

# Rodents from the Upper Miocene Tuğlu Formation (Çankırı Basin, Central Anatolia, Turkey)

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**Abstract** The upper Miocene assemblages of rodents collected from two layers of the type section of the Tuğlu Formation (Çankırı Basin, Central Anatolia, Turkey) are described. The assemblage from the lower level is considerably less diverse than that from the upper level. It contains *Progonomys* together with *Megacricetodon*, which is a very unusual association. The assemblage from the upper layer shows a relatively high diversity with four species of Gliridae instead of only one in the lower layer. Apart from the more diverse Gliridae, *Byzantinia* sp., *Spermophilinus*, *Keramidomys* and *Myocricetodon* appear in the upper layer. The absence of Murinae in the assemblage from the upper layer is very unexpected, because they usually become dominant soon after their arrival. Their unusual subsequent absence may be either due to a significant change from an open and humid environment to a more dry and wooded environment or to taphonomic bias. Both rodent faunas are assigned to local zone I, which is correlated to the lower Vallesian (MN9).

**Keywords** Central Anatolia · Late Miocene · Rodentia · Biostratigraphy

**Kurzfassung** Die obermiozänen Vergesellschaftungen von Rodentia aus zwei Lagen des Typus-Profiles der Tuğlu-Formation (Çankırı-Becken, zentral-Anatolien, Türkei) werden beschrieben. Die Vergesellschaftung der

unteren Lage ist deutlich weniger divers als jene aus der oberen Lage. Sie beinhaltet *Progonomys* zusammen mit *Megacricetodon*, was eine ungewöhnliche Assoziation darstellt. Die Vergesellschaftung aus der oberen Lage zeigt eine relativ hohe Diversität, mit vier Arten der Gliridae, gegenüber nur einer in der unteren Lage. Neben den diversen Gliriden kommen in der oberen Lage *Byzantinia* sp., *Spermophilinus*, *Keramidomys* und *Myocricetodon* vor. Das Fehlen der Murinae in der oberen Lage ist unerwartet, da diese üblicherweise schon bald nach ihrem Auftauchen dominant werden. Ihre ungewöhnliche Abwesenheit mag entweder auf einen drastischen Wechsel von einem offenen, humiden Lebensraum zu einem trockenen und bewaldeten Lebensraum oder auf einen taphonomischen Artefakt zurückzuführen sein. Beide Rodentier-Faunen werden der lokalen Zone I zugeordnet, die mit dem unteren Vallesium (MN9) korreliert ist.

**Schlüsselwörter** Zentralanatolien · Obermiozän · Rodentia · Biostratigraphie

## Introduction

An international interdisciplinary research team studied a number of Neogene key sections in the Çankırı Basin (Central Anatolia) within the framework of the VAMP project (Vertical Anatolian Movements Project) of the EUROCORES Topo-Europe program during the summers of 2008–2011. The aim of this article is to study the rodent assemblages from the fluvio-lacustrine deposits of a 24-m thick type section of the Tuğlu Formation, which yielded ostracods, benthic foraminifera, nannoplankton, charophytes, mollusks, fish remains, palynomorphs, crabs and micromammals (Mazzini et al. 2013; Kováčová et al.

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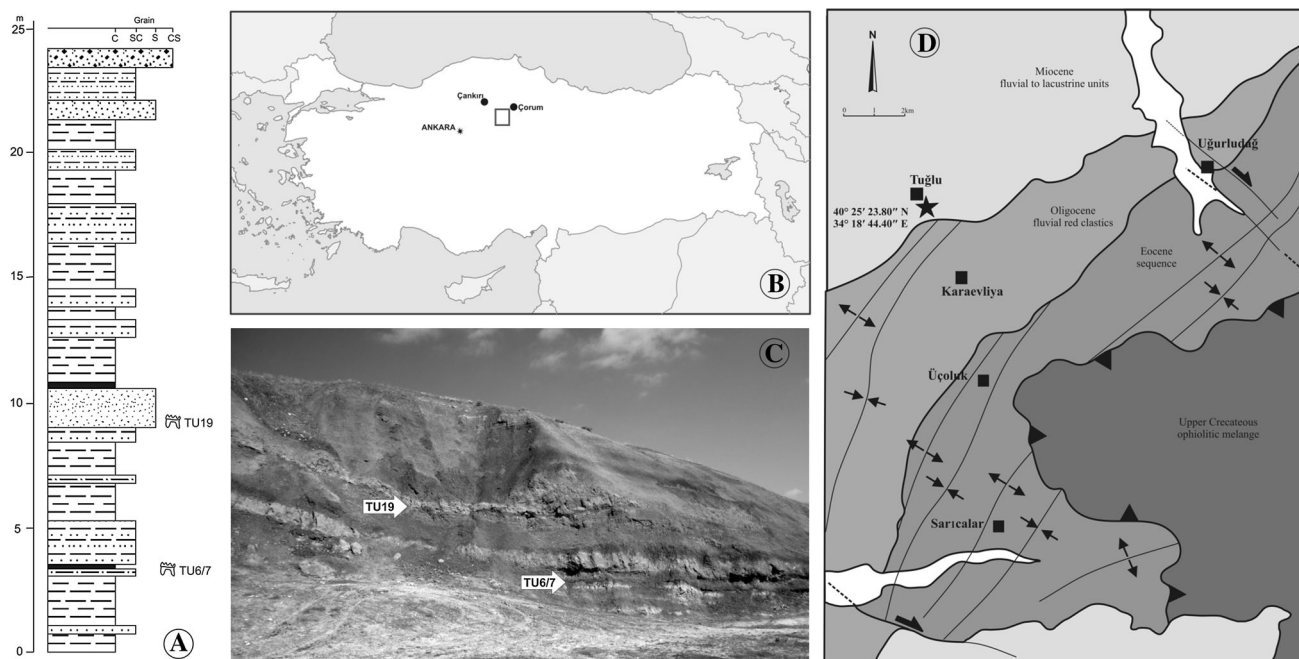
2010). The section, which is situated just south of the village Tuğlu (Fig. 1), is characterized by a succession of clays, silty and sandy clays, with patchy sand bodies. The age assigned to these deposits on the basis of a small micro-mammal assemblage collected from the bottom of the section in the late 1990s was Tortonian (de Bruijn in Kaymakçı 2000). The mammal remains were identified at the time as: *Parapodemus* sp., Cricetinae gen. indet., *Byzantinia* sp., *Zapodidea* gen. indet., *Myomimus* sp., *Schizogalerix* sp. and erinaceid indet. and evaluated as Late Miocene, Late Vallesian (MN10). The material that will be described below originates from two fossiliferous levels. The lower one (layer TU6/7) is exposed near the bottom of the section (all teeth collected in the late 1990s by HdB from this layer are included in the collection described from layer TU6/7), and the upper one (layer TU19) is situated approximately in the middle of the section (Fig. 1). The rodent teeth collected from these two levels allow a re-evaluation of the age of the deposits and suggest an older age than previously assumed.

## Methods

At least 2 tons of clay from each layer (TU19 and TU6/7) was sieved on a set of stable sieves (Daams and Freudenthal 1988) during the 2008–2011 fieldwork. The residue was subsequently dried, and the fossil remains were picked

manually. More than 300 teeth of rodents and insectivores, including a few specimens from the old collection, were recovered. The study of the insectivores is out of the scope of the present article.

The material described, including casts of the material collected by Hans de Bruijn (HdB), is housed in the collection of the Department of Geology and Paleontology of Comenius University, Bratislava, Slovakia. The original fauna collected by HdB is kept in the Natural History Museum of the MTA in Ankara, Turkey. Upper cheek teeth are indicated by upper case (P4, M1, M2, M3), lower cheek teeth by lower case (p4, m1, m2, m3). In case the distinction between first and second molars is questionable, they are indicated as m1/2 or M1/2. The measurements of the teeth were taken with a calibrated micrometer eyepiece on a Leica MZ75 stereomicroscope and in some cases on an analytical SEM microscope (Hitachi VP-SEM S-3700 N). The measurements taken are the maximum length (*L*) and width (*W*) of the occlusal surface of the cheek teeth. The results are given in mm. The terminology used for parts of the cheek teeth follows Daams and Freudenthal (1988) and Freudenthal et al. (1994) for the Cricetidae, de Bruijn (1967) for the Gliridae, Van de Weerd (1976) for the Murinae, Engesser (1990) for the Eomyidae and Cuenca Bescós (1988) for the Sciuridae. The taxa have been studied by comparison with material available at Utrecht University and using data available in the published descriptions of their type localities.



**Fig. 1** a The stratigraphic column of the section. b Map with the location of the Tuğlu locality. c Picture of the Tuğlu section with marked fossiliferous layers TU19 and TU6/7. d Schematic geological map of the Tuğlu section area with undifferentiated Miocene deposits

## Systematic paleontology

Order Rodentia Bowdich, 1821

Family Muridae Illiger, 1811

Subfamily Murinae Illiger, 1811

Genus *Progonomys* Schaub, 1938

*Progonomys cathalai* Schaub, 1938

(Plate 1, figs. 1–5)

## Material

TU6/7 1 M1 (TG010109), 2 M2 (TG010111, TG010112), 4 m1 (TG010101–0104), 2 m2 (TG010105, TG010106), 2 m3 (TG010107, TG010108). Measurements are in Table 1.

