Rodents, lagomorphs and insectivores

Sevket SEN

CR2P UMR 7207 (MNHN, CNRS, UPMC, Sorbonne Universités), Département Histoire de la Terre, Muséum national d'Histoire naturelle, case postale 38, 57 rue Cuvier, F-75231 Paris cedex 05 (France) sen@mnhn.fr

Published on 24 June 2016

urn:lsid:zoobank.org:pub:4D79A6D1-9508-4DF9-B1D6-FE8DC116D654

Sen S. 2016. — Rodents, lagomorphs and insectivores, *in* Sen S. (ed.), Late Miocene mammal locality of Küçükçekmece, European Turkey. *Geodiversitas* 38 (2): 299-314. http://dx.doi.org/10.5252/g2016n2a9

ABSTRACT

In the context of the present monograph on the late Miocene vertebrate locality of Küçükçekmece, this paper aims to provide a detailed analysis of rodent, lagomorph and insectivore remains. The Küçükçekmece fauna includes three species of rodents (*Byzantinia bayraktepensis* Ünay, 1980, Spalacidae indet. and *Chalicomys jaegeri* Kaup, 1832), one lagomorph (*Ochotona ozansoyi* Sen, 2003) and two insectivores (*Schizogalerix* sp. and *Crusafontina* cf. *endemica* Gibert, 1975). This assemblage is far from reflecting the complete spectrum of these groups in the community of the region. Several common late Miocene taxa are not represented in the material, which was collected by hand picking on the outcrops, not by screen washing of sediment. Among the species recovered, *B. bayraktepensis* and *O. ozansoyi* are known elsewhere in latest Astaracian (MN8) and early Vallesian (MN9) localities. The other taxa found at Küçükçekmece are common elements of European Vallesian faunas. Abundance of the beaver *C. jaegeri* suggests freshwater environment, while the insectivores of this locality indicate rather moist forests and subtropical climatic conditions.

KEY WORDS Rodentia, Lagomorpha, Insectivores, late Vallesian, Istanbul region.

RÉSUMÉ

Rongeurs, lagomorphes et insectivores.

Dans le cadre de la présente monographie sur le site à vertébrés du Miocène supérieur de Küçükçekmece, cette étude apporte une analyse détaillée des restes de rongeurs, de lagomorphes et d'insectivores. La faune de Küçükçekmece contient trois espèces de rongeurs (*Byzantinia bayraktepensis* Ünay, 1980, Spalacidae indet. and *Chalicomys jaegeri* Kaup, 1832), un lagomorphe (*Ochotona ozansoyi* Sen, 2003) et deux insectivores (*Schizogalerix* sp. and *Crusafontina* cf. *endemica* Gibert, 1975). Cet assemblage est loin de refléter le spectre complet de ces groupes dans la région. Plusieurs taxons communs dans les gisements du Miocène supérieur ne sont pas représentés dans le matériel, qui est récolté par ramassage des fossiles en affleurement, et non par lavage-tamisage de sédiments. Parmi ces espèces, *B. bayraktepensis* et *O. ozansoyi* sont connus ailleurs dans des localités datant de l'Astaracien supérieur (MN8) et du Vallésien inférieur (MN9). Les autres taxons trouvés à Küçükçekmece sont des éléments communs des faunes vallésiennes en Europe. L'abondance du castor *C. jaegeri* suggère un milieu d'eau douce, tandis que les insectivores de cette localité indiquent un environnement de forêts plutôt humide et des conditions climatiques subtropicales.

MOTS CLÉS Rodentia, Lagomorpha, Insectivores, Vallésien supérieur, région d'Istanbul.

INTRODUCTION

The Küçükçekmece vertebrate locality is known mostly to provide large vertebrates, in particular large sized mammals. This locality found in 1932 by Ahmet Malik Sayar is situated today in the western suburbs of Istanbul city. In their monograph on the Küçükçekmece vertebrate fauna, Malik & Nafiz (1933) also described a castorid, Steneofiber sp., of which they illustrated a left mandible bearing p4-m3 (see also Sickenberg et al. 1975; Saraç 2003). Later on, Père Jean Nicolas collected more fossils on the western banks of Küçükçekmece lagoon between 1956-1967 (see Sen, this volume for a detailed history of palaeontological investigations in the Istanbul region). Nicolas (1978: 456) provided a list of vertebrate taxa based on the fossils that he collected, among which he mentioned two insectivores ("Neomyiné forme primitive, Erinaceidé ou Galéridé ind."), one lagomorph (Ochotona sp.) and four rodents ("Chalicomys jaegeri Kaup, Monosaulax cf. eseri v. Meyer, Cricetodon decedens Schaub, Spalacidés ind." The systematic analysis of the available material shows that this list needs to be substantially revised.

MATERIAL AND METHODS

The studied material is housed in two different collections. The one at the Istanbul Technical University (ITU) consists of seven isolated teeth and two astragali of Castoridae and one upper incisor of Spalacidae. This material is in principle inherited from the excavations that Ahmet Malik and Hamit Nafiz undertaken in 1932, and occasionally in later years, in a sand quarry on the southeastern shore of Küçükçekmece lagoon near Küçükçekmece village. This locality is called here Küçükçekmece East, and the specimens are labeled KC. The substantial part of the studied material comes from the Nicolas collection at the Natural History Museum of Paris (MNHN). Nicolas (1978) has noted that he collected this material in a fossiliferous horizon that extends along the western shores of the Küçükçekmece lagoon and seashore cliffs next to the lagoon to the north of Marmara Sea. According to Nicolas (1978), all vertebrate remains issued from the one and same horizon where fossil pockets are scattered over several hundred meters. This locality is called here Küçükçekmece West, and the specimens are labelled TRQ.

The measurements of Castoridae teeth are taken using a Mitutoyo digital caliper, and other specimens were measured with a two-axis Mitutoyo measuroscope. All measurements are given in millimeters. Upper teeth are designated with capital letters (I, P, M), and lower teeth with small letters (i, p, m).

Dental terminology follows Hugueney (1999) for Castoridae, Mein & Freudenthal (1971) for muroid rodents, Engesser (1980) for Erinaceidae, Reumer (1984) for Soricidae, and Sen (1998, 2003) for lagomorphs.

SYSTEMATIC STUDY

Order RODENTIA Bowdich, 1821 Family Cricetidae Rochebrune, 1883. Subfamily Cricetodontinae Stehlin & Schaub, 1951

Genus Byzantinia de Bruijn, 1976

Type species. — Byzantinia pikermiensis de Bruijn, 1976.

Byzantinia bayraktepensis Ünay, 1980 (Fig. 1A-E)

TYPE LOCALITY. — Bayraktepe 1, Turkey, MN8.

MATERIAL. — From Küçükçekmece West: right M1 (3.32×2.19) , fragment of left maxillary with M2 (2.33×1.59) and M3 (1.76×1.36) , distal part of a right m1 $(-\times 1.79)$, right m2 (2.69×1.88) and left m2 (2.43×1.76) . Specimens numbered as MNHN.F.TRQ955 to TRQ959.

DESCRIPTION

All the molars are rather high-crowned, the lophs are thick and the ridges connecting the cusps are as high as the cusps. On the M1, the anterocone is deeply split into two cusps of similar volume. The labial anterocone has a thick spur connected to the base of the paracone, while the lingual one has a bulge on its lingual side. The sinus is directed distally. The ectoloph between the paracone and metacone is complete. This tooth has four roots, one mesial, one lingual and two distal.

