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On the brink: micromammals from the latest Villanyian from Bıçakçı (Anatolia)

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The locality of Bıçakçı (Çameli basin, Anatolia) has yielded a diverse fauna of micromammals. The arvicolines are the most diverse and abundant group. Their stage in evolution shows that the fauna is late Villanyian in age and can be placed in the lower part of the zone P of the Anatolian Neogene biozonation. Thus, it is on the brink of the important Villanyian/Biharian transition. The presence of three species of hamster, in combination with the occurrence of *Borsodia*, a high abundance of *Kalymnomys* and a near absence of insectivores, suggests a dry, open landscape. However, the important contribution of *Clethrionomys* in the vole fauna indicates the nearby presence of woodlands. Overall, the environment at the time of deposition appears to have been similar to that of the area today. Copyright © 2015 John Wiley & Sons, Ltd.

Received 17 May 2014; accepted 24 September 2014

KEY WORDS Early Pleistocene; Arvicolinae; Cricetinae; biogeography; biostratigraphy; Anatolia

1. INTRODUCTION

Because of its central position between three continents, Anatolia is a highly interesting area from a biogeographical perspective (Şen, 1977). As luck will have it, a large part of the history of the region has been preserved in sedimentary rocks in its many intramontane basins. The role that Anatolia played in the distribution of micromammals over the last 20 My is becoming clearer with every new locality that is published. However, research to date has mainly focussed on the Neogene (e.g. Şen, 1977; Engesser, 1980; De Bruijn and Saraç, 1991, 1992; De Bruijn *et al.*, 1992, 2006; Van den Hoek Ostende, 1992, 1995a, b, 1997; Ünay *et al.*, 2003; Alpaslan *et al.*, 2010). In comparison, the Quaternary micromammal record of Anatolia is scanty. One of the most important publications is that of Ünay and De Bruijn (1998), in which a series of small Plio-Pleistocene assemblages were described. Given the large number of assemblages in this paper, and the additional localities mentioned by Saraç (2003), the limited knowledge of Quaternary faunas is

certainly not a matter of lack of material. Following the discovery of *Homo erectus* in southwestern Anatolia (Kappelman *et al.*, 2008), the micromammals of the area have become of special interest, as they can help document the environmental changes that accompanied the migration out of Africa of early humans. This paper is a contribution to that knowledge, as we introduce the micromammals from the locality of Bıçakçı.

Bıçakçı is a new site for fossil micromammals in the Çameli basin of southwestern Anatolia (Figs. 1 and 2). The Çameli basin itself is a Neogene–Quaternary graben with a fill of terrestrial deposits, representing alluvial, fluvial and lacustrine depositional settings. The basin fill succession has been attributed to a Late Miocene to Late Pliocene age on the base of micromammal and macromammal associations (Alçıçek, 2001; Alçıçek *et al.*, 2005). The Bıçakçı locality represents a distal alluvial-fan setting arriving in a lacustrine environment and is located in the uppermost part of the basin fill succession. Initial studies have shown that the area contains several fossiliferous layers to the lacustrine marginal deposits and is thus a promising starting point to fill the gap in our knowledge on the micromammal fauna of Anatolia as a whole.

The site was discovered by Gerçek Saraç at the end of the last century and sampled by M. Cihat Alçıçek, who also

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†David Mayhew passed away on 3 October 2012.

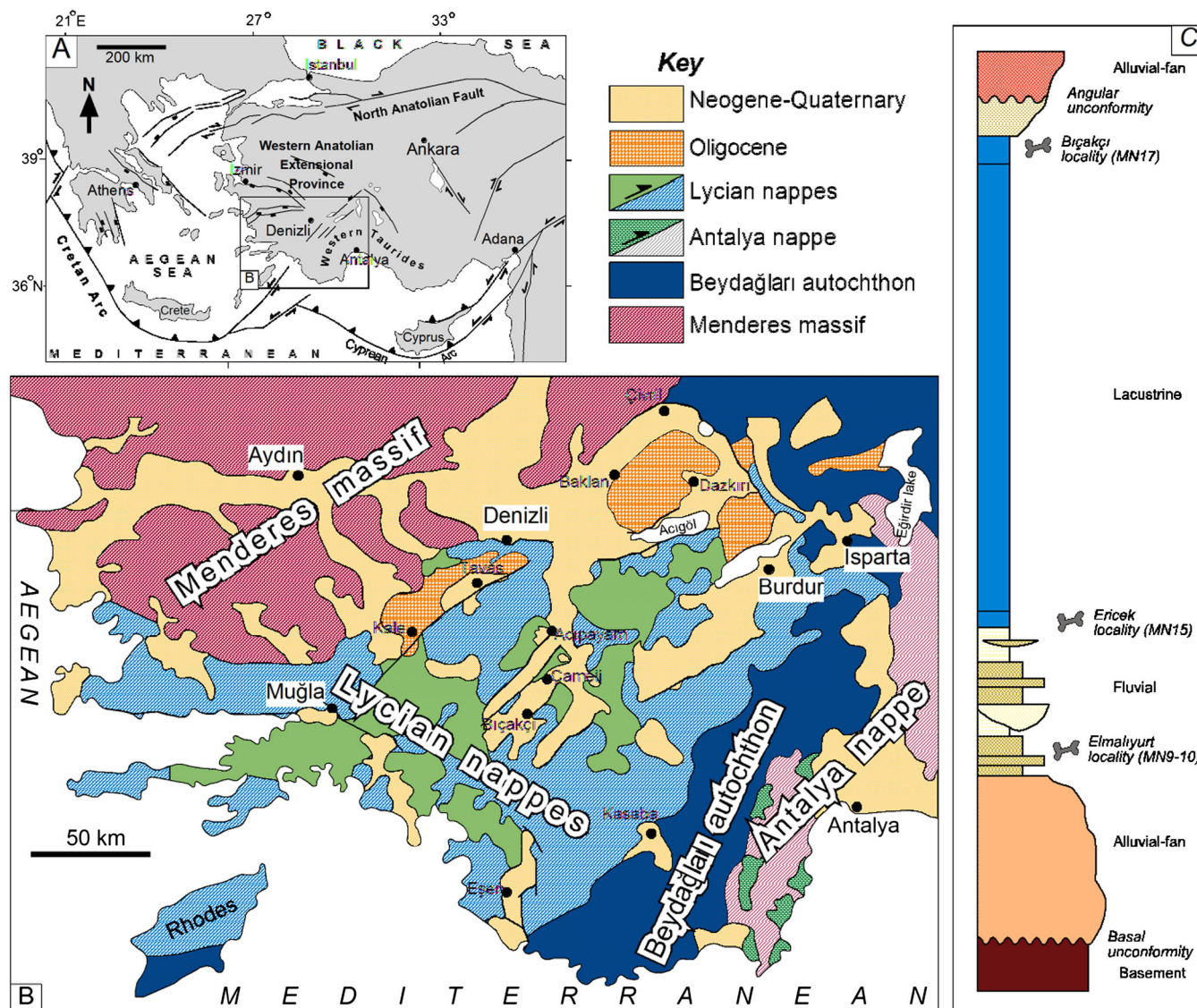


Figure 1. (A) Regional tectonic map of the eastern Mediterranean (after Alçiçek *et al.*, 2005, fig. 1). (B) Simplified geologic map of SW Anatolia (based on Konak & Şenel 2002). (C) Composite stratigraphy of the Çameli basin (not to scale, based on Alçiçek *et al.*, 2005). This figure is available in colour online at wileyonlinelibrary.com/journal/gj

documented the geology of the site. The faunal assemblage was studied by Flemming Diepeveen as an MSc project under the supervision of David Mayhew and Lars van den Hoek Ostende. The latter, together with Alexey Tesakov, prepared the manuscript. Our paper is intended as an introduction to the micromammals of Biçakçı. The material was collected as a bulk sample, but renewed study of the section suggested that possible multiple fossiliferous layers are present. As we found no major discrepancies in the ranges of the various micromammals, we assume that temporal mixing is limited. However, more detailed sampling is required to see if there are environmental changes recognizable within the section. A comprehensive paper,

dealing also with the other fossils from the site, is currently being prepared (Wesselingh *et al.*, research in progress).

2. MATERIALS AND METHODS

Most of the micromammals from Biçakçı were collected by wet-screening fossiliferous sediment, but some of the specimens described herein were surface finds. All molars were measured with a Leica MZ16A measuring microscope with associated software. All of the measurements in this study are given in millimetres. The material will be stored in the collection of the Natural History Museum of EGE-University (Izmir, Turkey).

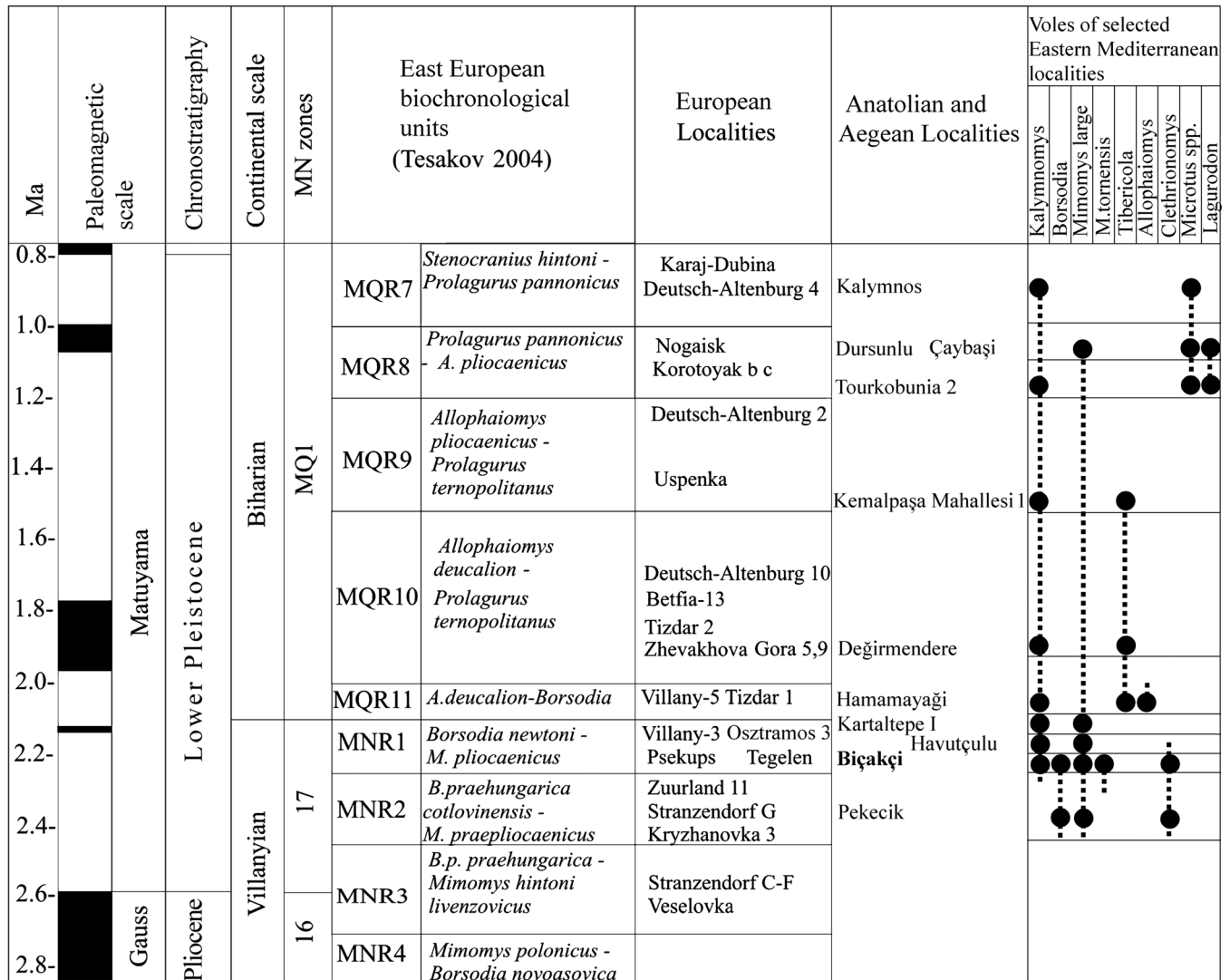


Figure 2. The stratigraphic position of Biçakçı based on the Arvicolidae of the locality.

