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The Early Miocene rodent faunas of Kargı, Anatolia, and their biostratigraphic implications

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Index

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Abstract

The assemblages found in the lignite mine of Kargı (Kargı 1, 2 and 3), Osmançik-Dodurga basin, Central Anatolia, contain a rich record of Late Oligocene and Early Miocene rodent species. Only the insectivore material of these assemblages has been formally studied before. The integrated faunal list of Kargı aids to the biostratigraphy of the Anatolian localities, which combined to the available tectonic and basin analyses, as well as the magnetostratigraphic studies, can provide a reliable dating of the localities. A large number of teeth (>300 molars and incisors) is examined; eight muroid genera and one dipodoid genus are identified in the Kargı assemblages, and described in detail; *Meteamys alpani* is the most frequent species found in the studied material and it is considered to be a characteristic species of the Oligocene/Miocene transition of Anatolia. Biostratigraphic correlations to other Anatolian localities of the time (Yeniköy, Inkonak, Kilçak, Harami, Keseköy) suggest that Kargı 1 is of Late Oligocene age (MP30), Kargı 2 is found during the Oligocene/Miocene transition (MP30/MN1 transition) and Kargı 3 is of Early Miocene age (MN1). Also, the composition of the Kargı faunas suggests a warm, humid/near lacustrine environment, which is supported by the presence of diatomites and lignites in the area.

1. Introduction

The central Anatolian locality of Kargı hosts a variety of species in the Oligocene/Miocene transition and the Early Miocene; the most frequent one is *Meteamys alpani*, which is considered characteristic of the Late Oligocene/Early Miocene of Anatolia. *Meteamys alpani* has not been extensively studied, except for the type locality of Inkonak (de Bruijn *et al.,* 1992).

The Paleogene and Neogene of Anatolia have been studied with respect to mammal distributions and migrations, and a local zonation of these ages has been established based on the rodents (Ünay *et al.,* 2003a, b). Tectonic and basin analysis studies have be aided by biostratigraphic studies of the Anatolian localities, and more specifically by rodent content examination, which shows a greater diversity and higher evolution rates than insectivores especially in these ages of Anatolia (van den Hoek Ostende, 2001b). The Anatolian assemblages from Early Miocene (**Fig. 1**) can provide largely accurate relative age estimates, due to the variety of the shared genera (de Bruijn *et al.,* 1992). Ünay *et al.* (2003b) constructed a preliminary zonation of the Anatolian Neogene, based on genus-level rodent evolution analyses, with Muroidea being the most significantly diverse superfamily. In this zonation, Kargı was estimated to be of Latest Oligocene age.

In this research, over three hundred specimens of rodent teeth were examined, of the Oligocene/Miocene transition and Early Miocene of Kargı, Central Anatolia. *Meteamys alpani* and *Cricetodon versteegi* are the most frequent rodent fossils in these assemblages; which contain seven more genera, as well. These fossils are stored in Utrecht University, Department of Earth Sciences.

We focus on taxonomical examination of the rodent teeth from Kargı 1, 2 and 3 with a detailed description, as well as a subsequent comparison of the affinities with other genera and species, in order to obtain more accurate age estimates. The biostratigraphical results are essential to conclude to the age of the Kargı assemblages, since previous studies were based on informal identifications of the Kargı faunas. An interpretation of the paleoenvironmental and paleogeographical evolution is also attempted. This research project lies within the framework of 'Terrestrial Oligocene and Miocene vertebrate Biostratigraphy' and is within the frame of the project "Biostratigraphy of the Neogene of Anatolia" of Dr. H. de Bruijn and Dr. W. Wessels.

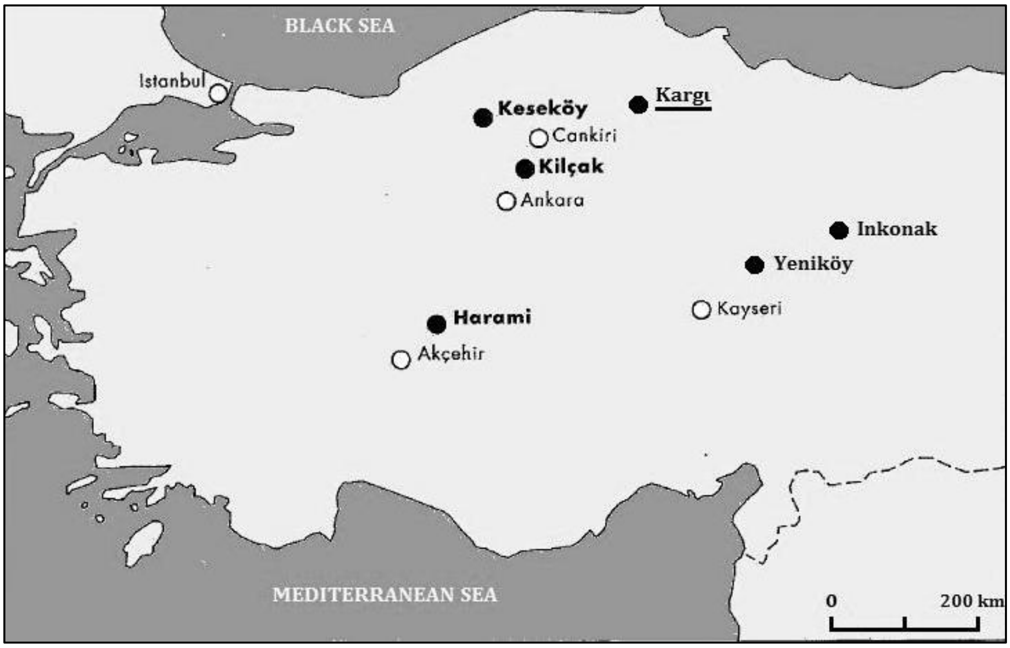


Fig. 1. Anatolian Mammal localities of the Upper Oligocene and Lower Miocene (modified after van den Hoek Ostende, 1995).

Geological setting

Central Anatolia has a complicated geology; during Oligocene time one large basin was formed, with gypsiferous, clastic and volcanic deposits, while after the Oligocene an "intra-cratonic" basin was developed (Görür *et al.*, 1998). In the lignite mine of Kargı a rich fossil mammal locality was discovered by Engin Ünay (M.T.A., Ankara) in 1994 (**Fig. 1**). This lignite mine belongs, among others, to the Osmançik-Dodurga intramontane basin. The diatomites of the Kargı mine have undergone less disturbance, due to the contiguity with the North Anatolian fault, than some other mines of the basin that contain clay (van den Hoek Ostende, 2001b). Magnetostratigraphy studies carried out by Krijgsman *et al.* (1996) mention a strong tectonisation of the Kargı mine sediments and a rhythmic alteration between limestones and dark green clays. Their studies were unable to estimate an accurate age for the Kargı levels, due to the high temperature of the samples in the demagnetisation curve of the IRM, and the low NRM intensities. However, they obtained magnetostratigraphic ages for the localities of Harami, Inkonak and Yeniköy and compared their biostratigraphy to Kargı in order to obtain ages for the latter (**Table 1**).

Biostratigraphy

A comparison of the lithostratigraphy of Kargı 1, 2 and 3 to other localities of Anatolia (Inkonak, Kilçak, Harami, Keseköy, Yeniköy) is unfeasible due to the difference of the basins to which they belong and the unattainable age estimation of Kargı. Biostratigraphic comparisons carried out by Krijgsman *et al.,* 1996 (based on informal identifications of the Kargı faunas) helped to derive relative positions of these assemblages according the evolution of mammal taxa, particularly Muroidea, and the gradual Early Miocene faunal change from *Meteamys alpani* - *Muhsinia steffensi* domination, to *Eumyarion* – *Spanocricetodon /Democricetodon* domination (Krijgsman *et al.,* 1996). However, the results of the current research show low content of *Muhsinia steffensi* in Kargı 2, the only Kargı level where this species is present.

The Inkonak assemblage (Late Oligocene) is dominated by *Meteamys alpani* and *Muhsinia steffensi* (de Bruijn *et al.*, 1992; Krijgsman *et al.,* 1996) and is the oldest from all the aforementioned assemblages, after Yeniköy. It is also the assemblage that resembles Kargı 1 the most. The Muroidea genera of *Eumyarion* and *Spanocricetodon*/ *Democricetodon* are more characteristic of the Early Miocene faunas (de

Bruijn *et al*., 1992; Krijgsman *et al.,* 1996). Kargı has been biostratigraphically dated between Inkonak and Kilçak (Krijgsman *et al.,* 1996; **Table 1**); Harami is younger than Kilçak, and Keseköy is the youngest of these central Anatolian mammal localities having newly entered genera (*Megacricetodon, Debruijnia, Sayimys*) according to the same authors.

Ünay *et al.* (2003b) grouped 42 localities into 16 zones based on species combination and the evolutionary stage of Muroidea and Zapodidae. Zone A (MP30) includes Inkonak and Kargı 1 and is grouped based on the dominance of *Meteamys alpani* and/or *Muhsinia steffensi*, combined to the presence of *Cricetodon* and *Spanocricetodon*. Zone B (MN1, Kilçak 0-3b and Kargı 2) and Zone C (MN2, Harami 1 and 3) contain *Eumyarion microps, Spanocricetodon sinuosus, Cricetodon versteegi* and *Heterosminthus cf. firmus*, differing on the species *Deperetomys* and *Mirabella* (in zone B and *Deperetomys intermedius* and *Mirabella anatolica* in zone C). Zone D (MN3, Keseköy) is dominated by: *Cricetodon kasapligili, Eumyarion intercentralis, Mirabella crenulata* and *Democricetodon doukasi.* The last occurrence of *Meteamys* and *Muhsinia* is in Zone B.

The distribution of Insectivora has been studied for the Late Oligocene/Early Miocene localities, by van den Hoek Ostende (2001b; **Fig. 2**). Kargı 1 and 2 have a low number of insectivores, but Inkonak has the lowest relative content (5%) of insectivores compared to the other faunas that have almost 20%. This low content of Kargı 1, 2 and Inkonak enhances their close resemblance that has been concluded from the rodent dominance of *Meteamys alpani* and *Muhsinia steffensi*. Kargı 3 is very rich in insectivores (40%) and is, thus, better correlated to Kilçak (van den Hoek Ostende, 2001a). However, the absence in Kargı 3 of talpids (*Suleimania* and *Theratiskos*) and a small soricid (soricid III), that are frequent in Kilçak and a rare dimylid (*Turkodimylus*), could possibly be due to the smaller sample sizes of Kargı or point to an older age of this assemblage, before the immigration of these species to Anatolia, according to van den Hoek Ostende (2001b).

The correlation of the Anatolian faunas to the European MN zones is difficult, since common species are absent between Anatolia or Central Asia and Europe and there is no other reference of the Anatolian species in any European fauna (except *Melissiodon*). According to Ünay *et al.* (2003a) the newly arrived species *Meteamys, Muhsinia, Cricetodon* and *Spanocricetodon* migrated during the late Oligocene from Iran through the Elbours-Kopetdagh corridor, which also agrees with the paleogeography of Paratethys of that time (Popov, 2010).

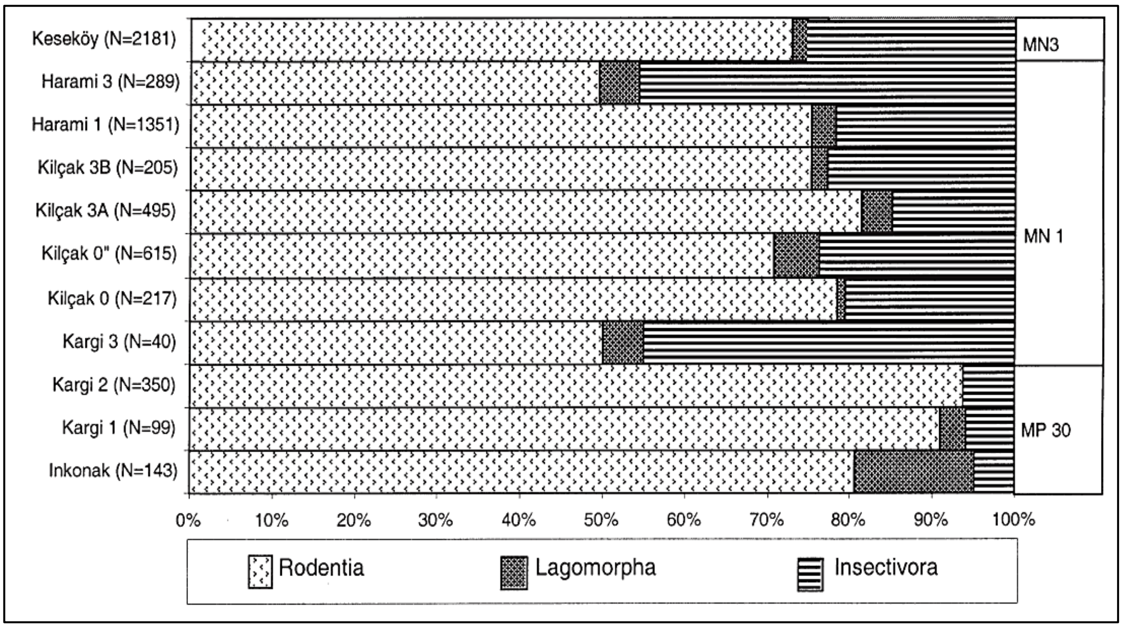


Fig. 2. Small mammals' relative abundance, after van den Hoek Ostende, 2000b.

Table 1. Correlation of some Anatolian fossil localities to the GPTS according to Krijgsman *et al.,* 1996, and their age in million years (Ma), (updated to GTS 2004).

	chron (CK 95)	Age (Ma)
Keseköy	C6n/C6An.1n/ C6An.2n	18,75/20,71/ 20,44
Harami 1	C6Bn.2n	22,1
Kilçak	?	
Kargı 3		
Kargı 2		
Kargı 1		
Inkonak	C6Br/C6Cn.1r/C8r	22,41/22,8/26
Yeniköy	C10r	29,2

Krijgsman *et al.* (1996) aged the Inkonak assemblages, which are dominated by *Meteamys* and *Muhsinia* (similar to Kargı but older, see also **Biostratigraphy**), to be of latest Oligocene-earliest Miocene age and make a correlation to chron C6Br, or C6Cn.1r or to C8r. With their paleomagnetic research, they achieved a correlation of the Anatolian assemblages to the European MN zonation: Inkonak, Kargı 1 and 2 are correlated to MP 30, Kargı 3, Kilçak and Harami to MN 1 and Keseköy to MN 3. However, de Bruijn *et al.* (1996) document the last occurrence of *Meteamys* at the end of MN1, the first occurrence of *Eumyarion* in lower MN1 and the first occurrence of *Deperetomys* in the middle of MN1; these genera are present in Kargı 2, indicating a correlation of this level to MN1. Van den Hoek Ostende (2001b) pointed out the gradual faunal change between Kargı 2 and Kargı 3, where also a large increase in the insectivore content takes place (**Fig. 2**), indicating a rapid shift in the environmental conditions. According to van den Hoek Ostende (2001b) there is no hiatus between these levels, indicating that a complete rodent turnover took place at the Oligocene/Miocene transition of Anatolia, mostly through the settling of immigrants.

The detailed study of the Kargı 1, 2 and 3 rodents and their correlation to the MN zonation, as well as the paleoecological changes that occur, will be discussed in the context of this report (see **Discussion and Conclusions**).

Muroidae

The current research project focuses on the rodent superfamily of Muroidae. As rodents, cricetids have ever-growing incisors with the enamel being present only buccally, and a large diastemma separating them from the molars. The lower jaw molars with their ridges and cusps move from the buccal to the lingual side, thus severing the food with this movement.

The muroid record of Kargı contains eight species, of which five are morphologically close in spite of the size differences. The species have only been ranked on the family level. A re-evaluation of the taxonomy for all Early Miocene Anatolian species will be discussed, after their detailed morphological descriptions.

Classification.

The superfamily of Muroidea has a controversial and very complex taxonomy (reviewed by Jansa & Weksler, 2004). Chaline *et al.* (1997) divided Muroidea into †Cricetidae, Nesomyidae, Rhizomyidae, Gerbillidae, Arvicolidae, Cricetomyidae and Muridae. The classification of McKenna and Bell (1977), which split Muroidea in Simimyidae and Muridae only, seems way too narrow. The subfamily division is even more complicated. The Early Miocene Anatolian species have been characterised as cricetids (e.g. Maridet and Ni, 2013; Theocharopoulos, 2000) or murids (e.g. de Bruijn *et al.,* 2012, in prep.); a ranking to Muridae is used in the current report. Also, a number of papers on Anatolia mention Eucricetodontidae as a family within Muroidae and Cricetodontinae, Eumyarioninae, Cricetopsinae as subfamilies among others (de Bruijn *et al*., 1992; de Bruijn *et al*., 1993; de Bruijn *et al*., 1994) or Eucricetodontinae and Eumyarioninae as the only two subfamilies (Ünay and de Bruijn, 1987).

De Bruijn *et al.* (1992) placed *Meteamys alpani* species in the subfamily of Eumyarioninae (family Eucricetodontidae) and De Bruijn and von Koenigswald (1994) placed *Enginia* in

Cricetopsinae. However, the morphological resemblance of *Meteamys* to *Deperetomys, Eumyarion, Cricetodon, Enginia* and *Muhsinia* should be reflected in the classification of these species on a level of family or subfamily. McKenna and Bell (1997) classified *Meteamys*, *Deperetomys* and *Cricetodon* in the Cricetodontini tribe and the Cricetodontinae subfamily, and separately classified *Muhsinia* and *Eumyarion* in the Paracricetodontinae subfamily and the tribe of Eucricetodontini, which is a very large taxonomical distance for species with that level of similarity. Thus, it would be an oversplitting to separate these genera on the subfamily level, in spite of their size differences and would not add any further information to their study, since the division into all the aforementioned subfamilies is nor clarified neither based on distinct characteristics.

In order not to oversplit into subfamilies, we use Muridae as the main ranking for the studied Muroidae material, and a lower number of subfamilies, than previously assigned. The genera *Meteamys, Cricetodon, Deperetomys, Muhsinia, Enginia* and *Eumyarion*, due to their morphological similarities, are placed to a different subfamily (Cricetodontinae) than *Spanocricetodon* (Copemyinae) and *Melissiodon* (Melissiodontinae), with which they have significant size and shape differences. The possibility of convergent evolution of the dental characters was also taken into account. However, since there has been no certain conclusion on whether the morphological similarities are due to convergence or common ancestry, we assumed that the subfamily division should be as parsimonious as possible.

The dipodoid found in the material, *Heterosminthus*, is classified as Lophocricetinae (Wessels *et al.*, 2003).

2. Material and Methods

Over three hundred teeth (incisors and molars) the Kargı localities (Kargı 1, 2 and 3) were examined; 130 teeth from Kargı 1, 180 teeth from Kargı 2 and 15 teeth from Kargı 3. They were discovered by Engin Ünay of the M.T.A., Turkey, in 1994 in the Kargı lignite mine near Dodurga village, 200 km NE of Ankara, and are stored in the collection of the Department of Earth Sciences, Faculty of Geosciences, Utrecht University. Only part of the Kargı collection had been previously examined and informally identified by Hans de Bruijn and that identification was used by Ünay *et al.* (2003a,b) for the examination of the Anatolian biostratigraphy.

The incisors, upper and lower, are not included in the description tables of the species, the graphs and the phylogenetic trees, since their structure is common among muroids of this age and no reliable enamel characters of the surface can be used for their identification and mostly the size of the incisors is used for the species identification in the present paper. The lower incisors in general are less curved throughout their length than the upper ones, due to smaller need to bend in the lower mandible, and the most prominent curve starts just before the incisor comes out of the gums. As for the upper incisors, there is little known difference in the tooth features among Miocene muroid species, which complicates their identification. Fortunately, the size grouping helped identifying the larger incisors or incisor fragments that belong to *Meteamys alpani*. Kalthoff (2006) carried out studies on the incisor enamel of Oligocene and Early Miocene hamsters and concluded on a reliable characterization of subfamilies based on the incisor schmelzmuster. Unfortunately, *Melissiodon* and *Eumyarion* are the only genera she studied that are found in the current material of our research.

The most common terminology used in literature is the one by Freudenthal et al. (1994); a modified terminology by Rodriguez *et al.* (2012) is also rather complete in minor lophs and ridges, such as metalophule I and II and protolophule I and II, which are very often used in the description of the genera and species found in the current thesis. An integrated terminology of the Late Oligocene/Early Miocene rodent molars is given in **Fig. 3**. In M1, the connection between protocone and anterocone is called anterolophule, but it is actually the connection of the anterolophule with the anterior protocone arm, thus it is sometimes interrupted. Protolophule I, not shown in **Fig. 3**, is never complete, but it is sometimes present on the anterior side of the protocone like a ridge parallel to protolophule II. Sometimes, there is a small ridge on the inner anterior side of paracone (e.g. **Plate 2, fig 4**), which is here named "paralophule". In M2, the anterior arm of the hypocone is extending to a long mesoloph, particularly long in *Meteamys alpani*. In m1 and m2, metalophulid II is positioned as a mesolophid, so its identification might be confusing, but in most specimens there is only metalophulid II, and rarely there is a true mesolophid, supporting that in the rest of the specimens only metalophulid II is present. Minor flattenings are present in the antero-labial, antero-lingual and meso-labial side of molars, and are hereby called valleys, except the antero-lingual valley of M1 which is usually wide enough to be called a protosinus, at list in the most abundant species, *Meteamys alpani*. The molar measurements taken are maximum length (L) and width (W1-maximum molar width; W2-maximum anterocone width, only for M1) (**Fig. 4**); they were made with 0,001 mm accuracy and are given here in mm. For *Meteamys* M1 it is typical that the maximum width is at paracone-protocone, but for the other species found, this is not always the case. No measurements were taken for the incisors. The measuring procedure was carried out at the Zoology/Marine Biology Department, Faculty of Biology, National and Kapodistrian University of Athens, on the stereoscope Nikon SMZ-2T with Nikon eyepieces 15x/14 and incident illumination of cold light instrument Olympus KL 1500LCD, through the system software of image analysis Image ProPlus 3.1. The L/W1 (Length to Width1) was calculated after obtaining L/W1 for each specimen separately and then calculated their mean. All statistical elaboration was carried out in Microsoft Excel software.

The specimens displayed on **Appendix Plates** are as if they are from the left side; all originally right side teeth are shown with an underlined number. Magnification will be pointed out for each plate separately. Upper molars are indicated by an uppercase M, and lower molars are indicated by a lowercase m. The morphological description characteristics for all species found are given in the **Appendix Tables**.

(next page) **Fig. 3.** Terminology of Late Oligocene/Early Miocene muroid rodents, on *Meteamys alpani* molars.