## Description

**M1** Only one specimen with a broken anterior part was found. Its t1 is placed posteriorly to t2 and t3. The t2 and t3 are broken; only their posterior parts are preserved. On the labial border next to the t3, a small t3 bis is developed. The valley between t1–t2–t3 and t4–t5–t6 is continuous, but very narrow between the t2 and t5. The t5 is situated more anteriorly than t6. The t4 is elongated and connected to the t5 by a ridge of medium height. The t6 and t9 are not connected. The t4 is connected to the t8 by a low ridge. The t9 is considerably smaller than the t8. The t12 is short, ridge-like and only connected to the t8. The roots of the M1 are not preserved.

**M2** The two specimens are very similar in morphology. The t3 is a small cusp placed more posteriorly than the t1 and t1 bis. The connection between the t3 and t1 bis is low and forms a narrow ridge in front of t5. The t4 has a posterior spur that reaches the t8. In one specimen this ridge is connected to a small spur of the t8. The t5 and t8 are about the same size. In one specimen there is a low connection between t6 and t9; in other this connection is absent. The t12 is ridge-like and connected to the t8. The roots of the M2 are not preserved.

**m1** The occlusal surface has a sub-elliptical outline. The lingual cusp of the anteroconid is slightly larger than the labial cusp in all specimens. The antero-central cusp (tma) is absent in three specimens, but in one specimen a small ridge-like structure is present. A low ridge is connecting the lingual anteroconid and metaconid. A low connection between the labial anteroconid and protoconid, which is present in two m1s, closes a small enamel lake. The labial and lingual anteroconid are divided by a shallow valley, so a connection is developed in the more worn specimens. The protoconid and metaconid, as well as the hypoconid and the entoconid, are connected by a ridge. The longitudinal ridge is absent. Two accessory labial cusps are present in three specimens. One is a small oval cusp that is

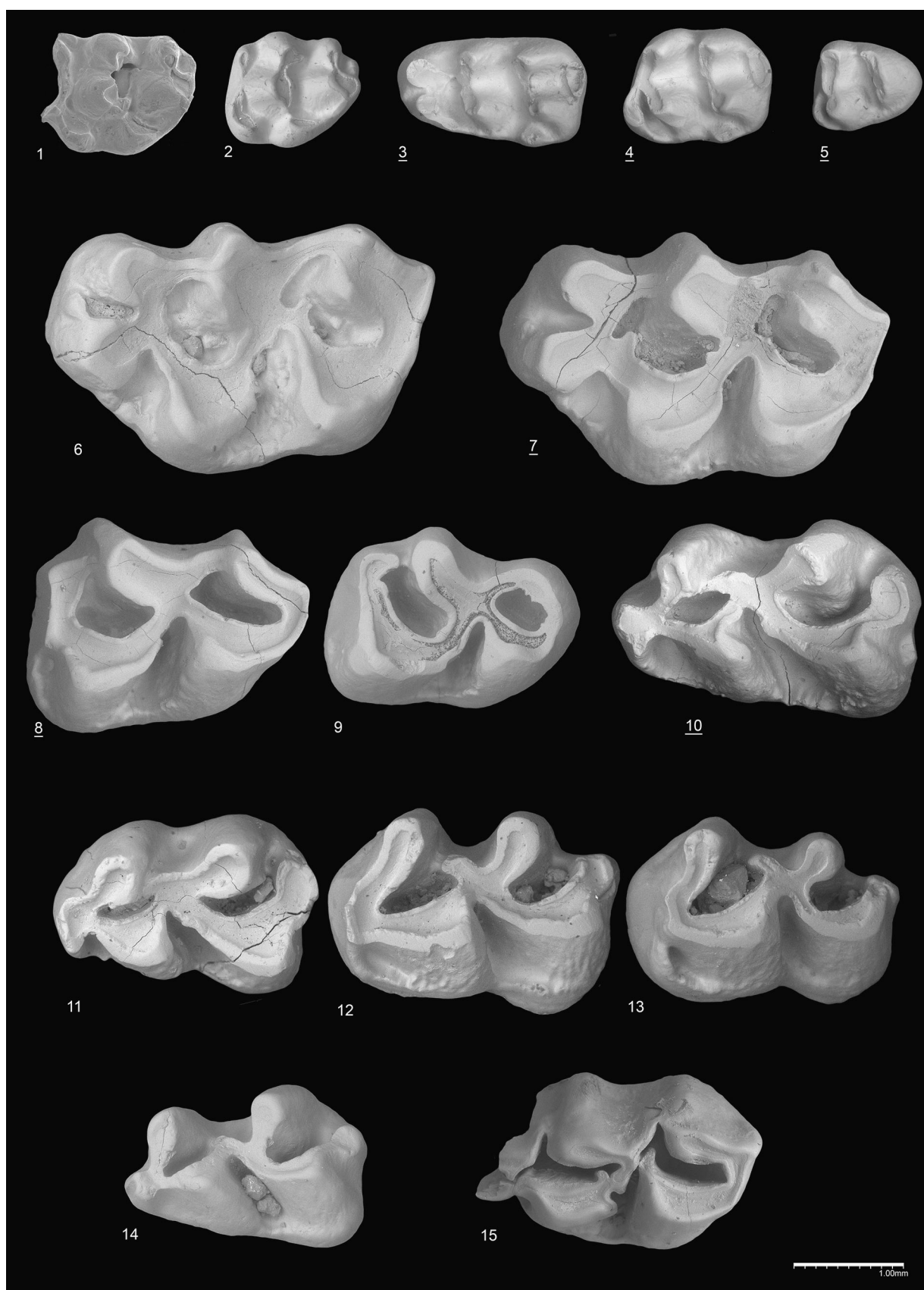
incorporated into the antero-labial cingulum. The c1 is developed as a small independent cusp and connected to the base of the hypoconid by a low ridge. In one specimen there is only a cingulum descending from the anteroconid to the protoconid. On this specimen, the c1 is present, but small and worn. The oval terminal heel is well developed, but deeply worn. The m1 has two roots.

**m2** Both specimens have the same morphology. The antero-labial cusp is elongated and connected to the ridge between the metaconid and protoconid. The hypoconid and entoconid are connected. Among the accessory cusps, only the c1 is developed as an isolated cusp. Because the longitudinal crest is absent, the sinusid is continuous from the labial to lingual border. The terminal heel is oval and deeply worn. The m2 has two roots.

**m3** Both specimens have the same morphology. Their outline is sub-triangular. The strong antero-labial cusp is connected to the ridge between the metaconid and protoconid. This connection is lower in the m3 than in the m2. The hypoconid and entoconid are fused. The longitudinal crest is absent. The entoconid is shifted anteriorly and connected to the metaconid. The central sinusid is continuous, but closed along the lingual border. The m3 has two roots.

## Comments

*Progonomys* was only found in the lower layer (TU6/7). All but one (m1 TG010101) of the eleven teeth correspond in size with the type material of *P. cathalai* from Montredon (France). The broken M1 (TG010109) shows all the characteristics of *P. cathalai*: a connection between the t1 and t2, absence of t1 bis, medium high connection between the t4 and the t5, the t4 connected to the t8 by a low ridge, absence of the t7 and separation of the t6 and t9 in M1 and M2. The lower molars are morphologically very close to the type material too; the connection between the antero-lingual cusp and metaconid is present in two out of four specimens only. Wessels (2009) gave a detailed description of the variation in the *Progonomys cathalai* material from the Turkish localities Altıntaş 1, 2 and Kütahya. She demonstrated that the presence/absence of the connection between the labial anteroconid and protoconid and between the anteroconid and metaconid are variable characters within single populations. Sen (2003) erected the species *P. minus*, which is smaller than *P. cathalai* and lacks the connection between the anteroconid and metaconid of the m1. One specimen from TU6/7 is considerably smaller (TG010101) than the others and shows low connections between the labial anteroconid and the protoconid and between the lingual anteroconid and the metaconid. This specimen falls within the lower part of the size range of *P. cathalai* from Altıntaş 1, 2 and Kütahya 1. Wessels (2009)



**Plate 1** *Progonomys cathalai*: 1 TG6/7 M1 (TG010109); 2 TG6/7 M2 (TG010111); 3 TG6/7 m1 (TG010103); 4 TG6/7 m2 (TG010106); 5 TG6/7 m3 (TG010108). *Byzantinia bayraktepens*: 6 TG19 M1 (TG020610); 7 TG19 M1 (TG020601); 8 TG19 M2 (TG020621); 9 TG19 M3 (TG020637); 10 TG6/7 m1 (TG010401); 11 TG19 m1 (TG020648a); 12 TG19 m2 (TG020648b); 13 TG19 m3 (TG020648c). *Byzantinia* sp.: 14 TG19 m1 (TG020655); 15 TG19 M1 (TG020615). *Underlined numbers* indicate reversed specimens

**Table 1** Measurements of *Progonomys cathalai* from layer TU6/7

	Length				Width			
	N	Min	Mean	Max	N	Min	Mean	Max
M1	0	–	–	–	1	1.17	1.17	1.17
M2	2	1.24	1.30	1.36	2	1.06	1.06	1.06
m1	4	1.52	1.65	1.72	4	0.83	0.95	1.03
m2	2	1.34	1.36	1.38	2	1.05	1.06	1.06
m3	2	0.97	0.98	0.99	2	0.82	0.83	0.83

considers *P. minus* a junior synonym of *P. cathalai* or *P. debruijni*. We agree with this opinion and include the smallest specimen from TU6/7 in the population of *P. cathalai*.