The dental terminology of the Cricetidae follows Cuenca-Bescós (2003). Dental terminology for the Arvicolinae is based on Van der Meulen (1973), and linea sinuosa measurements and terminology follow Rabeder (1981). The terminology for Muridae molars follows Şen (1977), whereas the Spalacidae dental terminology is based on descriptions by De Bruijn and Van der Meulen (1975). For the Soricidae, we follow Reumer (1984).

Some recent hamsters (*Cricetulus longicaudatus* and *Cricetulus barabensis*) and fossil material from the Dutch locality of Tegelen (*Beremendia fissidens*) from the collections of Naturalis in Leiden were used for comparison. For the *Apodemus* molars, a comparison was made with teeth (*A. atavus*, *A. mystacinus* and *A. dominans*) from the collections of the University of Utrecht. Also, the *Apodemus* molars were compared with *A. flavicollis* molars from the collection of Naturalis.

Photos were taken with a scanning electron microscope (SEM) at Naturalis. To facilitate comparison, all the non-voles teeth have been shown as if coming from the left side. Mirrored images are underlined on the plate. The classifications in the study follow Wilson and Reeder (2005).

3. SYSTEMATIC PALAEOLOGY

Class Mammalia Linnaeus, 1758
 Order Rodentia Bowdich, 1821
 Family Cricetidae Fischer, 1817
 Subfamily Cricetinae Fischer, 1817
 Genus *Cricetulus* Milne-Edwards, 1867
Cricetulus aff. *migratorius* (Pallas, 1773) (Fig. 3A–F)

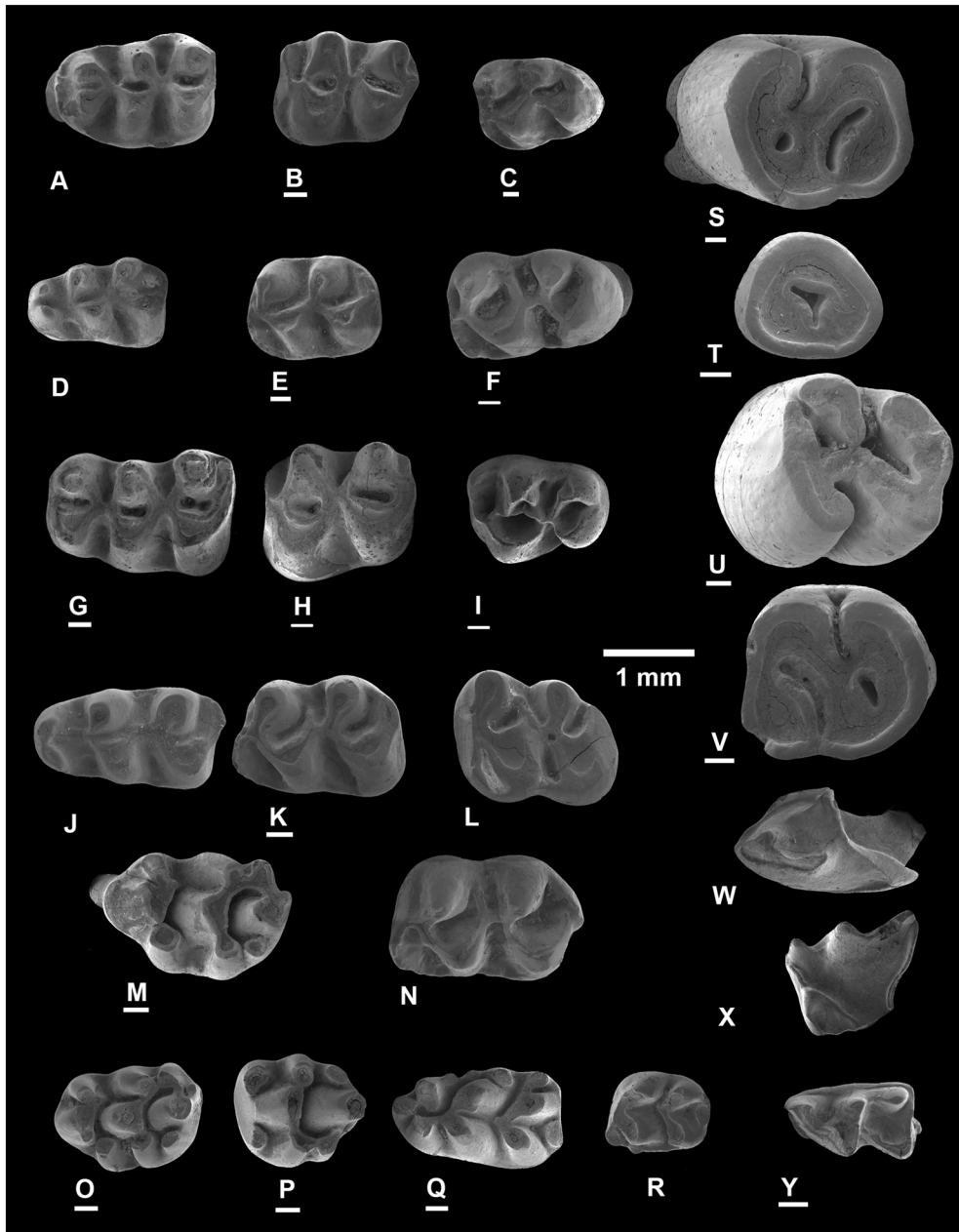


Figure 3. The non-arvicolid micromammals of Biçakçı. **A–F:** *Cricetulus* aff. *migratorius*, **A.** M1 sin. (EUNHM-PV 8528), **B.** M2 dext. (EUNHM-PV 8546), **C.** M3 dext. (EUNHM-PV 8533), **D.** m1 sin. (EUNHM-PV 8541), **E.** m2 dext. (EUNHM-PV 8532), **F.** m3 dext. (EUNHM-PV 8558). **G–L:** *Mesocricetus* aff. *primitivus*, **G.** M1 dext. (EUNHM-PV 8500), **H.** M2 dext. (EUNHM-PV 8501), **I.** M3 dext. (EUNHM-PV 8506), **J.** m1 sin. (EUNHM-PV 8539), **K.** m2 dext. (EUNHM-PV 8510), **L.** m3 sin. (EUNHM-PV 8517). **N.** *Cricetus* sp. m2 sin. (EUNHM-PV 8552). **M.** *Apodemus* cf. *flavicollis* M1 dext. (EUNHM-PV 8568). **O–R:** *Apodemus atavus*, **O.** M1 dext. (EUNHM-PV 8570), **P.** M2 dext. (EUNHM-PV 8576), **Q.** m1 dext. (EUNHM-PV 8577), **R.** m2 sin. (EUNHM-PV 8574). **S–V:** *Pliospalax* sp. **S.** M1 dext. (EUNHM-PV 8581), **T.** M3 dext. (EUNHM-PV 8584), **U.** M2 dext. (EUNHM-PV 8583), **V.** m2 dext. (EUNHM-PV 8686). **W.** *Beremendia* sp. p4 sin. (EUNHM-PV 8535). **X–Y:** *Soricinae* gen. et sp. indet., **X.** P4 sin. (EUNHM-PV 8686), **Y.** m1 dext. (EUNHM-PV 8687). Underlined letters indicate mirrored images.

Table 1. Length and width measurements and the number of molars per element of *Cricetulus* aff. *migratorius* from Bıçakçı. Data from the Pliocene locality of İğdeli (Alpaslan *et al.*, 2010) and the recent *C. migratorius* (Hír, 1993; lengths only) have been added for comparison

		Length			N	Width		
		Min	Mean	Max		Min	Mean	Max
M1	Recent	1.49	1.62	1.78	97	—	—	—
	Bıçakçı	1.73	1.80	1.91	3	1.01	1.17	1.24
	İğdeli	1.73	1.75	1.78	4	1.10	1.15	1.23
M2	Recent	1.03	1.17	1.28	87	—	—	—
	Bıçakçı	1.44	1.59	1.66	5	1.30	1.37	1.44
	İğdeli	1.30	1.34	1.40	4	1.00	1.09	1.15
M3	Recent	0.94	1.02	1.11	66	—	—	—
	Bıçakçı		1.26		1		0.98	
	İğdeli	1.00	1.09	1.25	7	0.80	0.96	1.02
m1	Recent	1.45	1.54	1.65	150	—	—	—
	Bıçakçı		1.52		1		1.00	
	İğdeli	1.65	1.71	1.76	4	1.00	1.02	1.05
m2	Recent	1.17	1.25	1.35	138	—	—	—
	Bıçakçı	1.35	1.39	1.43	3	1.07	1.11	1.14
	İğdeli	1.45	1.48	1.50	4	1.05	1.08	1.15
m3	Recent	1.06	1.19	1.30	110	—	—	—
	Bıçakçı	1.32	1.33	1.33	3	0.97	1.02	1.06
	İğdeli	1.20	1.27	1.31	3	1.00	1.02	1.05

Material. 4 M1, 5 M2, 1 M3, 1 m1, 3 m2, 3 m3

Measurements. The measurements are listed in Table 1.

Description. M1 is rectangularly shaped and relatively short. The two parts of the anterocone are similarly sized and clearly separated from each other. One specimen (RGM 814893) has a faint anterostyle. The main cusps are nearly in opposing position. The anterosinus is L-shaped, ending at the base of the paracone. The loph between the main cusps join in the centre, producing a conspicuous X-shape. The posteroloph runs against the posterior side of the metacone. The sinuses are bordered by cingulums, which vary in development between the four specimens from weak to quite strong.

M2 is subrectangular, the anterior side being only somewhat wider than the posterior side. The labial anteroloph is well developed and shows a tendency to connect to the paracone, encircling a relatively wide anterosinus. On the lingual side, an anterior cingulum is only found in the larger specimens. The four cusps stand nearly in opposition, and low ridges encircle deep pits between paracone and protocone, and metacone and hypocone, respectively. The sinus and mesosinus are wide and bordered by low cingulums. The posteroloph lies close to the metaconid, leaving a very narrow posterosinus.