M1: 1-labial anterocone cusp; 2-lingual anterocone cusp; 3-protosinus; 4-transverse ridge; 5-anterolophule; 6-antero-labial valley; 7-labial anterocone spur; 8-anterior protocone arm; 9-labial paracone curvature; 10-anterior paracone arm; 11-paralophule; 12-protocone; 13-paracone; 14-inner protocone curvature; 15-posterior protocone arm; 16-protolophule II; 17-entostyl; 18-meso-labial valley; 19-sinus; 20-posterior paracone spur; 21-mure; 22-mesoloph; 23-posterior metacone arm; 24-labial metacone curvature; 25-posterior hypocone arm; 26-remnant of metaloph; 27-hypocone; 28-metacone; 29-posterior hypocone arm; 30-postero-labial valley; 31-metalophule II; 32-hypoconulid; 33-posteroloph; 34-posterosinus.
M2: 1-labial anteroloph branch; 2-lingual anteroloph branch; 3-antero-labial valley; 4- antero-lingual valley; 5-anterior paracone arm; 6-anterolophule; 7-anterior protocone arm; 8-protocone; 9-paracone; 10-inner protocone curvature; 11-protolophule I; 12-anterior protocone arm; 13-meso-labial valley; 14-posterior paracone spur; 15-sinus; 16-protolophule II; 17-anterior metacone spur; 18-inner hypocone curvature; 19-mesoloph; 20-mure; 21-metacone; 22-posterior hypocone arm; 23-hypocone; 24-posterior metacone arm; 25-metalophule II; 26-metalophule I; 27-labial part of posteroloph; 28-lingual part of posteroloph.
M3: 1-anterior valley; 2-anteroloph; 3-lingual anteroloph branch; 4-antero-labial valley; 5-posterior protocone spur; 6-labial anteroloph branch (cusp-like); 7-anterosinus; 8-protocone; 9-anterior paracone spur; 10-protolophule; 11-mure; 12-paracone; 13-sinus; 14-posterior protocone spur; 15-mesosinus I; 16-entomesoloph; 17-protolophule vertical arm; 18-lingual valley; 19,20-mesoloph (interrupted); 21-mesosinus II; 22-anterior hypocone spur; 23-posterior paracone spur; 24-hypocone; 25-metalophule; 26-metaloph; 27-metacone; 28-posterosinus; 29-posteroloph.

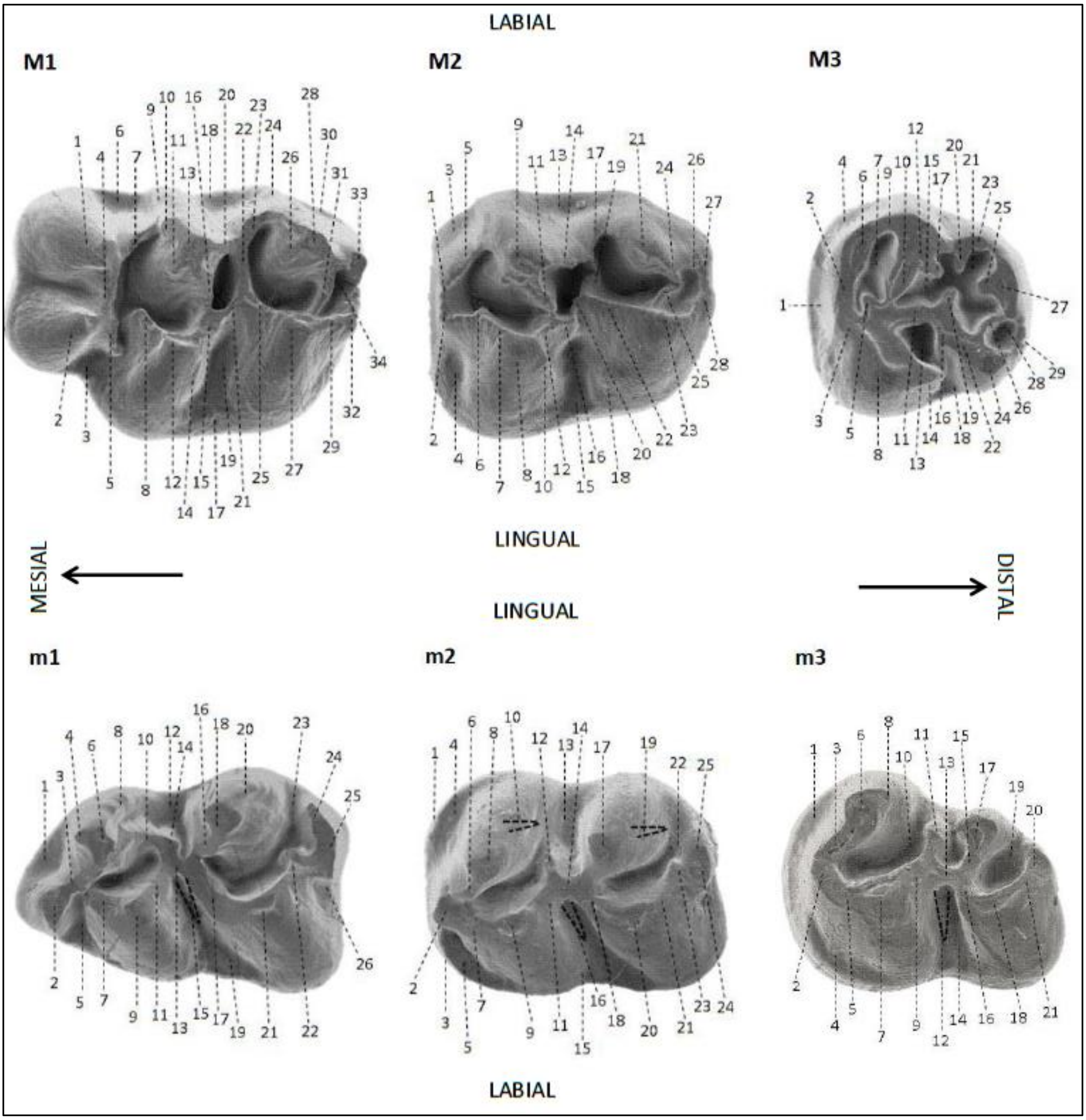


Fig. 3. Terminology of Late Oligocene/Early Miocene muroid rodents, on *Meteamys alpani* molars. (continued)

m1: 1-antero-lingual valley; 2-anteroconid; 3-anterolophulid; 4-metalophulid I; 5-antero-labial valley; 6-metaconid; 7-anterior protoconid arm; 8-posterior metaconid spur; 9-protoconid; 10,14-metalophulid II; 11-anterior protoconid arm; 12-(lingual) sinusid; 13-ectolophid; 15-ectomesolophid; 16-entolophid; 17-anterior hypoconid arm; 18-entoconid; 19-(labial) sinusid; 20-posterior entoconid spur; 21-hypoconid; 22-posterior hypoconid arm; 23-posterosinusid; 24-posterolophid; 25-hypoconulid; 26-posterior valley.

m2: 1-anterocingulid (lingual); 2-cusp-like anterolophulid; 3-anterocingulid (labial); 4-antero-lingual valley; 5-antero-labial valley; 6-metalophulid I; 7-anterior protoconid arm; 8-metaconid; 9-protoconid; 10-posterior metaconid spur; 11-posterior protoconid arm; 12-metalophulid II; 13-(lingual sinusid); 14-ectolophid; 15-(labial) sinusid; 16-ectomesolophid; 17-entoconid; 18-anterior hypoconid arm; 19-posterior entoconid spur; 20-hypoconid; 21,23-posterior hypoconid arm; 22-posterosinusid; 24-hypoconulid; 25-posterolophid.

m3: 1-antero-lingual valley; 2,5-anterior protoconid arm; 3-metalophulid I; 4-antero-labial valley; 6-metaconid; 7-protoconid; 8-anterior metaconid spur; 9-posterior arm of protoconid; 10-(lingual) sinusid; 11-mesolophid; 12-ectomesolophid; 13-ectolophid; 14-(labial) sinusid; 15-entolophid; 16-anterior hypoconid arm; 17-entoconid; 18-hypoconid; 19-posterosinusid; 20-posterolophid; 21-hypoconulid.

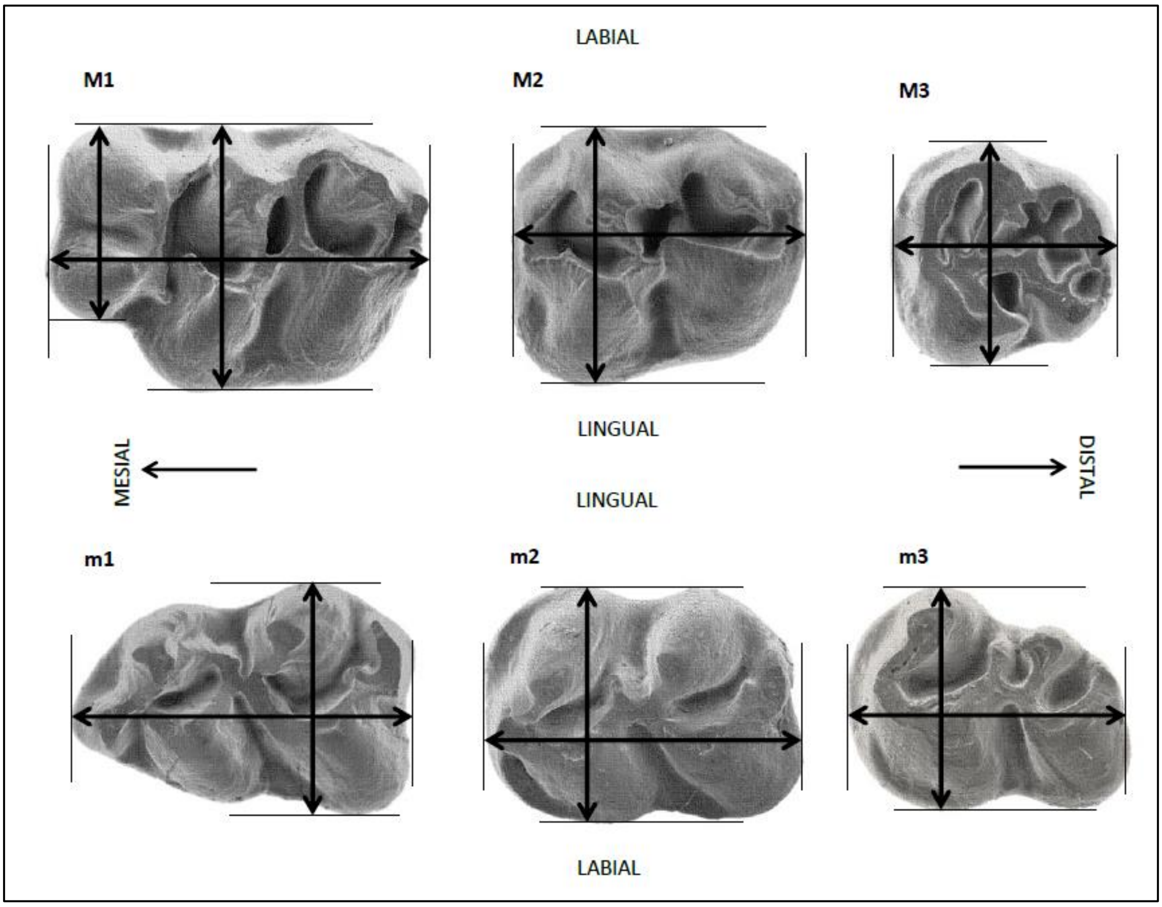


Fig. 4. Measurements of Late Oligocene/Early Miocene muroid rodents, on *Meteamys alpani* molars. The vertical lines (lingual to labial) indicate length (L) measurements, while all the horizontal lines (mesial to distal) indicate width (W1) measurements; in M1 the shorter line indicates maximum anterocone width (W2).

3. Systematics

RODENTIA

Superfamily MUROIDEA Miller & Gidley, 1918

Family MURIDAE Illiger, 1811

Subfamily CRICETODONTINAE Schaub, 1925

Genus ***Meteamys*** de Bruijn, Ünay, van den Hoek Ostende & Saraç, 1992

Meteamys alpani de Bruijn, Ünay, van den Hoek Ostende & Saraç, 1992

Stratigraphic and geographic distribution:
Late Oligocene/Early Miocene of Anatolia: Kargı 1, Kargı 2, Kilçak 0-3, Inkonak (type locality). In the present paper: Kargı 1, Kargı 2.

Material:
Kargı 1: 15 I, 13 M1, 22 M2, 7 M3, 10 i, 12 m1, 12 m2, 8 m3; **Plate 1, Figs. 1-6; Plate 2; Plate 3**. **Graphs 1-6.**
Kargı 2: 3 I, 12 M1, 20 M2, 16 M3, 16 m1, 14 m2, 9 m3; **Plate 4**. **Graphs 1-6.**

Measurements given in **Table 2** and **Table 3**.

Description:

I.

In Kargı 1 a large amount (25 specimens) of upper incisors' fragments was found, followed by a much smaller number (3 specimens) from Kargı 2. However, due to the large size difference among the specimens, the recognition of species was particularly difficult; the larger of the specimens were identified as *Meteamys alpani* (15 specimens), and the smaller ones could belong either to *Cricetodon*, which can be found in the Kargı assemblages, or to *Muhsinia steffensi*, which is a characteristic species for this level.

In *Meteamys alpani*, the upper incisors are bigger than the lower ones and flatter on the sides (**Plate 1**). Also on the sides there are two ridges than ran throughout the length of the tooth; on the one side it is situated more to the centre and on the other it is clearly distal, where the buccal side of the tooth starts. Close to the centre of the buccal side of the tooth on the longitudinal axis there is a change in the curvature of the enamel. The mesial part of the enamel is wider in the larger specimens that belong to *M. alpani* than the small ones, which have narrower, more proportional to the distal, mesial part.

M1.

Kargı 1. - This tooth is characterised by a wide anterocone complex with an average width of 1,45mm (Width2, or W2), and two clearly separated anterocone cusps, a lingual and a labial one. A valley is present between these two cusps, and a small ridge is rarely visible on the anterior side of the valley. The anterolophule connects the protocone equally often either to the lingual cusp of the anterocone, or to the ridge between the labial and the lingual anterocone cusp, even though in some of these specimens it is interrupted. Also, between the two anterocone cusps, a small spur is present in a few cases. The protolophule I is always absent, and the protolophule II is usually short and reaches to the posterior part of the protocone. Parallel to protolophule II is the metalophule II, which is absent in a few specimens, while in the most of the cases it is connected to the posterior part of the hypocone. The posterior spur of the paracone connects this cusp to the mesoloph, and it is interrupted in only three specimens. The mesoloph is usually complete, or very rarely interrupted. A mesostyl (small ridge on the labial end of mesoloph) is often quite visible, even though in some cases it is weak or absent. The mesosinus is often interrupted posteriorly. A character common of the first two upper molars of *Meteamys* is curvature that is visible on the labial side of both the paracone and the metacone. The posterosinus is present in most of the specimens, in variable shapes and depths, more or less narrow, long or shallow. A hypoconule is present in some specimens, even though in most of them it is very small. The (lingual) sinus is always wide and in many cases it also bordered by a cingulum and/or an entostyl (small ridge on the mid-lingual end of the sinus). The protosinus, a sinus postero-lingually of the anterocone complex and anteriorly of the protocone, is always present even though in three of the specimens it is significantly small; thereby a protostyl is present in very few cases. The antero-labial valley is either prominent or small, and absent in only one specimen. The meso-labial valley is more or less prominent, and also absent in only one specimen. The rather small postero-labial valley is rarely visible.

The M1 has three roots, a wide double one below the protocone and the hypocone, and two single ones below the anterocone and the metacone.

Kargı 2. - The anterocone complex is always wide, as in Kargı 1, but a valley is usually absent between the two anterocone cusps. The anterolophule almost always connects the protocone to the lingual cusp of the anterocone. The anterocone spur is present in one specimen. The protosinus is always quite prominent and a “protostyl” (small ridge on the protosinus) is present in half of the specimens. The protolophule I is present in only one case. Metalophule II is always present and in some cases it is fully or almost merged into the posteroloph (**Plate 4**, **fig. 1**). The labial curvature of the paracone and the one of metacone are always prominent, as well. The posterosinus is often very small. A hypoconule is very rarely present. The antero-labial valley is always prominent.

M2.

Kargı 1. - The anteroloph of this tooth consists of two branches, with the labial one being more prominent than the lingual one in most of the cases, resembling a parastyle in many of the

specimens. An interruption between the paracone and the “parastyle” is present in one specimen. The anterior arm of the protocone usually reaches to the anterolophule or a very weak protolophule I. The protolophule II is always directed posteriorly and connects to the mure. The metalophule II is present in all specimens, either weak or more prominent, and connected the anterior hypocone arm. As in M1, a paracone and metacone labial curvature is mostly present (**Plate 2**, **figs. 2, 4b**). The posteroloph is either equally prominent both labially and lingually, or one of the two parts is slightly less prominent than the other. The (lingual) sinus is always wide and only in a few cases it is bordered by a low entostyl or a cingulum. A hypocone inner lingual curvature is present only in a few specimens, a protocone inner lingual curvature is present in many cases (**Plate 2**, **figs. 2, 4b**). The antero-lingual valley is present, either wide or small, rarely bearing a small ridge; the antero-labial valley is mostly present but smaller than the antero-lingual one.
The roots of this tooth are as in M1, in which the lingual root is simple; only in one specimen it is split into two.

Kargı 2. - The anterior protocone arm connects to the anterolophule in one specimen. The protolophule II is almost always reaches to the mure behind the protocone but is in one specimen interrupted, and in another specimen a spur is pointing mid-anteriorly and closes the mesosinus lingually (**Plate 4**, **fig. 2**). The metalophule II is often quite strong, and in some of these cases it is merged into the posteroloph. The mesosinus is often open, while the posterosinus is in some cases not visible due to merging of the adjacent cusps and lophs. The metacone labial curvature is always present in the Kargı 2 specimens. The posteroloph branch is usually prominent labially. The antero-lingual valley is quite prominent in most cases. The (lingual) sinus is always wide and in more than half of the specimens it is bordered, as well.

M3.
Kargı 1. - The anteroloph shape in more than half of the specimens has much less prominent cusps than M2, especially the lingual one. The anterior arm of the protocone is in most cases it is developed as a spur, in a few others absent, or forming a protolophule I, and in one specimen it is merged into a complex of the protocone, the protolophule and the labial anteroloph. The protolophule is connected to the mure behind the protocone in most of the cases. The mesoloph is mostly long and complete, and in only one case it is interrupted. The sinuses show a variety of shape and connection: the lingual sinus is more often open lingually, or very rarely bordered by a posterior protocone spur, or by a structure resembling an “ectomesoloph”, which is only present in the Kargı 1 specimens; the protosinus is bordered in all specimens; the mesosinus I is usually bordered by a cingulum, or, in one case, it is open and connected to mesosinus II (sinus posteriorly of the central mesosinus I); the posterosinus, the anterosinus and the mesosinus II are always closed.
There are three roots, as in all the upper molars of *Meteamys*.

Kargı 2. - The anteroloph shape resembles the shape of M2 in most specimens; only in a few the cusps are not that prominent. The anterior arm of protocone is usually prominent and forms a protolophule I or it is merged into a complex of the protocone, the protolophule and the labial anteroloph. Protolophule connects the protocone to the mure in half of the specimens, or directly connects the paracone to the protocone in the others. The mesoloph is only in a few cases short and incomplete. The sinuses have the same features as in Kargı 1, except mesosinus I, which is often open or connected to mesosinus II, but usually it is bordered either by a cingulum or by a cusp vertical to mesoloph running through the middle of the sinus (**Plate 4**, **fig. 3**).

i.

Two ridges run throughout the centre of buccal/distal side of the tooth, on the longitudinal axis, and two more ridges are present on the side edges of the distal side. It is much narrower on the mesial side than the upper incisor, and generally a thin tooth. The structure of I with the two ridges on the sides can also be found here, with a ridge on the centre of the one side and one the other side situated clearly distally.

m1.

Kargı 1. - The anteroconid is positioned more labially on the longitudinal axis of the tooth. The metalophulid I is complete in most specimens, and interrupted in some, as well as metalophulid II, which is complete in most cases. A valley between the protoconid and the metaconid is elongated and bordered by metalophulid I and II, and this valley is either open antero-labially, or usually bordered by the anterolophulid. Both the metaconid and the entoconid always bear posterior spurs. The posterolophid is always connected to the posterior end of the entoconid, but not always strongly. The mesolophid is absent in almost all specimens, except one where it is present but weak. The hypoconulid is usually short. An antero-labial as well as an antero-lingaul valley is always present and usually quite wide; the lingual sinusid is always developed, as well; the antero-lingual valley sometimes bears a small ridge, but in some cases it is weak. The labial and the lingual sinusid are always wide, but the labial one is much more frequently bordered by a cingulum.
One root is present below the posterior side in the specimens that have a visible root.

Kargı 2.- The valley between the protoconid and the metaconid is either open antero-labially or bordered by the anterolophulid. The posterolophid strongly connected to the posterior entoconid spur. The mesolophid is more often absent than in Kargı 1, but also weak or even prominent in some specimens. The posterior arm of the hypoconid is usually long, but in some cases it is short or absent.

m2.

Kargı 1. - The cusp-like anterolophulid and the metalophulid I usually connect more labially off the central longitudinal axis of the anteroconid, and only in a few cases they meet on the middle of this axis (**Plate 2**, **fig. 10**). The metalophulid II is often long and extends until it reaches the metaconid, resembling a mesoloph, and even in the specimens where it is shorter, it is always developed. The labial sinusid is always in line with the axis of the development of metalophulid II. Both the metaconid and the entoconid have equally grown posterior spurs but often more prominent on the metaconid. The posterior hypoconid arm is directed anteriorly and in most cases it is short and with a variable width (mostly short and thin). The connection between posterolophid and entoconid is always interrupted, with a smaller or bigger notch in between. Both the antero-lingual and the antero-labial valleys are always present, and in most of the cases they are quite prominent. The labial and the lingual sinusids are always wide and usually bordered by cingulum.
The roots were broken in all specimens.

Kargı 2. - The cusp-like anterolophulid and the metalophulid I always connect more labially off the central longitudinal axis of the anteroconid. The posterior spur of the metaconid and the posterior spur of the entoconid are usually equally prominent.

m3.

Kargı 1. - The anterior protoconid arm and the metalophilid I connect anteriorly, on the central longitudinal axis of the tooth. As in m2, the labial sinusid and the metalophulid II are in line, and only in a few specimens they are more transverse. The metalophulid II reaches to the entoconid in a few specimens. The hypolophid is directed forwards and connects to the longitudinal ridge anteriorly of the hypoconid. The posterolophid reaches the entoconid in half of the specimens; otherwise, they are separated by a notch. The sinusids that are present in a variety of prominence are: a sinusid in the middle of the labial side, sometimes extending to the anterior end of the tooth or even to all the labial side, an antero-labial valley and an antero-lingual valley, which are prominent or at least small but developed in most of the cases.

Kargı 2.- The labial branch of anterolophid is often not as low as in Kargı 1, and the lingual one is in most cases absent. The labial sinusid and the metalophulid II are always in line. The antero-lingual valley is always prominent, but the antero-labial one is usually quite small.

<u>Discussion</u>: There is a general size increase of *Meteamys alpani* from Kargı 1 to Kargı 2. The large amount of the specimens also helped detecting some minor morpholophical differences between the two levels for this species, especially for the upper molars.

In spite of being a characteristic species for the Anatolian Oligo-Miocene (MP30), *Meteamys alpani* has only been morphologically described and measured by de Bruijn et al. (1992) for the type locality of Inkonak. As far as the differrences to the type locality are concerned, the Kargı specimens are larger, especially M1 and M2 with a wider range than Inkonak, and a significant length difference of 0,2mm (for M2 this only occurs in Kargı 1). The width differences don't exceed the 0,1mm, which indicates a general elongation of the teeth. The M1 mesoloph is complete for most Kargı specimens, while in Inkonak is always incomplete of medium length or long. Also labial curvatures are present on paracone and metacone in Kargı, but are absent in the type specimens. In M2, apart from the bordering of the sinuses there are not many differences between Kargı and Inkonak. In M3, the prominence of the various cusps and especially of the anteroloph, shows the most variability between Kargı and Inkonak. The lower teeth do not have as many differences as the upper ones, except the metalophulids and the bordering of the sinuses; the m3 is the most similar tooth between the two localities.