The M2 is elongated and tapers distally. The protosinus is a wide depression delimited mesially by a low lingual anteroloph. The labial anteroloph is strong and fused to the base of the paracone. The sinus is very oblique distally. There are four roots.

The M3 is similar to M2 in its general pattern, but with distal part notably reduced, in particular the hypocone and posteroloph. The sinus is directed distally, but is considerably reduced compared to that of M2. The M3 has three roots.

The preserved distal part of an m1 displays a strait sinusid directed forward and delimited by a thick cingulum. The posterolophid is cusp shaped.

The occlusal outline of the m2 is rather quadrangular. The anterosinusid is a shallow depression, while the protosinusid is deep due to the fact that the labial anterolophid is well developed. The mesolophid is a thick spur directed toward the metaconid. The sinusid is directed mesially. A thick cingulum runs along the labial face of the tooth. The posterolophid is cusp shaped. This tooth has three roots, one strong mesial and two small distal roots.

COMPARISON

The material described here above is rather homogenous in morphology and size, and therefore securely referred to the same species. It is important to clarify this aspect, because many late Miocene localities in Turkey and Greece yielded two species of *Byzantinia*. The subfamily Cricetodontinae

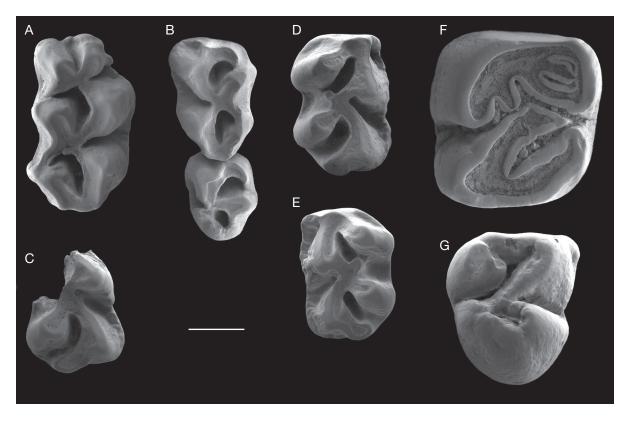


Fig. 1. — Byzantinia bayraktepensis from Küçükçekmece West, Turkey: A, M1 dext (MNHN.F.TRQ955); B, M2-3 sin (TRQ956); C, fragment of m1 dext (TRQ957); D, m2 dext (TRQ958); E, m2 sin (TRQ959). Spalacidae gen. and sp. indet. from Küçükçekmece: F, M2 sin (TRQ951); G, m3 sin (TRQ952). Scale bar: 1 mm.

is well documented in Turkey and in the Balkan countries since the early Miocene. Among several genera referred to this group, the specimens from Küçükçekmece fit with the genus Byzantinia in having rather high crowned molars with strong lophs between the cusps, well-divided anterocone on M1, and distally elongated M2 and M3. This genus is known by eleven species in this region during the latest middle Miocene and late Miocene.

The middle Miocene species *B. cariensis* (Sen & Ünay, 1979) and B. eskihisarensis (Tobien, 1978), as well as two late Miocene species B. nikosi de Bruijn, 1976 and B. ozansoyi Ünay, 1980 have molars smaller than the Küçükçekmece sample, and these species have a "funnel" structure on M1 and M2, which is absent on the M1 and M2 from Küçükçekmece. This funnel is formed by the connection of the protoloph, ectoloph, mesoloph and endoloph, it is apparently a character inherited from the ancestral genus Cricetodon.

Byzantinia unayae Rummel, 1998 from Karaözü (Sivas Basin, Turkey, MN10-11) is similar in size, but different in morphology from the Küçükçekmece species. Its M1 has lingual spurs of the anterocone and protocone, its M2 and M3 have labial anteroloph rather strait and not connected to the paracone, its M3 is not reduced distally, and the m2 and m3 taper mesially. Although not illustrated laterally, the description given by Rummel (1998) shows that the molars of this species are higher crowned than those of Küçükçekmece.

Another group of *Byzantinia*, including the species *B. dar*danellensis Ünay, 1980, B. hellenicus (Freudenthal, 1970) and

B. pikermiensis de Bruijn, 1976, is characterized with high crowned and lophodont molars, and lack of the funnel on M1 and M2. The cusps of both upper and lower molars are included in the lophs, the lophs are as high as the cusps, and the first and particularly the second molars are elongated. All these characters are not seen on the Küçükçekmece specimens.

The size and morphology of the Küçükçekmece specimens fit better with B. bayraktepensis Ünay, 1980. This species was initially described from Bayraktepe-1, a locality situated to the southeast of the Dardanelles Strait, and dated as latest middle Miocene because of the absence of murids in the fauna and the occurrence of Anchitherium and Listriodon in nearby horizons (Ünay 1980, 1981). Later on Rummel (1998) referred to this species the specimens from the localities of Dereikebir (Edirne, Thrace), Mahmutköy, Pişmanköy (Thrace) and Yenieskihisar (Muğla, SW Turkey). All these localities are correlated to MN8 or MN9, i.e. across the middle-late Miocene boundary. The material from Sinap Loc. 1 described by Sen (1990) as B. cf. dardanellensis can also be included in this species. Magnetostratigraphy of the Sinap Formation dated this locality to 9.68 Ma (Kappelman et al. 2003). Lately Joniak & de Bruijn (2015) attributed to this species the well-preserved material from the locality of Tuğlu 19 in the Çankiri Basin, central Anatolia. This locality is correlated to MN9 based on palaeontological and magnetostratigraphic data (Mazzini et al. 2013; Joniak & de Bruijn 2015).

Byzantinia orientalis (Lungu, 1981) from Buzhor-1 in Moldova could be a synonym of B. bayraktepensis. Its molars do

Table 1. — Measurements (in mm) of upper and lower teeth of *Chalicomys jaegeri* Kaup, 1832 from Küçükçekmece East and West.

	Length			Width		
Tooth	Range	X	N	Range	X	
l upper	4.93-7.21	6.44	12/9	5.32-7.15	6.53	
P4	7.34-8.71	7.99	6	7.91-8.62	8.37	
M1&M2	5.24-5.96	5.61	8	5.47-6.82	5.77	
M3	5.02-5.85	5.46	6	5.03-6.65	5.75	
I lower	5.41-7.30	6.42	19/9	5.66-7.30	6.66	
p4	8.90-11.15	10.12	14/16	6.53-8.41	7.48	
m1&m2	5.45-6.53	6.23	14/15	5.81-7.94	6.87	
m3	5.77-6.05	5.88	5	6.03-7.25	6.53	

not display any reliable morphological difference from those of *B. bayraktepensis* from its type locality Bayraktepe-1, although the size of molars as given by Lungu (1981) is either identical or larger than that of the type material. New measurements of the cricetodontine molars from Buzhor-1 are necessary for a reliable size comparison.

Family SPALACIDAE Gray, 1821

Spalacidae gen. and sp. indet. (Fig. 1F, G)

MATERIAL. — Left M2 (3.45 \times 3.45), right m3 (2.72 \times 2.56), two lower incisors of which the one almost complete (3.25 \times 3.12) and one left upper incisor (3.41 \times 3.02). These specimens are numbered as TUR 951 to 954, and the upper incisor KÇ 601.