M3 is strongly reduced, particularly in the metacone area. As a result, the molar has a sub-triangular outline. The protoloph is strongly curved and connects to the paracone, encircling a deep anterosinus. The mesosinus is bordered by a high labial ridge; a low lingual cingulum borders the sinus.

m1 is slender, continuously widening backwards. The main cusps are only slightly alternating. The anteroconid is

divided in a lingual cusp and a labial cusp, which are of similar size. The anterolophid connects to the labial cusplet of the anteroconid. The lingual sinusids are L-shaped; the labial sinusids are straight and slightly anteriorly directed. The mesolophid is absent. The posterolophid arches wide in posterolingual direction.

m2 is subrectangular with slightly alternating cusps. The anterolophid is well developed. It borders a wide anterosinusid. The small part of the anterolophid continues lingually, lying directly against the flank of the metaconid. The posterolophid bends sharply just behind the hypoconid and curves to connect low to the entoconid. The lingual sinusids are L-shaped and bordered by short lingual cingulums.

m3 is a long molar, showing reduction in the entoconid region only. The anterolophid continues all along the anterior side in two of the three specimens. Except for a lingual connection, these specimens also have a second connection to the metaconid by a short transverse ridge. In the third specimen, the lingual part of the entoconid ends against the anterior flank of the metaconid. The protoconid–entoconid connection shows a slight furcation at its end. The posterolophid is strongly curved and ends high against the entoconid.

Remarks. *Allocricetus* and *Cricetulus* are two closely related taxa and should most probably be considered a single genus. According to Mayhew (1978), *Allocricetus* was based on skull characteristics of uncertain taxonomic value, and the dentition of the two genera is quite similar. Purported differences suggested by Tchernov (1968) were according to this author not tenable. Hír (1993) demonstrated that differences between *Cricetulus* and *Allocricetus* dentitions lay with the proportion of morphotypes in an assemblage and size and concluded that the two could only be told apart with a sufficient sample size. In our opinion, these differences constitute differences between species, not genera. Cuenca-Bescós (2003) regarded the two genera as separate. As *Cricetulus* clustered with two species of *Allocricetus* (*A. teilhardi* and *A. jesreelicus*), she suggested that these two should be included in *Cricetulus*. However, in her analyses, she used multiple species of *Allocricetus*, whereas *Cricetulus* was included as a whole. Moreover, her matrix contained several characters which Hír (1993) has demonstrated to be variable within an assemblage and which are also variable in the Bıçakçı *Cricetulus*. Given these uncertainties, the cladogram (Cuenca-Bescós, 2003, fig. 2) only indicates that *Cricetulus* and *Allocricetus* are indeed morphologically very close. The only other taxon clustering with these two is *Cricetus*, again not separated into species.

Although a comprehensive review is needed to determine the relationships between species, there can be little doubt that *Cricetulus* and *Allocricetus* are congeneric. In this case, *Cricetulus* Milne-Edwards, 1867, has priority over *Allocricetus* Schaub, 1930. Nevertheless, Alpaslan *et al.*

(2010) described *Cricetulus* and *Allocricetus* from the Early Pliocene Anatolian locality of Iğdeli, stating that for both genera, it is the oldest record. From their tables (Alpaslan *et al.*, 2010, tables 4 and 5), it is clear that the two taxa are equal in size. As two morphologically similar and equally sized hamsters would certainly outcompete each other, it is clear that we are, in fact, dealing with one taxon; based on the descriptions and plates, the authors seem to have separated the simple and complex morphotypes *sensu* Hír (1993). As the oldest record of *Cricetulus*, the Iğdeli assemblage is very important. In Table 1, we have added the measurements of this assemblage, as calculated weighted means of the two tables of the original description. To the table, we have also added the data from the recent Syrian assemblage of Krak de Chevaliers (Pradel, 1981) as taken from Hír (1993). Unfortunately, we only have length measurement of the recent species.

Table 1 shows that three assemblages are all of similar size. There is no specific size trend, but, notably, Bıçakçı is consistently larger than the Recent *Cricetulus migratorius*. The size of the M2 and M3 from Bıçakçı is clearly larger than in the other two assemblages, with no overlap. Based on this, the best classification for the Bıçakçı assemblage is *Cricetulus aff. migratorius*, pending a review of all recent and fossil dwarf hamster species.

Genus *Mesocricetus* Nehring, 1898
Mesocricetus aff. primitivus De Bruijn, Dawson
 and Mein, 1970 (Fig. 3G–L)

Material. 2 M1, 3 M2, 4 M3, 3 m1, 10 m2, 16 m3

Measurements. The measurements are listed in Table 2.

Description. M1 is rectangular with a slightly concave labial side. The anterocone is clearly divided in two, the lingual cusp being slightly larger than the labial one. The protocone and hypocone are somewhat larger than their opposing labial cusps. The protolophule I is clearly lower than the protolophule II; both connect to the paracone. The posteroloph is slightly curved and ends against the posterolabial flank of the paracone, encircling a very narrow posterosinus. There is a faint and short transverse connection between the posterolophid and the posterolingual side of the metacone.

M2 has a subrectangular outline, the anterior side being wider than the posterior side. The protoloph is well developed and encircles an anterosinus which can be extremely narrow or relatively wide. One of the four specimens has a clear anterior cingulum, but this structure is absent in the other three. The sinus is wider than the mesosinus; both are bordered by low cingulum. The posteroloph encircles a wide posterosinus. In two specimens, the posteroloph shows a thickening at the postero-labial corner of the molar. The metalophule is lacking in one specimen, well developed in the others.

Table 2. Length and width measurements and the number of molars per element of *Mesocricetus aff. primitivus* from Bıçakçı. Measurements from *M. primitivus* from the Pliocene localities of Çalta (Şen, 1977) and Maritsa (De Bruijn *et al.*, 1970) are added for comparison, as well as those of sub-recent *M. auratus* from the locality of Meydan (Hír, 1992)

Element	Locality	Length			N	Width		
		Min	Mean	Max		Min	Mean	Max
M1	Meydan	2.26	2.36	2.85	68	1.20	1.49	1.62
	Bıçakçı	2.17	2.22	2.27	2	1.31	1.40	1.49
	Çalta	2.07	2.15	2.25	3	1.31	1.36	1.42
	Maritsa	—	—	—	—	—	—	—
M2	Meydan	1.83	2.07	2.35	87	1.32	1.53	1.74
	Bıçakçı	1.80	1.81	1.84	3	1.37	1.41	1.44
	Çalta	1.60	1.69	1.76	4	1.43	1.47	1.50
	Maritsa	1.55	1.66	1.76	2	1.43	1.47	1.50
M3	Meydan	1.71	1.94	2.17	77	1.22	1.39	1.61
	Bıçakçı	1.47	1.49	1.50	4	1.18	1.24	1.33
	Çalta	—	1.61	—	1	—	1.26	—
	Maritsa	1.47	1.57	1.62	4	1.29	1.33	1.40
m1	Meydan	2.04	2.20	2.46	77	1.05	1.20	1.36
	Bıçakçı	1.92	1.93	1.95	3	1.09	1.12	1.19
	Çalta	1.98	2.02	2.06	4	1.17	1.20	1.25
	Maritsa	—	—	—	—	—	—	—
m2	Meydan	1.72	2.18	1.94	101	1.18	1.33	1.53
	Bıçakçı	1.64	1.77	1.98	10	1.20	1.33	1.43
	Çalta	1.66	1.74	1.83	5	1.3	1.35	1.40
	Maritsa	1.52	1.71	1.85	5	1.31	1.37	1.47
m3	Meydan	2.00	2.16	2.52	71	1.23	1.34	1.65
	Bıçakçı	1.55	1.78	1.97	16	1.18	1.28	1.43
	Çalta	1.67	1.77	1.87	4	1.31	1.34	1.38
	Maritsa	1.72	1.74	1.75	2	1.28	1.31	1.34

M3 is elongated; the anterior side is clearly wider than the posterior side. The protoloph is short and encircles a relatively wide anterosinus. The sinus and mesosinus are of similar size and are both bordered by cingulums. The hypocone and metacone are somewhat reduced, there is no posteroloph.

m1 is very elongate, with nearly opposing cusps. The molar widens slightly towards the back. The anteroconid consists of two parts, the labial and lingual cusps being of equal size. One specimen also has a tiny anterostylid. In one relatively unworn specimen, the anterolophid is also double, connecting to both cusps of the anteroconid. The specimen with the anterostylid also has a mesostylid and shows a narrow basin between protoconid and metaconid. This structure is absent in the other m1. The anterosinusid and protosinusid, and the mesosinusid and sinusid are simple and stand directly opposite of one another. The posterosinusid is L-shaped. It is bordered by a thick and low posterolophid.

m2 is rectangular with slightly alternating cusps. The labial part of the anterolophid is relatively short and borders an anterosinusid that lies conspicuously