Meteamys alpani has a uniquely wide anterocone of M1 that makes it easy to recognize among every other Anatolian rodent of that period. Also, *Meteamys alpani* has a prominent sinus between the anterocone and the paracone of M1, which is small in *Cricetodon versteegi* and mostly absent in the rest of the species. The labial ridge of paracone and metacone are both present only in *Meteamys alpani*, only the paracone ridge is present in *Cricetodon versteegi* and they are both absent elsewhere. The posteroloph reaches the metacone labially in *Meteamys*, *Deperetomys* and *Cricetodon* but it is interrupted in *Muhsinia* and *Eumyarion*. In M2, the differences are fewer, mostly on the length of the posterior paracone spur, the length of the mesoloph (which is the longest in *Meteamys*), the existence of an antero-labial sinus (only present in *Meteamys*), and the bordering of the labial sinus. The last upper molar, M3, is only present in our samples for *Meteamys, Cricetodon* and *Deperetomys*; the inner sinuses show the largest amount of variability among the specimens. In m1, the Cricetodontinae species show a large amount of similarity, which also occurs for the present m2 specimens. Moreover, the m3 Cricetodontinae specimens found belong to *Meteamys alpani, Cricetodon versteegi* and *Eumyarion microps*, and in this case the highest similarity is detected between *Meteamys* and *Eumyarion*.

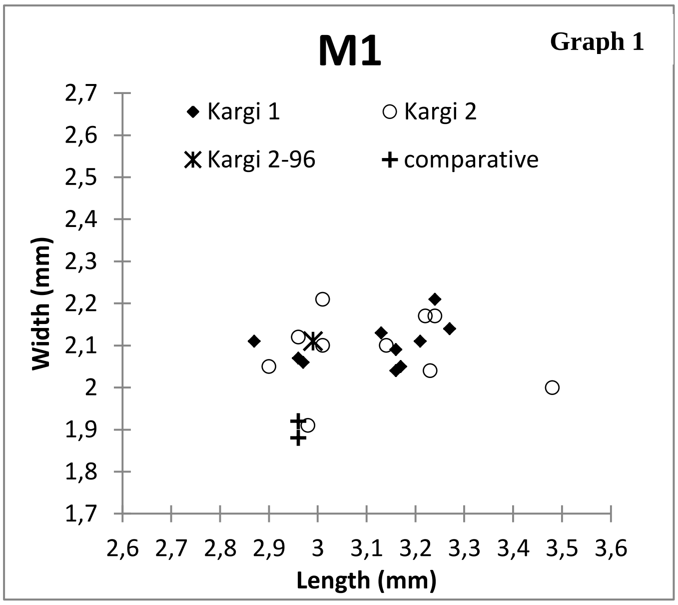
Table 2. The measurements of the Kargı 1 material of *Meteamys alpani*, in mm.

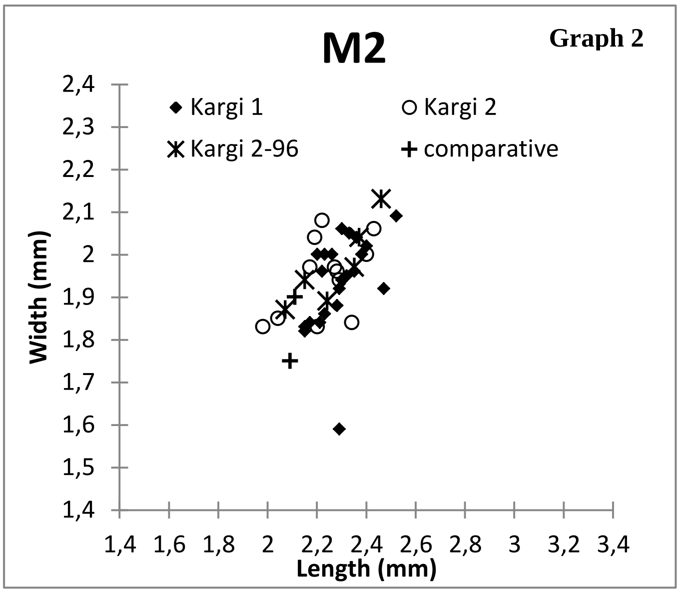
		mean			**N**	**SE**		**SD**		**Range**					
	L	**W1**	**W2**	**L/W1**		**L**	**W1**	**L**	**W1**	**L min**	**L max**	**W1 min**	**W1 max**	**W2 min**	**W2 max**
M1	3,11	2,09	1,46	1,48	10/11/10	0,042	0,019	0,134	0,063	2,87	3,27	1,97	2,21	1,30	1,61
M2	2,29	1,94		1,19	22	0,021	0,024	0,097	0,111	2,15	2,52	1,59	2,09		
M3	1,79	1,76		1,02	7	0,024	0,027	0,064	0,072	1,72	1,88	1,67	1,86		
m1	2,43	1,64		1,49	11	0,037	0,019	0,123	0,064	2,25	2,63	1,47	1,7		
m2	2,37	1,79		1,33	12	0,023	0,014	0,079	0,049	2,26	2,52	1,71	1,91		
m3	2,22	1,64		1,36	6/5	0,040	0,031	0,097	0,069	2,10	2,38	1,58	1,76		

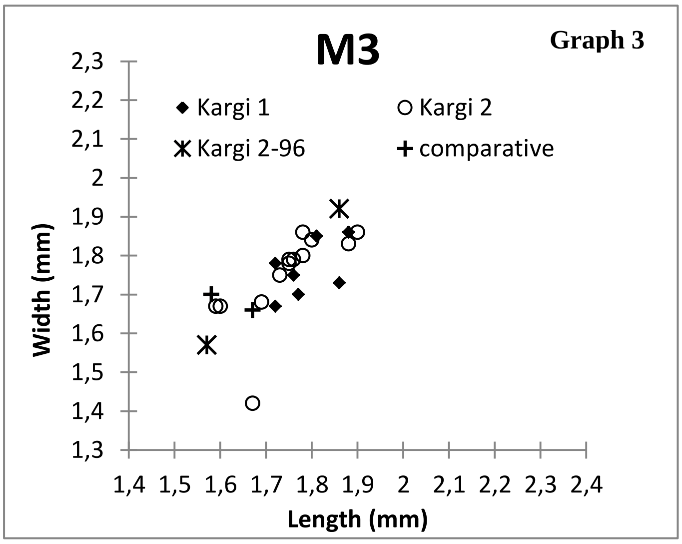
Table 3. The measurements of the Kargı 2 material of *Meteamys alpani*, in mm.

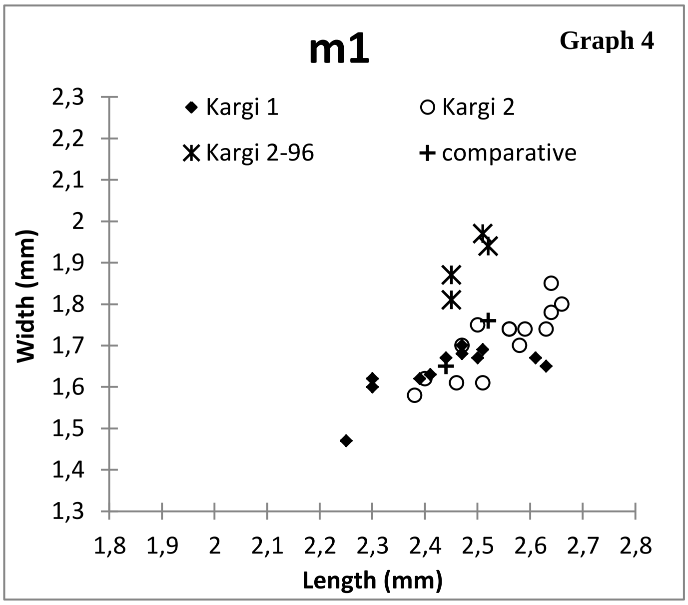
		mean			**N**	**SE**		**SD**		**Range**					
	L	**W1**	**W2**	**L/W1**		**L**	**W1**	**L**	**W1**	**L min**	**L max**	**W1 min**	**W1 max**	**W2 min**	**W2 max**
M1	3,11	2,09	1,45	1,49	12	0,048	0,024	0,165	0,082	2,9	3,48	1,91	2,21	1,33	1,65
M2	2,24	1,94		1,15	20/19	0,030	0,021	0,135	0,091	1,98	2,46	1,83	2,13		
M3	1,74	1,75		1,00	16/15	0,025	0,031	0,099	0,120	1,57	1,9	1,42	1,92		
m1	2,54	1,71		1,49	16	0,023	0,020	0,092	0,081	2,38	2,66	1,58	1,85		
m2	2,42	1,81		1,34	13/14	0,015	0,017	0,054	0,064	2,27	2,52	1,67	1,97		
m3	2,11	1,62		1,31	7/9	0,059	0,012	0,156	0,035	1,93	2,36	1,49	1,76		

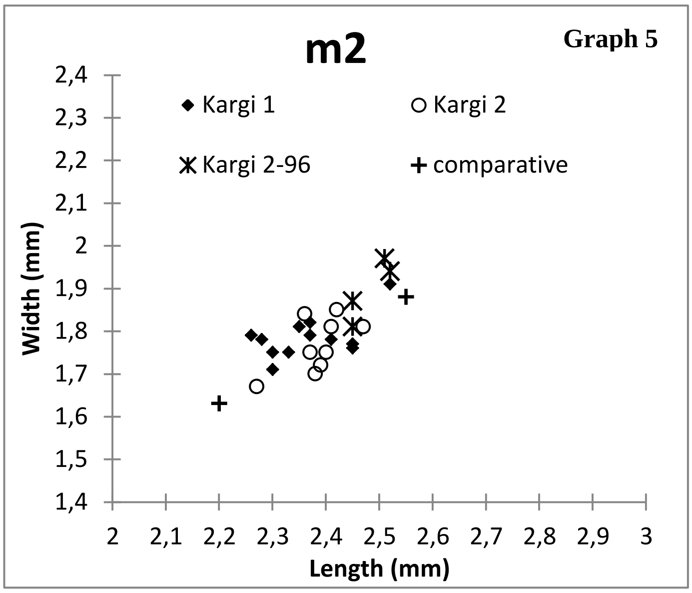
Graphs 1-6. *Meteamys alpani*. Note: The comparative material in the following graphs, are from the type locality of Inkonak M.R.6. Their measurements were taken with the same method as the rest of the material, by the current author.

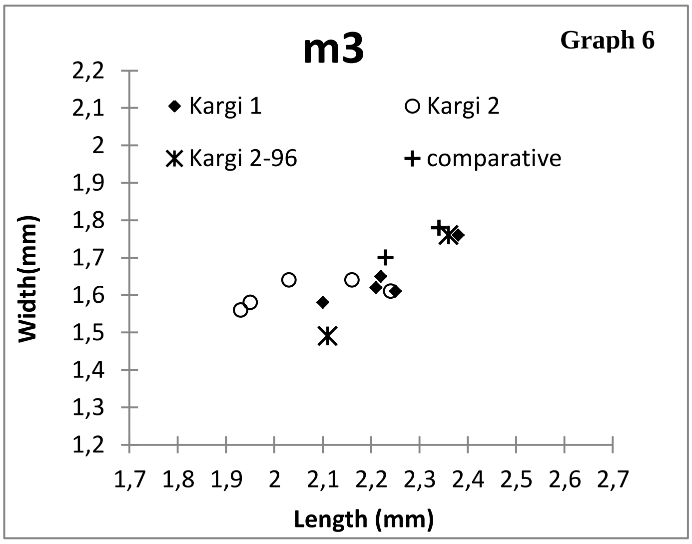












Genus ***Cricetodon*** Lartet, 1851

Cricetodon versteegi de Bruijn, Fahlbusch, Saraç & Ünay, 1993

Stratigraphic and geographic distribution:
Early Miocene of Anatolia: Kargı 2, Kilçak 0-3 (Kilçak 3a: type locality), Inkonak. In the present paper: Kargı 2, Kargı 3.

Material:
Kargı 2: 7 M1 (one broken), 10 M2, 11 M3, 6 m1(one broken), 6 m2 (one broken), 7 m3; **Plate 5, figs. 1-11. Graphs 7-12.**
Kargı 3: 2 M1 (2-2,07x1,34-1,4), 3 M2 (1,5-1,61x1,37-1,5), 1 m1 (1,57x1,05), 1 m2 (1,57x1,26), 1 m3 (1,49x1,22); **Plate 5, figs. 12-15. Graphs 7-9, 11-12.**

Measurements for Kargı 2 are given in **Table 4**.

Description:

M1.
Kargı 2. - This tooth has a wide anterocone complex, with the two equal cusps separated anteriorly by a valley which is sometimes bordered by a cingulum (**Plate 5**, **fig. 1**). The anterolophule extends to the anterior protocone arm in all specimens. The protolophule I is always absent; the protolophule II is short and usually connects the mure to the protocone; the posterior spur of the paracone reaches the base of the metacone in most specimens, as well. The mesoloph is always present and has a variable length; in half of the specimens it is quite long. The posterior paracone spur is always blunt and burgee-shaped. In only one specimen there is a connection between the posterior spur of paracone and the mesoloph. The metalophule II, either short or long, usually fully connected to the posteroloph; often there is a small interruption in between (**Plate 5**, **fig. 1**). The posteroloph reaches labially to the base of the metacone. A labial curvature is always present on the metacone. A mesostyl is more or less prominent, and in only one specimen it is absent. The protosinus bears a protostyl in two specimens. The lingual sinus is always wide and usually bordered by a cingulum; in one specimen there is also an entostyl. There is a small antero-labial valley, and a more prominent meso-lingual one. The posterosinus is always present, but it can be either bordered or open postero-labially. A small valley posteriorly of the hypocone is present in one specimen.
There are three roots.

Kargı 3. - In one of the two specimens the antercone complex is broken and missing; in the other one the anterocone complex is wider than in the Kargı 2 material (**Plate 5**, **fig. 12**). A protolophule I is present in one specimen and connects the paracone to the anterior protocone arm. The mesoloph is short in both specimens. In one of the specimens the posterior paracone spur is very weak, while in the other it is blunt and burgee-shaped. There is no labial metacone curvature. There is no protostyl in neither of the specimens.

M2.
Kargı 2. - The two branches of the anteroloph are of equal length and height in most cases, rarely the labial one is more prominent. The anterior arm of the protocone is always developed, as well as a posterior spur of the paracone, which is usually prominent. The protolophule II is usually absent; in two specimens it is short and does not reach to protocone. The metalophule II is usually short and connected to the anterior hypocone arm, but in two of the specimens it is longer, and in two it is absent. The mesoloph is always present, usually short and always incomplete. An anterior metacone spur is present and short in two specimens (**Plate 5**, **fig. 2**). The posteroloph is usually equally prominent labially and lingually. The antero-lingual valley is usually very developed and sometimes bordered by a cingulum. The (lingual) sinus is wide and bordered by a cingulum; the meso-labial valley is always prominent and bordered

by a cingulum or not bordered, with a mesostyl present in two cases.
There are three roots; the one below the anterior cusps is double.

Kargı 3. - There are three specimens of M2, bigger than most of the Kargı 2 specimens. In one specimen the labial anterocone branch is better developed than the lingual one (**Plate 5**, **fig. 13**). The metaloph is weak and in two of the specimens it connects to the anterior hypocone arm. The anterior metacone spur is always absent.

M3.
Kargı 2. - The outline of the occlusal surface is dominated by a very prominent and high paracone. The labial branch of the anteroloph is often more prominent than the lingual one; otherwise, both branches are equally well-developed. The anterolophule can be long or short. The protolophule is almost transverse and connects the paracone to the protocone in most specimens. Generally, the posterior part of the tooth is less developed than the anterior one. The mesoloph is almost always present but quite small. The (lingual) sinus is in most case closed by an “entomesoloph”-like structure, while the entoloph can be either small or more prominent. The antero-lingual valley is more prominent in some specimens, but frequently it is very small. The antero-labial valley is more often prominent, and occasionally bordered by a cingulum.

m1.
Kargı 2. - The anteroconid is prominent and always situated more labially than the central longitudinal axis. The anterior arm of the protoconid is usually long but ends free. The metalophulid I is either connected to the anterolophulid or the anteroconid. The metalophulid II is always complete and connects the posterior metaconid spur to the posterior arm of the protoconid. The metaconid and the entoconid usually have equally developed posterior spurs; in a few cases the metaconid spur is weaker. The hypolophulid always reaches the hypocone on the longitudinal ridge; a small hypoconulid is present on the posterolophid. A mesolophid is always absent. A mesostylid is developed in one specimen. The posterior arm of the hypoconid is always long and connects to the posteroconid. The posterolophid is sometimes fully connected to the entoconid, but usually they are separated by a notch. The lingual sinusid is always wide and in some specimens it is confluent to the labial sinus. The labial sinusid is always bordered by a cingulum. An antero-lingual valley is either very weak or absent; the antero-labial valley is usually bordered by an anterocingulid.
There are two strong roots, one below posteroconid/hypoconid/entoconid and one below protoconid/metaconid/anteroconid, both being equally strong throughout their length.

Kargı 3. - There is a single m1 specimen, with minor morphological differences from Kargı 2 and within its size range (**Plate 5**, **fig. 14**). The metalophulid I is connected to the anterolophid. The postero-lophid reaches the entoconid base. The labial and the lingual sinusids are confluent, and neither of them is bordered.

m2.
Kargı 2. - There is a cusp-like anterolophulid. The metalophulid I is connected to the anteroconid on the anterior side of the tooth; the metalophulid II is present in most specimens, and usually short, ending free in the lingual sinusid. The posterior spur of the metaconid is sometimes more prominent than the one of the entoconid, but more often these two spurs are equally prominent. The hypolophulid is short and directed forwards, conecting to the posterior arm of protocone; only in one specimen the hypolophulid connects to the longitudinal ridge in front of hypocone. The

posterolophid is wide in the middle and usually does not reach to the base of the entoconid. Both the lingual and the labial sinusids are wide, but the labial one is almost always bordered, unlike the lingual one. The antero-labial valley is always very prominent and bordered, and in most cases it is deep, as well. An antero-lingual valley is always absent.
There are two strong roots as in m1.

Kargı 3. - There is a single m2 specimen, with no considerable difference from Kargı 2, except of its slightly bigger size.

m3.
Kargı 3. - The anterior protoconid arm and the metalophulid I connect anteriorly on the central longitudinal axis. The metaconid is very high, and the protoconid is almost as high. The posteriorly directed mesolophid is more often long than short. The entolophid is present between the hypoconid and the entoconid, and in only one specimen it is not fully connected to entoconid; the entoconid is always fully connected to posterolophid. The labial sinusid is always developed and mostly bordered by a cingulum, or, in a few cases, by a mesostylid, as well. The lingual sinusid is always developed as well, but never bordered. An antero-labial valley is prominent in most specimens, quite deep and bordered by an antero-cingulid; an antero-lingual valley is always absent.
There are two roots.

Kargı 3. - There is a single m3 specimen, very similar to Kargı 2. The lingual sinusid is absent.

Discussion: Generally, the molars of *Cricetodon versteegi* are similar between Kargı 2 and Kargı 3. There are only a few morphological differences, between the two specimens of M1 from Kargı 2 and Kargı 3; the most considerable difference is the bigger size of the Kargı 3 specimens.
The material from Kargı 2 is smaller than the type material from Kilçak 3a (de Bruijn *et al.,* 1993) by a mean of 0,1mm, and closer to the measurements of Kilçak 0'' and 3b, whereas the material from Kargı 3 is larger than Kargı 2 and therefore close to the type measurements of Kilçak 3a. The M2 of Kargı 3 are generally the longest of all other localities. The morphology of the teeth is also very close to Kilçak 3b than any other Kilçak locality. The M1 has a rather wide anterocone with two separate cusps, and the posteroloph connects to the metacone. In M2, there are two almost equal anteroloph branches and the posterior spur of paracone never meets the short mesoloph, which is the case also for Kilçak 3b but sometimes happens in the Kilçak 3a and 0''. The metalophulid I of m1 always connects to anterolophulid, which is the case in only half of the type material of Kilçak 3a. The lingual anteroloph branch of m2 is never present in *Cricetodon versteegi*; in m2 we detect the fewest differences with the type locality material. In m3, the metalophulid I is always present and weak in Kargı 2, while in Kilçak 3b it can be absent or more developed, as well.

Cricetodon sp.

Stratigraphic and geographic distribution:
Early Miocene of Anatolia: Kargı 1, Kargı 2, Kilçak 0, Inkonak. In the present paper: Kargı 1, Kargı 2.

Material:
Kargı 1: 1 m1 (2,5x1,67).
Kargı 2: 1 m1 (2.43x1,61); **Plate 6, fig. 9. Graph 8.**

Description:

m1.
Kargı 1. - The anteroconid is prominent and situated more labially than the central longitudinal axis of the tooth. The anterior arm protoconid is very weak and no metalophulid is present. There is a curvature on the posterior side of metaconid. The hypolophulid reaches the hypocone on the longitudinal ridge. There is a long and complete mesolophid that reaches a

mesostylid on the lingual edge. The posterior hypoconid arm is long and connects to the posteroconid, which is separated by a notch from the base of the entoconid. The entostylid is very small. There is a weak antero-lingual valley. The lingual sinusid is wide and bordered by a cingulum.

Kargı 2. - The anteroconid is situated on the central longitudinal axis of the tooth. A metalophulid I is present and connects to the anterolophulid. The metalophulid II is complete and connects to the metaconid postero-labially and to the posterior arm of the protoconid, in an X-like shape. The posteroconid is fully connected to entoconid. The mesolophid is absent in the Kargı 2 specimen. There is a developed antero-lingual valley. The cingulum that borders the lingual sinusid only runs half-way, leaving the other half lingual edge open. There is a very small posterior cingulum.

Discussion: The m1 of *Cricetodon sp.* found in the Kargı 1 morphologically resembles the type material of *Cricetodon versteegi* from Kilçak 3a (de Bruijn *et al.,* 1993), but it is much larger. The size and the presence of a long and complete mesolophid, as well as the absence of metalophulid are closer to *Deperetomys anatolicus*. However, the absence of a ectomesolophid, the absence of a posterior hypocone arm, the weak antero-lingual valley, as well as the fact that the posterolophid does not reach the entoconid, point towards *Cricetodon* characteristics. The Kargı 2 specimen is also larger than a *Cricetodon versteegi* m1 and also has more morphological similarities to this species compared with *Deperetomys anatolicus*. The mesolophid is present. The two specimens share similar dimensions, but they also are separated by morphological differences. Thus, there was diversity within *Cricetodon* already from the Early Miocene, as stated by de Bruijn *et al.* (1993), but the material is too limited to be more specific on the species or even establish a new one.

Genus ***Deperetomys*** Mein & Freudenthal,1971

Deperetomys anatolicus de Bruijn, Fahlbusch, Saraç & Ünay, 1993

Stratigraphic and geographic distribution:
Early Miocene of Anatolia: Kargı 2, Kargı 3, Kilçak 0-3 (Kilçak 0'': type locality). In the present paper: Kargı 3.