DESCRIPTION AND COMPARISON

The M2 has occlusal outline square shaped, although the distal part is slightly narrower than the mesial part. In its present state of wear, the sinus and mesosinus are connected. The anterosinus is preserved as two enamel islands. The mesoloph is strong and thick, but it does not reach the labial border. The posterosinus is absent. In lingual view, the crown height is 4.04 mm and the sinus depth is 2.83 mm. In labial view, the crown height is much less (1.90 mm) indicating a strong unilateral hypsodonty, and the only sinus open is the mesosinus that extends on 0.75 mm along the crown height.

The m3 has an S-shaped occlusal pattern. A bulge on the mesiolabial angle seems to be a remnant of the labial anterolophid. The metaconid is a well-defined cusp that has a strong distolabial spur. The ridge between the protoconid and entoconid is strait. The maximum crown height on the labial side is 2.99 mm, and the sinusid depth is 2.29. On the lingual side the crown height is 1.93 mm at the metaconid, and the mesosinusid depth is 1.08 mm. Both teeth have roots broken.

The upper incisor is much thinner than the ones in the extant Spalax, and its anterior face bears two thin furrows in the enamel next to the lateral margin.

The lower incisor tapers mesially and has a chisel-shaped wear facet. The enamel of anterior face is smooth and slightly convex.

These teeth are, first of all, characterized by their larger size, larger than any named species of Spalacidae. The representatives of this family are known since the late Oligocene with

Vetusspalax progressus De Bruijn, Markovic & Wessels, 2013 from the locality of Banovici in Bosnia Herzegovina, dated to 24 Ma. During the early Miocene the family is represented with the genera Debruijnia Ünay, 1996 and Heramys Klein Hofmeijer & De Bruijn, 1985 known in Turkey and Greece. These are all small-sized species with rather low-crowned and less lophodont molars, compared to the later representatives of the family. During the middle and late Miocene, the dominant genus is Sinapospalax Sarica & Sen, 2003, which is known by six named species from Turkey (Sarica & Sen 2003; Sen & Sarica 2011). It includes medium to large-sized species with rather high-crowned and semihypsodont molars. The molars are already lophodont without, however, loosing the cusp shape in an early stage of attrition. Their lophodonty increases when molars are worn to 1/3 of their depth. The lophodonty of molars is notably stronger in late Miocene-Pleistocene genera *Pliospalax* Kormos, 1932 and *Spalax* Guldenstaedt, 1770. Even in rather young individuals the cusps of molars of those genera are not well defined, and a little attrition deletes any cusp appearance and includes them in strong lophs. In addition, the molars of these genera have lophs organized in a S-pattern that is typical for cheek teeth of the *Pliospalax* and *Spalax* species.

Based on these criteria, the specimens from Küçükçekmece fit best with the Sinapospalax species. Also, the presence of a free strong mesoloph, a parasinus which becomes a parafosset in early wear stages, and a mesially oblique sinus are characters that the M2 from Küçükçekmece shares with Sinapospalax. However, all species of this genus have much smaller molars (Fig. 2), preventing inclusion of the Küçükçekmece material in any known species. Such large molars already have been found in three localities in Turkey. Sarica & Sen (2003) described a large m1 (3.58 × 3.07 mm) from Sinap Loc 12 (Central Anatolia, MN10) as "Sinapospalax n. sp." [sic]. Ünay (1996) mentioned the presence of a spalacid M1 $(4.45 \times 4.30 \text{ mm})$ at Düzyayla 1 (Central Anatolia, MN11). The early Pliocene locality of Calta in the same region yielded an unpublished m3 (3.79 × 3.53 mm) that is even larger than the m3 from Küçükçekmece. One can wonder if these large teeth belonged to a discrete large sized species or they indicate the presence of some gigantic individuals in some spalacid populations.

Family CASTORIDAE Hemprich, 1820

Genus Chalicomys Kaup, 1832

Type species. — Chalicomys jaegeri Kaup, 1832.

Chalicomys jaegeri Kaup, 1832 (Figs 3, 4, 5)

TYPE LOCALITY. — Eppelsheim, Rhineland-Palatinate, Germany, MN 9|10.

MATERIAL. — From Küçükçekmece East (ITU collections) two upper incisors, one P4, two M1 or M2, one lower incisor, one m3 and two astragali, numbered as KÇ501 to KÇ509. From Küçükçekmece

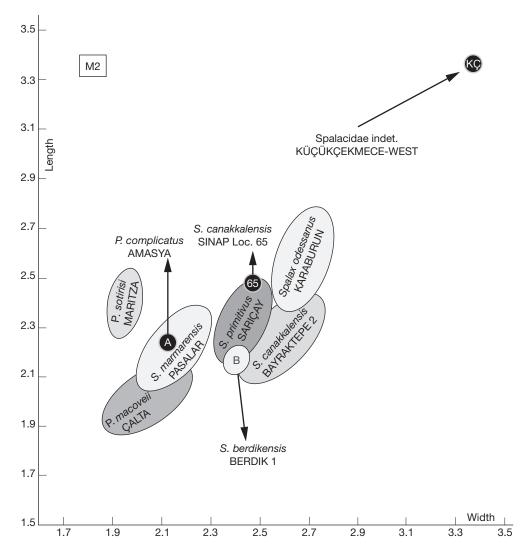


Fig. 2. - Length/width scatter diagram of the second upper molar (M2) in different species of Sinapospalax (S.), Pliospalax (P.) and Spalax. Note that only one M2 is noted from the localities of Sinap Loc. 65, Amasya and Küçükçekmece. Modified from Sen & Sarica 2011: fig. 4.

West (MNHN collections) 10 upper incisor fragments, five P4, nine M1 or M2, six M3, 14 lover incisor fragments, one mandible fragment with p4-m1, 17 p4, 12 m1 or m2, and five m3, numbered as MNHN.F.TRQ788 to TRQ866.

MEASUREMENTS. — See Table 1. Measurements of the length and width of cheek teeth are the maximum values that can be measured on teeth, often taken close to the base of the crown. Indeed, the cheek teeth, in particular when the attrition is not advanced, have occlusal surface shorter and narrower than near the base of the crown (see in particular Figures 3 and 4). In other words, in lateral and lingual views, the crown enlarges towards the root. Some authors provide measurements at the occlusal surface (Aldana Carrasco 1992; Apoltsev & Neofitny 2015) or occlusal surface and when possible largest dimensions of cheek teeth (Stefen 2009; Mörs & Stefen 2010). Largest dimensions are given here since the length and width of the occlusal surface generally increase with attrition.

DESCRIPTION

As shown in Figures 3 and 4, and Table 1, the specimens from Küçükçekmece display some size variation, in particular for incisors and p4, the larger teeth being 20 to 25% larger than the smaller ones. However, the Küçükçekmece material does

not show any size grouping, and the morphology of incisors and cheek teeth generally does not distinguish different species. Such a size variation has been observed in several other localities, when a sufficient number of specimens is available, as for the type locality of *Chalicomys jaegeri*, Eppelsheim (e.g., Stefen 2009: table 1). Size variation in castorids is explained by Hugueney (1999: 283) as being due "to the fact that castorid individual growth lasts during a long time (at least four years and perhaps all along the life, in extant *Castor*), so that size variation is very large".

The upper incisor has a wear facet 1.4 to 1.5 times longer than the width of the anterior face. The enamel is smooth and slightly convex. The section is rather rounded.