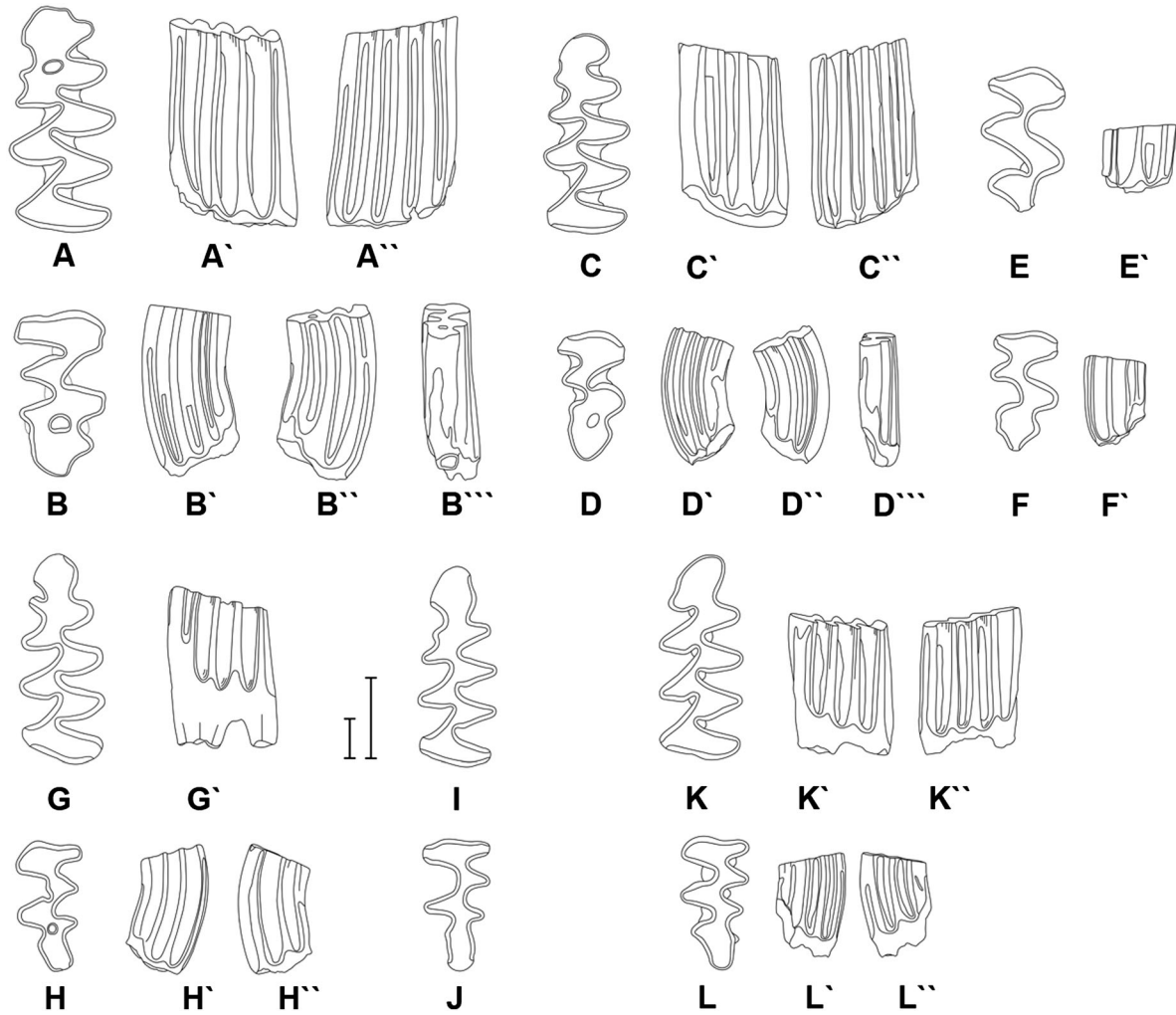


Figure 4. The arvicolids from Bıçakçı. **A–L**: occlusal view, (X) labial view, (X') lingual view, (X'') posterior view, (X''') lateral view. **A, B**: *Mimomys pliocaenicus*, **A**, m1 sin. (EUNHM-PV 8582), **B**, M3 dex. (EUNHM-PV 8666). **C, D**: *Mimomys* gr. *tornensis*, **C**, m1 sin. (EUNHM-PV 8675), **D**, M3 dex. (EUNHM-PV 8684). **E, F**: *Pitymimomys pitymyoides*, **E**, M2 dex. (EUNHM-PV 8693), **F**, M3 dex. (EUNHM-PV 8667). **G, H**: *Borsodia* gr. *newtoni-arankoides*, **G**, m1 sin. (EUNHM-PV 8589), **H**, M3 sin. (EUNHM-PV 8675). **I, J**: *Kalymnomys* sp., **I**, m1 sin. (EUNHM-PV 8588), **J**, M3 sin. unnumbered. **K, L**: *Clethrionomys kretzoi*, **K**, m1 sin (EUNHM-PV 8586), **L**, M3 sin. (EUNHM-PV 8707). Occlusal and lateral scales, 1 mm.

higher than the sinusid. The lingual part of the anterolophid is also short and lies directly adjacent to the metaconid. A short mesolophid is also present in

most specimens. The posterolophid is low and usually ends against the entoconid. It borders a narrow, L-shaped posterosinusid.

m3 is not reduced and quite variable in its shape; some specimens are subrectangular with a rounded posterior side, whereas others are clearly wider at the front than at the back. The cusps stand in slightly alternating positions. The lingual part of the anterolophid is formed as a ridge in about half the specimens. In the remaining molars, only patches of cingulum against the metaconid are preserved at most. The labial part of the anterolophid is rather short and slightly curved. In general, the mesolophid is of medium length and either ends freely just short of the metaconid or has a connection to that cusp. Some specimens have a long mesolophid. In one

Table 3. Measurements of *Clethrionomys kretzoi* from Bıçakçı

	Length				Width		
	Min	Mean	Max	<i>N</i>	Min	Mean	Max
m1	2.33	2.40	2.44	4	0.99	1.04	1.06
m2	1.41	1.46	1.51	2	0.84	0.88	0.91
m3	1.22	1.36	1.41	4	0.69	0.73	0.77
M1	1.91	2.06	2.3	5	1.02	1.14	1.25
M2	1.63	1.66	1.76	6	0.93	1.04	1.27
M3	1.90	1.65	1.74	6	0.80	0.84	0.90

specimen, the mesolophid is forked with both parts connecting to the metaconid. There is little reduction in the back part of the m3. The posterolophid is well developed and connects to the entoconid, enclosing a clear posterosinusid.

Remarks. Metrically, the middle-sized hamster from Biçakçı fits well with *Mesocricetus primitivus* from Çalta and Maritsa (Şen, 1977; De Bruijn *et al.*, 1970). Apart from the latter two localities, we have added in Table 2 the data of subfossil *M. auratus* from the Anatolian locality of Meydan (Hír, 1992). The latter is clearly larger than the Biçakçı hamster.

De Bruijn *et al.* (1970) defined *Mesocricetus primitivus* as having well-developed mesolophids on m2 and m3, and a relatively strong lingual branch of the anterior cingulum in M2 and M3. The latter character was erroneously given in the diagnosis as the *labial* branch but correctly identified in the discussion. The lingual branch is poorly developed in the Biçakçı M2 and M3. However, the mesolophids are well developed, particularly on m3. All in all, the assemblage is somewhat intermediate between the Pliocene and the recent representatives of the genus. Given the metrical similarity with *M. primitivus*, including the relatively short m2 and m3 which were considered typical for that species by De Bruijn *et al.* (1970), we classify the middle-sized hamster as *M. aff. primitivus*.

Genus *Cricetus* Leske, 1779
Cricetus sp. (Fig. 3N)

Material and measurements. 1 m2 (2.05 × 1.61)

Description. The m2 is subrectangular, with a general robust appearance. The main cusps are slightly alternating. The curved labial part of the anterolophid borders a wide anterosinusid. The lingual part forms a cingulum along the anterior flank of the metaconid. The mesolophid ends freely, just short of the metaconid. The posterolophid is thickest at the posteriormost part of the molar and curves to meet the entoconid, enclosing the posterosinusid. The sinusid is clearly wider than the mesosinusid. The various sinusids are bordered by low cingulums.

Remarks. In size and morphology, the described molar fits well with *Cricetus lophidens* from Maritsa (De Bruijn *et al.*, 1970). However, based only on one specimen, no confident determination to species level can be made. Other elements of the dentition are needed to ascertain the identity of the Biçakçı *Cricetus*.

Subfamily Arvicolinae Gray, 1821
Genus *Clethrionomys* Tilesius, 1850
Clethrionomys kretzoi (Kowalski, 1958) (Fig. 4K, L)

Material. 6 M1, 6 M2, 6 M3, 5 m1, 2 m2, 4 m3

Measurements. See Table 3.

Description. Small-sized vole with rooted molars with moderate cement accumulations and thick undifferentiated enamel. This is a moderately hypsodont vole; enamel-free areas (dentine tracts) are interrupted by wear at the stage of well-developed roots. Dentine tracts of anterior molars are 2.1–2.7 mm high. The posterior root of m2 is in semipleurohiz condition (partly shifted labially from the top of the incisor). All molars have two roots, except for M1 where two closely spaced anterior roots can separate in older specimens.

The m1 is composed of the posterior loop, three basic triangles and the anteroconid complex including broadly confluent T4–T5 and the cap. The cap is variable in shape. There is quite a broad connection between the dentine fields which tend to increase with wear. The anterior dentine tract is typically bifurcated. The HH-index in the least worn specimen (Fig. 4K') reaches 3.6.

The M3 is subdivided into anterior loop, three broadly fused intermediate triangles (T2–T4) and the posterior lobe. The first labial triangle is widely fused with the anterior loop except for early wear stages. The T3–T4 are characteristically broadly fused. The posterior loop has a shape of a rounded triangle with moderately expressed lingual and labial salient angles (LSA4 and BSA4). Dentine tracts range between 1.3 and 1.9. PA-index 2.2–2.6 ($n=3$).

Remarks. Small voles of the genus *Clethrionomys*, ancestral to the modern European bank vole, are known in arvicoline faunas since earliest late Villanyian. For the priority of *Clethrionomys* versus *Myodes*, see Tesakov *et al.* (2010). The Biçakçı wood vole fits the primitive earliest Early Pleistocene species *C. kretzoi* in morphology and hypsodonty level. Teeth of this small vole characteristically lack any mimomyine characters (like the *Mimomys* ridge and enamel islets) and show slightly negatively differentiated enamel, and moderately developed external cement. Hypsodonty indices of the Biçakçı wood vole overlap and slightly exceed the values known for its conspecifics from Psekups, Tegelen and Schemfeld (Tesakov, 1996, 1998; Carls and Rabeder, 1988). Thus, the hypsodonty level broadly matches latest Villanyian populations of *C. kretzoi* and is lower than in early Biharian *Clethrionomys hintonianus*.

Clethrionomys kretzoi shows strong similarity to the modern European bank vole that inhabits broad-leaved and mixed forests under temperate climatic conditions. The species *C. kretzoi* is the presumed direct Early Pleistocene ancestor (chronospecies) of the modern *C. glareolus* (Carls and Rabeder, 1988; Tesakov, 1996). Thus, a strong association with wood vegetation is suggested for *C. kretzoi*.

Genus *Mimomys* Forsyth Major, 1902
Mimomys pliocaenicus Forsyth Major, 1902 (Fig. 4A, B)

Material. 2 M1, 2 M2, 7 M3, 5 m1, 6 m2, 5 m3

Measurements. See Table 4.

Description. A large *Mimomys* with characteristic mimomyine morphology with a strongly negatively differentiated enamel band. This is the largest arvicolid found in the Bıçakçı locality. The hypsodonty level is advanced; dentine tracts in anterior molars are between 3.5 and 5 mm. All molars have two roots except some M1 in which two anterior roots can be still incompletely fused.

The m1 consists of a posterior loop, three basic triangles and the anteroconid complex. The connections between the dentine fields are nearly completely closed, as is the connection between the T3 and the anteroconid complex. The m1 bears anterior enamel islet and well-developed *Mimomys* ridge. Dentine tracts in m1 are 3.5–4.5 mm. HH-index is 5.3–6.05.

The m2 is situated labial to the incisor (pleurorhiz position, Fig. 4B^{'''}).

The M3 consists of the anterior loop, triangle T2 and posterior lobe with broadly confluent elements and posterior enamel islet. The islet is deep. It is apparent on the occlusal surface until at least the crown height of 3.4 mm. In one specimen, the traces of the islet are visible at crown height of 0.8 mm. Another specimen shows a deep posterolingual re-entrant without enamel islet. The dentine tracts of M3 range between 2.5 and 3.8 mm. Pa-index is 3.4–4.9.

Remarks. The material was compared with descriptions and measurements from Tegelen, Osztamos-3 and Schernfeld (Janossy and Van der Meulen, 1975; Carls and Rabeder, 1988; Tesakov, 1998). Morphologically and in size, the Bıçakçı material matches that from the other localities well. The hypsodonty level of the Bıçakçı vole is slightly higher than that of the conspecific form from Tegelen (Tesakov, 1998), but lower than in *Mimomys ostramosensis* from Schernfeld (Carls and Rabeder, 1988) and possibly from Osztamos 3 (Kościów and Nadachowski, 2002). The Bıçakçı vole differs from *M. ostramosensis* in the lack of separation of T4 from anteroconid and in more confluent elements of the posterior lobe of M3.

Because of its size, this large vole is commonly interpreted to be related in its ecology to riverine and lacustrine habitats. Some populations of this species group may have been related to the ancestry of the European water vole *Arvicola*.