Material:
Kargı 3: 1 M1 (- x1,78, broken), 1 M3 (1,87x1,85); **Plate 6, figs. 1,2**.

Description:

M1.
This tooth is broken on its anterior side, so it will be partially described. The protolophule II is short and inserts on the mure behind the protocone. The mesoloph is long and reaches to the posterior spur of the paracone and the anterior spur of the metaacone. The metalophule I is absent, and the metalophule II is anteriorly directed and connects to posteroloph, which extends beyond the metalophule II. The meso-labial valley is bordered by a cingulum and an entostyl, and the labial sinus is bordered by a cingulum and a low mesostyl. The cingulum that borders the meso-labial valley begins at the occlusal base of the paracone on the one side and of the metacone on the other side.

M3.
The lingual anteroloph branch is less developed than the labial one, which reaches to the base of the paracone. The protoloph is anteriorly directed and inserts on the mure behind the protocone. The posterior spur of the paracone is burgee-shaped and reaches to the occlusal edge, forming a "mesostyl". There is a short mesoloph and a short metaloph that doesn't extend to reach the hypocone. The posteroloph is separated from the metacone by notch. The (lingual) sinus is wide and not bordered.

Discussion: These two specimens from Kargı 3 are the only ones among the studies material that resemble the type material from Kilçak 0" (de Bruijn *et al.,* 1993) in both morphology and measurements.

Deperetomys* aff. *anatolicus

Stratigraphic and geographic distribution:
Early Miocene of Anatolia: Kargı 2. In the present paper: Kargı 2.

Material:
Kargı 2: 4 M1 (one broken), 3 M2, 1 m1; **Plate 6, figs. 3,4**. **Graphs 13,14.**

Measurements are given in **Table 5**.

Description:

M1.
The anterocone is wide with two cusps that are clearly separated in half of the specimens. The anterolophule is long and the shape is often like a burgee or sometimes more elongated; the anterolophule reaches to the base of the paracone in three specimens. The anterior arm of the protocone is usually connected to the lingual anterocone cusp, even though it can be connected to the anterolophule, as well. The protolophule is present and incomplete in most cases. The protolophule II is short and inserts on the mure behind the protocone. The mesoloph has medium length and ends free in the meso-labial valley. The posterior paracone spur and the anterior metacone spur are burgee-shaped and reach to the labial edge of the occlusal surface; they connect at the end of the mesoloph, near the labial edge. A metalophule I is usually absent (**Plate 6**, **fig. 3**), and the present metalophule II is anteriorly directed and connects to posteroloph. The posteroloph continues beyond the metalophule II, forming a rectacone. The (lingual) sinus is bordered by a cingulum and an entostyl in most specimens. The meso-labial valley is bordered by a cingulum in all specimens and a low mesostyl in half of them.

M2.
The lingual anteroloph branch is lower than the labial one, but both have the same length. The protoloph is posteriorly directed and inserts on the mure behind the protocone. The mesoloph is of medium length and ends free in the meso-labial valley (**Plate 6**, **fig. 4**). The posterior paracone spur has variable length from short to long. The anterior metacone spur also varies from short to long, but in one case it is absent; the same occurs for the entomesoloph. The metalophule I is usually present; the metalophule II is present in two of the specimens, strong and connected to posteroloph (**Plate 6**, **fig. 4**). The posteroloph is separated from the metacone by notch. The antero-lingual valley is bordered by the anterocingulum. The (lingual) and the meso-labial valley are both prominent and bordered by cingula.

m1.
The anteroconid of this tooth is rather developed; the anterolophid branches are both symmetrical. The anterior protoconid arm is short while metalophule I is anteriorly directed and connects to the anterolophid. The posterior protoconid arm is absent. The characteristic X-pattern of the cusps of *Deperetomys anatolicus* is absent from this specimen that has a pattern resembling an N-shape. The mesolophid is long, almost reaching to the rather short posterior metaconid spur. The anterior entoconid spur is short, too. The ectomesolophid is long and reaches to the labial edge of the occlusal surface. The posterolophid is parallel to the mesolophid and reaches to the posterior entoconid spur, thus enclosing a sinus that extends to hypoconid. The antero-lingual and antero-labial valleys are small and not bordered. The labial sinusid is wide and bordered by an ectomesolophid and a rather high cingulum; the lingual sinusid is wide but open lingually.

Discussion: The *Deperetomys* material from Kargı 2 is mostly larger and with more developed characteristics than *Deperetomys anatolicus* (type locality: Kilçak 0'') (de Bruijn *et al.,* 1993), but more primitive and smaller than *Deperetomys intermedius* (type locality: Harami). It is most likely an intermediate species between *Deperetomys anatolicus* and *Deperetomys intermedius* de Bruijn *et al.,* 1987. The size increase of the lower and the upper teeth is characteristic of the evolution of *Deperetomys* during the Early Miocene, as well as other morphological features e.g. weakening of the lingual anterolophid branch and shortening of the mesolophid and the ectomesolophid in the lower teeth, and strengthening of the lingual anteroloph cusp, lengthening of mesoloph and height increase of the crest that connect the main cusps in the upper teeth (see de Bruijn *et al.*, 1993, for the evolutionary trends of this genus). So, the lower m1 is morphologically similar with *Deperetomys anatolicus* but bigger, whereas the upper dentition material available (M1 and M2) are longer and wider by at least 0,15mm than the type *Deperetomys anatolicus*, but still not as strongly differentiated to be considered *Deperetomys intermedius*.

Genus ***Muhsinia*** de Bruijn, Ünay, van den Hoek Ostende & Saraç, 1992

Muhsinia steffensi de Bruijn, Ünay, van den Hoek Ostende & Saraç, 1992

Stratigraphic and geographic distribution: Oligo/Miocene of Anatolia: Kargı 1, Kargı 2, Inkonak (type locality). In the present paper: Kargı 2.

Material: Kargı 2: 2 M1 (2,15-2,25x1,36-1,13), 1 M2 (1,73x1,48), 2 m1 (1,83-1,96x1,29-1,91); **Plate 6, figs. 5,6. Graphs 15, 16.**

Description:

M1.
The anterocone complex differs between the two specimens; in one there are two distinct cusps, while in the other only one cusp is visible. The labial anterocone cusp extends to the base of the paracone and the lingual one can be either connected to the anterior arm of the protocone or not. The protocone is lower than hypocone, but it is also blunt. The anterior arm of the protocone can either be connected to the protolophule I or end free; the posterior arm of the protocone connects to the protolophule II, which is short and directed anteriorly or posteriorly. The paracone is of same size as the metacone. The posterior paracone spur is rather weak. The mesoloph is short in one specimen and of medium length in the other. The metacone and the posteroloph are fully connected. The meso-labial valley is prominent and bordered by a low cingulum and a very small mesostyl. The (lingual) sinus is bordered by a low entostyl.

M2.
The outline of the occlusal surface of this tooth is very close to a square. The lingual anteroloph branch is less prominent than the labial one. The anteroloph reaches labially to the paracone base. The protocone has a rounded shape, while the hypocone has a semi-circular shape; the paracone and the metacone have similar size and shape. The protolophule II reaches to the mure behind the protocone; the metalophule is transverse and connects to the hypocone. the mesoloph is of medium length and grown as an extension of the anterior arm of hypocone. The posteroloph is connected to the metacone base. The meso-labial valley is bordered by a cingulum, while the deep wide (lingual) sinus is open.

m1.
The anteroconid is low and situated on the central longitudinal axis, close to the metaconid. The anterolophulid is either short or absent. The metalophulid I is anteriorly directed and connects to the anteroconid, or there is an interruption between. The metalo-

phulid II connects to the protoconid. The mesolophid is of medium length (**Plate 6**, **fig. 6**). The hypolophid is rather anteriorly directed and connects to the ectolophid in front of the hypoconid; a hypoconulid is present. The labial posterolo-phid branch reaches to the base of the entoconid, while the labial posterolophid branch is prominent and borders a small valley. The antero-lingual valley is very small in one of the specimens and absent in the other; the antero-labial valley is developed and bordered by the anterocingulum. The labial sinusid is bordered by a low ectostylid in both specimens, and also by a low cingulum in one of them.

<u>Discussion</u>: The molars share morphological similarities with *Deperetomys anatolicus*, but the size and the general features are more like *Muhsinia steffensi*. Generally, the cusps are lower than *Deperetomys anatolicus* and the in between ridges are less prominent. Also, the mesoloph of M1 is rather shorter, the ectomesolopid is absent, and the posterior arm of paracone is not as strong as in *Deperetomys anatolicus*. The M2 of the material is closer to *Deperetomys anatolicus* than any other tooth of *Muhsinia steffensi*, with the square shape (more typical of Oligocene genera) and the mesoloph developed as an extension of the anterior arm of hypocone. The m1 is also similar to *Muhsinia steffensi*, with the exception of a longer mesolophid, an always present ectomesolophid and a very weak antero-lingual sinusid; it is also a bit longer and rather wider than the type material of Inkonak.
It is rather difficult to detect any significant differences from the type material of Inkonak, since *Muhsinia steffensi* has a much generalized dental pattern.

Genus ***Eumyarion*** Thaler, 1966

Eumyarion microps de Bruijn & Saraç, 1991

<u>Stratigraphic and geographic distribution</u>: Early Miocene of Anatolia: Kargı 2, Kilçak 0-3, Harami 1 (type locality), Harami 3 (aff.). In the present paper: Kargı 2.

<u>Material</u>:
Kargı 2: 2 M1 (1,66-1,77x1,06-1,18), 1 m1 (1,47x0,85), 1 m3 (1,13x0,97); **Plate 6, figs. 7,8**.

<u>Description</u>:

M1.
The anterocone cusps are distinctively separate in only one of the two specimens; in the second one they are merged into one cusp. There is a thin and straight posterior spur on the labial side of anterocone that curves to the posterior spur of paracone. The anterolophule is absent. The anterior protocone arm is somewhat transverse, and in one of the specimens it reaches to the paracone base. The metalophule reaches to the mure behind the protocone. The mesoloph is either of medium length or very long and reaching a mesostyl. There is an inner lingual protocone curvature. The antero-lingual valley is weak, and the antero-labial valley is absent. The (lingual) sinus is anteriorly directed and open in one specimen, and transverse and bordered by a small entostylid in the other. The posteriosinus is bordered, narrow, long and deep. The meso-labial valley is bordered by a mesostyl and a paracone posterior spur, and in one specimen it is bordered by a cingulum.

m1.
The anteroconid is small and low. The metalophulid I is short and incomplete, while the metalophulid II is complete. The mesolophid is long and almost transverse, slightly directed anteriorly, and ends free in the lingual sinusid. The ectomesolophid is short and transverse. The posterior hypoconid arm is prominent, long and transverse. The posterolophid is separated from the hypoconid by a notch. There is a hypoconid inner lingual curvature. The lingual sinusid is bordered by an indistinct mesostylid that merges with a

posterior metaconid spur and an anterior entoconid spur. The protosinusid is bordered by labial branch of the anterolophulid, while the labial sinusid is bordered by an ectostylid.

m3.
The posterior arm of the protoconid is very long, but doesn’t reach to the lingual side of the metaconid, which is very high. The metalophid I reaches to the anterior protoconid arm, closing the anterosinus. The metaconid is very high, while the entoconid is lower and connected to a prominent entolophid. The posterior hypoconid arm is long and thin, reaching to the base of the entoconid. The antero-labial valley is bordered antero-labially by the anterocingulid.

Discussion: This species was described in Harami (de Bruijn & Saraç, 1991), a locality younger than Kargı 2. The studied material closely resembles the type specimens. For the two M1, we see the same variety of the features as in the type material of Harami 1.

Genus ***Enginia*** de Bruijn & von Koenigswald, 1994

Enginia* aff. *djanpolati de Bruijn & von Koenigswald, 1994

Stratigraphic and geographic distribution:
Early Miocene of Anatolia: Kargı 2, Kargı 3, Kilçak 0-0”, Keseköy (type locality). In the present paper: Kargı 2, Kargı 3.

Material:
Kargı 2: 1 M1, 3 M2 (one broken), 3 M3, 5 m2 (two broken), 1 m3; **Plate 7, figs. 5-7**. **Graphs 17-19.**
Kargı 3: 2 M1 (2,19-2.57x2,1-2,15).

Measurements for Kargı 2 are given in **Table 6**.

Description:

M1.
The Kargı 2 specimen is very similar to the Kargı 3 ones. In fact, the very few deviations that are noticed are within the Kargı 3 specimens. Therefore, the M1 teeth of both levels are going to be described together. The two equal anterocone cusps of all cases are connected on their highest point, and anteriorly of them there is a small unbordered valley. The anterocone complex connects to the protocone via the anterolophule. There are two more anterocone ridges: one on the lingual margin of anteroloph, and another between the ridge connecting the anterocone cusps and the anterior arm of the protocone. The anterior protocone arm is posteriorly directed and it is short. The protolophule connects the paracone to the posterior protocone arm; the posterior paracone spur is prominent and rather blunt. The mesoloph is of medium length. The metalophule is the only character that has some deviations within the Kargı 3 specimens; in the one Kargı 2 and one Kargı 3 specimen it is longer (**Plate 7**, **figs. 5,6**) than the other rather short Kargı 3 specimen, but in all cases it is posteriorly directed, complete and bears a small spur antero-lingually. The posteroloph is separated from the metacone by a notch. The protosinus is wide and bears a protostyl. The meso-labial valley is bordered by a cingulum.

M2.
The labial anteroloph branch is more developed and bears a small cingulum. The anteroloph is connected to the protocone via the anterolophule in the one unbroken specimen where it is visible. The anterior protocone arm is complete in one specimen, and interrupted in the other. The two unbroken specimens have a protolophule II connecting the paracone to the posterior protocone arm; the posterior paracone spur is short and rather blunt in all specimens. The metalophule I is anteriorly directed and weak, but connects to the anterior hypocone arm; the metalophule II is posteriorly directed and connects to the posteroloph. The mesoloph is long and, in one case, it is connected to the base of the metacone. The posteroloph is more prominent on the labial part. There is an inner lingual curvature on both the protocone and the hypocone. The

antero-lingual valley is developed, and, in one case, it is bordered by a cingulum. The (lingual) sinus is developed and not bordered. The meso-labial valley is prominent, and in one case it is bordered by a cingulum.

M3.
This tooth is not described from the type locality of Keseköy. The labial anteroloph branch is more prominent, is in M2. The anterior arm of the protocone forms a protolophule I. The protolophule II inserts on the mure in one specimen, while in the other two it connects directly to the protocone; in one case protolophule II bears two spurs that are anteriorly directed. The posterior paracone spur is more prominent and long, almost reaching the metacone, in two of the specimens; in the third it is shorter. The mesoloph is quite long in two of the specimens and of medium length in the third. The posteroloph is always short but connected to metacone. There is also a small cingulum postero-labially of paracone in two of the specimens (**Plate 7**, **fig. 7**). The posterosinus is open, the mesosinus I and the mesosinus II are connected and viewed as one, the sinus between paracone and protocone is bordered, as well as the anterosinus. The protosinus is not bordered.

m2.
The anteroloph branches are equally developed. The anterior arm of the protoconid reaches to the anterior edge of the tooth, while the posterior arm of the protoconid ends freely in the central lingual sinusid less often than it connects to the mesoloph, extending to the lingual end of the central sinusid. The metalophulid II is always present, but short; the hypolophulid is anteriorly directed and reaches the longitudinal ridge before the hypoconid. The posterior arm of the hypoconid is usually long with a free end, but it can sometimes be short or even absent. The posterolophid reaches to the base of the entoconid. In half of the specimens there is a ridge dividing the postero-lingual valley. The ectomesolophid is frequently small, but can also be long or absent. The antero-lingual valley is wide, deep and bordered by an anterocingulid; the antero-labial one is more narrow and also bordered by the anterocingulid. The labial sinusid is bordered by a cingulum in most specimens, but in one it is bordered by an ectomesostylid. The posterior sinusid can be more or less developed.

There two roots, one below the anterior and one below the posterior cusps.

m3.
This tooth is not described from the type locality of Keseköy. In one specimen of this tooth from Kargı 2 the anterior protoconid arm and the metalophulid I are of equal height, while in the other specimen the anterior protoconid arm one is lower. The metalophulid is anteriorly directed and connects to the anterolophulid. The posterior protoconid arm is quite long; the protoconid is connected to the hypoconid by a long zigzag longitudinal ridge. The mesolophid is short. The hypolophulid is anteriorly directed and connects to the hypoconid. The posterolophid is long and connects to the entoconid. Both the lingual and the labial sinusid are bordered by cingula, and the anterocingulid borders both the antero-labial and the antero-lingual valley.

<u>Discussion</u>: The majority of the material shows features from both *Enginia beckerplateni* as well as *Enginia djanpolati*. Only M1 and M2 are described from both Kargı and Keseköy. Generally, there are very few specimens found of *Enginia djanpolati* (de Bruijn & von Koenigswald, 1994) complicating a valid comparison and a possible variability of features. The upper teeth are more similar to the type specimens than the lower teeth, but M2 also resembles *Enginia beckerplateni* with the more vertical and less sideways directed cusps and the open lingual sinus.

Subfamily COPEMYINAE Jacobs and Lindsay, 1984

Genus ***Spanocricetodon*** Li, 1977

Spanocricetodon sinuosus Theocharopoulos, 2000

Stratigraphic and geographic distribution:
Early Miocene of Anatolia: Kargı 1, Kargı 2, Kilçak 0-3 (Kilçak 3a: type locality). In the present paper: Kargı 1, Kargı 2.

Material:
Kargı 1: 2 M2, 2 m1, 1 m2, 3 m3; **Plate 7, figs. 1-4**. **Graphs 20-22**.
Kargı 2: 1 M1 (0,94x -).

Measurements for Kargı 1 are given in **Table 7**.

Description:

The M1 from Kargı 2 is so worn, that it cannot be properly described. All the other descriptions for the Kargı 1 specimens are given below.

M2.
The labial anteroloph branch is more prominent and longer than the lingual one; the lingual and the labial branch reach to the base of the protocone and the paracone, respectively. The protolophule is anteriorly directed and connects to the anterolophule. The posterior protocone arm connects to the anterior hypocone arm in the middle of the distance between the two cusps. A posterior paracone spur is present in one of the two specimens. The mesosinus is quite wide and closed by a small labial ridge (a mesostyl). The mesoloph is short in both specimens and the entoloph is low and runs antero-lingually – postero-labially. The metalophule is anteriorly directed and connects to the anterior arm of the hypocone. The posteroloph is developed and reaches the base of the metacone, thus, bordering the posterosinus. The meso-labial valley is wide and anteriorly directed, bordered by a hypocone ridge. All the other present valleys (antero-labial, antero-lingual) and the (lingual) sinus are developed and bordered.

m1.
The labial anteroloph branch is longer than the lingual one, and extends to the base of the protoconid, bordering the protosinusid. The lingual anteroloph branch is low and not fully connected to the base of the metaconid, but separated by a notch. The anterior arm of the protoconid is short or long, but in both cases it ends free; the posterior arm of the protoconid is short in the one specimen that is unworn enough to detect its length. A posterior metacone ridge descends steeply from the metaconid and connects to the base of the entoconid, forming a cingulum. The metalophulid is anteriorly directed and connects to anterolophulid in one specimen, while ends free in the other. The mesosinusid is lingually bordered by the posterior metacone ridge. The mesolophid is absent in both specimens. The ectolophid is U-shaped and connects to the protoconid and the hypoconid. The ectomesolophid is of medium length or short. The hypolophulid is posteriorly directed, reaching to the anterior arm of the hypoconid in one specimen. The posterolophid either reaches to the base of the entoconid or ascends to the entoconid. The posterosinusid is wide with a faint posterolophid in one specimen, but quite small in the other. Both the labial and the lingual sinusid are wide but rather shallow; the labial one is bordered by an ectostylid, while the lingual one is either bordered or not. The anterosinusid is open labially; the antero-lingual valley is wider or smaller, and the antero-labial valley is wide and bordered.

m2.
The labial anterolophid branch is better developed than the lingual one, and extends to the base of protoconid. The lingual anterolophid branch extends to the lingual border of the occlusal surface and reaches to the metaconid, bordering the anterosinusid. The metalophulid is very faint, but the posterior arm of the protoconid is long and connected to

metalophulid. There is no metaconid curvature, mesolophid or ectomesolophid. The ectolophid is low and straight. The hypolophulid is posteriorly directed and extends to the ectolophid; there is also an indistinct hypoconulid. The posterosinusid is bordered by a posterolophid. The postero-lingual valley is wide and transverse. The antero-lingual valley is wider than the antero-labial one. Both the lingual and the labial sinusid are developed.

m3.
The anterior protoconid arm and the metalophulid I connect anteriorly on the central longitudinal axis. The metalophulid is absent in one specimen, but in the other two it is anteriorly directed either extending lingually of anterolophulid are reaching to the lingual branch of the anterolophid. The posterior metalophulid spur is absent in two out of three specimens (**Plate 7**, **fig. 4)**. The mesosinusid is wide and bordered by a cingulum, which is either high or low and reaches to metaconid. The entoconid is well developed, but in one case it is merged with the lingual cingulum. The mesolophid is always absent. The hypoconid is more anteriorly directed and rather convex, while hypolophulid is rather transverse and reaches to the apex of the sinusid. A lingual posterolophid is present in two out of three specimens. The posterosinusid is wide and rather deep. The labial sinusid is usually transverse and bordered by a cingulum.

Discussion: In the studied material of this species, we do not detect the typical primitive features as stated by de Bruijn *et al.* (1992); there is no wide anterolophid in m2, when there are single metalophulids, and a mesolophid is absent in all lower molars. Also, the measurements are close to the ones from the type locality of Kilçak 3a, which confirms the statement of Theocharopoulos (2000) that the size of this species does not fluctuate significantly. However, there are some primitive (according to de Bruijn *et al.*, 1992) characters: a double metalophulid is present in m1 and m2, and the mesolophid is absent in spite of the tendency of size increase of this feature in younger localities. Therefore, the Kargı 2 specimens are closer to the younger assemblages.

Subfamily MELISSIODONTINAE Schaub, 1925

Genus ***Melissiodon*** Schaub, 1920

Melissiodon sp.

Stratigraphic and geographic distribution:
Oligo/Miocene and Early Miocene or Europe (France, Germany, Switzerland), Early Miocene of Kargı 2. In the present paper: Kargı 2.

Material:
Kargı 2: 1 M3 (- x2,09), 1 m1 (1,95x2,12); **Plate 7, figs. 8,9**.

Description:

M3.
This tooth has much thinner cusps than any other M3 that is described in this paper. The protocone and the paracoce are robust and high. The anterior paracone arm reaches to the anterocingulum, enclosing a bordered valley. The paracone also bears a labial curvature and an inner lingual curvature. The paracone posterior spur is long and complete and also bears a ridge labially. The mesoloph is short and incomplete. The (lingual) sinus is open, while the posterosinus is present between the metacone and the hypocone and is bordered by a cingulum. There is only one mesosinus.

m1.
This tooth has a broken anterior side, so it will be described from its middle backwards. The metalophulid II is anteriorly directed and connects to the postero-lingual edge of the metaconid. The entoconid is prominent and bears two ridges lingually and one more posteriorly. The anterior arm of the entoconid starts on the inner side of this cusp and reaches to the lingual base of the paracone. The

ectolophid is anteriorly directed and curves twice, forming two small conulids, before reaching the anterior entoconid arm. The anterior hypoconid arm reaches to the posterior protoconid arm. The entoconid and the posterolophid are separated by a notch. There is a ridge posteriorly of the posterolophid. There is also a sinusid on the inner side of entoconid and it is open postero-lingually, while a sinusid on the outer side of entoconid is open.