Subfamily Cricetodontinae Schaub 1925

Genus *Byzantinia* de Bruijn 1976

*Byzantinia bayraktepens* Ünay 1980

(Plate 1, figs. 6–13)

## Material

TU6/7 2 fragments of M1 (TG010410, TG010412), 1 M2 (TG010408 2.47 × 1.62), 2 m1 (TG010401 2.48 × 1.83; 1 fragment of anterior part of m1 TG010409), 1 fragment of anterior part of m2 (TG010403), 2 m3 (TG010404 2.46 × 1.62; TG010411 2.33 × –).

TU19 14 M1 (TG020601–020614), 10 M2 (TG020620–020629), 14 M3 (TG0206030–020643), 12 m1 (TG020648a, TG020650–020654, TG020656–020660, TG020662, TG020663), 15 m2 (TG020648b, TG020668–020681), 12 m3 (TG020648c, TG020686–020696). Measurements are in Table 2.

## Description

**M1** The anterocone is broad and symmetrically divided into two cusps by a deep groove. In one specimen an extra small tuberculum (anterostyle) is developed on the anterior wall of the anterocone. The lingual spur of the anteroloph is absent. The ectoloph is complete. One specimen shows a short mesoloph. The lingual cingulum is formed by irregular small cusps. The “funnel structure” is absent. The molars have four roots.

**Table 2** Measurements of *Byzantinia bayraktepens* from layer TU19

	Length				Width			
	N	Min	Mean	Max	N	Min	Mean	Max
M1	6	2.84	3.29	3.53	13	1.80	2.11	2.34
M2	5	2.36	2.60	2.72	8	1.74	1.86	2.00
M3	8	2.12	2.22	2.36	9	1.52	1.67	1.80
m1	9	2.50	2.62	2.88	9	1.56	1.67	1.78
m2	8	2.56	2.72	2.88	14	1.62	1.74	1.86
m3	10	1.96	2.34	2.66	10	1.38	1.52	1.68

**M2** The anterior part of the M2 is wider than the posterior one. The ectoloph is complete in all specimens. The lingual cingulum is developed as a chain of irregular small cusps. The lingual wall of the protocone and hypocone is often ornamented. The M2 has four roots.

**M3** The posterior part of the M3 is not much reduced. The labial spur of the anteroloph is connected to the paracone in worn specimens. In young specimens the labial spur is constricted close to paracone. The weak lingual branch of the anteroloph is of variable length. The protocone is the largest cusp. The ectoloph is complete. In one specimen a small “funnel” is developed. The hypocone and metacone are distinctive cusps. The roots or traces of roots are preserved in four specimens. The M3 has four roots: two anterior of approximately equal size and two posterior. The labial posterior root is stronger than the lingual one, which is placed more anteriorly.

**m1** The small anteroconid is rounded and bears a labial spur (anterolophid). Metalophulid 1 is connected to the anteroconid. Metalophulid 2 is formed by the forward-directed mesolophid. The anterior sinusid is closed. The strong posterolophid is always separated from the entoconid. The labial wall of the protoconid and hypoconid is somewhat ornamented. The m1 has two roots.

**m2** The labial branch of the anterolophid descends to the base of the protoconid. The lingual branch is absent. The metalophulid and hypolophulid are directed forwards. The well-developed mesolophid is separated from the metaconid. The strong posterolophid does not reach the entoconid in seven specimens; in two others the posterolophid is connected to the entoconid. The labial wall of the protoconid and hypoconid is slightly ornamented. The m2 has one anterior and two posterior roots (preserved in four specimens).

**m3** The posterolophid is short and reduced. The entoconid is smaller than the metaconid. The rest of the morphology is the same as in the m2. The roots or traces of roots are preserved in five specimens. The m3 has one anterior and one posterior root with a tendency to bifurcate (2/10).



*Byzantinia* sp.

(Plate 1, figs. 14, 15)

## Material

TU19 1 M1 (TG020615 –  $\times 1.84$ ), 2 m1 (TG020655  $2.28 \times 1.48$ ; TG020661  $2.14 \times 1.44$ ).

## Description

**M1** (TG020615) The anterior part of this tooth is damaged. The labial spur of the anterocone (anterior ectoloph) of this rather narrow M1 is not connected to the base of the paracone. The lingual part of the anteroloph is connected to the lingual part of the protocone. Protolophule 1 is absent, and the posteriorly directed protolophule 2 is connected to the endoloph. The half-way constricted posterior arm of the protocone determines the shape of the sinus. A short mesoloph (anterior arm of the hypocone?) is present.

**m1** These two m1s are considerably smaller than those of *B. bayraktepenis*. The anteroconid is small and rounded. The mesolophid (metalophulid 2) is absent in one specimen (TG020655). In the other (TG020661), a short mesolophid is present. The posterolophid is developed as a rounded cusp that is slightly larger than the anteroconid.

## Comments

The subfamily Cricetodontinae Schaub (1925) is used here in a restricted sense including genera that are considered to be phylogenetically affiliated to the genus *Cricetodon* Lartet (1851). The material found in Tuğlu corresponds to two different taxa: *B. bayraktepenis* found in both levels and *Byzantinia* sp. recovered only in the upper level and poorly represented by three teeth. While teeth of *Byzantinia* are quite rare in level TU6/7, this genus is dominant in the upper level (TU19). The larger sample of *Byzantinia* M1 from the upper level clearly shows the absence of a “funnel” and the lingual spur of the anterolophule, which is characteristic for both *B. bayraktepenis* and *B. dardanellensis*. However, the teeth of *B. dardanellensis* are larger and more hypsodont, and the M3 is relatively short and narrow. After Ünay (1980), the length ratio of the M1/M3 is 1.84 in *B. dardanellensis* and 1.51 in *B. bayraktepenis*. Comparison of hypsodonty is difficult, because the type material of *B. dardanellensis* and *B. bayraktepenis* has been figured from the occlusal view only. Moreover, the majority of the specimens from TU19 are heavily worn. Since the length ratio of the *Byzantinia* M1/M3 from level TU19 is 1.48, these teeth are assigned to *B. bayraktepenis*. The limited material of *Byzantinia* from the lower level falls within the size range of *B. bayraktepenis* and shows

**Plate 2** *Megacricetodon* cf. *yenicekentensis*: 1 TG6/7 M1 (TG010236); 2 TG6/7 M1 (TG010229); 3 TG6/7 M2 (TG010242); 4 TG19 M2 (TG020507); 5 TG19 M2 (TG020506); 6 TG6/7 M3 (TG010246); 7 TG6/7 m1 (TG010206); 8 TG6/7 m1 (TG010203); 9 TG6/7 m2 (TG010212); 10 TG19 m2 (TG020505); 11 TG19 m3 (TG020508); 12 TG6/7 m3 (TG010226). *Myocricetodon* cf. *eskihisarenensis*: 13 TG19 m2 (TG020502); 14 TG19 M1 (TG020512). *Myomimus dehmi*: 15 TG6/7 P4 (TG010304); 16 TG6/7 M1/2 (TG010305); 17 TG6/7 M1/2 (TG010316); 18 TG6/7 M3 (TG010318); 19 TG6/7 p4 (TG010323); 20 TG6/7 m1/2 (TG010333); 21 TG6/7 m1/2 (TG010338); 22 TG6/7 m3 (TG010345). *Myoglis* cf. *ucrainicus*: 23 TG19 M1 (TG020201). *Microdromys complicatus*: 24 TG19 P4 (TG020301); 25 TG19 p4 (TG020302); 26 TG19 m1 (TG020303); 27 TG19 m2 (TG020304). *Muscardinus* aff. *thaleri*: 28 TG19 P4 (TG020101); 29 TG19 p4 (TG020102); 30 TG19 M3 (TG020103); 31 TG19 m1 (TG020104); 32 TG19 m2 (TG020105); 33 TG19 m3 (TG020106). *Spermophilinus* cf. *besana*: 34 TG19 P4 (TG020801); 35 TG19 M1/2 (TG020802); 36 TG19 M3 (TG020804); 37 TG19 p4 (TG020805); 38 TG19 m1/2 (TG020806). *Keramidomys* sp.: 39 TG19 M1/2 (TG020704); 40 TG19 M1/2 (TG020703); 41 TG19 m1/2 (TG020702); 42 TG19 m1/2 (TG020701); 43 TG19 m3 (TG020705). Underlined numbers indicate reversed specimens

the same dental characters as the specimens from the upper level, so these are also assigned to *B. bayraktepenis*.

The teeth described under the heading *Byzantinia* sp. differ in size and morphology from *B. bayraktepenis*. They are somewhat similar to *B. dardanellensis* in the undulation of the enamel of the posterior arm of the protocone, but are not so narrow. The straight backwards-directed protolophule and the constricted endoloph make the M1 from TU19 clearly different. Although the morphological variability in *Byzantinia* is quite large, these specimens are not considered to be aberrant *B. bayraktepenis* teeth, but seem to represent a different species. This is the more so because the presence of two species of *Byzantinia* in one assemblage is quite common (Ünay 1980).