Table 4. Measurements of m1 and M3 of *Mimomys pliocaenicus* from Bıçakçı

	Length				Width		
	Min	Mean	Max	N	Min	Mean	Max
m1	3.16	3.36	3.63	3/7	1.30	1.51	1.63
M3	1.73	2.03	2.17	7	1.05	1.12	1.18

Mimomys gr. *tornensis* Janossy and Van der Meulen, 1975 (Fig. 4C, D)

Material. 9 M1, 7 M2, 6 M3, 5 m1, 6 m2, 5 m3

Measurements. See Table 5.

Description. A smaller *Mimomys* species showing hypsodont molars and abundant crown cement. The enamel band shows strong negative differentiation with leading edges thinner than trailing ones. The m2 is positioned labial to the incisor (pleurorhiz condition). Molars are very hypsodont. Dentine tracts are interrupted by wear at early stages of root formation; in young specimens of m1 and M1, their height is more than 4.0–4.3 mm. All molars have two roots. The anterior root of M1 shows traces of fused anterior and anterolingual roots.

The m1 consists of the posterior loop, three basic triangles and the anteroconid complex. Triangles of occlusal surface have rounded outlines. The connections between the dentine fields are nearly completely closed, due to the very deep re-entrant folds. The connections in the anteroconid complex are broad. The m1 do not show traces of an enamel islet even in the youngest specimens. The *Mimomys* ridge is strongly reduced in expression and depth; it is elevated above the crown base at 3.7 mm. Dentine tracts are higher than 4.0 mm. HH-index of the least worn molar is close to 5.4. The M3 consists of the anterior loop broadly confluent with T2 and a posterior lobe which bears posterior enamel islet. The islet is apparent on occlusal surface at crown height higher than 2.7–3.0 mm. This molar shows anterior dentine tracts higher than 2.7–3.0 mm.

Remarks. The combination of characters excludes the attribution of this species from the lineage of *Mimomys hintoni-reidi-pusillus* and suggests its similarity with voles of the *M. tornensis* group. This species group is abundant in latest Villanyian assemblages of central and northwestern Europe like those from Tegelen, Osztamos 3 and Schernfeld.

Morphologically, the material fits well with that described from Osztamos-3 and Schernfeld (Janossy and Van der Meulen, 1975; Carls and Rabeder, 1988). However, *Mimomys tornensis* of Bıçakçı is slightly smaller than *M. tornensis* from Osztamos-3 and Schernfeld. The HH-index fits well with the Schernfeld material. The HH-index was also compared with *M. tigliensis* from Tegelen (Tesakov, 1998), which seemed to be a little higher than the Bıçakçı material. The large amount of crown cement and the very high HH-index suggest placement in *M. tornensis* rather than in *M. tigliensis*.

Table 5. Measurements of m1 and M3 of *Mimomys* gr. *tornensis* from Bıçakçı

	Length				Width		
	Min	Mean	Max	N	Min	Mean	Max
m1	2.43	2.49	2.60	5	1.05	1.12	1.25
M3	1.35	1.45	1.55	5	0.74	0.79	0.87

Mimomys tornensis belongs to the *Mimomys* (*Tcharinomys*) group of small voles showing hypsodont molars with abundant cement and reduction of mimomyine characters. Their molar morphology strongly resembles that of rootless *Microtus s.l.* of Early Pleistocene to Recent age, and it has been suggested that this group of small *Mimomys* is ancestral to common voles *s.l.* (Rabeder, 1986; Tesakov, 1998). It is thus probable that this species indicates meadow habitats characteristic for many extant species of *Microtus*.

Genus *Pitymimomys* Tesakov, 1998

Pitymimomys pitymyoides (Janossy and Van der Meulen, 1975) (Fig. 4E, F)

Material. 2 M2, 2 M3

Measurements. Length and width of M2 are 1.70×1.06 and 1.76×1.02 ; those of M3 are 1.55×0.78 and 1.47×0.84 .

Description. This small vole is only represented in the fauna by upper molars which show the typical morphology with broadly confluent dentine fields. The hypsodonty index (HH-index) of M2 is higher than 5.65. The index of posterior lobe to occlusal length (P) in M3 is 0.75 and 0.66.

Remarks. This extinct vole is common in European late Villanyian faunas with dominance of voles adapted to mesic habitats. The exact environmental preferences of this species are unknown. The broadly confluent elements of the occlusal surface are similar to those of modern underground voles of the genus *Terricola*, which have a burrowing life mode in mesic, possibly meadow ecotopes.

Genus *Borsodia* Janossy and Van der Meulen, 1975

Borsodia gr. *newtoni* Forsyth Major, 1902–*arankoides* Alexandrova, 1976 (Fig. 4G, H)

Material. 1 M2, 1 M3, 2 m1, 1 m2

Measurements. The single intact m1 (Fig. 4G): length 2.55, width 1.04, anteroconid length 1.15, anterosinusid >2.45 , hyposinusid >2.05 , hyposinulid >2.28 , HH-index >3.2 . The damaged m1 (unnumbered): anteroconid length 1.09, width 0.9, anterosinusid >2.62 . m2: length ca. 1.57, width 0.95, HH-index >2.9 . M2: length 1.67, width 0.98, anterosinusid >3.60 , protosinusid ≥ 3.38 , PA-index >4.9 . M3: length 1.61, width 0.89, posterior lobe length 0.73, anterosinusid 2.76, protosinusid ≥ 2.94 , PA-index ≥ 4.03 .

Description. The enamel band is positively differentiated with leading edges thicker than trailing ones. The hypsodonty level determined by the least worn molar M3 (Fig. 4H) is quite high. Dentine tracts in upper molars are more than 3.0 mm.

The single intact m1 (Fig. 4G) consists of posterior loop, three basic triangles (T1, T2 and T3) and the anteroconid complex. The well-developed and deep *Mimomys* ridge has a high mimosinuid tract. The connections between dentine

fields are nearly completely closed. The connection between the cap and the rest of the anteroconid complex is broad.

The M3 (Fig. 4H) consists of anterior loop, three alternating triangles (T2–T4) and the posterior loop of rectangular shape. The first lingual re-entrant (LRA2) shows a slight indentation, known as a lagurine denticle. This feature is typical for rootless lagurines of the Pleistocene, but rarely occurs in rooted *Borsodia*. The posterior enamel islet is of rounded shape. The index of posterior lobe (P/L) measured as the ratio of combined length of T4 and posterior loop to the occlusal length is 0.43.

Remarks. This material resembles *Borsodia newtoni* because of the characteristic features it shares with specimens from East Runton and Schernfeld (Mayhew and Stuart, 1986; Carls and Rabeder, 1988), such as positively differentiated enamel, the absence of crown cement and the closed dentine fields. This form has differentiated enamel, which indicates it is a highly evolved form of *Borsodia* (Tesakov, 1993). The hypsodonty level also matches that of latest Villanyian *Borsodia* from the northern coast of the Black Sea (Tesakov, 2004). The form closely resembles *Borsodia* of the *newtoni-arankoides* complex (Tesakov, 2004). The deep *Mimomys* ridge in m1 and lagurine denticle in anterolingual re-entrant of M3 may suggest the assignment to *B. arankoides*, a presumed ancestor of *Lagurodon arankae*. More material is needed for determining the species status of the Late Villanyian *Borsodia* from Anatolia.

Genus *Kalymnomys* von Koenigswald, Fejfar and Tchernov, 1992

Kalymnomys sp. (Fig. 4I, J)

Material. 4 M1, 5 M2, 3 M3, 5 m1, 5 m2, 7 m3

Measurements. See Table 6.

Description. This vole has rootless molars. Enamel band is uniformly thick with somewhat thinner portions inside re-entrants. Younger molars show a slight trend towards positive enamel differentiation (thicker leading and thinner trailing edges). Occlusal elements alternate but show considerable degree of confluence.

The m1 has a posterior loop, three basic alternating triangles and an anteroconid complex with constantly present *Mimomys* ridge (Fig. 4I). Occlusal elements are moderately confluent. Among the basic triangles, T2–T3 are most confluent. The anteroconid has an elongated or rounded shape.

Table 6. Measurements of m1 and M3 of *Kalymnomys* sp. from Biçakçı

	Length				Width		
	Min	Mean	Max	<i>N</i>	Min	Mean	Max
m1	2.24	2.37	2.47	5	0.95	0.97	0.99
M3	1.39	1.53	1.61	3	0.77	0.80	0.83

The anteroconid index (A/L) ranges between 1.00 and 1.17, with a mean value of 1.05 ($n=5$).

The M3 consists of an anterior loop, three triangular elements (T2–T5) and a posterior loop. All elements broadly communicate. The posterior loop has an elongated shape and may have a poorly developed lingual salient angle (Fig. 4J). The length of the posterior lobe (T4+posterior loop) has a range of 0.75–0.87 and mean 0.80 ($n=3$), forming about half the occlusal surface (P/L index is 0.49, 0.54, 0.54).

Remarks. This peculiar vole has an m1 that resembles that of *Pitymimomys pitymyoides* in general outline and broad communication of occlusal elements. However, it differs from the latter form in having a uniformly thick enamel band and the lack of cement in the re-entrant folds. The *Kalymnomys* from Bıçakçı, characterized by its simple M3, apparently belongs to a yet undescribed species ancestral to *Kalymnomys major*, a species widespread in early Biharian faunas of Anatolia and Greece (Ünay *et al.*, 1995). This taxon will be described elsewhere. The primitive morphology and co-occurrence with large *Mimomys pliocaenicus* in Bıçakçı and Havutçulu (Ünay *et al.*, 1995) localities indicate a late Villanyian age. *Kalymnomys* is the first rootless arvicoline species in fauna of Anatolia and southern Europe.

Family Muridae Illiger, 1811

Subfamily Murinae Illiger, 1811

Genus *Apodemus* Kaup, 1829

Apodemus atavus Heller, 1936 (Fig. 3O–R)

Material. 4 M1, 5 M2, 3 m1, 1 m2

Measurements. See Table 7.

Description. The M1 is a robust and elongated molar. There is a strong connection between the t2 and t3; the connection between t2 and t1 is weaker. The accessory cusp t0 is absent. The cusps t4, t5, t6 and t9 form a ring in which they are all strongly connected. In most specimens, there is also a weaker connection between the ring of cusps and t8. In completely worn teeth, the t7 cusp is also connected to the ring. A small, well-developed posterior cingulum is visible in most specimens. The specimens have three or four roots.

The M2 has well-developed t1 and t3 cusps. The t4, t5, t6 and t9 cusps are strongly connected. There is also a weak

connection between t4 and t7. The t8 is well developed. In some specimens, a clear posterior cingulum is present.

The m1 is an elongated molar. The cusps tE–tF, tC–tD and tA–tB are all paired. They are separated by a valley between the paired cusps. The antero-central cusp is quite large. In one specimen, a weak connection between this cusp and the tE–tF pair is visible. All three specimens have three accessory cusps. These cusps are isolated and do not seem to fuse with wear. The posterior cingulum is rounded. The postero-central cusp is variable in size. The specimens have three roots.

The m2 has obviously paired tC–tD and tA–tB cusps. The tE cusp, which is in the antero-labial part of the molar, is also well developed and completely isolated. Only one weak accessory cusp is visible, which has a weak connection with the tC cusp. The terminal heel is rounded to oval-shaped and quite low. The postero-central cusp is quite large. The specimen has two roots.