Discussion: These fragmentary specimens of *Melissiodon* are the only record of this genus in Anatolia, since it is only known from the Late Oligocene and the Early Miocene of Europe. The separate subfamily, to which this species is assigned, is also supported by the Kalthoff (2006) inscisor internal enamel studies.

Superfamily DIPODOIDAE Fischer von Waltheim, 1817

Family DIPODIDAE Fischer von Waltheim, 1817

Subfamily LOPHOCRICETINAE Savinov, 1970

Genus ***Heterosminthus*** Schaub, 1930

Heterosminthus* cf. *firmus Lopatin & Zazhigin, 2000

Stratigraphic and geographic distribution:
Miocene of China and Libya, Early Miocene of Kargı 2. In the present paper: Kargı 2.

Material:
Kargı 2: 1 m1 (1,34x0,96), 2 m2 (1,34-x1,14-0,96); **Plate 7, figs. 10,11**.

Description:

m1.
The anteroconid is developed as a single cusp, and there is no anterolophid. The protoconid and the metaconid have exactly the same shape and size and both connect posteriorly to metalophulid II. There is a distinct free-ending mesolophid, which also connects to metalophulid II. The ectolophid connects the mesoconid to the hypoconid, while the entolophid connects the mesoconid to the entolophid; the entoconid and the hypoconid are not connected. The hypoconulid is very prominent, forming a parastyl-like structure. The posterolophulid extends to the entoconid base. The lingual sinusid is partially bordered by a metaconid spur.

m2.
One of the two specimens is broken anteriorly. The complete one has no anterolophulid and a long and complete metalophid, and they are separated by a narrow valley. The mesolophid is long and complete in both specimens, and reaches to the lingual edge, forming a mesostyl-like structure. The posterior protoconid arm is short, and the mesoconid is faint. The ectolophid is prominent and reaches to the anterior hypoconid arm in both specimens. The antero-lingual valley is open in front of the metaconid, and is confluent with the antero-labial valley, which is open in front of the protoconid. Both sinusids are quire wide. The lingual sinusid is bordered by a mesostylid, and the labial sinusid is bordered in only one of the specimens, by an ectostylid. The posterior sinusid is open lingually and there is also a small valley posteriorly of the posterolophid.

Discussion: *Heterosminthus* is known from the Early Miocene of Kazakhstan, and the Oligocene/Miocene boundary and Middle Miocene of Mongolia with a separate lineage for each of these localities (Ünay *et al.*, 2003a). Morphologically it is not far from the description of *Heterosminthus firmus* from the Loh Formation, Central Mongolia (Daxner-Höck, 2001) but the specimens especially the m2, are too fragmentary to derive certain conclusions.

Table 4. The measurements of the Kargı 2 material of *Cricetodon versteegi*, in mm.

	mean			**N**	**SE**		**SD**		**Range**			
	L	**W1**	**L/W1**		**L**	**W1**	**L**	**W1**	**L min**	**L max**	**W1 min**	**W1 max**
M1	1,93	1,30	1,49	6/7	0,019	0,017	0,046	0,046	1,86	1,98	1,23	1,35
M2	1,37	1,30	1,08	10	0,028	0,019	0,088	0,061	1,27	1,59	1,43	1,43
M3	1,15	1,21	0,95	12	0,020	0,015	0,071	0,053	1,06	1,27	1,32	1,32
m1	1,62	1,08	1,50	5	0,024	0,015	0,053	0,034	1,54	1,67	1,10	1,10
m2	1,44	1,19	1,21	7	0,018	0,014	0,048	0,037	1,40	1,52	1,26	1,26
m3	1,43	1,24	1,15	7	0,024	0,027	0,063	0,071	1,31	1,50	1,34	1,34

Table 5. The measurements of the Kargı 2 material of *Deperetomys* aff. *anatolicus*, in mm.

	mean			**N**	**SE**		**SD**		**Range**			
	L	**W1**	**L/W1**		**L**	**W1**	**L**	**W1**	**L min**	**L max**	**W1 min**	**W1 max**
M1	2,90	1,78	1,63	4	0,015	0,035	0,030	0,07	2,86	2,92	1,85	1,85
M2	2,06	1,76	1,18	3	0,151	0,174	0,262	0,30	1,78	2,3	1,96	1,96
m1	2,35	1,57	1,50	1								

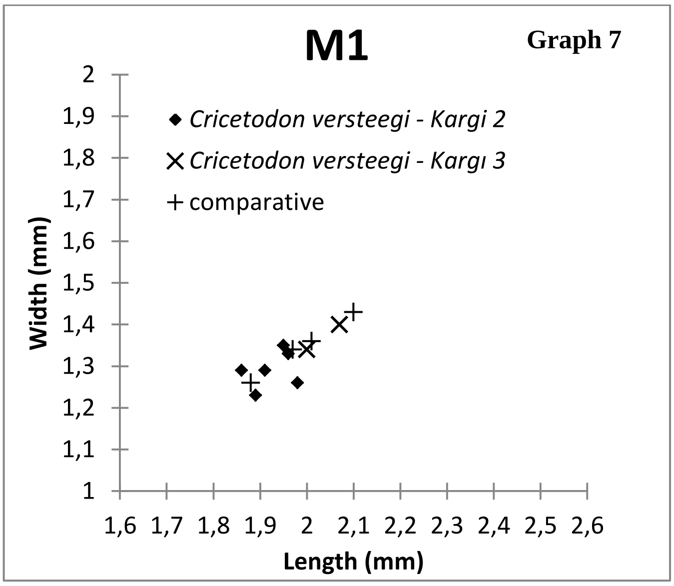
Table 6. The measurements of the Kargı 2 material of *Enginia* aff. *djanpolati,* in mm.

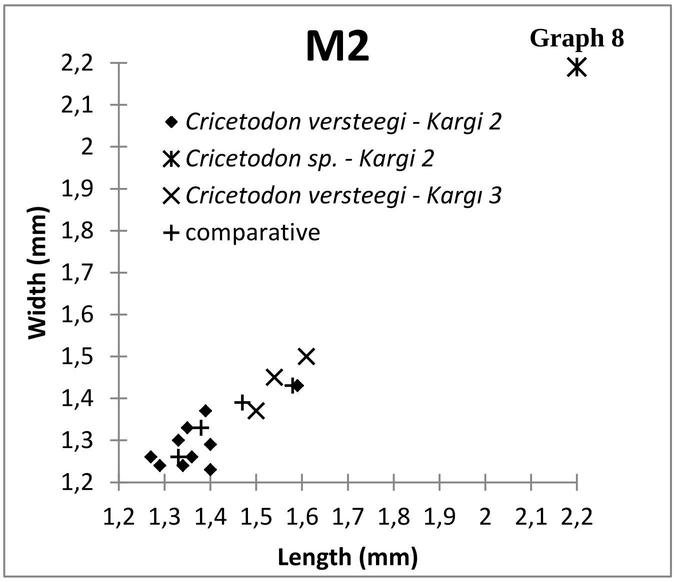
	mean			**N**	**SE**		**SD**		**Range**			
	L	**W1**	**L/W1**		**L**	**W1**	**L**	**W1**	**L min**	**L max**	**W1 min**	**W1 max**
M1	3,74	2,39	1,56	1								
M2	2,3	2,22	1,04	3/2	0,031	0,040	0,053	0,057	2,26	2,36	2,26	2,26
M3	1,82	2,02	0,90	3	0,131	0,106	0,227	0,183	1,63	2,07	1,86	2,22
m2	2,5	2,03	1,23	5/6	0,088	0,076	0,197	0,187	2,31	2,8	2,3	2,3
m3	2,4	1,93	1,24	1								

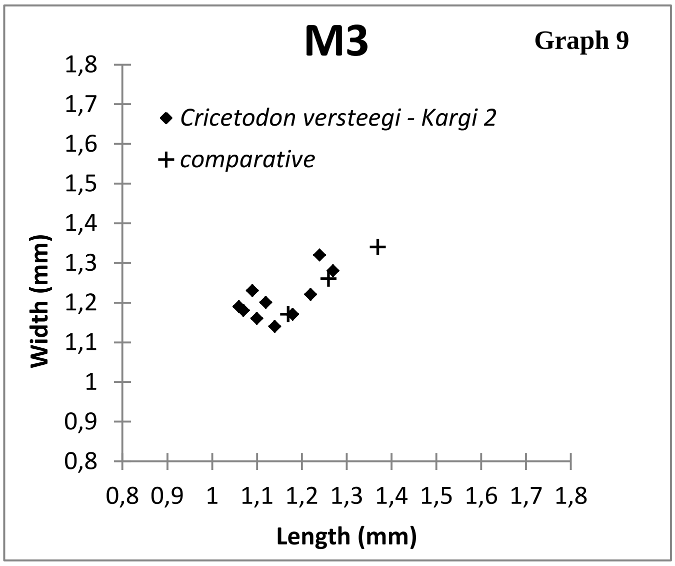
Table 7. The measurements of the Kargı 1 material of *Spanocricetodon sinuosus,* in mm.

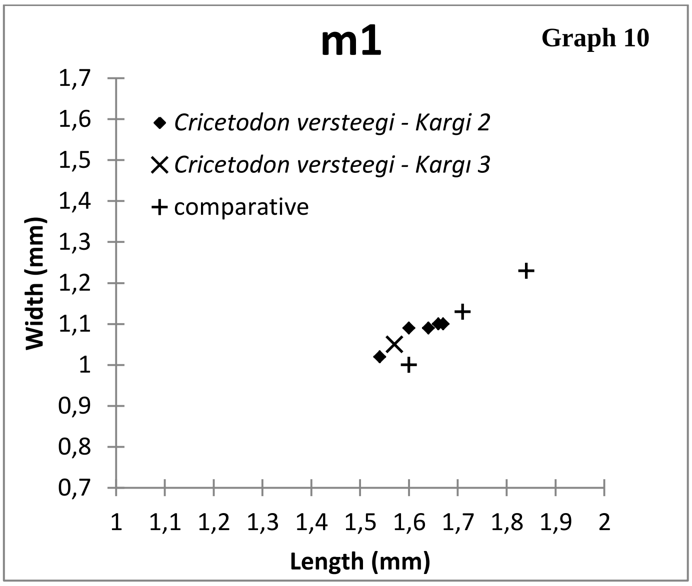
	mean			**N**	**SE**		**SD**		**Range**			
	L	**W1**	**L/W1**		**L**	**W1**	**L**	**W1**	**L min**	**L max**	**W1 min**	**W1 max**
m1	1,14	0,79	1,45	2	0,015	0,035	0,021	0,049	1,12	1,15	0,82	0,82
m2	1,04	0,92	1,13	3	0,020	0,032	0,035	0,055	1,01	1,08	0,96	0,96
m3	0,89	0,71	1,24	3	0,007	0,009	0,012	0,015	0,88	0,90	0,73	0,73

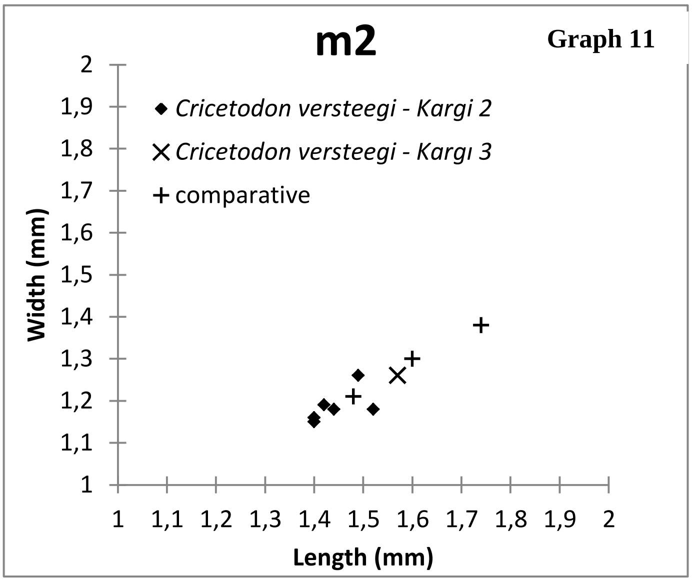
Graphs 7-12. *Cricetodon versteegi*, Kargı 2, M1-M3, m1-m3. The measurements of the comparative material are the minimum, maximum and mean measurements of the type locality Kilçak 3a according to de Bruijn *et al*. (1993), therefore they are not taken with the same method as the material studied in the current paper.

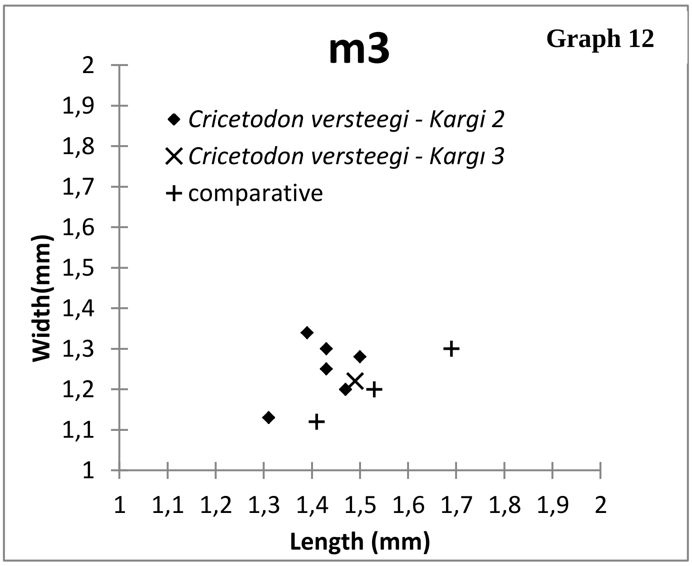




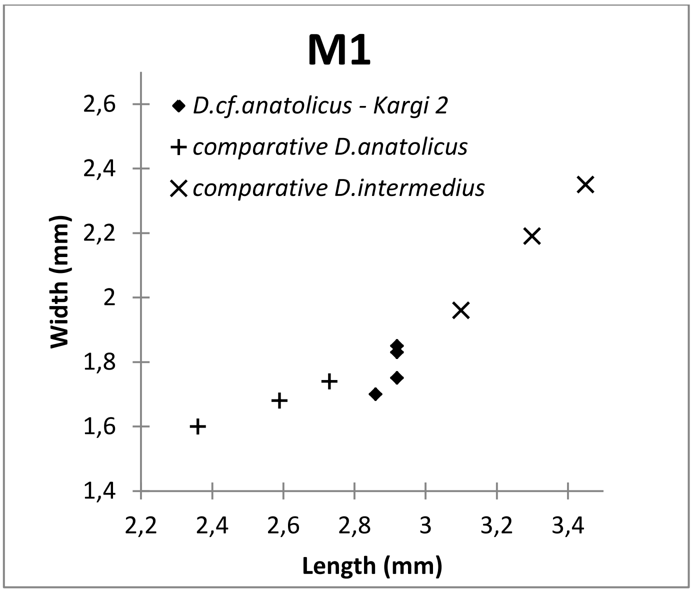




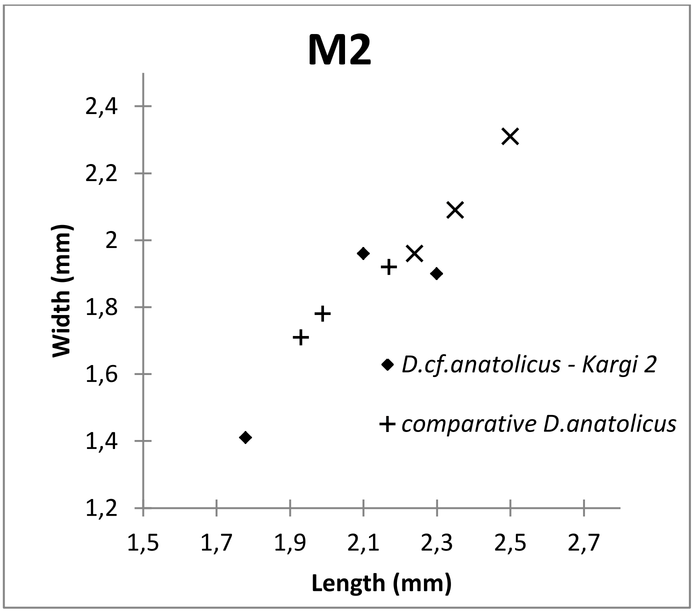




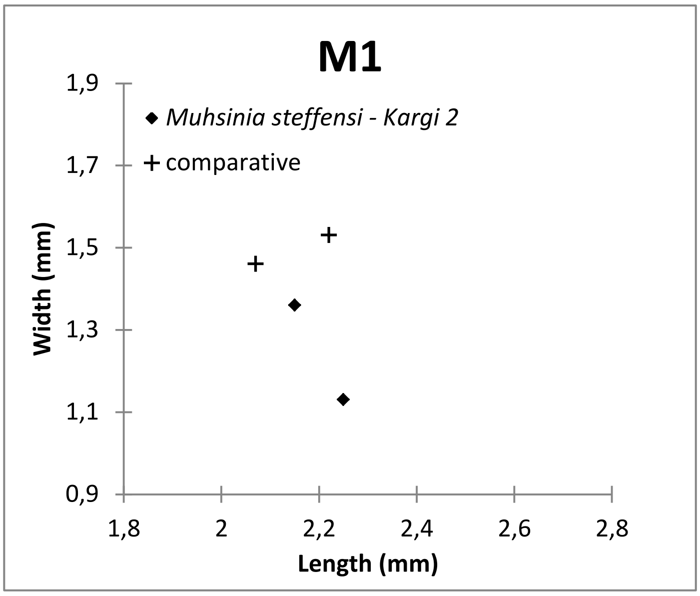
Graph 13. *Deperetomys* aff. *anatolicus*, Kargı 2, M1. The measurements of the comparative material are the minimum, maximum and mean measurements of *Deperetomys anatolicus* of the type locality Kilçak 0'' and the minimum, maximum and mean measurements of *Deperetomys intermedius* of the type locality Harami 1 according to de Bruijn *et al*. (1993), therefore they are not taken with the same method as the material studied in the current paper.



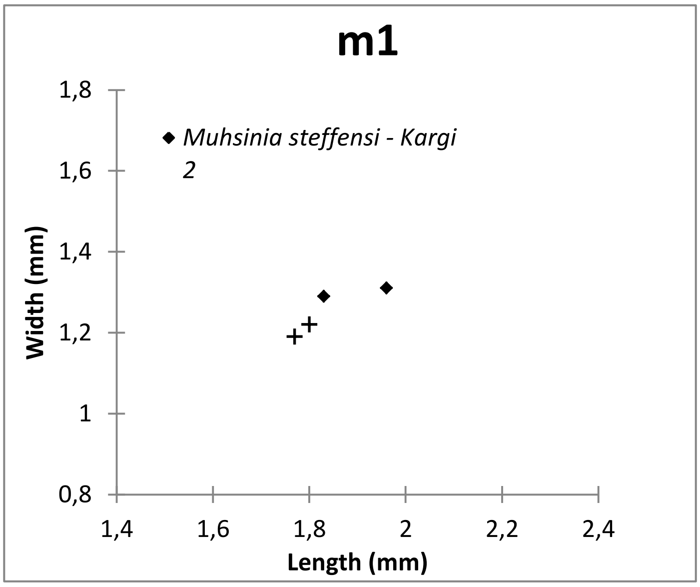
Graph 14. *Deperetomys* aff. *anatolicus*, Kargı 2, M2. Measurements of the comparative material as in Graph 13.



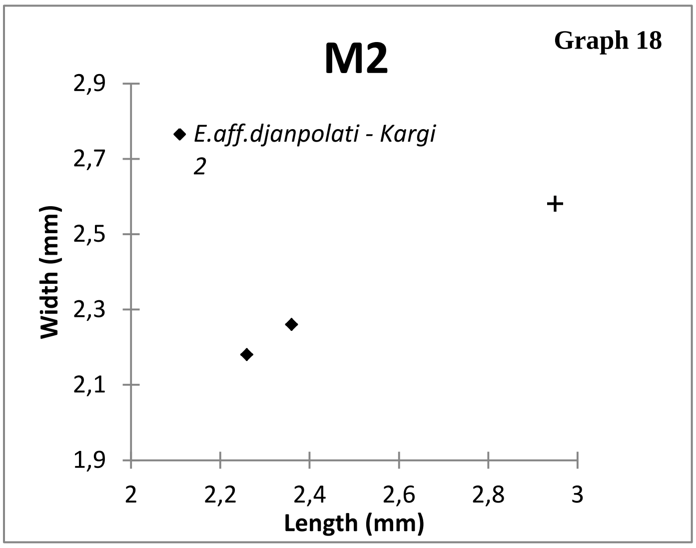
Graph 15. *Muhsinia steffensi*, Kargı 2, M1. The measurements of the comparative material are from the type locality Inkonak M.R.6, and were measured by the present author.

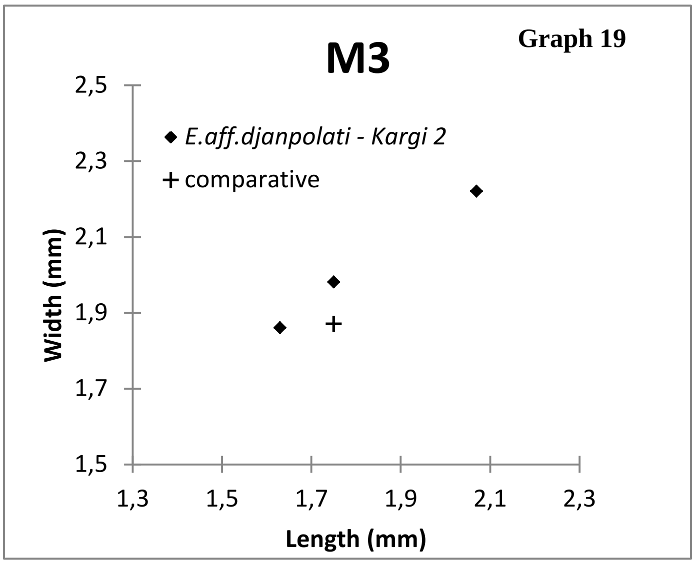


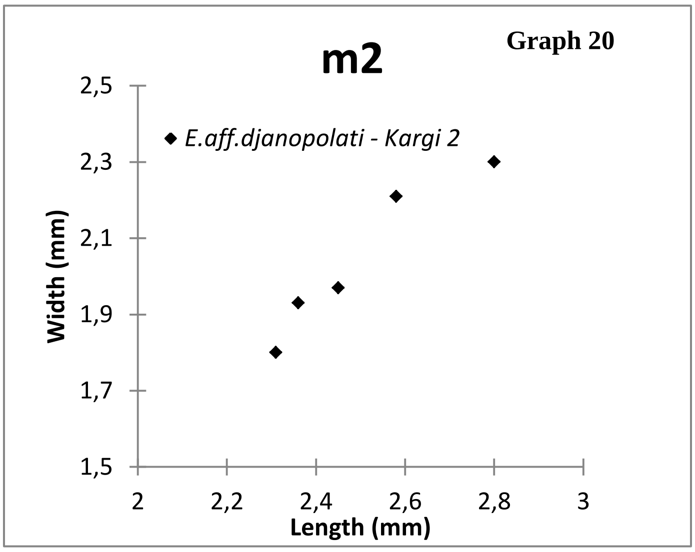
Graph 16. *Muhsinia steffensi*, Kargı 2, m1. Measurements of the comparative material as in Graph 21.