Subfamily Megacricetodontinae Mein and Freudenthal 1971

Genus *Megacricetodon* Fahlbusch 1964

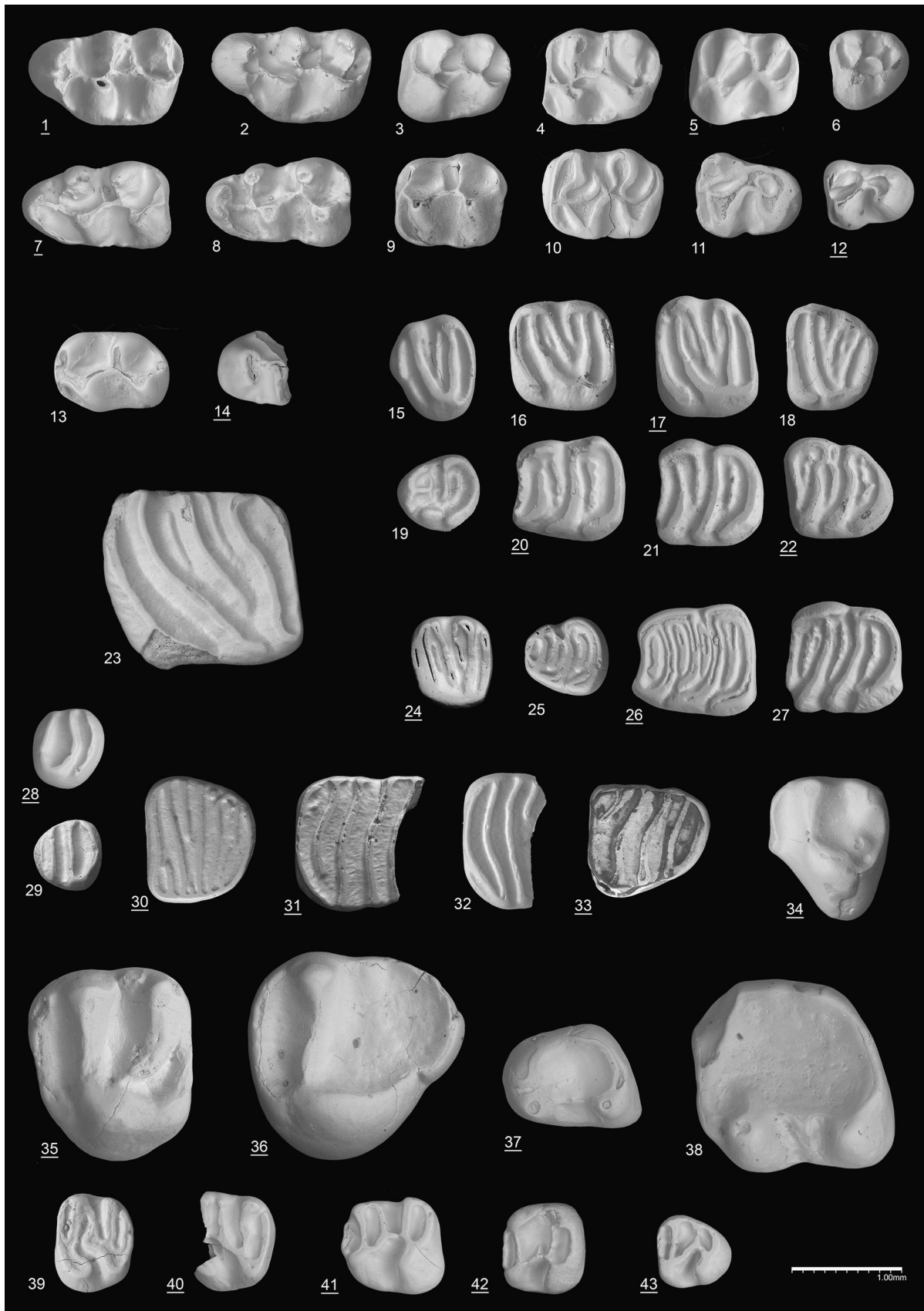
*Megacricetodon* cf. *yenicekentensis* Erten, Sen and Görmüş 2014

(Plate 2, figs. 1–12)

## Material

TU6/7 11 M1 (TG010229–239), 6 M2 (TG010240–245), 2 M3 (TG010246–247) 11 m1 (TG010201–211), 13 m2 (TG010212–224), 4 m3 (TG010225–228). Measurements are in Table 3.

TU19 2M2 (TG020506  $0.98 \times 0.88$ ; TG020507  $1.06 \times 0.87$ ), 1 m1 (TG020501 –  $\times 0.82$ ), 1 m2 (TG020505  $1.09 \times 0.82$ ) 1 m3 (TG020508  $0.98 \times 0.88$ ).



**Table 3** Measurements of *Megacricetodon* cf. *yenicekentensis* from layer TU6/7

	Length				Width			
	N	Min	Mean	Max	N	Min	Mean	Max
M1	6	1.43	1.49	1.56	9	0.84	0.88	0.94
M2	6	0.98	1.04	1.1	6	0.82	0.87	0.93
M3	2	0.72	0.76	0.79	2	0.73	0.75	0.77
m1	7	1.34	1.36	1.38	8	0.79	0.82	0.84
m2	9	0.99	1.06	1.12	12	0.79	0.85	0.93
m3	3	0.82	0.94	1.09	4	0.66	0.75	0.78

## Description

**M1** The anterocone is slightly asymmetrically split into a larger labial and a smaller lingual cusp. The anterolophule is bifurcated with one branch connected to each cusp of the anterocone enclosing a small rounded basin. In one specimen a short labial spur of the anterolophule is present, but the labial branch of the anterocone is well developed and closes the labial anterosinus in most specimens. The lingual cingulum is low around the protocone and bears a small entostyle between the protocone and hypocone in five specimens. The short protolophule is more or less transverse. Seven out of ten specimens have a short posterior spur of the paracone. In four M1s, the posterior arm of the protocone is connected, or almost connected, to the mesoloph. The mesoloph is of medium length in eight specimens and long in the two others. The metalophule joins the posteroloph in eight specimens; in two others it inserts on the hypocone. In two specimens a weak metalophule 1 connects the metacone to the mesocone. The sinus is directed forwards. The depth of the closed posterossinus is variable.

**M2** The labial branch of the anteroloph is better developed than the lingual one and forms a labial anterosinus. The lingual branch of the anteroloph descends to base of the protocone, but is absent in two specimens. The protolophule is double in all but one specimen (TG020506). The connection between protolophule 2 and the protocone is well developed in one specimen; in the six other specimens it is incomplete. The mesoloph is of medium length in two, but long in six specimens. In two specimens it is connected to the base of the paracone. The metalophule curves forwards and is connected to the anterior arm of the hypocone. The posteroloph reaches the base of the metacone, enclosing a wide posterossinus.

**M3** The labial branch of the anteroloph descends to the base of the paracone, enclosing a labial anterosinus. The lingual branch of the anteroloph is absent in one specimen and weak, but distinctive, in the second specimen. The mesoloph is well developed in one specimen; in the other it

is reduced. The hypocone is incorporated into the posteroloph, but distinctive, forming a small sinus in one specimen. The slightly forward-directed metalophule inserts on the endoloph. The metacone is a small cusp on the posteroloph.

**m1** The anteroconid is simple, but in unworn specimens it shows a tendency to form two or three small tips. The strong labial branch of the anteroconid descends to the base of the protoconid. The short lingual branch of the anteroconid bears a small cusp in four specimens; in the five specimens this cusp is absent. The anterolophulid is connected to the labial side of the anteroconid in four, to the lingual side in two and to the center in two m1s. This ridge is absent in one specimen. The metalophulid is directed forwards and inserts on the anterolophulid. The mesolophid is of medium length in all but one m1 in which it reaches the lingual cingulum. The sinusid is wide and almost transverse. The hypolophulid is directed forwards and inserts on the ectolophid. The posterolophid joins the base of the entoconid and encloses the posterossinusid.

**m2** The lingual branch of the anterolophid is either absent or very weak. The labial branch of the anterolophid descends to the base of the protoconid, enclosing the anterosinus. The metalophulid is directed forwards. The mesolophid is of medium length, curved slightly forwards and reaches the base of the metaconid in two specimens. In one specimen the mesolophid is short. The hypolophulid is simple and curves forwards. The posteriorly directed sinusid is bordered by a cingulum on the labial side in eight out of eleven specimens. This cingulum is interrupted in one specimen forming two small cusps; in six others it is either a ridge or a small cusp. The posterolophid joins the base of the entoconid, closing a wide posterossinusid.

**m3** The labial branch of the anterolophid is developed, but the lingual branch is absent. The posterior part of the m3 is narrow because of reduction of the entoconid. The mesolophid is connected to the lingual cingulum. The sinus is oriented posteriorly. The entoconid is incorporated into the posterolophid.

## Comments

A large number of *Megacricetodon* species have been formally named. Many of these show an overlap in size and morphology. Many of the “distinctive characters” are within the intraspecific variation, e.g., the length of the mesoloph/-id, which is considered to be an environmentally dependent character (Hooper 1952; Daams et al. 1999). The genus *Megacricetodon* seems therefore to have been grossly oversplit. The *Megacricetodon* teeth from Tuğlu have the same size as the type material of *M. col-longensis* from Vieux Collonges. Morphologically they differ from that sample by the stronger separation of the



cusps of the anterocone of the M1 and by not having a fully developed double protolophule in the M2. Wessels et al. (2001) gave a short overview of the *Megacricetodon* material from Turkey and concluded that two size groups can be distinguished: the *M. collongensis* ‘group’ and *M. minor* ‘group’. The Turkish species within each of these groups share many morphological characters, while clear morphological differences between samples from different localities are absent. Recently, Erten et al. (2014) described a new species, *Megacricetodon yenicekentensis*, from locality Yenicekent 3 dated as MN8. They compared it with small-sized species of *Megacricetodon*, although it falls in the upper range of the “small-sized” group. As distinctive characters, they interpreted the presence of a forked anterolophule in M1 and a long mesoloph in M1 and M2. The anteroconid of the m1 is simple and rounded. *Megacricetodon* from Tuğlu is slightly larger than *M. yenicekentensis*, but morphologically shares almost all characters. It slightly differs in having mesoloph in M1 of medium length in most specimens and in the tendency to form two or three small tips on the anteroconid in unworn specimens of m1.