Remarks. *Apodemus* from Bıçakçı was compared to congeneric material from several other localities, Çalta (Şen, 1977), Maritsa (De Bruijn *et al.*, 1970), Tourkobounia-I (De Bruijn and Van der Meulen, 1975), and Yenice-I, Ta ova, Ortalica and Tozaklar (Ünay and de Bruijn, 1998). The material from Bıçakçı is close to the earlier described material of *A. dominans* and *A. atavus* in both morphology and size (Table 3). Based on direct comparison with *Apodemus* assemblages in the collection of Utrecht University, the material was assigned to *Apodemus atavus*.

Apodemus cf. flavicollis Melchior, 1834 (Fig. 3M)

Material and measurements. 1 M1 (2.05 × 1.37)

Description. The M1 is remarkably robust. A strong connection is present between the t2 and the t3. A weaker connection is present between t2 and t1. The accessory cusp t0 is absent. The cusps t4, t5, t6, t8 and t9 form a ring which has strong connections between them. Cusp t7 is isolated from the ring. A small posterior cingulum is present. The specimen has three roots.

Remarks. This molar cannot be placed with the other Bıçakçı *Apodemus* because of several morphological differences. First of all, the molar is larger than the *Apodemus atavus*. The molar is also more robust, and the t8 cusp has a strong connection with the rest of the ring of cusps, which is not the case in *A. atavus*. In size, the molar falls in the range of the measurements from Hatay, Turkey (Suata Alpaslan, 2011). The molar is both morphologically and in size quite similar to the Recent *A. flavicollis* from the Naturalis collection, in which, however, considerable intraspecific variability can be seen. Therefore, the Bıçakçı species cannot be confidently placed in the species *A. flavicollis* based on one molar only and is best classified as *Apodemus cf. flavicollis*.

Family Spalacidae Gray, 1821

Genus *Pliospalax* Kormos, 1932

Pliospalax sp. (Fig. 3S–V)

Table 7. Length and width measurements of *Apodemus atavus* from Bıçakçı

	Length			<i>N</i>	Width		
	Min	Mean	Max		Min	Mean	Max
M1	1.85	1.89	1.94	4	1.17	1.20	1.22
M2	1.24	1.33	1.40	5	1.15	1.17	1.23
m1	1.75	1.83	1.89	3	1.06	1.07	1.09
m2	—	1.24	—	1	—	1.02	—

Material. 2 M1, 1 M2, 1 M3, 1 m2

Measurements. The measurements are listed in Table 8.

Descriptions. Both M1 are quite worn. A deep lingual re-entrant fold is present in both specimens. The antero-labial and postero-labial folds have become enamel islets around the same wear stage of the molar. There is a plank-shaped root (consisting of two merged roots) on the lingual side of the molars and two roots with a circular cross section on the labial side.

The M2 is also in a quite worn state; just like the available M1, the occlusal surface is flat. The molar has a very deep lingual re-entrant fold, and two enamel islets on the labial side as remains of the antero-labial and postero-labial folds. The roots are similar to the roots of the M1. On the lingual side of the molar, there is a plank-shaped (merged) root, and there are two roots with a circular cross section on the labial side of the molar.

The M3 is shaped like a rounded triangle. The occlusal surface of this molar is flat. The molar is in such a far worn state that there are no re-entrant folds left. There is a triangular enamel islet in the centre of the crown surface. Just like in the other upper jaw molars, there is a plank-shaped (merged) root on the lingual side and two roots with a circular cross section on the labial side of the molar.

The m2 is relatively unworn. The occlusal surface of this molar is not flat, like the more worn upper jaw molars. The molar has one deep labial re-entrant fold; it closes at around one third from the crown basis up. The anterolingual re-entrant fold is quite deep and closes around half-way up the crown. The posterolingual fold is still present, which indicates that the molar represents a very young individual.

Table 8. Length and width measurements and the number of molars per element of *Pliospalax* sp. from Biçakçı. Measurements from *P. sotirisi* from Maritsa (De Bruijn *et al.*, 1970) are added for comparison

Element	Locality	Length				Width		
		Min	Mean	Max	N	Min	Mean	Max
M1	Biçakçı	1.95	1.96	1.97	2	1.65	1.66	1.68
	Maritsa	—	2.54	—	1	—	2.45	—
M2	Biçakçı	—	1.75	—	1	—	1.65	—
	Maritsa	1.93	1.95	1.96	3	2.25	2.36	2.54
M3	Biçakçı	—	1.51	—	1	—	1.34	—
	Maritsa	—	1.43	—	1	—	1.50	—
m1	Biçakçı	—	—	—	—	—	—	—
	Maritsa	—	2.00	—	1	—	1.65	—
m2	Biçakçı	—	1.48	—	1	—	1.33	—
	Maritsa	—	2.03	—	1	—	1.65	—
m3	Biçakçı	—	—	—	—	—	—	—
	Maritsa	—	—	—	—	—	—	—

Remarks. Kuss and Storch (1978) placed the genus *Pliospalax* and the species *Spalax* cf. *nehringi* and *Microspalax nehringi* in one group, *Spalax*. However, the difference in labial re-entrant folds seems to be a clear enough difference to distinguish between the groups even if the wear state is taken into account. *Pliospalax tourkobouniensis* from Tourkobounia-1 (De Bruijn and Van der Meulen, 1975) differs from the Biçakçı material in having a posterior cingulum and a mesoloph in the M1. For *Pliospalax macoveii* from Çalta (Şen, 1977), the same difference can be seen. Morphologically, the Biçakçı material is extremely similar to *Pliospalax sotirisi* from Maritsa (De Bruijn *et al.*, 1970). However, the Rhodes material is so much larger than the Biçakçı specimens that placement in the same species is not possible (Table 4). The sample is also too small to be able to describe a new species. The material is therefore assigned to *Pliospalax* sp.

Order Eulipotyphla Waddell, P. J., Okada, N. & Hasegawa, M., 1999

Family Soricidae Fischer, 1814

Subfamily Soricinae Fischer, 1814

Genus *Beremendia* Kormos, 1934

Beremendia sp. (Fig. 3W)

Material and measurements. 1 p4 (2.15 × 1.03)

Description. The p4 is a remarkably robust tooth. The tooth has a long labial arm compared to the lingual arm. Only one root is visible.

Remarks. A comparison was made with the *Beremendia fissidens* from Tegelen, described and measured by Reumer (1984). The teeth are quite similar in size but differ morphologically in some aspects, such as the length of the labial arm. Also, the Tegelen specimens appear to be more developed lingually.

Soricinae gen. et sp. indet. (Fig. 3X, Y)

Material and measurements. 1 (P4 BL 1.54, PE 0.87), 1 m1 (1.47 × 0.67 × 0.84)

Description. The P4 is slightly damaged under the hypocone. It is not very antero-posteriorly compressed. The protocone is quite high. The parastyle and the paracone are both quite high. The remainder of a valley separating the protocone and hypocone is visible. Part of the hypoconal flange is missing. The parastylar crest is quite low and also quite short.

The m1 is an elongated molar which has a long talonid and trigonid basin. A remarkable feature of the molar is that the hypolophid is directly connected to the lingual cingulum. No ectostylid is visible in between. The lingual cingulum itself is slightly developed. A short entoconid crest is visible, which is not very high. A weak buccal cingulum is present. A small mesoconid is visible on the oblique crest.

Remarks. The two specimens can be placed in the Soricinae because of the long talonid of the m1 and not much antero-posteriorly compressed P4 (Marc Furio, personal communication). A remarkable feature of the m1 is the hypolophid that is directly connected with the lingual cingulum, which to our knowledge is not known from any other Pleistocene shrew. This might indicate that we are dealing with a new taxon. However, the material is too limited for a species or even genus designation.

4. DISCUSSION

4.1. Age of the Bıçakçı fauna

The arvicoline association of Bıçakçı enables an accurate placement of the fauna in European and Eurasian biochronological schemes (Fig. 2). The dominant mimomyine voles are represented by hypsodont forms close in evolutionary level to voles of late Villanyian (MN17) faunas of Europe. Moreover, most vole species of the fauna are common in late Villanyian faunas of northwestern, central and eastern parts of Europe. Especially characteristic are large *Mimomys pliocaenicus*, *Mimomys* gr. *tornensis* and *Pitymimomys pitymyoides*. Lagurines are represented by the widespread late Villanyian species, *Borsodia* ex gr. *newtoni-arankoides*, and *Kalymnomys* sp., a form endemic to Anatolia, the Aegean islands and the Near East. *Kalymnomys* are known to characterize Biharian faunas of the region (Ünay and De Bruijn, 1998; Sarica, 2000). The primitive morphological stage of this vole, however, also indicates latest Villanyian. The primitive wood vole, *Clethrionomys kretzoi*, is more advanced in its hypsodonty stage than the late Villanyian conspecific forms (Tesakov, 1998) and less evolved than the Biharian *C. hintonianus*, thus also confirming the late Villanyian age of the fauna. In terms of small mammal regional biochronological units of Europe and western Asia, the Bıçakçı association matches MNR1 zone defined as the concurrent range zone of *Borsodia* gr. *newtoni-arankoides* and *Mimomys pliocaenicus* (Tesakov, 2004; Tesakov et al., 2007). The fauna also matches Zone P (*Mimomys pliocaenicus*–*Tibericola sakaryaensis*) of the Anatolian Neogene biozonation (Ünay et al., 2003). This zone can obviously be subdivided into subzones. The lower subzone, where the Bıçakçı fauna should be placed, is defined by the co-occurrence of *Mimomys pliocaenicus*, *Borsodia* and earliest *Kalymnomys*. The upper subzone hosts faunas with the first rootless Arvicolinae–*Tibericola* and *Allophaiomys* co-occurring with the advanced *Kalymnomys* major. Thus, the Bıçakçı arvicoline fauna immediately precedes the stage of dramatic restructuring of Holarctic small mammalian faunas near the Villanyian–Biharian transition marked by the mass

arrival of voles with rootless cheek dentitions such as *Allophaiomys*, *Prolagurus* and *Lagurodon*, and decline of primitive voles with rooted cheek dentitions (Tesakov, 2004; Martin et al., 2008). In the international chronostratigraphic scheme, the Bıçakçı assemblage correlates with the Early Pleistocene, latest Gelasian, and fits the time interval between ca. 2.2 and 1.9 Ma (Tesakov, 2004; Mayhew, 2013).

The other micromammals fit the age range indicated by the arvicolines. Two different species of murids have been found in the Bıçakçı material, *Apodemus atavus* and *Apodemus* sp. The last known record of *A. atavus* dates from the Early Pleistocene (Martín Suárez and Mein, 1998). It is considered a descendant of *A. dominans*, which lived throughout the Pliocene (Martín Suárez and Mein, 1998). In turn, *A. atavus* is believed to be the ancestor of *A. flavicollis* and *A. sylvaticus*. According to Martín Suárez and Mein (1998), these two extant species must have arisen after the Early Pleistocene. *Apodemus flavicollis* has been reported since the Pliocene, but in Anatolia, it is known since the Biharian (Suata Alpaslan, 2011). That would suggest that the *Apodemus* cf. *flavicollis* from Bıçakçı is the oldest known occurrence of this species in Anatolia. Co-existence of *A. atavus* and a species that resembles *A. flavicollis* closely confirms an age near the Villanyian/Biharian transition. The hamsters *Cricetulus* aff. *migratorius* and *Mesocricetus* aff. *primitivus* both represent, as could be expected, an evolutionary stage between the recent species and their Neogene ancestors. The rare elements in the Bıçakçı fauna are *Cricetus* sp., *Pliospalax* sp., *Beremendia* sp. and Soricinae indet. The hamster and the indeterminate shrew are not very indicative. However, *Pliospalax* ranges from Late Ruscinian to the Biharian (De Bruijn and Van der Meulen, 1975; Ünay and de Bruijn, 1998; Şen, 1977; Koufos, 2001), and the genus *Beremendia* is known from assemblages from the Pliocene to the Middle Pleistocene (Furió et al., 2010; Rofes and Cuenca-Bescós, 2009). Thus, for both taxa, the age Bıçakçı falls within the known range.