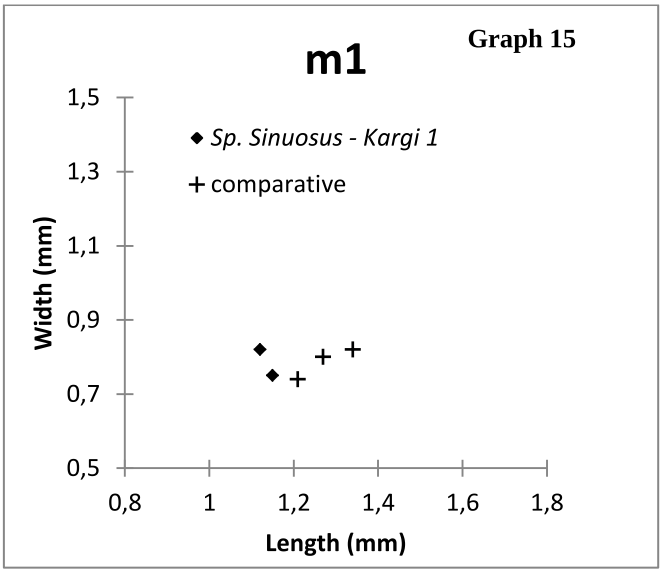
Graphs 17,18,19. *Enginia* aff. *djanopolati*, Kargı 2, M2-M3, m2. The measurements of the comparative material are the minimum, maximum and mean measurements of the type locality Keseköy for M2 and the relative measurements for *Enginia* aff. *djanpolati* of Kargı 2 for M3 according to de Bruijn *et al*. (1994), therefore they are not taken with the same method as the material studied in the current paper. There are no comparative measurements for m2.

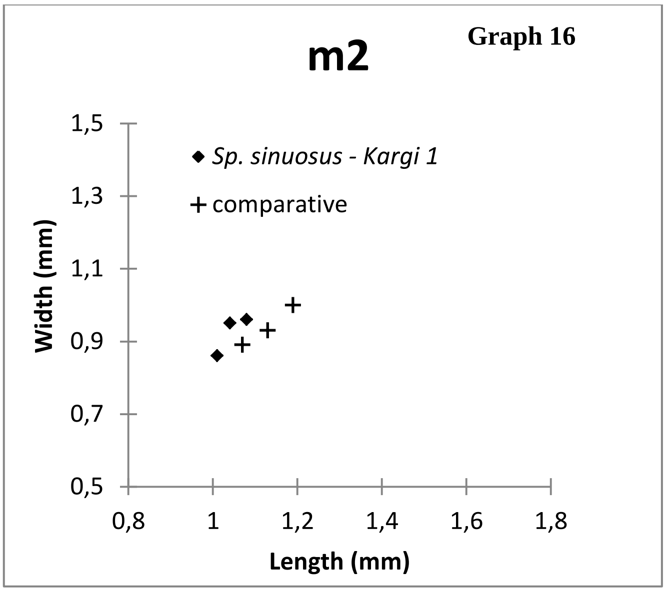






Graphs 20, 21, 22. *Spanocricetodon sinuosus*, Kargı 1, m1-m3. The measurements of the comparative material are the minimum, maximum and mean measurements of the type locality Kilçak 3a according to Theocharopoulos (2000), therefore they are not taken with the same method as the material studied in the current paper.





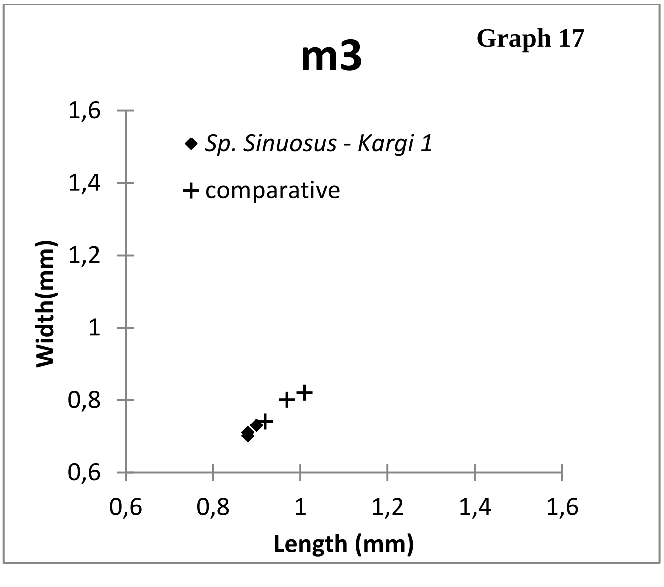


Table 8. List of the studied Kargı species, and other Anatolian fauna from literature. The grey highlighted cells indicate the presence of a species. The striped area means that there is no *D.anatolicus* but there is *D.intermedius*.

	Inkonak	Kargı 1	Kargı 2	Kilçak 0''	Kargı 3	Kilçak 3a	Kilçak 3b	Harami	Keseköy
Age (Ma)	26-22,41		23,03					22,1	20,71-18,75
MN zone correlation	MP30			MN1				MN2	MN3
	<u>Oligocene</u>			<u>Miocene</u>					
Meteamys alpani	■	■	■						
Cricetodon versteegi			■	■	■	■			
Cricetodon sp.	■	■	■	■			■	■	
Deperetomys anatolicus				■	■	■	■	■	
D. aff. *anatolicus*			■	■				▤	
Eumyarion microps			■					■	
Muhsinia steffensi	■		■						
Spanocricetodon sinuosus		■	■	■					
Enginia djanpolati					■				■
E. aff. *djanpolati*			■						
Melissiodon sp.			■						
Heterosminthus cf. *firmus*			■						

4. Discussion and conclusions

In **Table 8**, we have summed all the examined species from Kargı 1, 2 and 3; the age assignment of Inkonak, Harami and Keseköy is according to the magnetostratigraphic studies by Krijgsman *et al.* (1996). When comparing the Kargı assemblages with others from Anatolia, we can define their relative biostratigraphic position. Kargı 1 is the locality level closer to Inkonak in spite of the fact that *Muhsinia steffensi* is absent from Kargı 1, but present in Kargı 2. This might be due to the fact that *Muhsinia steffensi* had not migrated to Inkonak until the deposition of Kargı 2, where it is also of bigger size than Inkonak.

The richest fauna on genus level is found in Kargı 2, that hosts all the genera found in Kargı; it is clear that a faunal change takes place during this level. Kargı 2 also shares species with the late Oligocene localities of Inkonak and Kargı 1. Therefore, it is most possible that this level was deposited during the Oligocene/Miocene transition, hosting the last record of the Late Oligocene species *Meteamys alpani* and *Muhsinia steffensi*, as well as the first record of all the newly entered Early Miocene species. Also, we notice that some species (*Melissiodon* sp., *Heterosminthus* cf. *firmus*) are only found in Kargı 2 during the Early Miocene of Anatolia. This is rather unexpected since the Early Miocene environmental conditions were quite similar among the localities and would favour the survival of these species. However, it is not rare that a newly entered species, which has migrated from somewhere else, does not make it to establish its presence and finally disappears from the new locality.

Kargı 3 not only has the fewest species from all the Kargı levels, but there is a great decrease in the quantity of the rodent material. A great increase is noted in the percentage of the insectivores and a relative significant decrease in the rodents' percentage in the total small mammal fauna (van den Hoek Ostende, 2001b). This clearly indicates an environmental change.

Previous studies place all Kargı levels together below Kilçak. However, it is quite clear from **Table 8** that the rodent fauna of Kargı 2 and Kilçak 0'' are much closer to each other than Kargı 2 and Kargı 3. Therefore, it is logical to assume a relative biostratigraphic position of

Kilçak 0'' between Kargı 2 and Kargı 3, or even an age overlap between the younger part of Kargı 2 and the oldest part of Kilçak 0''. Also, Kargı 3 seems much closer to the younger locality of Kilçak 3a. It is essential to point out that all the Kargı and all the Kilçak are chronically close, and, without any proper magnetostratigraphic data available, it is very easy to misinterpret their relative positions.

There is also another faunal turnover, of a smaller extend than Kargı 2, between Harami and Keseköy. After the MN2/MN3 transition, we detect a disappearance of all the Early Miocene Anatolian species; *Enginia* is the only common rodent genus between Keseköy and all the other Early Miocene Anatolian localities. This can be justified by a significant geological change of the time, as it will be discussed subsequently.

Additionally, a size increase is detected from older to younger levels; the most abundant species, *Meteamys alpani* and *Cricetodon versteegi*, increase in size. This is indicative of environmental and/or ecological change, and will be discussed subsequently.

As far as other areas outside Anatolia are concerned, there are very few similarities among the localities. *Heterosminthus* cf. *firmus* is the only of the studied species from Kargı that can be found elsewhere in Asia than Anatolia, more specifically at the Oligocene/Miocene transition of Kazakhstan. Also, *Melissiodon*, *Eumyarion, Deperetomys* and *Cricetodon* are genera which are known from the Miocene of Europe and from younger Anatolian localities, represented by different species than in the Early Miocene of Anatolia.

Since there is a large number of data for the rodent content of various Anatolian assemblages, we can also conclude to the migration patterns. All studied species are very unlikely to be the descendants of older Anatolian species; therefore there is a visible turnover of the fauna near the Oligocene/Miocene transition (see Kargı 2 in **Table 8**). It has been stated assumed that these newly entered species arrived there from the Iranian block (Popov *et al.* 2004; Wessels 2009; **Fig. 5**). After Harami there is also a (smaller) faunal turnover. *Melissiodon*, *Eumyarion, Deperetomys* and *Cricetodon* must have migrated from Harami and Keseköy to Europe where other species of these genera evolved.

According to Akgün *et al.* (2007), the climate was warm (16,5-21°C in some Central Anatolian basins like Sivas basin and Çankiri basin) during the Early Miocene of Turkey, as indicated by their palynological studies and the presence of reefal limestones (Görür *et al*., 1998). They pointed out vegetational shifts during the Oligocene/Miocene transition (MP30/MN1) and the Early Miocene, as well as an uplift of Turkey towards the end of MN2. The vegetation of central and western Anatolia during the Oligocene/Miocene was consisted of mesophytic and near-shore forests, while it became more terrestrial due to the elevation that occurred in the MN2. Therefore, the faunal change at Keseköy can be explained by this geological change, since the humidity-preferring Early Miocene species could not thrive in these new more terrestrial conditions. So, the paleogeographical data agree with the interpreted rodent turnovers that occurred during the MP30/MN1 transition (Kargı 2) and the end of MN2 (Harami).

We can now derive final conclusions on the paleoecology of our three Kargı levels. First, the diatomites of the Kargı mine show a flourishing of diatoms and therefore of an aquatic depositional environment, which can be further specified to a lacustrine environment due to the deposition of lignites. Therefore, the studied rodents of Kargı were living in a near-lacustrine environment. *Melissiodon* and *Eumyarion* indicate wet environment (according to studies by Daams *et al*., 1998, on Spanish rodent faunas), as well. The absence of any organisms that prefer dry environment also enhances the conclusion of wet, near-shore conditions at Kargı. The increase of insectivores after the MP30/MN1 transition, according to van den Hoek Ostende (2001b) also supports the increase in humidity and warmth as suggested by the rodents and the pollen, with a further increase during the deposition of Kargı 3. The small rodent turnover between the Harami and Keseköy assemblages also agrees with a turnover in rodents, which points to somewhat drier conditions than the younger localities. This is quite expected from the paleo-geographical data of an increased elevation in Anatolia at that time. Furthermore, the absence of large animals indicates possibly the lack of proper conditions for their burial, as is a near-shore environment that favours the burial of smaller mammals.

The taxonomy of the studied genera is still very controversial, and needs to be thoroughly studied in its entity, from the species (all the aff. and cf. assigned material of this research) to the family level. The studied species from Kargı are frequent in the Early Anatolian faunas and also some of them are characteristic of their biostratigraphic levels, so a cohesive reliable taxonomy is essential. Finally, more a new complete rodent biozonation of the Early Miocene of Anatolia should be carried out in order to include the official and complete species identification of Kargı. An integrated and complete biostratigraphy is significant, because it adds to a more accurate age estimation of Kargı and Kilçak, localities that cannot be dated according the correlation with the polarity time scale.

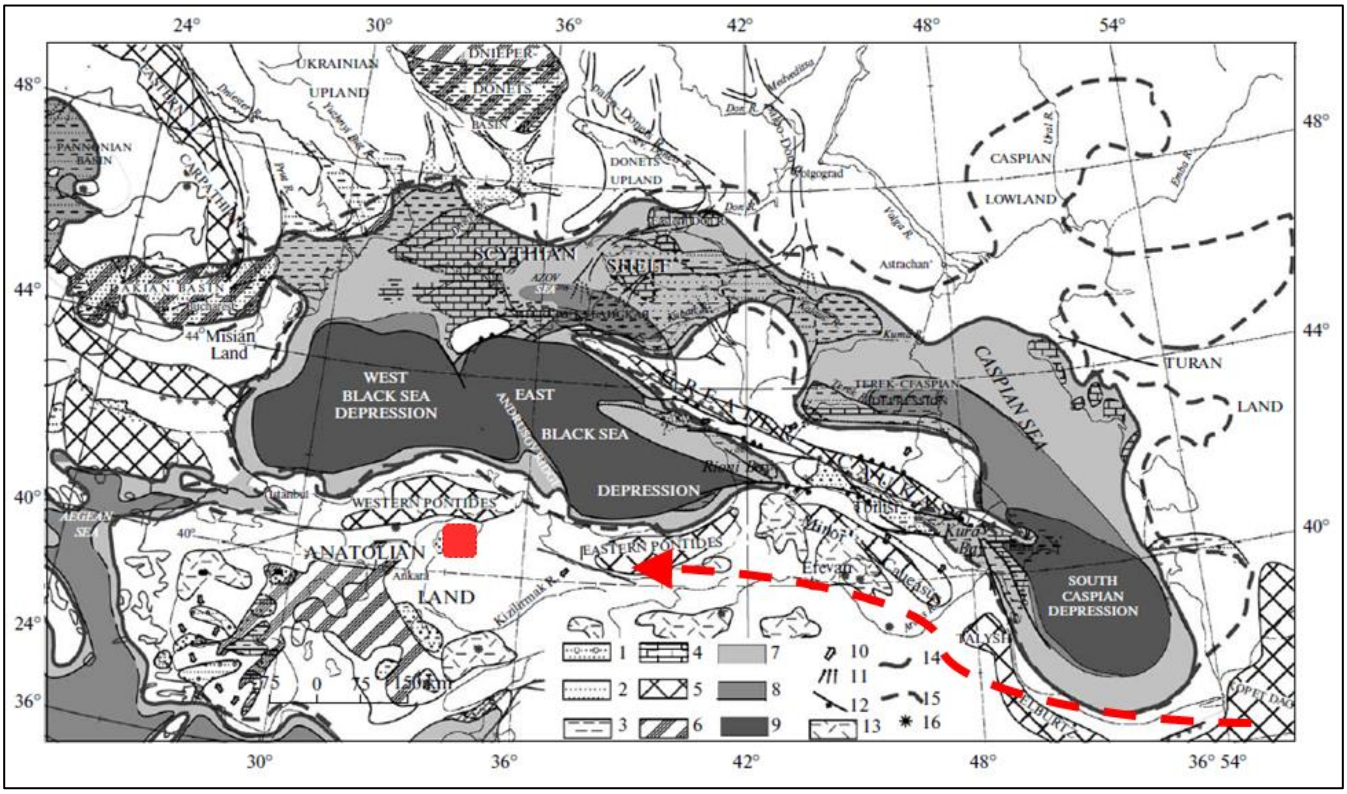


Fig. 5. Migration pathway of rodents during the Oligocene/Miocene transition towards Anatolia. The square indicates the area of Kargı, and the dotted line indicates the migration pathway through the Elbours-Koppedagh corridor. Map of Paratethys modified after Popov *et al.*, 2004.

5. Acknowledgements

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8. Appendix

Plates

Plate 1. Incisor specimens from Kargı 1

Fig. 1 – *Meteamys alpani* upper incisor, distal view
Fig. 2 – *Meteamys alpani* upper incisor, mesial view
Fig. 3 – *Meteamys alpani* upper incisor, labial view
Fig. 4 – *Meteamys alpani* upper incisor, lingual view
Fig. 5 – *Meteamys alpani* lower incisor, distal view
Fig. 6 – *Meteamys alpani* lower incisor, labial view
Fig. 7 – lower incisor incertae sedis, lingual view

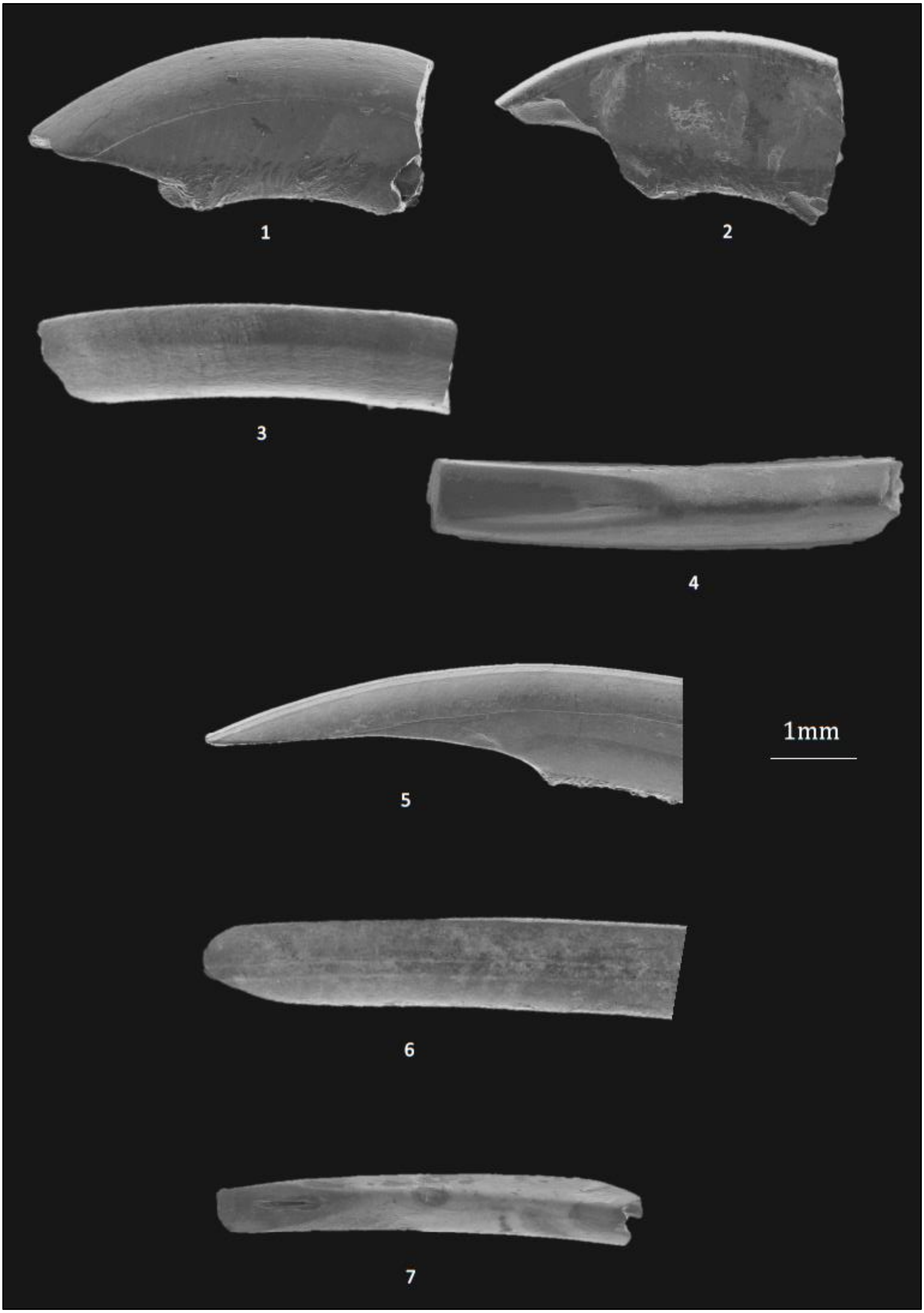

1
2
3
4
1mm
5
6
7

Plate 2. *Meteamys alpani* molar specimens from Kargı 1

Fig. 1, 4a - M1, occlusal view
Fig. 2, 4b - M2, occlusal view
Fig. 3, 5 – M3, occlusal view
Fig. 6, 9 – m1, occlusal view
Fig. 7, 10 – m2, occlusal view
Fig. 8 – m1, occlusal view