*Megacricetodon* is represented only by five teeth in upper layer TU19, while it is relatively abundant in lower layer TU6/7 (47 specimens). The teeth from upper layer TU19 share all morphological characters with those from the lower layer TU6/7, but one specimen from upper layer TU19 slightly differs in having a single protolophule in M2. Although the specimens from Tuğlu 6/7 and Tuğlu 19 fall within the size range of the type material of *M. collongensis* and are slightly larger than *M. yenicekentensis*, they are very close in morphology to the type material of *M. yenicekentensis*. This induced us to identify this material as *M. cf. yenicekentensis*. The *Megacricetodon* from Tuğlu is probably the youngest occurrence of this genus from Central Anatolia so far.

Subfamily Myocricetodontinae Lavocat, 1961

Genus *Myocricetodon* Lavocat, 1952

*Myocricetodon* cf. *eskihisarensis* Wessels et al. 1987

(Plate 2, figs. 13, 14)

#### Material

TU19 1 anterior part of M1 (TG020512) and 1 m2 (TG020502 1.04 × 0.74).

#### Description

**M1** The anterocone is divided into two small cusps and placed centrally. The anterolophule is connected to the labial cusp of the anterocone. Neither the lingual nor labial

branch of the anteroloph is present. A small protostyle is developed on the lingual edge of the protosinus.

**m2** The posterior part of the occlusal surface is slightly narrower than the anterior part. The labial branch of the anterolophid is well developed, but not connected to the base of the protoconid. The metaconid is connected to the very short lingual branch of the anterolophid. The wide and shallow sinusid is directed posteriorly. The entoconid is connected to the ectolophid. A distinct hypoconulid is developed on the strong posterolophid, which ends at the postero-lingual base of the entoconid.

#### Comments

The morphology and size of the material of *Myocricetodon* from TU19 resembles *Myocricetodon eskihisarensis* Wessels et al. 1987 from Yeni Eskihsar.

Family Gliridae Muirhead, 1819

Genus *Myomimus* Ognev, 1924

*Myomimus dehmi* (de Bruijn, 1966)

(Plate 2, figs. 15–22)

#### Material

TU6/7 4 P4 (TG010301-0304), 7M1 (TG010305-03011), 5 M2 (TG010312-0316), 6 M3 (TG010317-0321), 7 p4 (TG010323-0329), 5 m1 (TG010330-34), 10 m2 (TG010335-0344), 3 m3 (TG010345-0348). Measurements are in Table 4.

TU19 3 P4 (TG020401-0403), 4 M1 (TG020407-0410), 3 M2 (TG020404-0406), 1 M3 (TG020411), 1 p4 (TG020420), 1 m1 (TG020421) 1 m2 (TG020422), 5 m1/2 (fragments TG020423-0427), 2 m3 (TG020428, TG020429). Measurements are in Table 4.

#### Description

**P4** TU6/7: The protoloph and the metaloph are complete and connected to the main cusps, thus forming a U-shaped trigon. The long anteroloph is lower on the labial and lingual side than in the middle and reaches the bases of the protocone and paracone. The anterior centroloph is short. In one worn specimen, it is absent. The posterior centroloph is long, reaching to at least the lingual half of the occlusal surface. In three specimens it is connected to the metacone; in one unworn specimen it is connected to the basis of the metacone. The posteroloph is the longest ridge; it connects the protocone to the metacone. The P4 has three roots. TU19: the specimens from TU19 and TU6/7 have the same morphology, but the anterior centroloph is absent in all specimens from TU 19.

**Table 4** Measurements of *Myomimus dehmi* from layer TU6/7 and TU19

	Length				Width			
	N	Min	Mean	Max	N	Min	Mean	Max
Layer TU 6/7								
P4	4	0.66	0.75	0.80	4	0.73	0.89	0.98
M1	5	0.91	0.99	1.06	5	1.05	1.14	1.20
M2	4	0.94	0.99	1.00	4	1.13	1.18	1.22
M3	6	0.81	0.86	0.90	6	0.99	1.05	1.11
p4	6	0.71	0.74	0.78	6	0.60	0.66	0.73
m1	5	0.95	1.01	1.09	5	0.80	0.94	1.04
m2	6	1.00	1.02	1.07	7	0.91	0.99	1.07
m3	3	0.89	0.97	1.02	3	0.90	0.92	0.93
Layer TU 19								
P4	3	0.69	0.72	0.75	3			
M1	4	0.95	0.96	0.97	3	0.85	0.87	0.89
M2	3	1.06	1.07	1.09	3	1.07	1.14	1.21
M3	1	–	0.83	–	0	1.20	1.24	1.28
p4	1	–	0.79	–	1	–	–	–
m1	1	–	1.00	–	1	–	0.79	–
m2	1	–	1.02	–	1	–	1.01	–
m3	2	0.97	0.98	0.99	1	–	0.99	–

**M1 TU6/7:** The shape of the concave occlusal surface is sub-rectangular, but the anterior part is slightly narrower than the posterior part. The anteroloph is connected to the paracone, but separated from the protocone. The protocone is situated halfway to the lingual border. The paracone and metacone are well developed. The protoloph and metaloph are always complete, connected to the main cusps and forming a U-shaped trigon. The anterior centroloph is long, reaching to at least the middle of the occlusal surface. The posterior centroloph is always shorter than the anterior centroloph. The posteroloph is complete and connects the protocone to the base of the metacone. A small extra ridge between the protoloph and anterior centroloph is present in six out of seven specimens. The M1 has three roots. The material of *M. dehmi* from the levels TU19 and TU6/7 is very similar in all aspects, but the posterior centroloph is absent in one specimen from TU19 (TG020409).

**M2 TU6/7:** The shape of the outline is sub-rectangular, but the posterior part is slightly narrower than the anterior part. The occlusal pattern is very similar to that of the M1, but the posteroloph is separated from the metacone in all specimens. The extra ridge between the protoloph and anterior centroloph is longer than in the M1. The material of *M. dehmi* from TU19 and TU6/7 is very similar, but in one specimen from TU19 (TG020405), a small ridge connects the anteroloph with the protoloph approximately halfway.

**M3 TU6/7:** The posterior outline of the M3 is rounded because the metacone is reduced. The anteroloph is

separated from the protocone in four out of six specimens, so there is a tendency to form an endoloph. In two specimens the endoloph is fully developed. The protoloph and metaloph are connected to the paracone and metacone, but in one specimen, the protoloph is interrupted at the base of the paracone. The pattern of the centrolophs shows much variation: in some specimens, these are connected to the paracone and metacone, while they are separate ridges or a chain of small isolated cusps in others. The posterior centroloph is longer than the anterior one. A posterior extra ridge of variable length is always present. The only M3 from TU19 (TG020411) does not differ from specimens from TU 6/7.

**p4 TU6/7:** The outline of the occlusal surface is oval. The anterolophid is curved and bears a small cusp in its central part. The metalophid is interrupted and incomplete in all specimens. A short longitudinal ridge connects the anterolophid and the metalophid. The posterolophid and mesolophid form the posterior valley, which is completely enclosed in three out of seven specimens. A posterior extra ridge is present in the majority of the specimens; in one p4 it is developed as a small cusp, and in one it is absent. The mesoconid is developed as a separate cusp in three specimens; in two others it is connected to the posterolophid, and in two specimens it is absent. The p4 has one root. Only one worn and slightly damaged specimen is available from TU19 (TG020420). In this specimen the posterior extra ridge is developed as a small cusp.

**m1 TU6/7:** The outline of the m1 is sub-rectangular. The anterior part is slightly narrower than the posterior part. The anterolophid is connected to the metaconid and almost reaches the protoconid. The metalophid is constricted before reaching the metaconid. The long centrolophid does not reach the labial outline of the occlusal surface. The endolophid is interrupted between the centrolophid and the mesolophid. The mesolophid and posterolophid incorporate the entoconid, forming a U-shaped posterior valley. The posterior extra ridge is well developed in all specimens. The m1 has three roots. TU19: In the only complete specimen from TU19, the centrolophid and posterior extra ridge are relatively short.

**m2 TU6/7 and TU19:** The shape of the outline is sub-rectangular, but the posterior part is slightly narrower than the anterior part. In all other characters, the m2s are the same as the m1. The m2 has three roots. The centrolophid and the posterior extra ridge are restricted to the lingual half of the occlusal surface in the specimen from TU19 (TG020422).