All cheek teeth have flexi/ids filled with cement, and in some teeth, the cement covers parts of or even all faces of the crown (e.g., Fig. 4F, G). The root is open in young individuals, but closed with cement layers in older ones. Upper cheek teeth are strongly convex lingually and twisted distally, while lower cheek teeth are slightly convex labially and curved mesially. The crown is high; the maximum crown heights measured

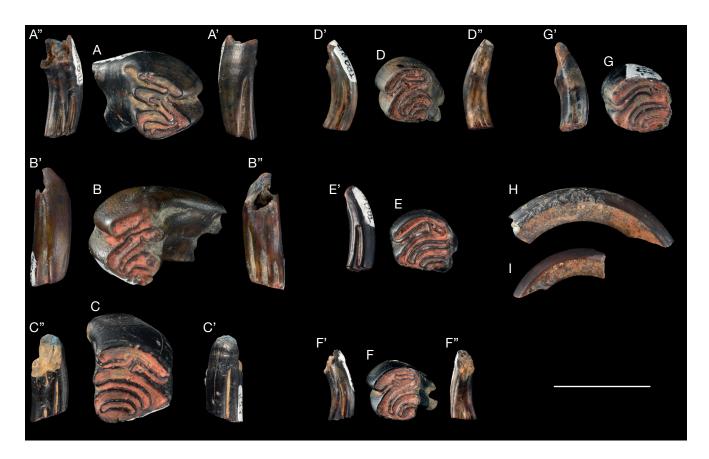


Fig. 3. — Chalicomys jaegeri Kaup, 1832 from Küçükçekmece West. Upper incisors and cheek teeth. A, right P4 (MNHN.F.TRQ829) in occlusal (A), lingual (A') and labial (A") views; B, left P4 (TRQ830) in occlusal (B), lingual (B') and labial (B") views; C, right P4 (TRQ831) in occlusal (C), lingual (C') and labial (C") views; D, left M1 or M2 (TRQ822) in occlusal (D), lingual (D') and labial (D") views; E, left M1 or M2 (TRQ819) in occlusal (E) and lingual (E') views; F, left M1 or M2 (TRQ817) in occlusal (F), lingual (F") views; G, left M3 (TRQ834) in occlusal (G) and lingual (G') views; H, right upper incisor fragment (TRQ791) in lateral view; I, left upper incisor fragment (TRQ801) in lateral view. Scale bar: occlusal view of cheek teeth, 10 mm; lingual and labial views of cheek teeth and incisors, 5 mm.

on fresh teeth are 21.8 mm for a p4 (MNHN.F.TRQ843) and 24.3 mm for a P4 (TRQ830).

On the P4, the hypoflexus is strongly directed forward and penetrates deep inside the occlusal surface; in one P4 (MNHN.F.TRQ830, Fig. 3B) it is connected with the paraflexus. On other P4s these two flexi face each other. The metaflexus is labially closed in very early stage of wear, and in one specimen it has a distal extension (TRQ829, Fig. 3A). The mesoflexus is arc-shaped and remains lingually open, as does the paraflexus, until late stages of wear. In lingual view, the depth of the hypostria is somewhat variable: in 1/3 of P4s it reaches the base of the crown (Fig. 3B), while in the others its ends far from the base of the crown. In labial view, the depth of strii increases from metastria to parastria (Fig. 3B"), although the metastria disappears in very early stages of wear, while the mesostria and parastria are preserved quite late; their depth does not exceed half of the crown height in unworn specimens. Crown height is three times more than the length in unworn or moderately worn specimens.

The M1 and M2 are much smaller than the P4. Their occlusal outline is roughly square. The hypoflexus is strongly directed forward, and it ends in front of the paraflexus, which is an island in all specimens. The mesoflexus remains open quite late in wear, while the metaflexus becomes closed in

moderately worn teeth. The hypostria does not reach the base of the crown; it ends about 7-8 mm above it. On two fresh M1-2, (MNHN.F.TRQ817 and 819), its depth is about ½ of the crown height. The mesostria and metastria are equally deep (Fig. 3D", F"), but they disappear in moderately worn specimens.

The M3 is similar in size to M1-2 or slightly smaller. The crown is twisted lingually and distally, more than in the other upper cheek teeth. The other characters are similar to that of M1-2.

The lower incisor has a wear facet much longer than that of the upper incisor, and its length is twice its anterior enamel width. The enamel of the anterior face is smooth and rather flat. The section is triangular.

The p4 is by far the largest cheek tooth. Its occlusal surface tapers mesially in young individuals, but becomes rounded in adult ones. The hypoflexid is strongly distally oblique and does not reach the metaflexid. Its depth increases with wear progress. The paraflexid is mesially twisted and bifurcated into two branches. The mesoflexid and metaflexid are slightly oblique mesially or rather transverse. On some fresh specimens, such as the p4 MNHN.F.TRQ813 (Fig. 4E), there is a remnant of proparafossettid which becomes an enamel island with a little wear; this is also seen in some lower molars (Fig. 4J, K).



B, right lower incisor fragment in lateral view (TRQ797); C left mandible fragment with p4-m1 (TRQ846) in occlusal (C) and labial (C') views; D, right p4 (TRQ845) in occlusal (D), labial (D') and lingual (D') views; E, left p4 (TRQ813) in occlusal (E), labial (E') and lingual (E') views; F, right p4 (TRQ843) in occlusal (F), labial (F) and lingual (F") views; G, right mandible fragment with p4 (TRQ864) in occlusal (G), labial (G') and lingual (G") views; H, right m1 or m2 (TRQ857) in occlusal (H) and labial (H") views; I, right m1 or m2 (TRQ855) in occlusal (I), labial (I') and lingual (I") views; J, right m3 (TRQ860) in occlusal (J), labial (J') and lingual (J") views; K, right m3 (TRQ837) in occlusal (K), labial (K') and lingual (K') views. Scale bar: occlusal view of cheek teeth, 10 mm; lingual and labial views of cheek teeth and incisors, 5 mm.

In labial view, the hypostriid reaches the base of the crown in all specimens. In lingual view, the depth of the three striids increases posteriorly, the deepest being the metastriid, which reaches half of the crown height in fresh p4s (see Fig. 4E").

m1 and m2 are smaller and in particular shorter than p4. The occlusal pattern is similar to that of p4, except that the paraflexid and mesoflexid are rather transverse and gently curved. Contrary to p4, the metaflexid becomes closed earlier than the other flexids. In labial view, the hypostriid reaches or may not reach the base of the crown. In lingual view, the deepest striid is the mesostriid, while the metastriid is the shorter.

The m3 has a similar occlusal pattern to m1 and m2, except that the hypostriid is less oblique. In all m3s, the hypostriid reaches the base of the crown. In lingual view, the height of mesostriid and parastriid is similar, but the metastriid is shorter.

The ITU collection also includes two astragali of beaver from Küçükçekmece East (Fig. 5A, B). They are complete, well preserved and may belong to the same individual. Their dimensions in mm are as follows (left – right): maximum length = 21.2-21.2; maximum width = 18.6-18.5; maximum width of trochlea = 13.3-13.5; maximum width of the head = 11.0-10.5.