4.2. Palaeoecology

The most abundant groups from the locality of Bıçakçı are the arvicolines and the cricetids. Given that we are dealing with a Pleistocene fauna, the dominance of voles (63%) is hardly surprising. However, the high proportion of hamsters (27%) is remarkable. Murines (7%), spalacids (2%) and shrews (1%) only represent small constituents to the fauna.

According to García-Alix et al. (2008), *Cricetus*, *Cricetulus* and *Mesocricetus*, the three hamster genera found in Bıçakçı, all lived in an open steppe environment. The latter two have representatives living in Anatolia today; *Cricetus* has a bit more northern distribution and is found in eastern Europe and the open fields of the Ukraine. The presence of *Borsodia* certainly confirms the presence of an

open habitat. These primitive lagurines with rooted molars dominate most faunas of the steppe belt in middle latitudes of Eurasia throughout the Late Pliocene and beginning of Early Pleistocene (Tesakov, 1993). The group is ancestral to Pleistocene to Recent steppe-lemmings or lagurines specialized to steppe and semi-desert open habitats. However, *Borsodia* is only present in small numbers (2%). The most common vole is *Kalymnomys* (19%). Unfortunately, its environmental preferences are not known. However, by analogy with Early Pleistocene to Recent 'steppe-lemmings' of the tribe Lagurini, the rootless dentition of *Kalymnomys* suggests a preference for open steppe-like habitats. The same holds presumably true for *Pliospalax* (5%). The subterranean rodent is extinct, but its extant relative *Spalax* inhabits the open fields and grass steppes of southeastern Europe (Nowak, 1991).

Mimomys pliocaenicus is well represented in the fauna (11%). Based on its size, this large vole is commonly interpreted to be related in its ecology to riverine and lacustrine habitats. Some populations of this species group may have been ancestral to European water vole *Arvicola*. Given the sedimentology of the site, the presence of a semi-aquatic species is hardly surprising, and presumably it lived close to the area of deposition. *Mimomys* gr. *tornensis* strongly resembles in its molar morphology the rootless *Microtus s.l.* of Early Pleistocene to Recent and has been suggested to be ancestral to common voles *s.l.* (Rabeder, 1986; Tesakov, 1998). Thus, it is probable that this species, accounting for 15% of the Bıçakçı fauna, indicates meadow habitats characteristic for many extant species of *Microtus*. Such meadows can easily be envisioned in the direct surroundings of the lake.

More puzzling is the high proportion of *Clethrionomys* (14%). *Clethrionomys kretzoi* shows strong similarity to the modern European bank vole that inhabits broad-leaved and mixed forests under temperate climatic conditions and is considered the direct Early Pleistocene ancestor (chronospecies) of the modern *C. glareolus* (Carls and Rabeder, 1988; Tesakov, 1996). Thus, *C. kretzoi* indicates the presence of a wooded environment. The same holds true for the two species of *Apodemus*, which together constitute 7% of the fauna. Although some of the recent species of *Apodemus* can also survive in scrublands, extant *Clethrionomys* is associated with relatively moist woodlands (Torre and Arrizabalaga, 2008).

Overall, the micromammals give a mixed picture of the palaeoenvironment, in which the representatives of a steppe environment hold the majority. Also, the virtual absence of insectivores argues for a relatively dry environment. Moreover, one of the two insectivores found is a species of *Beremendia*, which is considered to be an opportunistic shrew (Reumer, 1984; Furió *et al.*, 2010), capable of surviving under relatively harsh conditions.

On the other hand, *Clethrionomys* and *Apodemus* require woodlands. This mixture could result from mixing material from different periods, but as the faunal composition consistently indicates the same age, a spatial separation of the two habitats is more probable. The Çameli Basin lies in a mountainous region, in which different environments can be found at a relatively short distance. If this is the case, the presumed agent of accumulation for most micromammal assemblages, the pellets of owls and raptors, would cause a bias in the thanatocoenosis. Open fields provide a far more suitable hunting environment for birds of prey than forest, leading to an overrepresentation of the rodents indicating an open environment. In order to get a more comprehensive view of the palaeoenvironment of the site, a paper comparing the results from different proxies is being prepared (Wesselingh *et al.*, research in progress).

5. CONCLUSIONS

The new locality of Bıçakçı has yielded a diverse micromammal assemblage, providing a glimpse of the Anatolian small mammal community at the very end of the Early Pleistocene. The age of the site is based on the stage of evolution of the rodent assemblage and fits the MNR 1 zone in the biochronology of Europe and western Asia. In the Anatolian mammal zonation of Ünay *et al.* (2003), it fits the lower part of zone P. The high proportion of steppe elements and the very few finds of insectivores suggest a dry, open landscape. However, *Clethrionomys* is well represented in the assemblage, which indicates that woodlands were present in the surroundings of the site.

ACKNOWLEDGEMENTS

It is with great pleasure that we dedicate this paper to Andy Currant, for his contributions to the field of vertebrate palaeontology as a scientist, but also as a splendid host for many colleagues. Hans de Bruijn helped with the identification of the Muridae molars and allowed access to the University of Utrecht collection. Marc Furió offered advice in determining soricids. A. Tesakov and M. C. Alcicek benefited from bilateral project of TUBITAK-RFBR (111Y192), and MCA was additionally granted by TUBA-GEBIP (Outstanding Young Scientist Award by the Turkish Academy of Sciences). The paper was reviewed by Bob Martin, Steve Donovan and Simon Parfitt. Their help is greatly appreciated. Delia van Oijen assisted in making the photographs and plate of the non-voles. We would like to acknowledge the grants of SYTHESYS and Martin/Temmick by NATURALIS.

REFERENCES

- Alexandrova, L.P. 1976.** *Rodents of Anthropogene of the European Part of the USSR*. Moscow: Nauka.
- Alçiçek, M.C. 2001.** *Sedimentological investigation of Çameli basin (Late Miocene–Late Pliocene, Denizli, SW Anatolia)*. Unpublished PhD thesis, Ankara University.
- Alçiçek, M.C., Kazancı, N., Özkul, M. 2005.** Multiple rifting pulses and sedimentation pattern in the Çameli basin, southwestern Anatolia, Turkey. *Sedimentary Geology* **173**, 409–431.
- Alpaslan, F.S., Ünay, E., Ay, F. 2010.** İğdeli (Gemerek, Sivas) Lokalitesi Erken Pliyosen Fauna İstifinin Rodentia ve Lagomorpha (Mammalia) Fosilleri: Biyokronolojik ve Paleobiyoçografik Anlamları. [The Rodentia and Lagomorpha (Mammalia) from the Early Pliocene from İğdeli (Gemerek, Sivas): biochronological and paleogeographical implications.] *Fen Bilimleri Dergisi* **31**, 1–29. [in Turkish]
- Bowdich, T.E. 1821.** *An Analysis of the Natural Classifications of Mammalia, for the Use of Students and Travelers*. Paris: J. Smith.
- Carls, N., Rabeder, G. 1988.** Die Arvicoliden (Rodentia, Mammalia) aus dem Ältest-Pleistozän von Schernfeld (Bayern). *Beiträge zur Paläontologie von Österreich* **14**, 123–237.
- Cuenca-Bescós, G. 2003.** Análisis filogenético de *Allocricetus* del Pleistoceno (Cricetidae, Rodentia, Mammalia). *Coloquios de Paleontología* **1**, 95–113.
- De Bruijn, H., Dawson, M.R., Mein, P. 1970.** Upper Pliocene Rodentia, Lagomorpha and Insectivora (Mammalia) from the Isle of Rhodes (Greece). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B* **73**, 535–584.
- De Bruijn, H., Mayda S., Hoek Ostende, L.W. van den, Kaya, T., Saraç, G. 2006.** Small mammals from the Early Miocene of Sabuncubeli (Manisa, S.W. Anatolia, Turkey). *Beiträge zur Paläontologie* **30**, 57–87.
- De Bruijn, H., G. Saraç 1991.** Early Miocene rodent faunas from the eastern Mediterranean area. Part I. The genus *Eumyarion*. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, **94**, 1–36.
- De Bruijn, H., G. Saraç 1992.** Early Miocene rodent faunas from the eastern Mediterranean area. Part II. *Mirabella*. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* **95**, 25–40.
- De Bruijn, H., Van der Meulen, A.J. 1975.** The Early Pleistocene rodents from Tourkobounia-1 (Athens, Greece). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B*, **78**, 314–338.
- De Bruijn, H. de, Ünay, E., van den Hoek Ostende, L.W., Saraç, G. 1992.** A new association of small mammals from the lowermost Lower Miocene of Central Anatolia. *Geobios* **25**, 651–670.
- Engesser, B. 1980.** Insectivora and Chiroptera (Mammalia) aus dem Neogen der Türkei. *Schweizerische Paläontologische Abhandlungen* **102**, 37–363.
- Fischer, J.G. 1814.** *Zoognosia tabulis synopticis illustrata, in usum praeractionum academiae imperialis medico-chirurgicae Mosquensis edita. Volumen tertium. Quadrupedum reliquorum, cetorum et montrymatum descriptionem continens*. Moscow: Nicolai Sergeidis Vsevolosky.
- Fischer, G. 1817.** Adversaria zoologica. *Mémoires de la Société Impériale des Naturalistes Moscou* **5**, 357–472.
- Forsyth Major, C. 1902.** Exhibition on and remarks upon some jaws and teeth of Pliocene voles (*Mimomys* gen. nov.). *Proceedings of the Zoological Society of London* **1902**, 102–107.
- Furió, M., Agustí, J., Mouskhelishvili, A., Sanisidro, Ó., Santos-Cubedo, A. 2010.** The paleobiology of the extinct venomous shrew *Beremendia* (Soricidae, Insectivora, Mammalia) in relation to the geology and paleoenvironment of Dmanisi (Early Pleistocene, Georgia). *Journal of Vertebrate Paleontology* **30**, 928–942.
- García-Alix, A., Minwer-Barakat, R., Martín Suárez, E., Freudenthal, M., Martín, J.M. 2008.** Late Miocene–Early Pliocene climatic evolution of the Granada Basin (southern Spain) deduced from the paleoecology of the micromammal associations. *Palaeogeography, Palaeoclimatology, Palaeoecology* **265**, 214–225.
- Gray, J.E. 1821.** On the natural arrangement of vertebrate animals. *London Medical Repository* **15**(1), 296–310.
- Heller, F. 1936.** *Eine Forest Bed-Fauna aus der Schwäbischen Alb*. *Sitzungsberichte der Heidelberger Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse* **1936**, 1–29.
- Hír, J. 1992.** Subfossil *Mesocricetus* population from the Toros Mountains (Turkey)(Mammalia). *Folia Historico Naturalia Musei Matraensis* **17**, 107–130.
- Hír, J. 1993.** *Cricetulus migratorius* (PALLAS 1773) (Rodentia, Mammalia) population from the Toros Mountains (Turkey) (with a special reference to the relation of *Cricetulus* and *Allocricetus* genera). *Folia Historico Naturalia Musei Matraensis* **18**, 17–34.
- Illiger, C. 1811.** *Prodromus systematis mammalium et avium additis terminis zoographicis utriusque classis*. Berlin: C. Salfield.
- Janossy, D., Van der Meulen, A.J. 1975.** On *Mimomys* (Rodentia) from Osztramos-3, north Hungary. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B* **78**, 381–391.
- Kappelman, J., Alçiçek, M.C., Kazancı, N., Schultz, M., Özkul, M., Şen, Ş. 2008.** First *Homo erectus* from Turkey and implications for migrations into temperate Eurasia. *American Journal of Physical Anthropology* **135**, 110–116.
- Kaup, J. 1829.** *Skizzierte Entwicklungsgeschichte und Natürliches System der Europäischen Thierwelt*. Darmstadt/Leipzig: C.W. Leske.
- Konak N., Şenel, M. 2002.** *Geological map of Turkey in 1/500.000 scale: Denizli sheet*. Publication of Mineral Research and Exploration Directorate of Turkey.
- Kormos, T. 1932.** Neue Pliozäne Nagetiere aus der Moldau. *Paläontologische Zeitschrift* **14**, 193–200.
- Kormos, T. 1934.** Neue Insektenfresser, Fledermäuse und Nager aus dem Oberpliozän der Villanyer Gegend. *Földtani Közlemények* **64**, 296–321.
- Kościów, R., Nadachowski, A. 2002.** Type populations of some *Mimomys* species (Arvicolidae, Rodentia) at the Pliocene/Pleistocene boundary in Central Europe. *Folia Zoologica* **51**(Supplement 1), 93–104.
- Koufos, G.D. 2001.** The Villafranchian mammalian faunas and biochronology of Greece. *Bollettino della Società Paleontologica Italiana* **40**, 217–223.
- Kowalski, K. 1958.** An Early Pleistocene fauna of small mammals from the Kadzielnia Hill in Kielce (Poland). *Acta Palaeontologica Polonica* **3**, 25–41.
- Kuss, S.E., Storch, G. 1978.** Eine Säugetierfauna (Mammalia: Artiodactyla, Rodentia) des älteren Pleistozäns von der Insel Kalymnos (Dodekanés, Griechenland). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* **4**, 206–227.
- Leske, N.G. 1779.** *Anfangsgründe der Naturgeschichte*. Leipzig: S.L. Crusius.
- Linnaeus, C. 1758.** *Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomis I*. Stockholm: Laurentii Salvii, Holmiae.
- Martin, R.A., Peláez-Campomanes, P., Honey, J.G., Fox, D.L., Zakrzewski, R.J., Albright, L.B., Lindsay, E.H., Opdyke, N.D., Goodwin, H.T. 2008.** Rodent community change at the Pliocene–Pleistocene transition in southwestern Kansas and identification of the *Microtus* immigration event on the Central Great Plains. *Palaeogeography, Palaeoclimatology, Palaeoecology* **267**, 196–207.
- Martin Suárez, E., Mein, P. 1998.** Revision of the genera *Parapodemus*, *Apodemus*, *Rhagamys* and *Rhagapodemus* (Rodentia, Mammalia). *Geobios* **31**, 87–97.
- Mayhew, D.F. 1978.** Late Pleistocene small mammals from Arnissa (Macedonia, Greece). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B* **81**, 302–321.
- Mayhew, D.F. 2013.** West European arvicolid evidence of intercontinental connections during the Early Pleistocene. *Quaternary International* **284**, 62–73.
- Mayhew, D.F., Stuart, A.J. 1986.** Stratigraphic and taxonomic revision of the fossil vole remains (Rodentia, Microtinae) from the lower Pleistocene deposits of Eastern England. *Philosophical Transactions of the Royal Society of London B* **312**, 431–485.
- Melchior, H.B. 1834.** *Den Danske Stats og Norges Pattedyr* [Mammals of Denmark and Norway]. Copenhagen: Gyldendalske Forlag.
- Milne-Edwards, A. 1867.** Observations sur quelques mammifères du nord de la Chine. *Annales des sciences naturelles. Zoologie et biologie animale* **7**(5), 375–377.