**m3 TU6/7:** The posterior part of the m3 is rounded. Apart from that, the pattern is the same as in the m1 and m2. In one specimen, the anterolophid is not connected to the metaconid. In this specimen, the metaconid is developed as a cusp, separated from the centrolophid by a notch. In

another specimen, the metalophid is interrupted approximately in its middle. In two specimens, a weak anterior extra ridge is developed. The roots are not preserved. The specimen from TU19 (TG020428) has a shorter centrolophid, and the posterior extra ridge developed as small cusp.

#### Comments

The most striking character of *Myomimus* is the three-rooted lower molars, which make these teeth distinctive from those of *Peridyromys* and *Miodyromys*, which have an overall similar dental pattern, but only two roots. However, after Mayr (1979) *Miodyromys biradiculus* differs from *M. hamadryas* in having two instead of three roots in m2. On the other hand, the *M. biradiculus* differs from our *Myomimus* specimens by the larger size and slightly more complicated dental pattern. The “lineage” *M. dehmi*-*M. maritsensis*-*M. roachi* shows a tendency toward simplification of the dental pattern and size increase of the molars (Daams, 1981; Ünay 1994). The teeth of *M. dehmi* from Tuğlu are about the same size as the material from Nombrevilla and are only slightly larger than the material from the type locality. *M. dehmi* from Tuğlu shows a relatively complex dental pattern, which is considered to be a primitive feature in this genus (Daams 1981; Daxner-Höck 1995). The higher complexity makes it distinctive from *M. maritsensis*. Daams (1981) provides the distribution of standard morphotypes of *M. dehmi* from different localities in Spain and Greece. The complexity of *M. dehmi* from TU 6/7 and TU 19 is similar to that in the teeth from Nombrevilla (Spain, MN9) and Escobosa de Calatañazor (Spain, MN7/8) and is more complex than in *M. dehmi* from the type locality Pedregueras 2C (Spain, MN9) and from Pikermi (Greece, MN9). This difference in complexity is most striking in the P4/p4 and M3. The P4/p4 from Tuğlu resembles *P. dehmi* from Nombrevilla (Spain). The scatter diagram of the average number of ridges of M1,2 and m1,2 in different *Myomimus* species through time in Daams (1981, p.94 fig. 40) shows a linear relationship. The M1,2s from TU 6/7 have an average of 6.7 and those from TU 19 an average of 6.3 ridges, while the lower molars always have 6 ridges. In this respect, the Tuğlu material occupies a position between that from Pedregueras 2C and Nombrevilla.

The stratigraphic range of the occurrences of *Myomimus dehmi* in Turkey is from MN9 to MN12. Besides the common occurrences of this species in SW Europe (Spain, France), it is also known from Miocene localities in Austria [Kohfidish and Eichkogel (MN11); Daxner-Höck and Höck 2009], Greece [Lefkon (MN10), Daxner-Höck 1995; Pikermi, Chomateres (MN12), de Bruijn 1976] and from Moldava reported as *Myomimus dehmi/maritsensis* [Chimishliya, Gradishte, Gura Galbene (MN12), Delinschi 2013].

Genus *Myoglis* Baudelot, 1965

*Myoglis* cf. *ucrainicus* Nesin and Kowalski, 1997 (Plate 2, fig. 23)

#### Material

TU19 2 M1 (TG020201  $1.80 \times 1.62$ ; TG020202  $1.74 \times -$ ), 1 broken m1 (TG020203  $1.67? \times -$ )

#### Description

**M1** The shape of the outline is sub-rectangular. Its pattern consists of the four main ridges, a lingually as well as labially isolated anterior centroloph and two extra ridges inside the trigon. The main ridges are symmetrical in cross section. The anteroloph is isolated. The protoloph is lingually separated from the metaloph in one specimen, but connected by a weak ridge in the other. The metaloph is lingually connected to the posteroloph. The anterior centroloph is long, reaching the lingual half of the occlusal surface. The extra ridges are situated anteriorly and posteriorly of the anterior centroloph. In one specimen a short third extra ridge, situated labially between the metaloph and posteroloph, is present. The roots are not preserved.

**m1** The lingual half of one m1 is preserved. The anterolophid is short and separated from the metalophid. The anterior extra ridge is almost as high as the main ridges and connected to the anterolophid approximately in the middle. A small second extra ridge is developed on the lingual part of the posterior slope of anterior extra ridge. The centrolophid is a discontinuous low ridge. The lingual end of the posterolophid curves toward the mesolophid. The roots are not preserved.

#### Comments

The measurements of the *Myoglis* teeth from TU19 fall within the size range of *M. meini* as well as of *M. ucrainicus*. The protoloph separated from the metaloph is one of the morphological features that are typical for *M. ucrainicus*. In one specimen from TU19, the protoloph is separated from the metaloph, while in a second specimen a weak connection is present. In this aspect, they strongly resemble *M. ucrainicus*; however, only three specimens of *Myoglis* available from TU19 led us to identify it as *M. cf. ucrainicus*.

Representatives of genus *Myoglis* are relatively rare in Miocene assemblages from Europe. According to Nemetschek & Mörs (2003), the genus contains five species: *M. tuyolsi*, which is the oldest species of genus (MN2), *M. houlezi* (MN3), *M. antedens* (MN3–MN5), *M. meini* (MN4/5–MN10) and *M. ucrainicus* (MN9–MN10). The occurrences of *Myoglis* listed by these authors are

restricted to Europe. The type locality for *M. ucrainicus* is Gritsev in Ukraine (MN9). This species is also known from Austria (Richardhof-Golfplatz (MN9), Götzendorf (MN9), Richardhof-Wald (MN10) and Schernham (MN10); Daxner-Höck and Höck 2009). *Myoglis* cf. *ucrainicus* described from Rudabanya (MN9, Hungary; Daxner-Höck 2005). The presence of *M. cf. ucrainicus* from TU19 proves that the geographical range of this genus was much larger than assumed.

Genus *Microdyromys* de Bruijn, 1966

*Microdyromys* cf. *complicatus* de Bruijn, 1966

(Plate 2, figs. 24–27)

#### Material

TU19 1 P4 (TG020301  $0.74 \times 0.86$ ) 2 p4 (TG020302  $0.76 \times 0.71$ , TG020303  $0.68 \times 0.57$ ), 2 m1 (TG020304  $1.11 \times 1.01$ ; TG020305 –  $\times$  –), 1 m2 (TG020306  $1.06 \times 1.02$ ), 1 m3 (TG020307  $1.05 \times 0.98$ ).

#### Description

**P4** The occlusal surface has a rounded shape, with the four main ridges and the anterior centroloph, posterior centroloph and an extra ridge between the protoloph and the anterior centroloph. The anteroloph is short and united to the protoloph. The endoloph is complete. The protoloph, metaloph and posteroloph are connected to the endoloph. The anterior centroloph is longer than the posterior centroloph. The posteroloph is not connected to the metacone. The roots are not preserved.

**p4** The occlusal outline is oval, narrower anteriorly than posteriorly. In addition to the anterolophid, metalophid, centrolophid, mesolophid and posterolophid, there is a posterior extra ridge. The hypoconid and mesoconid are separated. The centrolophid is connected to the metaconid. The mesoconid is connected to protoconid in one specimen (TG020302). The p4 has one posteriorly placed root.

**m1** The shape of the occlusal surface is trapezoid; the anterior part is narrower than the posterior part. The anterolophid is connected to the protoconid. The metalophid is connected to the metaconid. The centrolophid is connected to the metaconid, but separated from the mesoconid by a narrow and shallow valley. The posterolophid, entoconid and mesolophid form a U-shaped continuous ridge. The endolophid is not complete. Four extra ridges of about the same length are situated in the valleys between the main ridges. Traces of the two roots are preserved.

**m2** The occlusal surface has a trapezoid shape and is slightly narrower posteriorly. The four main ridges, a long centrolophid and two extra ridges are developed. The extra

ridges in front and behind the centrolophid present in the m1 are missing in the m2. The anterolophid is separated from the protoconid by a notch. The roots are not preserved.

**m3** The tooth is morphologically similar to m2, but is more reduced posteriorly. The anterolophid is connected to the protoconid.

#### Comments

Except one upper premolar, only the lower cheek teeth of *Microdyromys* were recovered from layer TU 19. These teeth of *Microdyromys* are similar in size and morphology to the type material of *M. complicatus*, but since we do not have the M1/2, we identify these teeth as *M. cf. complicatus*.

Genus *Muscardinus* Kaup, 1829

*Muscardinus* aff. *thaleri* de Bruijn, 1966

(Plate 2, figs. 28–33)

#### Material

TU19 1 P4 (TG020101  $0.63 \times 0.72$ ), 1 M3 (TG020103  $0.98 \times 1.14$ ), 1 p4 (TG020102  $0.60 \times 0.62$ ), 1 fragment m1? (TG020104 –  $\times$  1.22?), 1 fragment m2? (TG020105 –  $\times$  1.22?), m3 (TG020106  $1.09 \times 1.02$ ).

#### Description

**P4** The occlusal surface is rounded with three ridges. The two anterior ridges are connected lingually, forming a U-shaped structure. The posterior ridge is transverse, ending labially and lingually free. The tooth has one main root and another small one placed anterolabially.

**M3** The outline of the tooth is oval, narrower in the posterior part. Six complete ridges are developed on the occlusal surface. All ridges are connected to the endoloph. Between the first (anteroloph) and second complete ridge (protoloph), an extra ridge is developed. A centrally interrupted ridge is developed between the second and third complete ridge. In the posterior part of the tooth, two extra ridges/cusps on the labial margin are developed (between the posterior centroloph and metaloph, and also between the anterior centroloph and posterior centroloph). The roots are not preserved.

