)	<i>Arvicola</i>	no	11	116.5	4	106 - 128	3.41	4	3.17 - 3.60	Maul et al., 1998
Visogliano/A-2 (Italy)	<i>Arvicola</i>	no	11	122.8	2	118 - 128	3.47	2	3.47 - 3.47	Maul et al., 1998
Visogliano/B (Italy)	<i>Arvicola</i>	no	11	125.5	3	109 - 137	3.28	3	3.21 - 3.35	Maul et al., 1998
Marathousa 1 (Greece)	<i>Arvicola mosbachensis</i>	no	12/11	122.0	25	102 - 149	3.62	40	3.18 - 3.96	this paper
Boxgrove (UK)	<i>Arvicola mosbachensis</i>	no	13	139.0	13	140 - 164	3.40	80	2.84 - 3.92	Maul & Parfitt, 2010
Miesenheim I (Germany)	<i>Arvicola mosbachensis</i>	no	13	152.0	78	126 - 180	3.50	18	3.21 - 3.71	van Kolfschoten, 1990
Mosbach 2 (Germany)	<i>Arvicola mosbachensis</i>	no/yes	15	133.3	44	118 - 159	3.25	44	3.06 - 3.55	Maul et al., 2000
Isernia (Italy)	<i>Arvicola mosbachensis</i>	no/yes	15	130.3	7	113 - 142	3.47	6	3.13 - 3.63	von Koenigswald and van Kolfschoten, 1996; Maul et al., 1998
Choremi IV (Greece)	<i>Mimomys savini</i>	yes		117.9	3	108 - 129	3.37	2	3.34 - 3.40	this paper
Choremi III (Greece)	<i>Mimomys savini</i>	yes		137.1	7	117 - 168	3.74	6	3.38 - 4.01	this paper
Choremi II (Greece)	<i>Mimomys savini</i>	yes		144.9	2	144,7 - 145	3.64	2	3.61 - 2.67	this paper
Choremi I (Greece)	<i>Mimomys savini</i>	yes		148.3	5	132 - 160	3.68	4	3.45 - 3.82	this paper
West Runton upper levels (UK)	<i>Mimomys savini</i>	yes		139.2	23	115 - 157	3.10	24	2.89 - 3.72	Maul & Parfitt, 2010
West Runton lower levels (UK)	<i>Mimomys savini</i>	yes		138.9	26	115 - 163	3.34	26	2.98 - 3.66	Maul & Parfitt, 2010
Prezletice (Czech Republic)	<i>Mimomys savini</i>	yes		133.0	17					Heinrich, 1990
Voigtstedt (Germany)	<i>Mimomys savini</i>	yes		139.1	10	122 - 166	3.53	16	3.30 - 3.71	Heinrich, 1990
Villány 8/10-11 (Hungary)	<i>Mimomys savini</i>	yes		138.6						Heinrich, 1990
Koneprusy C718 (Poland)	<i>Mimomys savini</i>	yes		141.7	20					Heinrich, 1990

<i>Microtus cf. arvalis</i>		N	Mean	Range	St Dev
m1	L	5	3.3	3.14-3.51	0.18
m1	W	5	1.06	0.88-1.04	0.15
m1	a	6	0.37	0.04-1.12	0.5
m1	b	6	0.14	0.04-0.36	0.14
m1	c	6	0.13	0.05-0.27	0.1
m1	d	3	0.34	0.28-0.38	0.05
m1	e	3	0.92	0.8-1.02	0.11
M3	L	5	2.3	2.25-2.32	0.033
M3	W	6	1.03	0.9-1.08	0.017

<i>Apodemus sp.</i>	Length		Width	
	Mean	N	Mean	N
m1	1.75	1	1.08	1

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I have the pleasure to submit, on behalf on all the authors, the article entitled *The small mammal fauna from the Palaeolithic site Marathousa 1 (Greece)* for publication in Quaternary International. (special issue: **The Gates of Europe**)

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