The size and proportions of these astragali are similar to those of *Castor fiber* (Fig. 5). In dorsal view, the trochlea is faintly and asymmetrically convex. Its lateral condyle is sharper than the medial condyle. The cotylar fossa is rather shallow. These characters are also seen in *C. fiber*. The lateral condyle extends distally up to the neck, like an U-shaped tongue, while the facet of the medial condyle is much larger and shorter. In *C. fiber*, the lateral and medial articular facets of the trochlea are V-shaped, and consequently the interarticular rugose area has an arrow shape that penetrates the trochlea. This area is ∩-shaped on the astragali of Küçükçekmece due to the parallel borders of the distolateral and distomedial articular facets of the trochlea. The head is short and the navicular facet appears crescent-shaped along its distal margin.

In plantar view, the ectal facet extends more medially than in *C. fiber*, and its medial margin is more rounded than in this species. The trochlear facet and sustentacular facet (for calcaneus) are separated on the Küçükçekmece astragali by a rugose area, while in *C. fiber* these two facets are connected and their limit is marked by a roughly mediolateral ridge. In *C. fiber* the sustentacular facet is constricted at the level of the neck, while this constriction is tenuous on the Küçükçekmece astragali. Distally, the sustentacular facet joins the cuboid facet of the head on our samples. In *C. fiber*, these two facets are partly separated by a lateral notch that penetrates the distal face to form a sulcus between these facets. In summary, the astragali of Küçükçekmece and *C. fiber* are similar in size and in their proportions, but different in the shape and connections of articular facets.

As far as I know from the literature, the astragalus of *Chalicomys* is undescribed to date. The astragalus from Sansan (France, MN6), described by Hugueney & Duranton (2012) and referred to *Euroxenomys minutus*, has similar proportions but is notably smaller than the Küçükçekmece astragali. In plantar view, the shape of the ectal facet is similar, but the sustentacular facet occupies more space on the head, and

its outline is different compared to that of Küçükçekmece. The same differences are also observed with the astragalus of *E. minutus* from Aumeister near Munich (MN9, Stromer 1928: pl. 2, fig. 19). Hugueney & Duranton (2012) also illustrated an astragalus of *Steneofiber castorinus* from St Gérand Le Puy (France, MN2; see also Stefen 2011 for the systematic status of this species). This astragalus (max. L × W = $16 \times 11.5 \text{ mm}$) is also smaller than that of Küçükçekmece, and the head is proportionally elongated. These characters and many other detailed morphological differences prevent any reliable comparison with the Küçükçekmece astragali.

DISCUSSION

Malik & Nafiz (1933) described *Steneofiber* sp. from the locality Küçükçekmece East based on four lower jaws, about twenty isolated cheek teeth and ten incisors. They illustrated one lower jaw with p4-m3 (Fig. 5A). Most of the fossils from Küçükçekmece East were lost during the fire that devoured Geological Institute of Istanbul University on February 28, 1942 (Sen 2016). The remaining specimens, which are housed now at the ITU collection, do not contain any mandible but only isolated teeth and two astragali. We do not know how much of this material is inherited from the initial collection of Malik & Nafiz (1933).

The beaver remains from both Küçükçekmece localities cannot be referred to Steneofiber. The largest species of this genus S. depereti has cheek teeth as large as or somewhat smaller than the Küçükçekmece specimens (see diagrams in Mörs & Stefen 2010: fig. 7). In morphology, the cheek teeth of S. depereti are characterized by shorter hypostriae/ iids, the lack of labial striae/iids except mesostria/iid, and the absence of substantial cement. As described above, the beaver of Küçükçekmece has hypsodont cheek teeth (height three time more than length) with tetralophodont occlusal pattern, occurrence of pro-parafossettid on fresh teeth, hypostria/iid reaching or ending close to the base of the crown, abundant cement in striae/iids or even outside and long para- and mesostriae/iids. In all these characters, and also in size, the beaver of Küçükçekmece resembles Chalicomys jaegeri. Stefen (2009) restudied the type material from Eppelsheim. The size of premolars and molars, their occlusal pattern, as well as the length of striae and striids are very similar, and there is not any substantial difference between the assemblages of Steinheim and Küçükçekmece. Consequently, the material from Küçükçekmece is identified as C. jaegeri.

In her review of European castorids, Hugueney (1999) retained three species of *Chalicomys*: the type species *C. jaegeri*, *C. subpyrenaicus* (Lartet, 1851) from Villefranche d'Astarac (France, MN7) and *C. plassi* Storch, 1975 (in Franzen & Storch 1975) from Dorn-Dürkheim (Germany, MN11). Casanovas-Vilar *et al.* (2008) added two more species from Spain: *C. catalaunicus* (Bataller, 1938) from Trinxera del Ferrocarril in Sant Quirze (MN7/8) and a new species *C. batalleri* from Abocador de Can Mata (MN7/8). Stefen (2009) and Mörs & Stefen (2010) suggest that the specimens from Abocador de Can Mata should rather be referred to *Stene-ofiber* than to *Chalicomys*, because the crenulations of enamel

and the labiomesially open paraflexid in lower cheek teeth are indicative of the juvenile state in Steneofiber. Further, in this Spanish species, the hypostriid does not reach the base of the crown, and the size of the specimens from Abocador de Can Mata falls within the size range of S. depereti. For Hugueney (1999) C. catalaunicus should be included in Eucastor Leidy, 1858 or Schreuderia Aldana Carrasco, 1992, while for Stefen (2009), the systematic status of this species needs re-examination, and its assignment to the genus Steneofiber seems more appropriate. Casanovas-Vilar & Alba (2011) refuted the assignment of these two Spanish species to any other genus than Chalicomys, arguing that in these species, the cheek teeth are four lophed, the hypostriae/iids of P4 and p4 approach the base of the crown, the striae/iids are filled with cement, and the P4 has three moderately developed striae on the labial side of the crown (only the mesostria is present in S. depereti). Chalicomys plassi from Dorn-Dürkheim is poorly documented, and the dimensions of the unique p4 are in the lower size range of C. jaegeri. Casanovas-Vilar et al. (2008) follow Hugueney (1999) in accepting C. subpyrenaicus as a separate species of Chalicomys. Mörs & Stefen (2010) also discussed the characters and systematic status of *C. subpyrenaicus*, and they concluded that the size of this species overlaps with Steneofiber depereti Mayet, 1908, and the morphology of its cheek teeth is quite similar in having a short hypostriid and only a mesostriid on lower cheek teeth, which are characters shared with Steneofiber species. They suggest maintaining it as a distinct species of Steneofiber pending the revision of the material referred to it by Lartet (1851), Gervais (1859) and Hugueney (1999). As seen from this short review, the systematic status of several species referred to the genus Chalicomys is debated, and there is no agreement on their attribution to Chalicomys and affiliation with the type species C. jaegeri.