**p4** The occlusal surface is rounded, narrower in the anterior part. The tooth has four ridges. The first anterior ridge is short, weak and almost completely worn. The two posterior ridges are connected lingually and nearly so labially. The posterior ridge is curved, whereas the other ridges are straight and transverse. The tooth has one root.

**m1?** This fragment seems to represent the anterior part of a damaged m1. The anterolophid is curved, its edges

(lingual and labial) are free and directed backwards. The third transversal ridge (metalophid) is complete, ending free on both margins and curved forwards on the labial side. The second ridge (extra ridge between the anterolophid and the metalophid) reaches the lingual margin but not the labial margin of the occlusal surface. It ends free in the labial half of the tooth surface. A small ridge/cusp near the lingual end of the valley between the anteroloph and second ridge is developed. The fourth transversal ridge is curved forwards. The rest of the last preserved fifth ridge shows the same morphology as the fourth ridge. The posterior part of the tooth is not preserved.

*m2?* This fragment seems to represent the anterior part of m2 or m1. All preserved ridges are curved slightly forwards. The anterolophid is connected lingually with the second transversal ridge. The third transversal ridge ends free on both margins. A short accessory ridge situated lingually is developed between the third and fourth ridge.

*m3* The shape of the molar is sub-triangular, narrower and rounded in the posterior part. Five complete transversal ridges are on the occlusal surface. The anterolophid is straight, perpendicular to the longitudinal axis of the tooth. The anterolophid continues to the lingual border of the occlusal surface toward the second ridge. The second ridge is incomplete, developed as a small ridge only on the lingual side of the occlusal surface of the tooth. This ridge extends from the lingual border of the tooth toward the lingual part of the anterolophid, delimiting the small basin/valley on the anterolingual corner of the occlusal surface. The last two posterior ridges are connected labially and lingually. Traces of three roots are preserved on the tooth.

#### Comments

The identifications of the fragments of *Muscardinus* are tentative. The few *Muscardinus* teeth from TU19 are morphologically close to *M. thaleri*, *M. hispanicus* and *M. topachevskii*. The size of the teeth is similar to those of *M. thaleri* from Arroyo del Val VI (Spain) and slightly larger than the teeth of *M. topachevskii* from Grytsiv and *M. hispanicus* from Pedreueras 2C. The m3 only has five ridges, which is a feature of *M. hispanicus* and *M. thaleri*. The here-studied P4 displays three ridges, whereas the P4 of *M. thaleri* possesses four. Daams (1985) defined the main distinctive characters between *M. thaleri* and *M. hispanicus*: “The second transverse ridge of the m1 and m2 does not reach the labial border in *M. thaleri*, whereas this ridge is complete in *M. hispanicus*; the presence of the small accessory lingually situated ridge between the third and fourth ridge of the m1 and m2 of *M. thaleri*”. Regarding this, the material from TU 19 fits more to *M.*

*thaleri*. Moreover, the transverse ridges in the m1 and m2 of *M. thaleri* tend to be straight, whereas these ridges are curved strongly forwards in *M. hispanicus* (Daams 1985). In this respect, the material from TU 19 occupies an intermediate position. We present these teeth under the heading *Muscardinus* aff. *thaleri* on the basis of their overall similarity in size and morphology with that species and the recognition that there are differences in the material from the type area.

Family Sciuridae Fischer de Waldheim, 1817  
Genus *Spermophilinus* de Bruijn and Mein, 1968  
*Spermophilinus* cf. *besana* Cuenca Bescós, 1988  
(Plate 2, figs. 34–38)

#### Material

TU19 1 D4 (TG020801  $1.12 \times 1.32$ ), 3 M1/2 (TG020802  $1.54 \times 1.80$ , TG020803 –  $\times 2.05$ ; TG020811 –  $\times -$ ), M3 (TG020804  $2.01 \times 1.90$ ), 1 d4 (TG020805  $1.17 \times 1.02$ ), 1 m1/2 (TG020806  $1.82 \times 1.78$ ).

#### Description

*D4* The shape of the occlusal surface is sub-triangular. The dominant cusp is the protocone. The paracone and metacone are about the same size. The hypocone is indistinct, and the metaconule is small. The anteroloph is low, but distinctive. The straight protoloph narrows toward the protocone. The roots are not preserved.

*M1/2* The occlusal surface is sub-quadrate. The three main cusps are well developed. The protocone is wide and dominant. A mesostyle is developed in all three specimens. The metaloph is slightly curved and bears a weak metaconule. The metaloph is constricted next to the protocone. The protoloph is straight, transverse and connected to the protocone. The anteroloph is connected to the base of the paracone and protocone, forming a narrow basin. The weak hypocone is united with the protocone. The posteroloph is connected to the base of the metacone. The roots are not preserved.

*M3* The tooth has a sub-triangular outline with rounded corners. The protocone is the dominant cusp. The paracone is small, but well developed. The paracone is connected to the protocone by the transverse, slightly curved protoloph. The anterior basin is fully closed by the anteroloph. The posterior basin is wide and surrounded by the posteroloph. The posteroloph is separated from the hypocone by a notch. The metacone is incorporated into the posteroloph. The roots are not preserved.

*d4* The occlusal surface is oval to sub-triangular. The protoconid and metaconid are roughly the same size and are situated close to one another. They are separated only by a very shallow furrow. The weak mesoconid is situated



close to the protoconid. The hypoconid is pronounced. The posterolophid, which encloses the talonid basin, is about equally high all over. The entoconid is incorporated into the posterolophid. The surface of the talonid basin surface is smooth.

*m1/2* The proroconid, hyposonid and metaconid are dominant. The entoconid is incorporated into the posterolophid, but distinctive. The mesoconid is a distinct cusp on the ectolophid. The metalophid is weak in one specimen, but better developed in the broken one. The anterolophid is short, connected to the metaconid and ending near the protoconid. The surface of the talonid basin is smooth. The roots are not preserved.

## Comments

Since the few sciurid teeth available from Tuğlu have a morphology and relative size as expected in one species, our working hypothesis is that they represent one species of primitive ground squirrel. The only specimen that allows unequivocal generic identification is the M3. The notch that separates the hypocone from the posteroloph in that tooth is characteristic for the M3 of *Spermophilinus*. The other teeth might be allocated to either *Spermophilinus* or *Tamias*. The teeth from Tuğlu share characters such as the convergent protoloph and metaloph in the M1/2, the slanting postero-internal corner of the m1 and m2, the smooth surface of the talonid basin and the well-developed posterior lobe of the M3 with *Spermophilinus*. As mentioned by de Bruijn (1995), the most striking feature of the species of *Spermophilinus* is that they share the same dental pattern, so differences between species are based on size. The specimens from Tuğlu are somewhat smaller than those of all contemporary samples of *Spermophilinus* and fall into the size range of *S. besana*, a species assumed to be restricted to the Early Miocene. Whereas *Spermophilinus* teeth from European sites show a size increase through time, some samples from Turkey contain teeth that are smaller than their European counterparts (de Bruijn 1995; Bosma et al., 2013). Since the sample from Tuğlu is poor, a sampling bias cannot be excluded. We therefore present this material under the heading *S. cf. besana*.

Family Eomyidae Depéret and Dauxami, 1902

Genus *Keramidomys* Hartenberger, 1966

*Keramidomys* sp.

(Plate 2, figs. 39–43)

## Material

TU19 2 M1/2 (TG020703 –  $\times 0.97$ , TG020704  $0.75 \times 0.95$ ), 2 m1/2 (TG020702  $0.91 \times 0.87$ ; TG020701  $0.74 \times 0.82$ ) 1 m3 (TG020705  $0.67 \times 0.69$ ).

## Description

*M1/2* The occlusal surface is wider anteriorly than posteriorly. The longitudinal crest is absent in one specimen and weak in the second one. The mesoloph is long and connected to the paracone in one specimen. The metaloph is complete and connected to the longitudinal crest. The posteroloph is long and not connected to the metacone. The roots are not preserved.

*m1/2* The anterolophid is well developed and connected to the base of the protoconid and metaconid. The longitudinal crest is complete, but constricted before reaching the hypolophid in unworn specimens. The strong posterolophid is connected to the entoconid, enclosing the fourth synclinid. The mesolophid is long and connected to the metaconid in one specimen, but short and ending free in the other one.

*m3* The four main ridges, anterolophid, metalophid, hypolophid and posterolophid, are present. The hypolophid is constricted before it reaches the entoconid. The mesolophid is absent.

## Comments

The molars from TU19 are similar in size to *K. mohleri* from Anwil (Engesser 1972) and fit within the upper part of the range of *K. ermannorum* from the Late Miocene of Austria (Daxner-Höck and Höck 2009). They are slightly larger than those of *K. carpathicus* from Neudorf (Fejfar 1974). In some morphological characters, such as the tendency to develop lophodonty, the labial and lingual connections of the loph(id)s and the presence of a low but complete, longitudinal crest in one M1/2, the material resembles *Keramidomys ermannorum*. However, the reduction of the mesolophid in one of the lower molars is very similar to *K. anwilensis* and *K. cf. carpathicus* from Maramena (de Bruijn 1995). The latter occurrence was later re-allocated to *K. ermannorum* (Daxner-Höck and Höck 2009). The collection of *Keramidomys* from TU19 is too small to be identified to the species level because the morphological variation in *Keramidomys* assemblages is high.