- Nehring, A. 1898. Über *Cricetus*, *Cricetulus* und *Mesocricetus* n. subg. *Zoologischer Anzeiger* **21**, 493–495.
- Nowak, R.M. 1991. *Walker's Mammals of the World (5th edition, Volumes I & II)*. Baltimore: Johns Hopkins University Press.
- Pallas, P.S. 1773. *Reise durch verschiedene Provinzen des Russischen Reichs, Vol. 2*. St. Petersburg: Russian Academie of Sciences.
- Pradel, A. 1981. Biometrical remarks on the hamster *Cricetulus migratorius* (Pallas, 1773) (Rodentia, Mammalia) from Morovitsa Cave (North Bulgaria). *Acta Zoologica Cracoviensia* **32**(13), 271–292.
- Rabeder, G. 1981. Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. *Beiträge zur Paläontologie Österreich* **8**, 1–373.
- Rabeder, G. 1986. Herkunft und frühe Evolution der Gattung *Microtus* (Arvicolidae, Rodentia). *Zeitschrift für Säugetierkunde (Mammalian Biology)* **51**, 350–367.
- Reumer, J.W.F. 1984. Ruscinian and early Pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (The Netherlands) and Hungary. *Scripta Geologica* **73**, 1–173.
- Rofes, J., Cuenca-Bescós, G. 2009. First record of *Beremendia fissidens* (Mammalia, Soricidae) in the Pleistocene of the Iberian Peninsula, with a review of the biostratigraphy, biogeography and palaeoecology of the species. *C. R. Palevol* **8**, 21–37.
- Saraç, G. 2003. *Türkiye Omurgalı Fossil Yatakları. Mineral Research and Exploration Directory Turkey (MTA), Scientific Report 10609*, 208 pp. [in Turkish].
- Sarica, N. 2000. The Plio-Pleistocene age of Büyük Menderes and Gediz grabens and their tectonic significance on N–S extensional tectonics in West Anatolia: mammalian evidence from the continental deposits. *Geological Journal* **35**, 1–24.
- Schaub, S. 1930. Quartäre und jungtertiäre Hamster. *Abhandlungen der Schweizerische Paläontologische Gesellschaft* **49** (6), 1–49.
- Şen, Ş. 1977. La faune de Rongeurs pliocènes de Çalta (Ankara, Turquie). *Bulletin du Muséum National d'Histoire Naturelle* **465**, 89–171.
- Suata Alpaslan, F. 2011. Some small mammal fossils of Üçağızlı Cave (Hatay, Turkey). *Turkish Journal of Zoology* **35**, 755–768.
- Tchernov, E. 1968. Succession of rodent faunas during the Upper Pleistocene of Israel. *Mammalia depicta* **3**, 1–152.
- Tesakov, A.S. 1993. Evolution of *Borsodia* (Arvicolidae, Mammalia) in the Villanyian and in the Early Biharian. *Quaternary International* **19**, 41–45.
- Tesakov, A.S. 1996. Evolution of the bank voles (Clethrionomys, Arvicolidae). *Acta Zoologica Cracoviensia* **39**, 541–547.
- Tesakov, A.S. 1998. Voles of the Tegelen fauna. *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO* **60**, 71–134.
- Tesakov, A.S. 2004. *Biostratigrafiya srednego plio-tsena—eopleistotsena vostochnoi Evropy [Biostratigraphy of the Middle Pliocene–Eopleistocene of Eastern Europe]*. Russian Academy of Sciences, Transactions of the Geological Institute Nauka **554**, 1–247. [In Russian]
- Tesakov, A.S., Lebedev, V.S., Bannikova, A.A., Abramson, N.I. 2010. *Clethrionomys* Tilesius, 1850 is the valid generic name for red-backed voles and *Myodes* Pallas, 1811 is a junior synonym of *Lemmus* Link, 1795. *Russian Journal of Theriology* **9**(2), 83–86.
- Tesakov A.S., Vangengeim, E.A., Pevzner, M.A. 2007. Arvicolid zonation of continental Pliocene of East Europe. *Courier Forschungsinstitut Senckenberg* **259**, 227–236.
- Tilesius, W.G. 1850. Gliriumspecies in Bavaria nonnullae. *Isis* **2**, 27–29.
- Torre, I., Arrizabalaga A. 2008. Habitat preferences of the bank vole *Myodes glareolus* in a Mediterranean mountain range. *Acta Theriologica* **53**, 241–250.
- Ünay, E., De Bruijn, H. 1998. Plio-Pleistocene rodents and lagomorphs from Anatolia. *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO* **60**, 431–466.
- Ünay, E., de Bruijn, H., Saraç, G. 2003. A preliminary zonation of the continental Neogene of Anatolia based on rodents. In: *Distribution and Migration of Neogene Mammals in Eurasia*, Reumer, J.W.F., Wessels, W. (eds.). *Deinsea* **10**: 530–547.
- Ünay, E., Göktas, F., Hakyemez, H.Y., Avsar, H., San, Ö. 1995. Dating the sediments exposed at the northern part of the Büyük Menderes Graben (Turkey) on the basis of Arvicolidae (Rodentia, Mammalia). *Geological Bulletin of Turkey* **38**, 63–68.
- Van den Hoek Ostende, L.W. 1992. Insectivore faunas of the Lower Miocene of Anatolia. Part 1: Erinaceidae. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* **94**, 437–467.
- Van den Hoek Ostende, L.W. 1995a. Insectivore faunas from the Lower Miocene of Anatolia. part 2: Heterosoricidae. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* **98**, 1–18.
- Van den Hoek Ostende, L.W. 1995b. Insectivore faunas from the Lower Miocene of Anatolia. part 3: Dimylidae. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* **98**, 19–38.
- Van den Hoek Ostende, L.W. 1997. Insectivore faunas from the Lower Miocene of Anatolia. Part 4. The genus *Desmanodon*, with the description of a new species from the Lower Miocene of Spain. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* **100**, 27–65.
- Van der Meulen, A.J. 1973. Middle Pleistocene smaller mammals from the Monte Peglia (Orvieto, Italy) with special reference to the phylogeny of *Microtus* (Arvicolidae, Rodentia). *Quaternaria* **17**, 144.
- von Koenigswald, W., Fejfar, O., Tschernov, E. 1992. Revision einiger alt- und mittelpleistozäner Arvicoliden Rodentia, Mammalia aus dem östlichen Mittelmeergebiet (Ubeidiya, Jerusalem und Kalymnos-Xi). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **184**, 1–23.
- Waddell, P.J., Okada, N., Hasegawa, M. 1999. Towards resolving the interordinal relationships of placental mammals. *Systematic Biology* **48**(1), 1–5.
- Wilson, D.E., Reeder, D.M. (eds) 2005. *Mammal Species of the World. A Taxonomic and Geographic Reference* (3rd edition). Baltimore: Johns Hopkins University Press.