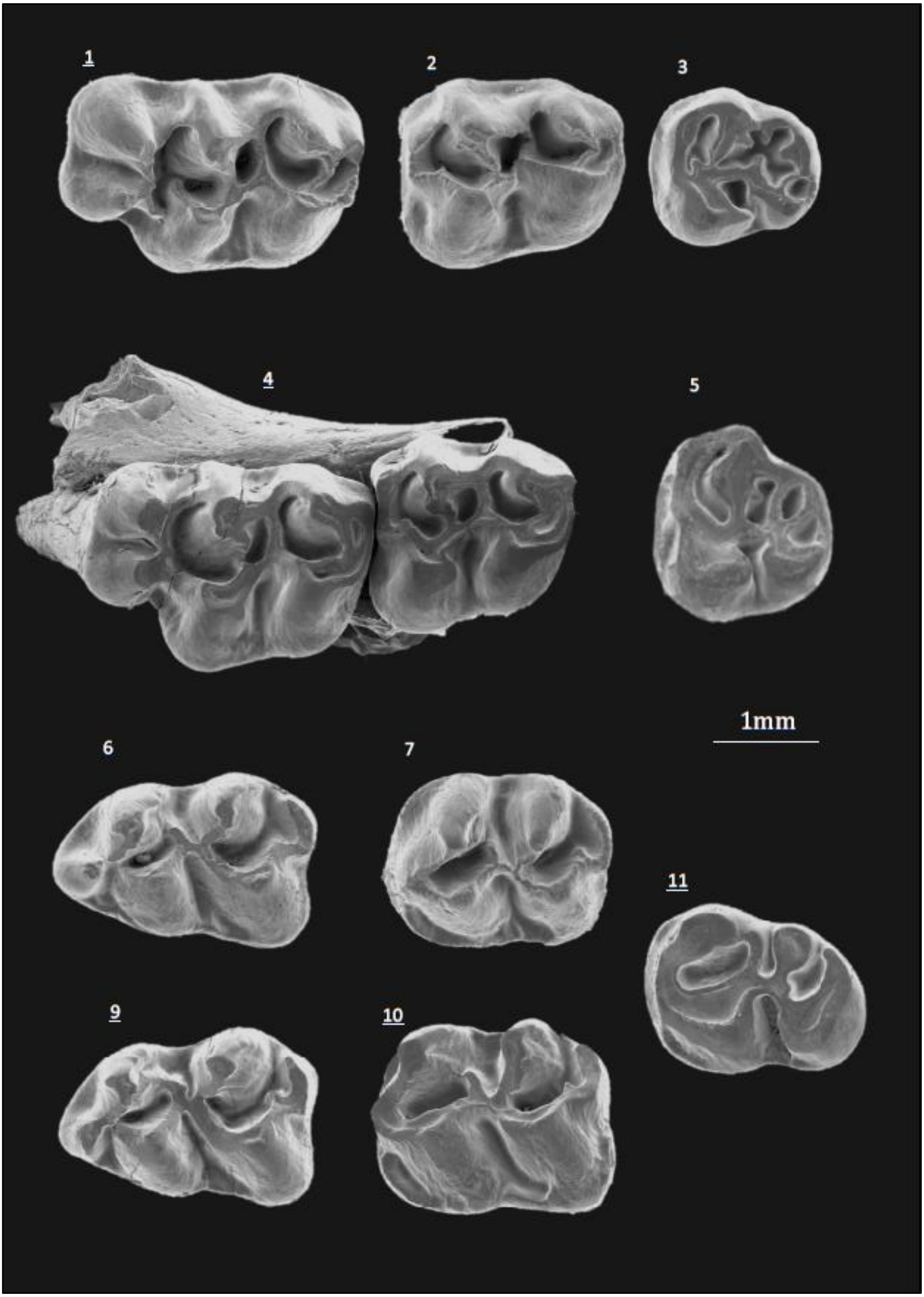
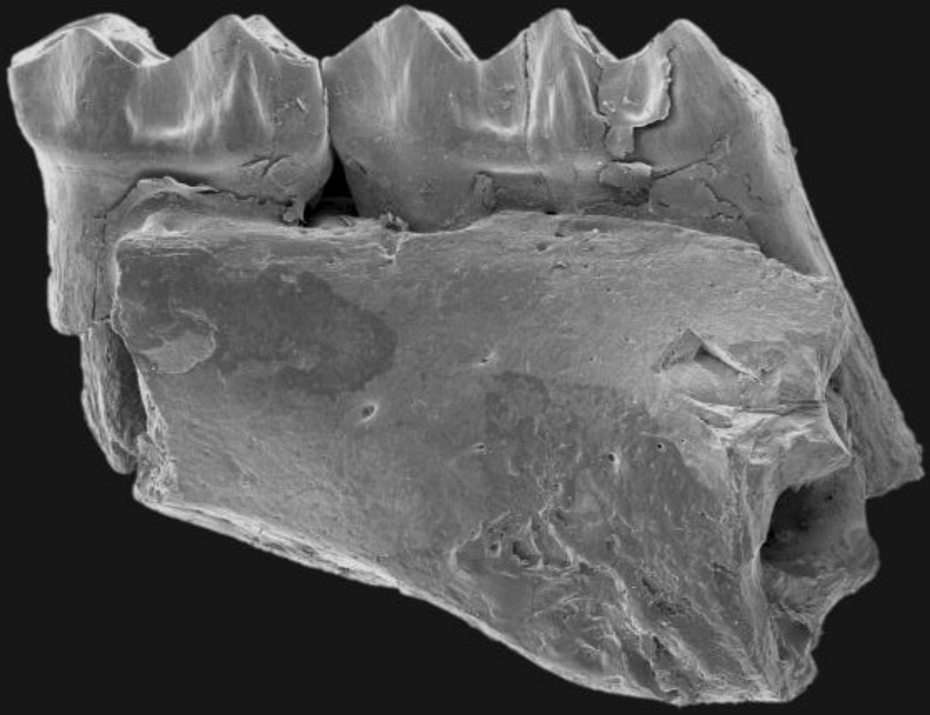

1
2
3
4
5
1mm
6
7
11
9
10

Plate 3. *Meteamys alpani* M1 and M2 on mandible, from Kargı 1

Fig. 1 - M1 and M2 on mandible, lingual view
Fig. 2 - M1 and M2 on mandible, labial view

1



2

Plate 4. *Meteamys alpani* molar specimens from Kargı 2

Fig. 1, 4 - M1, occlusal view
Fig. 2, 5 - M2, occlusal view
Fig. 3, 6 – M3, occlusal view
Fig. 7, 10 – m1, occlusal view
Fig. 8, 10 – m2, occlusal view
Fig. 9, 11 – m1, occlusal view

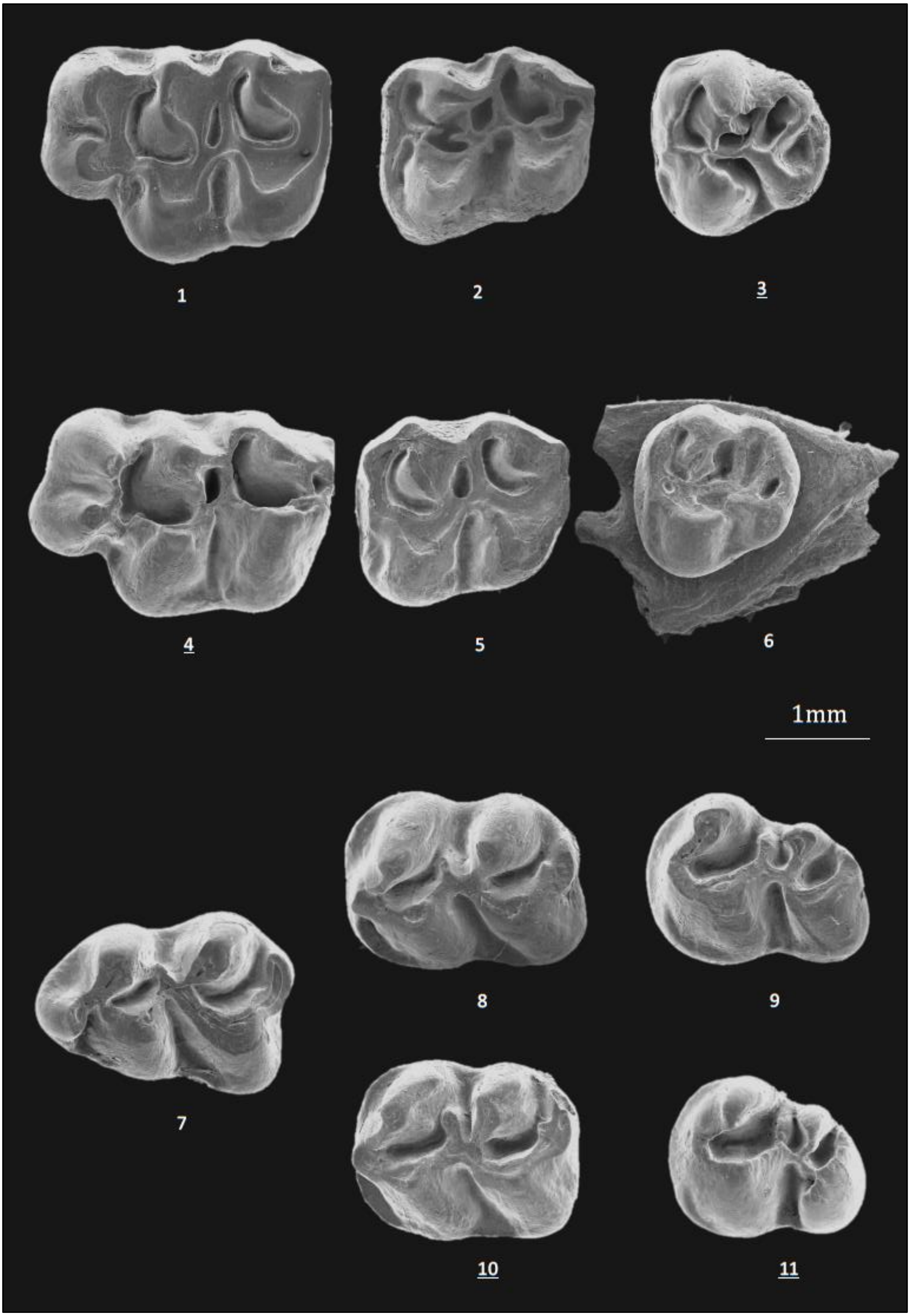

1
2
3
4
5
6
1mm
7
8
9
10
11

Plate 5. *Cricetodon versteegi* molar specimens

from Kargı 2
Fig. 1, 4 - M1, occlusal view
Fig. 2 - M2, occlusal view
Fig. 3, 5 – M3, occlusal view
Fig. 6, 9 – m1, occlusal view
Fig. 7, 10 – m2, occlusal view
Fig. 8, 11 – m1, occlusal view
from Kargı 3
Fig. 12 – M1, occlusal view
Fig. 13 – M2, occlusal view
Fig. 14 – m1, occlusal view
Fig. 15 – m3, occlusal view

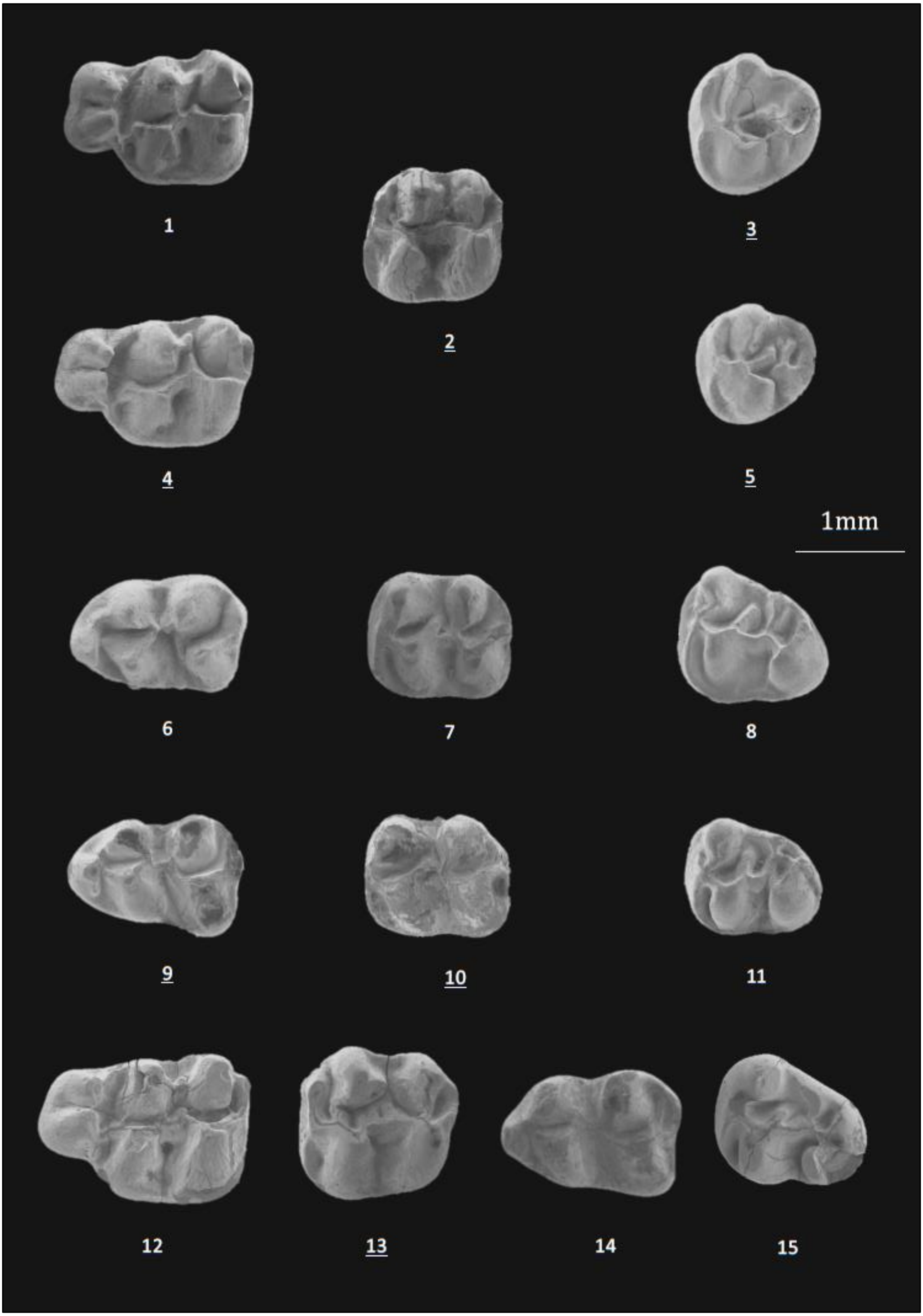

1
2
3
4
5
1mm
6
7
8
9
10
11
12
13
14
15

Plate 6. Other Cricetodontinae molar specimens

-*Deperetomys anatolicus* from Kargı 2
Fig. 1 – M1, occlusal view
Fig. 2 – M3, occlusal view

-*Deperetomys* aff. *anatolicus* from Kargı 2
Fig. 3 – M1, occlusal view
Fig. 4 – M2, occlusal view

-*Muhsunia steffensi* from Kargı 2
Fig. 5 – M2, occlusal view
Fig. 6 – m1, occlusal view

-*Eumyarion microps* from Kargı 2
Fig. 7 – m1, occlusal view
Fig. 8 – m3, occlusal view

-*Cricetodon* sp. from Kargı 2
Fig. 9 – m1, occlusal view

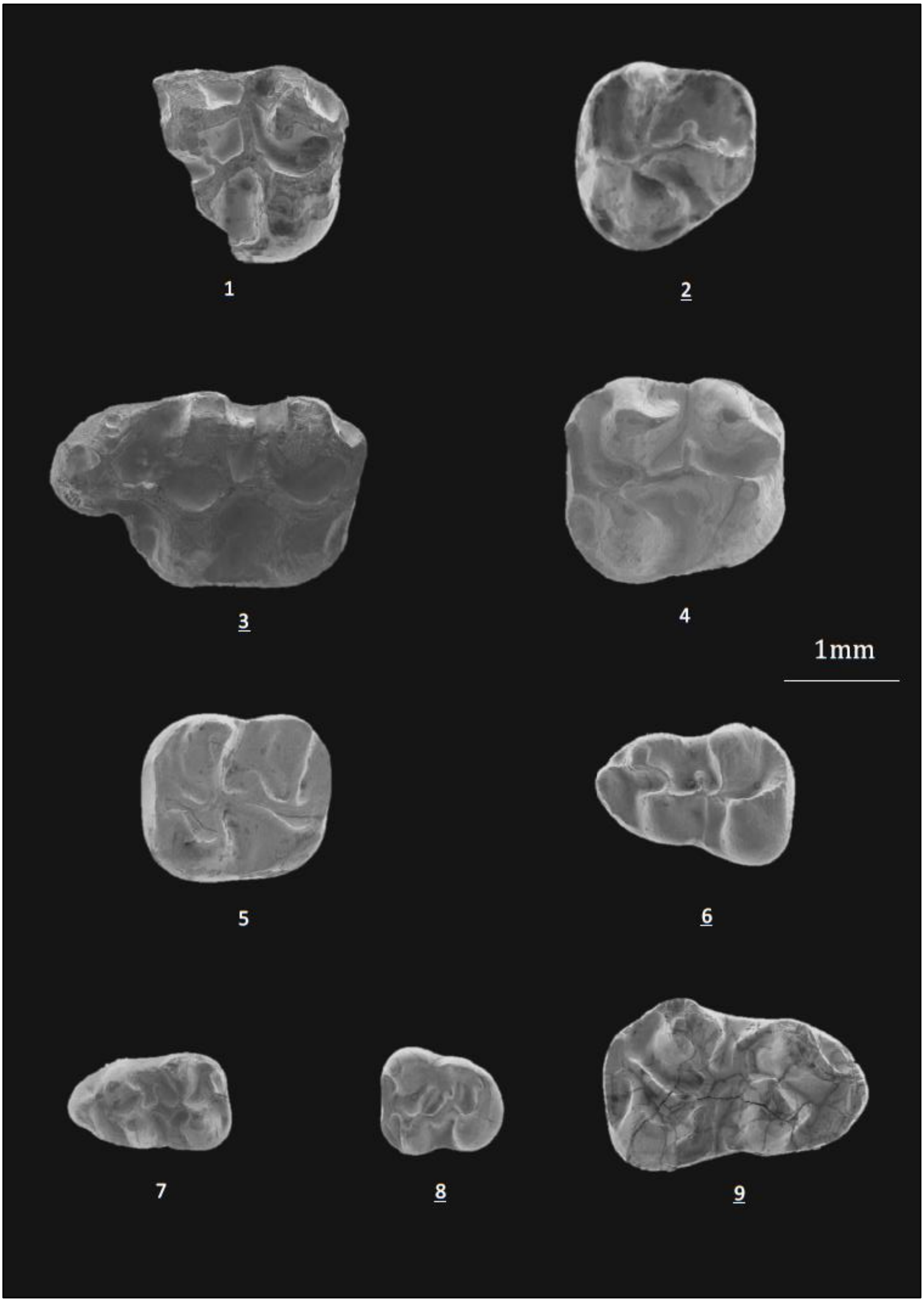

1
2
3
4
1mm
5
6
7
8
9

Plate 7. Other molar specimens

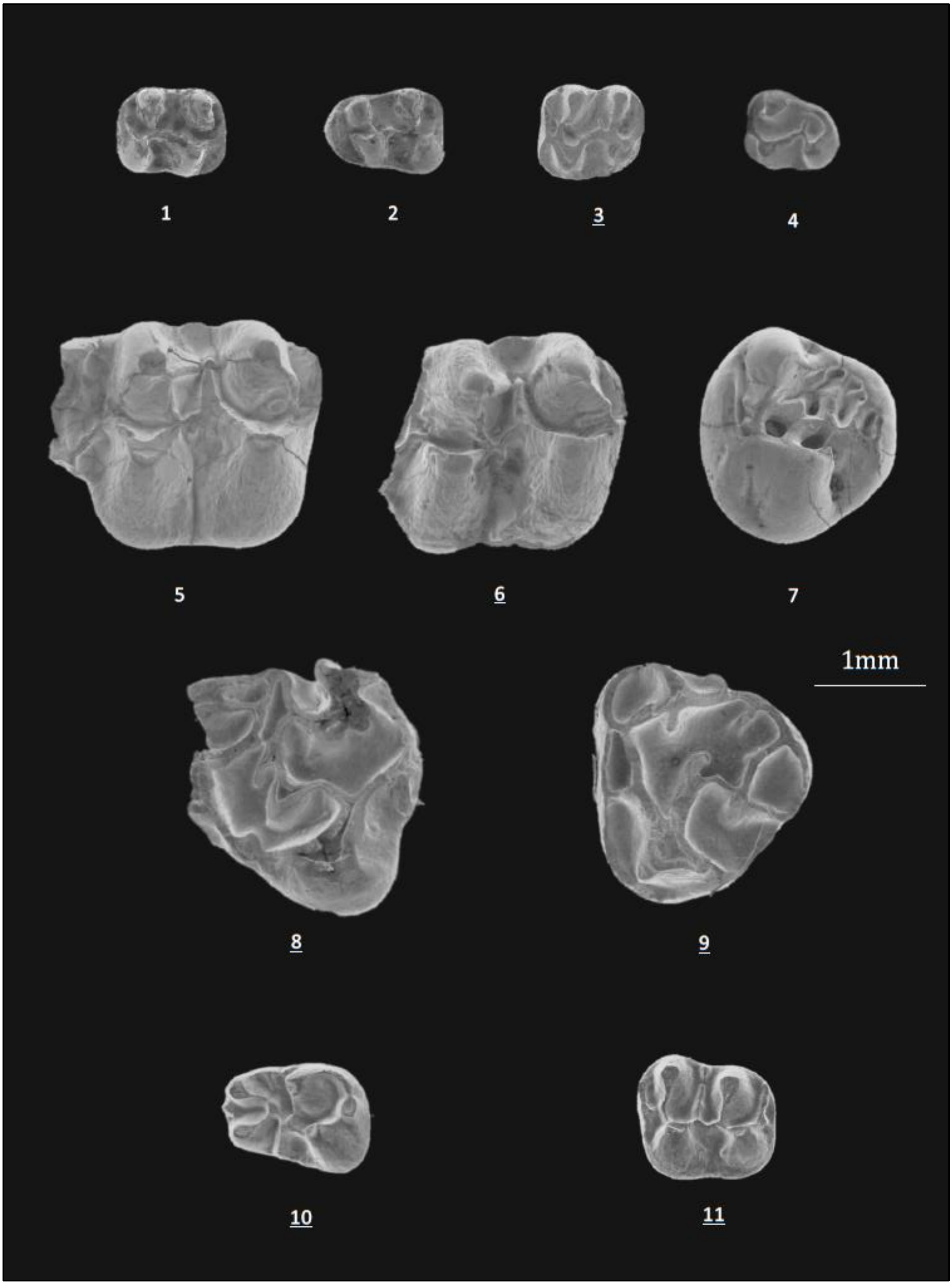
Spanocricetodon sinuosus from Kargı 1
Fig. 1 – M2, occlusal view
Fig. 2 – m1, occlusal view
Fig. 3 – m2, occlusal view
Fig. 4 – m3, occlusal view

-*Enginia* aff. *djanpolati* from Kargı 3
Fig. 5, 6 – M1, occlusal view

-*Enginia* aff. *djanpolati* from Kargı 2
Fig. 7 – M3, occlusal view

-*Melissiodon sp.* from Kargı 2
Fig. 8 – m1, occlusal view
Fig. 9 – m3, occlusal view

-*Heterosminthus* cf. *firmus* from Kargı 2
Fig. 10 – m1, occlusal view
Fig. 11 – m2, occlusal view