## Composition of the assemblages

The rodent assemblages from the levels TU6/TU7 and TU19 differ considerably in composition. The lower layer (samples TU6/TU7) yielded 123 identifiable teeth and fragments of teeth and contains *Megacricetodon* cf. *yenicekentensis* (49 %), *Myomimus dehmi* (33 %), *Progonomys cathalai* (11 %) and *Byzantinia bayraktépensis* (7 %). The rodent assemblage from upper layer TU19 (136

identifiable teeth) is dominated by *Byzantinia bayraktensis* and *Myomimus dehmi* (57 and 16 %). Other taxa represent approximately one quarter of the all specimens: *Byzantinia* sp. (3 %), *Microdyromys* cf. *complicatus* (3 %), *Myoglis* cf. *ucrainicus* (3 %), *Muscardinus* aff. *thaleri* (2 %), *Spermophilinus* cf. *besana* (4 %), *Keramidomys* sp. (4 %), *Megacricetodon* cf. *yenicekentensis* (4 %) and *Myocricetodon* cf. *eskihisarensis* (2 %). The percentages are based on the sum of the lower and upper first and second molars of each species with respect to the total number of lower and upper first and second molars (Table 5).

The striking difference between the assemblages from two different layers was probably caused by a change of environmental conditions. Mazzini et al. (2013) provide a detailed paleoenvironmental interpretation of the Tuğlu section based on an array of multidisciplinary analyses. The lowermost part of the profile is characterized by a hyperhaline lake with the presence of foraminifera. The occurrence of foraminifera at the base of the section is interpreted by passive transport into a lake environment with suitable salinity and not by a marine connection. Layer TU6/7 is located on the transition from hyperhaline to shallow fresh water to oligohaline lake or marsh. A shallow lake with oligohaline waters persists until the change to a fresh water lake with macrophytes. Our layer TU19 represents the fluvial input at the beginning of this change. A shallow lake with fluctuating salinity (fresh water to oligohaline) persists up to the uppermost part of section, where slowly flowing, oxygenated water conditions prevailed. As demonstrated above, both layers containing small mammals are connected with environmental changes in the lake system. Layer TU6/7 was deposited in the low energy shallow lake, and layer TU19 is characterized by higher energy with water flow input. Whether a significantly different composition of rodent assemblages was caused by a change in the depositional bias, by an overall change in the environment or by a combination of both cannot be clearly explained for now.














The assemblage from layer 6/7 is considerably less diverse than the assemblage from TU19 and contains an unusual association of *Megacricetodon* cf. *yenicekentensis* and *Progonomys cathalai*. *Megacricetodon* cf. *yenicekentensis* should be considered as inhabitant of humid environments (Daams et al. 1999). On the basis of comparison with extant *Myomimus personatus*, *Myomimus dehmi* can be considered as a ground-dweller in open country. On the other hand, the assemblage from TU19 is dominated by *Byzantinia bayraktensis* (57 %), which is considered to have preferred drier biotopes (de Bruijn et al. 1993). The upper layer TU19 shows a higher diversity mainly among dormice. This is documented by the presence of four species of Gliridae in the upper layer instead of only one

species in the lower layer. Moreover, *Myoglis* cf. *ucrainicus* is the first occurrence of the genus outside of Europe. The presence of *Muscardinus* aff. *thaleri*, *Microdyromys* cf. *complicatus* and *Myoglis* cf. *ucrainicus* as well as the appearance of the eomyid *Keramidomys* sp. suggests a more forested environment. In addition, *Byzantinia* sp., *Spermophilinus* cf. *besana*, *Myocricetodon* cf. *eskihisarensis* and *Megacricetodon* cf. *yenicekentensis* appear in upper layer TU19, where the Murinae are missing. This unique situation is not known from other localities so far. A possible explanation for this unexpected absence could be that the fauna in sample TU19 is re-deposited. However, the preservation of the fossils lacks evidence of long transport. Another option may be that selection by birds of prey has introduced a bias in the composition. Last but not least, an explanation could be the gradual geographical spreading of *Progonomys* during its western migration. The Tuğlu assemblages probably represent a short time slice when the prograding *Progonomys* community was still not stable in the area and thus very sensitive to environmental changes. Since the age interval represented between sample TU6/7 and sample TU19 is estimated to have been relatively short, the absence of *Progonomys* in the sample TU19 remains a mystery for the time being.

### Age of the assemblages

The rodent assemblages described above allow a more precise correlation to the European MN scale and to the local biozones (de Bruijn et al. 2013) than was hitherto possible. Our revised age estimate is primarily based on the co-occurrence of *Progonomys cathalai* and *Megacricetodon* cf. *yenicekentensis* in layer TG 6/7 and the presence of rodent species in the overlying layer TU 19 that are indicative of MN7/8. The stratigraphical range of the Anatolian *Megacricetodon* is from MN4 (Keseköy-local Biozone D) to MN7/8 (Yeni Eskihisar, Sofca and Yenicekent-local Biozone H). The occurrence of *Megacricetodon* younger than MN7/8 (local Biozone H) is not known from Turkey so far. The genus *Megacricetodon* survived in Europe slightly longer and disappeared during the Early Vallesian (MN9). The first *Progonomys* species appear in Anatolia during Biozone I, which is correlated with MN9 (Altıntaş 1, Altıntaş 2, Bayraktepe 2, Mahmutköy, Kütahya A, Kütahya C, Aşağıçığıl, Sinap loc 8A and Güney), and the last appearance is in Biozone J correlated with MN10 (Karaözü) (Wessels 2009; Erten et al. 2014). According to Wessels (2009), the first *Progonomys* is not known before  $\approx 10$  MA in Europe. The association of the genera *Progonomys* and *Megacricetodon* is only otherwise known from Pedregueras 2C, Spain (Van Dam et al. 2001; Álvarez-Sierra et al. 2003), Can Lobateres, Spain (Alberdi

**Table 5** Composition of the rodent assemblages from layers TU6/7 and TU19 and stratigraphical ranges of the taxa

TG 6/7 N (%)	TG 19 N (%)	Taxa	Stratigraphic range of the taxa in Turkey				Comment
			MN 6	MN7/8	MN9	MN10-11	
9 (11)	0	<i>Progonomys cathalai</i>					species range
6 (7)	51 (57)	<i>Byzantinia bayraktepenensis</i>					species range
0	3 (3)	<i>Byzantinia</i> sp.					genera range
41 (49)	4 (5)	<i>Megacricetodon</i> cf. <i>yenicekentensis</i>					species range
0	2 (2)	<i>Myocricetodon</i> cf. <i>eskihisarensis</i>					species range
27 (33)	14 (16)	<i>Myomimus dehmi</i>					species range
0	3 (3)	<i>Myoglis</i> cf. <i>ucrainicus</i>					not known
0	3 (3)	<i>Microdyromys</i> cf. <i>complicatus</i>					species range
0	2 (2)	<i>Muscardinus</i> aff. <i>thaleri</i>					genera range
0	4 (5)	<i>Spermophilinus</i> cf. <i>besana</i>					genera range
0	4 (5)	<i>Keramidomys</i> sp.					genera range
83(100)	90 (100)	N = m1 + m2 + M1 + M2	zone G	zone H	zone I	zone J	Local zone

Continuous lines indicate known ranges, dashed lines indicate extended ranges based on this study

et al. 1981; Agustí et al. 2001), and Castelnou 1B, France (Aguilar et al. 1991). Since the fauna from Can Llobateres is the reference for MN9, the association from layer TU 6/7 can be correlated to that unit (=Early Vallesian) with confidence. It seems that the assemblage from the TU 6/7 bed contains the last occurrence of *Megacricetodon* as well as the first occurrence of *Progonomys* in Anatolia so far. What this means in terms of absolute age remains to be demonstrated, because it seems unlikely that the entry of *P. cathalai* in Anatolia and Spain took place simultaneously, and *Megacricetodon* has been suggested to have gone extinct earlier in Anatolia than in Spain. Also peculiar is the composition of the assemblage from upper layer TU19, which shows a close affinity to Biozone H (MN7/8). This is suggested by the absence of the *Progonomys* as well as by the presence of the species that have their stratigraphical range limited to Biozone H (*Byzantinia bayraktepenensis*, *Myocricetodon* cf. *eskihisarensis* or *Megacricetodon* cf. *yenicekentensis*). The paleomagnetic data from the Tuğlu section (Mazzini et al. 2013) indicate that all the samples have a normal polarity. This supports the age constraint to one of the normal polarity events at the base of the MN9 zone. Anyway, the biostratigraphical correlation of the Tuğlu faunas to MN 10–12 as suggested by Kaymakcı (2000) and Karadenizli (2011) was obviously at least one MN unit too young.

## Conclusions

The Tuğlu locality is unique in having yielded rodent associations that are essentially different from two beds that are stratigraphically only a few meters apart. Moreover, Murinae were found in the lower level, but not in the upper level, which is strange because after entry this subfamily soon becomes dominant elsewhere. These peculiar observations are, for the time being, explained by assuming a drastic change of the environment between the TU 6/7 and TU 19 levels, but since there is no indication of such a change from other sources, this is a working hypothesis.

The rodent assemblages from TU6/7 and TU19 are both correlated with MN9 of the European standard scale and thus considered to have an Early Vallesian, early Late Miocene age.

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