Castorids are known in Turkey in localities ranging in age from Oligocene to Pleistocene. Saraç (2003) mentioned their occurrence in at least 30 localities in Turkey, referred to the genera Dipoides, Trogontherium, Euroxenomys, Steneofiber, Chalicomys and Castor. However, the castorid remains from most of these localities are not described, except for that of Erenköy (Calvert & Neumayr 1880), Küçükçekmece East (Malik & Nafiz 1933), Bayraktepe 1 and 2 (Ünay 1976, 1981), Çatakbagyaka (Ünay 1977), Manisa-Develi (Ozansoy, 1961), Paşalar (Flynn & Jacobs 1990) and Emirkaya 2 (Montuire et al. 1994). The material from the first four localities can be securely referred to Chalicomys. The fragmentary remains from Çatakbagyaka (MN7/8) are described as a new subspecies, Trogontherium minutus ozansoyi (Ünay 1977), and Ozansoy (1961) described a new species of Dipoides, D. anatolicus from Manisa-Develi (MN13). The unique M3 from Paşalar (MN5; Flynn & Jacobs 1990) was referred to cf. Chalicomys jaegeri because of its relatively large size (5.5 × 5.5, h = 14 mm) and the presence of a long hypostria that ends 5 mm above the base of the crown. Such characters are not sufficient for a reliable identification of the Paşalar castorid. Castor fiber was reported from the Emirkaya 2 fissure filling, correlated to the Middle Pleistocene (Montuire et al. 1994). The cheek teeth from Küçükçekmece are similar in size and morphology to those of Erenköy, Bayraktepe 1 and Bayraktepe 2. Bayrak-



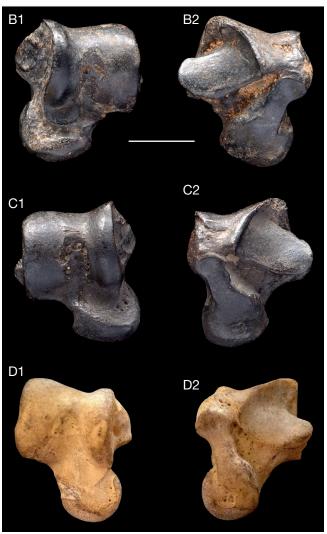


Fig. 5. - Chalicomys jaegeri Kaup, 1832 from Küçükçekmece East and an astragalus of Castor fiber for comparison: A, right mandible with p4-m3 in occlusal view, as illustrated by Malik & Nafiz 1933, pl. XII, fig. 8; B, left astragalus (KÇ 118) in dorsal (B1) and plantar (B2) views; C, right astragalus (KÇ 117) in dorsal (C1) and plantar (C2) views; D, right astragalus of extant C. fiber in dorsal (D1) and plantar (D2) views (MNHN.F, no number). Scale bar: 10 mm.

tepe 1 is correlated to latest middle Miocene (MN7/8) while the others to early late Miocene (MN9/10) (Ünay 1981; Saraç 2003; Ünay et al. 2003).

According to Hugueney (1999), the earliest occurrence of Chalicomys is at the locality of Riedern in Switzerland,

TABLE 2. — Measurement (in mm) of upper and lower cheek teeth of *Ochotona ozansoyi* Sen, 2003 from Küçükçekmece West. Abbreviations: No, catalog number of specimen; **Want**, width of anterior loph; **Wpost**, witdth of postrior loph.

No	Tooth	Length	Want	Wpost
MNHN.F.TRQ965	P2 sin	0.95	1.94	_
MNHN.F.TRQ966	P2 sin	0.89	1.72	_
MNHN.F.TRQ967	P4/M1 dex	1.57	_	_
MNHN.F.TRQ968	P4/M1 dex	1.54	2.79	2.72
MNHN.F.TRQ969	P4/M1 sin	1.56	2.52	2.71
MNHN.F.TRQ970	P4/M1 sin	1.51	2.85	2.67
MNHN.F.TRQ971	M2 sin	1.76	2.30	2.42
MNHN.F.TRQ972	p3 dext	1.76	1.78	-
MNHN.F.TRQ973	m1 dext	1.62	1.71	1.67
Mandible	m2 dext	1.65	1.71	1.67
MNHN.F.TRQ974	Lower molar	1.90	1.52	1.60
MNHN.F.TRQ975	Lower molar	1.82	1.82	2.02

correlated to MN6, and its latest occurrence is at Polgárdi 4 in Hungary correlated to the early part of MN13. However, Mörs & Stefen (2010) noted that occasional occurrence of some characters of *Chalicomys jaegeri* in individuals of MN5-MN6 beaver populations do not confirm their attribution to *Chalicomys*. Some individual teeth of *S. depereti* from Hambach and Eggingen–Mittelhart show an elongated hypostriid and cement filling of synclines. They concluded (Mörs & Stefen (2010: 196) that "the occasional occurrence of single *C. jaegeri* features in MN5 populations of *S. depereti* supports the European lineage from *S. depereti* to *C. jaegeri*". *Chalicomys jaegeri* is frequently recorded in European localities with wet environmental conditions dated to the latest middle Miocene and late Miocene, *c.* between 12-6.5 Ma.

Order LAGOMORPHA Brandt, 1855 Family OCHOTONIDAE Thomas, 1897

Genus Ochotona Link, 1795

Type species. — Ochotona daurica (Pallas, 1776).

Ochotona ozansoyi Sen, 2003 (Fig. 6)

Type locality. — Loc. 84 in the Sinap Formation, Yassiören village, Ankara, Turkey. MN10, *c.* 9.4 Ma.

MATERIAL. — Two left P2, Two left and two right upper cheek teeth, one left M2, a right mandible fragment bearing m1-m2 and the alveoli of p4 and m3, one right p3 and three lower cheek teeth, all numbered from MNHN.F.TRQ965 to TRQ976.

MEASUREMENTS. — See Table 2.

DESCRIPTION

All upper cheek teeth are labially curved. The enamel is thick on the mesial and lingual margins of the lophs but thin on their distal and in particular labial margins. The P2 is short and wide. Its unique anteroflexus is oblique distolabially. The following upper cheek teeth have occlusal pattern formed of

two sub equal lophs separated by a deep and distally curved hypoflexus. The M2 has a strong distolingual spur.

The mandible is broken, missing its anterior part and most parts of the ramus. In lateral view, its height below m2 is 6.5 mm. There are one large foramen and several small foramina below m1 close to the ventral margin. The ramus is gently inclined distally. In medial view, the distal end of the incisor reaches the base of the p4 according to the hole it left on the body. The p3 has a triangular occlusal outline. The anteroconid is triangular and without any lateral or medial depression. It is connected to the posterior complex by a rather large enamel bridge. The paraflexid is short and oblique posteriorly, while the protoflexid is transverse. The hypoflexid is also transverse and does not reach the middle of the occlusal surface. The lower cheek teeth have a diamond-shaped anterior lophid and a triangular posterior lophid, both connected by cement infill. On the mandible, the alveolus of m3 is single and rounded.

DISCUSSION

The ochotonid remains from Küçükçekmece West can be attributed without doubt to the genus Ochotona because the P2 has a simple occlusal pattern with one flexus, M2 has a distolingual spur, and the p3 has a triangle-shaped anterocone and almost transverse protoflexid and paraflexid. The oldest species of Ochotona in Turkey, O. ozansoyi, has been reported from Loc. 84 and O. cf. ozansoyi from Inönü in the Sinap Formation. In this species, the P2 is identical in size and morphology to that of Küçükçekmece West, except that on the P2 from Loc. 84 the paraflexus is less deep, indicating an early stage of evolution. The other upper cheek teeth from Küçükçekmece West are identical both in size and morphology to that of Sinap Loc.8 and Inönü. For lower teeth, the general pattern of p3 is identical to that of O. ozansoyi, but its length is about 5% smaller than the largest p3 of O. ozansoyi (Sen 2003). As known, the length and width of p3 increase with attrition, and consequently such a difference should be considered as an intraspecific variation.