1
2
3
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7
1mm
8
9
10
11

Character tables

M1		***Meteamys alpani***		***Cricetodon versteegi***		***Deperetomys anatolicus***	***Deperetomys aff. anatolicus***	***Eumyarion microps***	***Enginia aff. djanpolati***		***Muhsinia steffensi***	***Meteamys alpani* comparative**	***Muhsinia steffensi* comparative**
		Kargı 1 (10)	Kargı 2 (12)	Kargı 2 (6)	Kargı 3 (2)	Kargı 3 (1)	Kargı 2 (4)	Kargı 2 (2)	Kargı 2 (1)	Kargı 3 (2)	Kargı 2 (2)	Inkonak (2)	Inkonak (2)
Anterocone complex	wide	9	12	6	2	-	4	1	0	0	0	2	0
	narrow	1	0	0	0	-	0	1	1	2	2	0	2
Anterocone cusps	equal	6	7	6	2	-	2	1	1	2	1	1	1
	labial more prominent	4	5	0	0	-	0	0	0	0	0	1	0
	lingual more prominent	0	0	0	0	-	0	0	0	0	0	0	0
Low ridge closes anterior anterocone	yes	2	0	2	0	-	0	0	0	0	0	2	0
	no	8	12	4	1	-	4	2	1	2	2	0	2
Anterolophule	present	7	8	6	1	-	4	0	1	2	2	2	2
	absent	3	4	0	0	-	0	2	0	0	0	0	0
Anterocone labial cusp	reaches paracone base	10	12	5	1	-	4	2	1	1	2	2	2
	does not reach	0	0	1	1	-	0	0	0	0	0	0	0
Anterocone-protocone connection	via anterocone lingual cusp	4	11	4	2	-	3	0	1	2	1	1	2
	via anterolophule	0	0	0	0	-	1	0	0	0	0	0	0
	via transverse ridge of anterocone	3	1	0	0	-	0	0	0	0	0	0	0
	interrupted	3	0	2	0	-	0	2	0	0	1	1	0
Protocone anterior arm	transverse	0	0	0	0	-	0	2	0	0	0	0	0
	anteriorly directed	10	12	6	2	-	4	0	0	0	0	1	0
	posteriorly directed	0	0	0	0		0	0	1	2	0	0	0
	reaches paracone	0	0	0	0	-	0	1	0	0	0	0	0
	does not reach	0	0	0	2	-	0	1	1	2	2	0	2
Protolophule I	absent	10	11	6	1	-	1	2	0	0	0	2	2
	present	0	1	0	1	-	3	0	1	2	2	0	0
	...anteriorly directed	0	1	0	0	-	0	0	0	0	1	0	0
	...posteriorly directed	0	0	0	1	-	3	0	1	2	1	0	0
	connects paracone to anterior protocone	0	0	0	1	0	0	0	0	0	1	0	0
	connects paracone to posterior protocone	0	0	0	0	-	0	0	1	2	0	0	0
Protolophule II	reaches to mure	10	12	5	2	1	4	1	0	0	2	2	2
	does not reach	0	0	1	0	0	0	1	1	2	0	0	0
Metalophule II	absent	3	0	0	0	0	0	0	0	0	2	0	0
	present	7	12	6	1	1	4	2	1	2	0	2	2
	complete	7	12	4	1	1	4	2	1	2	0	2	0
	long but incomplete	0	0	2	0	0	0	0	0	0	0	0	0
	short	9	11	0	1	0	0	0	1	0	0	0	2
Metalophule II merged to posteroloph	yes	0	2	0	0	1	4	0	0	0	0	0	0
	almost	0	4	0	0	0	0	0	0	0	0	1	0
	no	10	6	6	2	1	4	2	1	2	2	1	2
Mesoloph	complete	9	11	0	0	0	0	1	0	0	0	2	0
	incomplete	1	1	6	2	1	4	1	1	2	2	0	2
	...short	0	0	2	2	0	0	0	0	0	1	0	0
	...medium length	0	0	0	0	0	4	1	1	2	1	0	1
	...long	0	1	4	0	1	0	0	0	0	0	0	1
Paracone posterior spur	blunt	10	12	6	1	1	4	2	1	2	0	2	2
	burgee-shaped	10	12	6	1	1	4	2	1	2	0	1	1
	weak	0	0	0	1	0	0	0	0	0	2	0	1
	connects to mesoloph	10	12	0	0	1	1	0	0	0	0	2	0
	does not connect	0	0	0	2	0	3	2	1	2	0	0	0

M1		***Meteamys alpani***		***Cricetodon versteegi***		***Deperetomys anatolicus***	***Deperetomys* aff. *anatolicus***	***Eumyarion microps***	***Enginia* aff. *djanpolati***		***Muhsinia steffensi***	***Meteamys alpani* comparative**	***Muhsinia steffensi* comparative**
		Kargı 1 (10)	Kargı 2 (12)	Kargı 2 (6)	Kargı 3 (2)	Kargı 3 (1)	Kargı 2 (4)	Kargı 2 (2)	Kargı 2 (1)	Kargı 3 (2)	Kargı 2 (2)	Inkonak (2)	Inkonak (2)
Labial paracone curvature	present	10	12	0	0	0	0	0	0	0	0	2	0
	absent	0	0	6	2	1	4	2	1	2	2	0	2
Labial metacone curvature	present	10	12	6	0	0	0	0	0	0	0	2	0
	...very weak	3	0	0	0	0	0	0	0	0	0	0	0
	absent	0	0	0	2	1	4	2	1	2	2	0	2
Inner lingual curvature	only at hypocone	0	0	0	0	0	0	0	0	0	0	0	0
	at both	7	7	0	0	0	0	0	0	0	0	2	0
	at neither	0	1	6	2	1	4	0	1	2	2	0	1
Posteroloph reaches metacone labially	yes	10	12	6	2	1	4	0	0	0	0	2	0
	no	0	0	0	0	0	0	2	1	2	2	0	2
Hypoconule	prominent	0	2	0	0	0	0	0	0	0	0	1	0
	very small	5	0	0	1	0	0	0	0	0	0	0	0
	no	5	10	6	1	1	4	2	1	2	2	1	2
Mesostyl	more prominent	5	8	0	1	0	0	2	0	0	0	1	2
	less prominent	4	3	0	1	0	2	0	0	0	2	1	0
	absent	1	1	6	0	1	2	0	1	2	0	0	0
"Protostyl"	present	2	6	2	0	0	4	0	1	2	0	2	1
	...very small	1	3	0	0	0	0	0	0	0	0	1	1
	absent	8	6	4	2	1	0	2	0	0	2	0	1
Protosinus	yes	10	12	6	1	-	4	2	1	2	0	1	2
	...wide, bearing a small ridge	0	0	4	0	-	0	0	0	0	0	1	1
	...wide, bearing a protostyl	0	0	2	0	-	4	0	1	2	0	1	1
	...small	1	0	0	0	-	0	2	1	2	0	0	2
	...very small	2	0	0	0	-	0	0	0	0	0	0	0
	absent	0	0	0	0	-	0	0	0	0	2	0	0
Sinus (lingual)	bordered by entostyl	4	6	6	0	1	4	1	0	0	2	2	2
	...and cingulum	3	3	0	0	1	4	0	0	0	0	2	2
	bordered only by	4	5	0	2	0	0	0	1	1	0	0	0
	not bordered	2	2	0	0	0	0	1	0	1	0	0	0
Antero-labial valley	prominent	6	12	0	1	-	0	0	0	0	0	2	0
	small	3	0	6	0	-	0	0	0	0	0	0	0
	very small	0	0	0	0	-	0	0	0	0	1	0	0
	absent	1	0	0	0	-	4	2	1	2	1	0	2
Meso-labial valley	prominent	2	9	6	2	1	4	2	1	2	2	0	2
	small	6	3	0	0	0	0	0	0	0	0	1	0
	very small	1	0	0	0	0	0	0	0	0	0	1	0
	absent	1	0	0	0	0	0	0	0	0	0	0	0
Postero-labial valley	prominent	0	0	0	0	0	0	0	0	0	0	1	0
	small	0	1	0	0	0	0	0	0	0	0	0	0
	very small	1	1	0	0	0	0	0	0	0	0	1	0
	absent	9	10	0	2	1	4	2	1	2	2	0	2
Valley postero-lingually of posteroloph	small	1	3	1	0	0	0	0	0	0	0	1	0
	absent	9	9	0	2	1	4	0	1	2	2	1	2

M2		***Meteamys alpani***		***Cricetodon versteegi***		***Cricetodon*** **sp.**	***Deperetomys*** **aff.** ***anatolicus***	***Spanocricetodon sinuosus***	***Enginia*** **aff.** ***djanpolati***	***Muhsinia steffensi***	***Meteamys alpani*** **comparative**	***Muhsinia steffensi*** **comparative**
		Kargı 1 (22)	Kargı 2 (20)	Kargı 2 (10)	Kargı 3 (3)	Kargı 2 (1)	Kargı 2 (3)	Kargı 2 (2)	Kargı 2 (2)	Kargı 2 (1)	Inkonak (2)	Inkonak (2)
Anteroloph	equal	0	0	8	2	0	0	0	0	0	0	1
	Lingual branch more prominent	3	1	0	0	0	3	2	2	1	0	1
	Labial branch more prominent	19	18	2	1	1	0	0	0	0	2	0
Anterior arm of protocone	reaches anterolophule	19	16	10	3	1	2	2	1	1	2	2
	reaches protolophule I	6	2	0	0	0	1	0	0	0	0	0
	absent	3	2	0	0	0	0	0	0	0	0	0
Protolophule II	posteriorly directed	22	19	0	0	1	3	2	2	1	2	2
	reaches to the mure behing protocone	22	19	0	0	1	3	2	2	1	2	2
	interrupted	0	1	2	0	0	0	0	0	0	0	0
	absent	0	0	8	0	0	0	0	0	0	0	0
Posterior paracone spur	blunt, burgee-shaped	22	20	10	3	0	1	1	2	1	2	1
	short	0	0	4	2	1	1	0	2	1	0	0
	long	22	20	6	0	0	2	1	0	0	2	0
	absent	0	0	0	2	0	0	1	0	0	0	1
Mesoloph	long	22	20	1	0	1	0	0	2	0	2	0
	medium length	0	0	2	0	0	3	0	0	1	0	0
	short	0	0	9	3	0	0	2	0	0	0	2
	complete	20	17	0	0	0	0	0	0	0	2	0
	incomplete, ends free	2	3	10	2	1	3	2	0	1	0	2
	reaches to metacone base	0	0	0	0	0	0	0	2	0	0	0
Anterior metacone spur	blunt	22	20	2	0	1	2	1	2	1	2	2
	short	0	0	10	0	0	1	1	0	1	0	1
	long	22	20	0	0	1	1	1	2	0	2	1
Metalophule II	weak	0	0	6	0	0	0	0	2	0	0	0
	more prominent	22	20	2	1	1	2	2	0	1	2	2
	connects to posteroloph	0	0	0	0	0	0	0	0	0	0	1
	connects to anterior hypocone arm	22	20	7	1	1	2	2	2	1	2	1
	absent	0	0	2	0	0	1	0	0	0	0	0
Posteroloph	equally prominent sides	8	6	7	0	0	2	0	0	0	0	2
	lingually less prominent	8	11	2	1	1	0	0	2	1	0	0
	lingually more prominent	6	1	1	0	0	1	2	0	0	2	0
Inner lingual curvature	only at protocone	9	6	9	0	0	2	0	1	0	0	2
	only at hypocone	0	0	0	0	0	0	0	0	0	0	0
	at both	6	14	1	0	0	1	0	1	0	1	0
	at neither	8	0	0	1	1	0	2	0	1	1	0
Antero-lingual valley	wide	10	18	9	0	0	3	2	2	1	2	2
	…bordered by anterocingulum	4	7	9	0	0	3	2	1	1	2	2
	faint	12	2	1	0	0	0	0	0	0	0	0
	absent	0	0	0	1	1	0	0	0	0	0	0
Antero-labial valley	small to wide	18	15	0	0	0	0	2	2	0	1	0
	…bordered by cingulum	0	0	0	0	0	0	2	2	0	0	0
	absent	4	5	10	1	1	3	0	0	1	1	2
Sinus (lingual)	wide	22	20	8	1	1	3	2	2	1	2	2
	…bordered by cingulum	4	12	8	0	0	3	2	0	0	1	2
Meso-labial valley	bordered by cingulum	1	0	6	1	1	3	2	1	1	1	2
	not bordered	21	19	4	0	0	0	0	1	0	1	0
	anteriorly directed	22	20	3	0	0	3	2	2	1	0	2
	mesostyl present	0	2	2	1	1	0	0	0	0	0	2
	mesostyl absent	22	18	8	0	0	3	0	0	1	2	0
Roots	as in M1	-	1	10	-	-	-	-	-	-	-	-
	Lingual root splitting all the way	-	1	0	-	-	-	-	-	-	-	-
	Lingual root no splitting	-	9	10	-	-	-	-	-	-	-	-

M3		***Meteamys alpani***		***Cricetodon versteegi***	***Deperetomys anatolicus***	***Enginia* aff. *djanpolati***	***Melissiodon* sp.**	***Meteamys alpani* comparative**
		Kargı 1 (7)	Kargı 2 (16)	Kargı 2 (11)	Kargı 3 (1)	Kargı 2 (3)	Kargı 2 (1)	Inkonak (2)
Anteroloph branches	labial more prominent	3	14	7	1	3	0	0
	both less prominent, especially lingual	4	2	0	0	0	1	1
	both equally prominent	0	0	4	0	0	0	1
Protolophule	inserts behind the protocone on the mure	6	8	0	1	1	1	1
	directly connects paracone to protocone	1	8	10	0	2	0	1
	anteriorly directed and ends free	0	0	1	0	0	0	0
	bears two extra spurs	0	0	0	0	1	0	0
Posterior paracone spur	reaches anterior metacone spur	7	16	8	1	0	1	2
	does not reach	0	0	3	0	3	0	0
	absent	0	0	0	0	0	0	0
Inner paracone ridge	present	0	0	0	0	0	1	0
	absent	7	16	11	1	3	0	2
Mesoloph	long and complete	6	11	0	0	0	0	2
	long and interrupted	1	1	1	0	2	0	0
	short	0	4	5	1	1	1	0
	faint	0	0	4	0	0	0	0
	absent	0	0	1	0	0	0	0
Antero-lingual valley	wide	0	3	5	0	3	0	2
	...bordered by anterocingulum	0	2	0	0	3	0	2
	small/faint	5	9	6	1	0	0	0
	absent	2	4	0	0	0	1	0
Antero-labial valley	wide	0	0	7	0	0	0	0
	...bordered by anterocingulum	0	0	4	0	0	0	0
	small/faint	0	2	4	0	0	0	0
	absent	7	14	0	1	3	1	2
Sinus (lingual)	lingually open	4	13	3	1	3	1	1
	closed by posteriorly directed spur of protocone	1	3	0	0	3	0	1
	closed by "ectomesoloph"	2	0	8	0	0	0	0
Posterosinus	open	0	0	0	1	0	1	0
	closed	7	16	11	0	3	0	2
Anterosinus	open	0	0	3	0	0	0	0
	closed	7	15	8	1	3	1	2
Protosinus	open	0	1	6	1	3	1	0
	closed	7	14	5	0	0	0	2
Mesosinus I	open	1	5	10	10	3	1	0
	...connected to mesosinus II	1	4	10	1	3	0	0
	closed	6	11	0	0	0	0	2
	...middle of sinus is ran by protolophule vertical arm	0	4	0	0	0	0	0
Mesosinus II	open	7	15	10	1	3	1	0
	closed	0	0	0	0	0	0	2

m1		***Meteamys alpani***		***Cricetodon versteegi***	***Cricetodon* sp.**		***Deperetomys* aff. *anatolicus***	***Spanocricetodon sinuosus***	***Eumyarion microps***
		Kargı 1 (11)	Kargı 2 (16)	Kargı 2 (5)	Kargı 1 (1)	Kargı 2 (1)	Kargı 2 (1)	Kargı 1 (2)	Kargı 2 (1)
Anteroconid positioned more labially	yes	12	16	0	1	0	1	2	1
	no	0	0	5	0	1	0	0	0
Lingual anterolophid branch	more developed	0	0	0	0	1	1	0	0
	very low	0	4	0	0	0	0	2	1
	absent	11	12	5	1	0	0	0	0
Metalophulid I	connects to anterolophulid	0	2	3	0	1	1	1	0
	connects to anteroconid	9	9	2	0	0	0	0	0
	interrupted	2	5	0	0	0	0	1	1
	absent	0	0	0	1	0	0	0	0
Metalophulid II	not interrupted	9	14	5	0	1	1	0	1
	...x-shape formed by cusps	8	11	5	0	1	0	0	0
	interrupted	2	2	0	1	0	0	1	0
Metaconid and entoconid have posterior crests	both	11	16	3	0	0	1	0	1
	more prominent at entoconid	0	0	2	0	0	0	0	0
	only at metaconid	0	0	0	1	1	0	1	0
	neither	0	0	0	0	0	0	1	0
Posterolophid confluent to	yes	11	14	2	0	1	1	1	0
	no, interrupted	0	2	3	1	0	0	1	1
Mesolophid	long	0	5	0	0	1	1	0	1
	...complete	0	5	0	0	1	0	0	0
	weak	1	3	0	0	0	0	0	0
	absent	10	8	5	1	0	0	2	0
Mesostylid	more prominent	0	0	5	0	0	0	0	0
	less prominent	0	1	0	1	1	0	0	1
	absent	11	15	0	0	0	1	2	0
Ectomesolophid	long	0	1	0	0	1	1	0	0
	medium length	0	1	0	0	0	0	1	0
	short	0	2	0	0	0	0	1	1
	absent	11	12	5	1	0	0	0	0
Antero-labial valley	wide	11	11	2	0	1	1	2	1
	...bordered by anterocingulid	11	11		0	1	1	2	1
	weak	0	0	3	0	0	0	0	0
	absent	0	0		1	0		0	0
Antero-lingual valley	wide	8	16	5	0	1	0	1	0
	...bordered by anterocingulid	4	7	2	0	0	0	0	0
	weak	2	0	0	0	0	1	1	1
	very faint	1	0	0	0	0	0	0	0
	absent	0	0	0	1	0	0	0	0
Labial sinusid	wide	11	16	5	1	1	1	2	1
	...bordered by cingulum	11	16	5	0	1	1	2	0
	...bordered by ectostylid	4	3	0	0	1	0	0	1
Lingual sinusid	wide	11	15	5	1	1	1	2	0
	...bordered by cingulum	2	1	0	1	1	0	1	0
	weak	0	1	0	0	0	0	0	0
	absent	0	0	0	0	0	0	0	0

m1		***Muhsinia steffensi***	***Melissiodon* sp.**	***Heterosminthus* cf. *firmus/lanzhouensis***	***Meteamys alpani* comparative**	***Muhsinia steffensi* comparative**
		Kargı 2 (2)	Kargı 2 (1)	Kargı 2 (1)	Inkonak (2)	Inkonak (2)
Anteroconid positioned more labially	yes	2	-	0	2	2
	no	0	-	1	0	0
Lingual anterolophid branch	more developed	0	-	0	0	0
	very low	0	-	0	1	0
	absent	2	-	1	1	2
Metalophulid I	connects to anterolophulid	2	-	0	0	2
	connects to anteroconid	0	-	0	1	0
	interrupted	0	-	0	1	0
	absent	0	-	1	0	0
Metalophulid II	not interrupted	2	1	1	2	2
	...x-shape formed by cusps	0	0	0	2	0
	interrupted	0	0	0	0	0
Metaconid and entoconid have posterior crests	both	1	1	0	2	2
	more prominent at entoconid	0	0	1	0	0
	only at metaconid	1	0	0	0	0
	neither	0	0	0	0	0
Posterolophid confluent to	yes	2	0	1	1	2
	no, interrupted	0	1	0	1	0
Mesolophid	long	2	1	0	0	1
	…complete	0	1	0	0	1
	weak	0	0	0	0	1
	absent	0	0	1	2	0
Mesostylid	more prominent	0	1	1	0	0
	less prominent	0	0	0	0	1
	absent	2	0	0	2	1
Ectomesolophid	long	0	0	1	0	0
	medium length	0	1	0	0	0
	short	2	0	0	0	1
	absent	0	0	0	2	1
Antero-labial valley	wide	2	-	0	2	2
	…bordered by anterocingulid	2	-	0	2	2
	weak	0	-	0	0	0
	absent			1	0	0
Antero-lingual valley	wide	0	-	0	2	1
	…bordered by anterocingulid	0	-	0	1	1
	weak	1	-	1	0	0
	very faint	0	-	0	0	1
	absent	1	-	0	0	0
Labial sinusid	wide	2	1	1	2	2
	…bordered by cingulum	2	1	0	2	2
	…bordered by ectostylid	1	1	1	2	1
Lingual sinusid	wide	2	1	1	2	2
	…bordered by cingulum	1	0	0	0	1
	weak	0	0	0	0	0
	absent	0	0	0	0	0

m2		***Meteamys alpani***		***Cricetodon versteegi***	***Spanocricetodon sinuosus***	***Enginia* aff. *djanpolati***	***Heterosminthus* cf. *firmus/lanzhouensis***	***Meteamys alpani* comparative**
		Kargı 1 (12)	Kargı 2 (14)	Kargı 2 (6)	Kargı 1 (1)	Kargı 2 (5)	Kargı 2 (2)	Inkonak (2)
Anterolophulid	equally prominent sides	2	0	0	0	5	0	0
	more labially cusp-like anterolophulid	10	14	6	1	0	0	2
	more lingually cusp-like anterolophilid	0	0	0	0	0	2	0
Metalophulid I	grown but short	3	6	0	0	4	0	0
	long	8	7	0	0	1	0	2
	faint	0	0	0	1	0	0	0
	absent	0	0	6	0	0	2	0
Metalophulid II	long	0	0	0	0	0	2	0
	complete	2	4	0	0	0	2	0
	short (mesolophid-lke)	12	14	5	0	5	0	2
	absent	0	0	1	1	0	0	0
Ectomesolophid	more prominent	0	0	0	0	2	0	0
	short	0	0	0	0	1	0	0
	absent	12	14	6	1	3	2	2
Posterior spurs of metaconid and entoconid	metaconid more prominent	9	3	2	1	2	0	1
	equally prominent	3	11	4	0	3	0	1
	absent	0	0	0	0	0	2	0
Posterior arm of hypoconid	long and thick	0	3	6	1	3	0	2
	short and thin	10	10	0	0	1	2	0
	absent	2	1	0	0	1	0	0
Posterolophid - entoconid	connected	0	0	4	1	5	1	1
	interrupted	12	14	2	0	0	0	1
Antero-lingual valley	wide	10	14	0	1	5	2	0
	...bordered by anterocingulid	8	10	0	1	5	0	0
	small	1	1	0	0	0	0	2
	absent	0	0	6	0	0	0	0
Antero-labial valley	wide	12	13	6	1	5	2	2
	...bordered by anterocingulid	12	13	6	0	5	0	2
	small	0	1	0	0	0	0	0
Labial sinusid, wide	bordered by cingulum	10	11	0	0	4	0	2
	bordered by ectomesostylid	9	2	0	0	1	1	0
	not bordered	0	3	6	1	0	1	0
Lingual sinusid, wide	bordered by cingulum	4	3	5	0	0	0	0
	bordered by mesostylid	0	1	0	0	0	2	0
	not bordered	8	10	1	1	5	0	2

m3		***Meteamys alpani***		***Cricetodon versteegi***	***Spanocricetodon sinuosus***	***Enginia* aff. *djanpolati***	***Eumyarion microps***	***Meteamys alpani* comparative**
		Kargı 1 (8)	Kargı 2 (9)	Kargı 2 (7)	Kargı 1 (3)	Kargı 2 (1)	Kargı 2 (1)	Inkonak (2)
Anterolophid branches	lingual faint, labial prominent	2	2	3	3	-	0	0
	only labial present	6	7	4	0	-	0	2
	equal length, labial lower	0	0	0	0	-	1	0
Anterior protoconid arm	reaches anterocone position	8	9	7	3	1	1	2
	does not reach	0	0	0	0	0	0	0
Metalophulid I	reaches anterocone position	8	8	4	3	0	1	2
	does not reach	0	1	0	0	1	0	0
Mesolophid	long	8	7	4	0	0	0	0
	short	0	2	3	0	1	1	2
	absent	0	0	0	3	0	0	0
Entoconid	prominent	0	0	7	3	0	0	1
	lower than metaconid	8	9	0	0	1	1	1
Entolophid	connects to entoconid	8	7	6	2	1	0	1
	does not connect	0	2	1	1	0	1	1
Posterolophid - entoconid	complete	4	5	7	3	1	1	2
	interrupted	4	4	0	0	0	0	0
Antero-labial valley	prominent	6	4	7	3	1	1	2
	…bordered by anterocingulid	6	2	7	3	1	1	2
	small	0	1	0	0	0	0	0
	faint	2	4	0	0	0	0	0
Antero-lingual valley	prominent	2	7	0	3	1	1	2
	…bordered by anterocingulid	2	5	0	3	1	1	2
	small	4	2	0	0	0	0	0
	faint	2	0	0	0	0	0	0
	absent	0	0	7	0	0	0	0
Labial sinusid	wide	7	9	7	3	1	1	2
	…bordered by cingulum	5	6	5	3	0	1	1
	…bordered by cingulum and ectomesostylid	2	3	2	0	0	0	1
	faint	1	0	0	0	0	0	0