Late Miocene representative of Ochotona are poorly documented (see review in Sen 2003). The best known species *Ochotona eximia* Khomenko, 1914 from Taraklia in Moldova is clearly larger than the pika from Küçükçekmece (Erbajeva 1988; Sen 2003). Erbajeva (2003) and Erbajeva *et al.* (2006) described several new species of *Ochotona* from late Miocene localities in China and Mongolia. Among these species, *O. chowmincheni* Erbajeva, Flynn, Li & Marcus, 2006 is larger and its p3 has a trefoil-shaped anteroconid. *O. gudrunae* Erbajeva, Flynn, Li & Marcus, 2006 and *O. tedfordi* Erbajeva, Flynn, Li & Marcus, 2006 are similar in size to the Küçükçekmece pika, but their p3 is different in having a round anteroconid in *O. gudrunae*, and deep and oblique flexids in *O. tedfordi*.

Ochotona antiqua Argyropulo & Pidoplichko, 1939 is a well-known species in eastern European Pliocene localities. Čermák & Rekovetz (2010) gave a complete account on its morphology and dispersal. Suata-Alpaslan (2009) described a new species, O. mediterranensis, from the early Pliocene (MN14) locality of Iğdeli in central Turkey, similar in size and tooth pattern to O. antiqua. Both species are smaller than

the pika from Küçükçekmece, and the p3 has paraflexid and protoflexid deeper and directed obliquely. In summary, the specimens from Küçükçekmece fit better with O. ozansoyi than any other species of Ochotona.

Order EULIPOTYPHLA

Waddell, Okada & Hasegawa, 1999 Family Erinaceidae Fischer von Waldheim, 1817

Genus Schizogalerix Engesser, 1980

Type species. — Schizogalerix anatolica Engesser, 1980.

Schizogalerix sp. (Fig. 7D)

MATERIAL. — Right m2, MNHN.F.TRQ961 (2.26 × 1.69) from Küçükçekmece West.

DESCRIPTION AND COMPARISON

In occlusal view, the trigonid is notably shorter than the talonid and has a narrow trigonid basin. The protoconid and metaconid are of the same height. The paraconid is ridge shaped. On the talonid, the entoconid is much higher than the hypoconid. The mesiolabial cingulum is strong and continues labially up to the base of the hypoconid. The metaconid has a strong posterior spur (metastylid) that ends freely in the mesosinusid. The posterior arm of hypoconid is directed to the middle of the hypoconulid and its middle part is thickened as a poorly defined cusp. The hypoconulid is almost bilobed. The strong posterior cingulum reaches the distolabial corner at the base of the hypoconid. There are two roots.

All characters of this tooth (size and morphology) fit with that of the genus Schizogalerix, which occurs in Turkey and southeastern Europe since latest early Miocene (Hoek Ostende & Doukas 2003) through late Miocene. The middle Miocene representatives of this genus are different in having the posterior arm of the hypoconid either connected to the posterior part of the hypoconulid (S. pasalarensis Engesser, 1980), and in that case the posterior cingulum is a separate low ridge, or connected to the posterior cingulum (S. anatolica Engesser, 1980), and in that case the posterior cingulum is short and weak. The latter configuration is also preserved in S. voesendorfensis (Rabeder, 1973) and S. moedlingensis (Rabeder, 1973) from the late Vallesian-early Turolian localities of Central Europe (Engesser 1980). The m2 from Küçükçekmece West has a talonid pattern similar to that of S. intermedia Selänne, 2003 and S. sinapensis Sen, 1990 from the Vallesian localities of Central Anatolia, and also to that of S. zapfei (Bachmayer & Wilson, 1970) from early Turolian localities of the Balkans and Central Europe. Unfortunately the unique m2 does not allow further comparison and thus it cannot be identified at the species level.

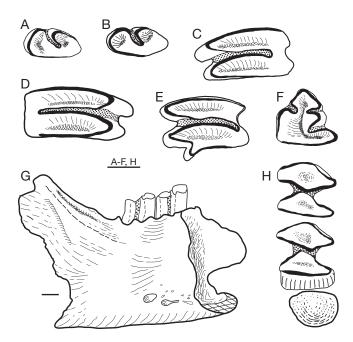


Fig. 6. - Ochotona ozansoyi Sen, 2003 from Küçükçekmece West: A, B, P2 sin; C, P4 or M1 sin; D, P4 or M1 dext; E, M2 sin; F, p3 dext; G, mandible dext in lateral view; H, m1, m2 and alveoli of m3 of the same mandible. Cheek teeth in occlusal view. Black areas, enamel; dotted areas, cement infill.

Order SORICOMORPHA Gregory, 1910 Family Soricidae Fischer von Waldheim, 1817 Subfamily Soricinae Fischer von Waldheim, 1817 Tribe Anourosoricini Anderson, 1879

Genus Crusafontina Gibert, 1975

Type species. — Crusafontina endemica Gibert, 1975.

Crusafontina cf. endemica Gibert, 1975 (Fig. 7A-C)

TYPE LOCALITY. — Can Llobateres 1, Vellès-Penedes Basin, Spain,

MATERIAL. — Right mandible (MNHN.F.TRQ962) with complete ramus and part of the body bearing m1 (2.12 × 1.21), right mandible (TRQ963) without ramus and with m1 (1.95 × 1.14), left mandible body fragment (TRQ964) with alveoli of m1-m3, all from Küçükçekmece West.

DESCRIPTION

The MNHN collection includes three fragments of mandibles, two of which have m1 and the alveoli of m2 and m3. The third one has only the alveoli of m1-m3. In labial view, the body has rather sub-parallel lines from below m1 to below m3. The ventral margin is flat below the molars, and slightly curved upward toward the angular process. The foramen mentale is positioned at mid-depth either below the protoconid of m1 (2/3) or below its talonid (1/3). There is a second foramen below the anterior root of m2. The masseteric crest is absent on this face. The ascending ramus is high, and forms an angle of

Table 3. — Comparative measurements of first lower molar (m1) for the European species of *Crusafontina* from some selected European localities. Type localities are indicated in bold characters. The localities are ordered by their relative age. Measurements are given in millimetres.

Species	Locality	MN zone	N	Length range	Length mean	Width range	Width mean	References
C. kormosi (Bachmayer &								
Wilson, 1970)	Polgárdi 4	MN13	87	2.50-3.20	2.72	1.16-1.64	1.37	Mészáros 1998
C. kormosi	Tardosbánya	MN12	51	2.38-2.84	2.61	1.20-1.48	1.38	Mészáros 1998
C. kormosi	Kohfidisch	MN11	2	2.5-2.6	2.55	1.4-1.5	1.45	Bachmayer & Wilson 1970
C. endemica Gibert, 1975/								
C. kormosi	Sümeg	MN10	9	2.39-2.72	2.56	1.24-1.34	1.29	Mészáros 1998
C. endemica	Masia del Barbo 2A	MN10	10	1.90-2.24	2.04	1.04-1.52	1.22	Van Dam 2004
C. endemica	Masia del Barbo 2B	MN10	3	2.01-2.11	2.06	1.08-1.20	1.14	Van Dam 2004
C. cf. endemica	Küçükçekmece	MN10	2	1.95-2.12	2.04	1.14-1.21	1.18	This study
C. aff. endemica	Götzendorf	MN9	4/9	2.15-2.35	2.25	1.10-1.23	1.15	Ziegler 2006
C. endemica	Can Llobateres 1	MN9	1	_	2.15	_	1.18	Van Dam 2004
C. aff. endemica	Rudabánya	MN9	3	2.02-2.15	2.09	1.18-1.25	1.21	Ziegler 2005
C. exculta (Mayr &								
Fahlbusch, 1975)	Hammerschmiede 3	MN8/9	17/10	1.81-2.21	1.96	1.03-1.24	1.12	Prieto & Van Dam 2012
C. exculta	Hammerschmiede 1	MN8/9	16	1.84-2.25	2.01	1.01-1.26	1.15	Prieto & Van Dam 2012

100° with the body. The coronoid process is slightly enlarged and rounded on its tip. The external temporal fossa is well marked in its upper part, while its lower part is rather shallow; the coronoid spicule, which divides this fossa in two parts, is thick and does not reach the distal margin of the coronoid process. The angle of the upper sigmoid notch is about 95°. The angular process is reduced, being faintly marked by the shallow lower sigmoid notch.

The lingual face of the body is smooth and rather flat. On the ramus, the internal temporal fossa is very large, drop shaped, and is deepest at the mid-level of the articular process, or above the occlusal plan of m3, if preserved. The mandibular foramen is situated just below the internal temporal fossa, but separated from it by a thick ridge that connects the lingual alveolar edge to the base of the articular process. On the articular process, the upper and lower articular facets are broadly connected to form a boomerang-shaped single articular facet. Its upper part is rather triangular, while its lower part is oblong. The pterygoid fossa is deep and bordered disto-ventrally by the articular facet, and mesio-dorsally by a ridge that descends from the dorsal part of the articular facet. The articular process is L-shaped in distal view.

The unique preserved tooth, m1, does not show pigmentation. The trigonid covers about ½ of the occlusal length. The blades of the protoconid and paraconid form an angle of 105°. The paraconid and metaconid are much lower than the protoconid, the lowest being the paraconid. On the talonid the oblique crest is directed toward the lingual arm of the protoconid. The hypoconid is ridge shaped. The entostylid is separated from the entoconid by a narrow notch. The entoconid crest joins the base of the metaconid. There are two cinguli, the mesial one below the paraconid, and the distal one along the distal margin of the tooth, both being rather weak and low.

The length of alveoli m1-m3 varies between 4.04-4.41 mm, with an average of 4.14 mm (n=3). According to the alveoli, the m2 is two-rooted and smaller than m1. The two small alveoli of m3 (length about 1 mm) indicate that this molar was reduced and lingually displaced.

DISCUSSION

The mole shrew remains from Küçükçekmece can be referred to the tribe Anourosoricini because the mandibular body is regularly deep below the molars, the ramus is high and has a deep and drop-shaped internal temporal fossa, and the entoconid crest is present on the m1 (Van Dam 2004).

Among the genera of this tribe, the genus *Paranourosorex* Rzebik-Kowalska, 1975 includes, compared to the Küçükçekmece mole shrew, larger sized species. On their mandible, the internal temporal fossa is oblique to the vertical axis of the ramus, the mandibular foramen is situated higher and close to the internal temporal fossa the articular process has two distinct articular facets, the angle between these facets is narrower, the m1 is particularly enlarged compared to m2, its talonid is larger (about 45% of total length), and the trigonid is wide open lingually (Rzebik-Kowalska 1975; Storch & Zazhigin 1996). Species referred to this genus span the latest Turolian to late Ruscinian (Van Dam 2004).

The genera *Anourosorex* Milne-Edwards, 1872 and *Amblycoptus* Kormos, 1926 group the largest species of Anourosoricini. For Storch & Zazhigin (1996) these two genera are closely allied in having common derived features such as hypertrophied parastyle and subdued mesostyle on M1, very elongated trigonid and reduced hypoflexid on m1. In addition the m3 is lost in *Amblycoptus*. These characters are not seen on the specimens of Küçükçekmece. The oldest occurrence of *Anourosorex* was reported from Lufeng in China (MN12), while the oldest occurrence of *Amblycoptus* is in Europe at the locality of Polgárdi (MN13) in Hungary (Kormos 1926; Rzebik-Kowalska 1975; Mészáros 1998, 1999). Such a geographic distance in their first occurrences makes a suggestion of common origin doubtful, without proposing a dispersal from Eastern Asia to Europe during the Turolian.

Among the Anourosoricini, the specimens from Küçükçekmece compare better with the species referred to the genus *Crusafontina*. Thus far this genus is known in Europe with

five species: C. endemica Gibert, 1975 (type loc. Can Llobateres 1, Spain, range MN9-10), C. kormosi (Bachmayer & Wilson, 1970) (type loc. Kohfidisch fissures, Austria; range MN10-13), C. exculta (Mayr & Fahlbusch, 1975) (type loc. Hammerschmiede, Germany, range MN9), C. fastigata Van Dam, 2004 (type loc. Los Aguanaces 5A, Spain, age MN10), and C. vandeweerdi Van Dam, 2004 (type loc. Tortajada C, Spain, age MN11-12). Ziegler (2005, 2006) suggested the synonymy of C. exculta with C. endemica considering that the length of m2 and m3 has the same degree of reduction with respect to the length of m1, and its stage of evolution corresponds to that of C. endemica. However, Van Dam (2010) and Prieto & Van Dam (2012) maintained this species as valid, because it is smaller, and several characters of its dentition differ from those of C. endemica.

From these European species, C. fastigata and C. vandeweerdi are endemic to Spain. The mandible and lower molars of C. fastigata and C. vandeweerdi are not known, preventing any comparison with the specimens from Küçükçekmece. The latter species is known as being the largest species of Crusafontina (Van Dam 2004). C. kormosi has lately been the subject of detailed studies by Mészáros (1998, 2000) and Ziegler (2006) based on the specimens from Hungarian and Austrian localities, respectively. This species is clearly larger than C. endemica, it has a more reduced m2 and m3 (e.g., Mészáros 1998: pl. 1, figs 3, 5), and the trigonid of m1 is stretched mesially to form a wide angle of about 140°. These characters are different from the ones observed on the specimens of Küçükçekmece. C. kormosi is mainly known in central and southeastern Europe from localities correlated to MN10-early MN13 (Van Dam 2004).

Up to date Crusafontina exculta is known from its type locality Hammerschmiede and Hillenloh, both in Bavaria (Germany), and both correlated to MN8 or early MN9 (Mayr & Fahlbusch 1975; Van Dam 2004, 2010; Prieto & Van Dam 2012). The size of cheek teeth is in the lower limits of *C. endemica* (see Table 3). It differs from the latter species, and also from the material of Küçükçekmece, in having lower molars with oblique crests, not sub-parallel to the entoconid crest as in other species, larger talonid on lower molars (on the m1 talonid occupies 45% of the total length), and the trigonids of m1 and m2 less stretched longitudinally compared to other Crusafontina species. In addition, the mandibles from Hammerschmiede display a well-marked lower sigmoid notch and strong angular process. On the mandibles from Küçükçekmece, the lower sigmoid notch is faint and the angular process is not formed.

The size and the characters of mandible and dentition of the Küçükçekmece specimens fit with *C. endemica* (Table 3). Van Dam (2004) redescribed and illustrated mandibles and dentition of C. endemica from its type locality Can Llobateres 1 and from other localities in Spain (Gibert 1975; Van Dam 2004, 2010). The material from Küçükçekmece does not show any reliable difference, and the dimensions of the mandibles as well as the m1 are within the size range of this species. Although in all characters the Küçükçekmece shrew fits with this species, the poor state of the material and the

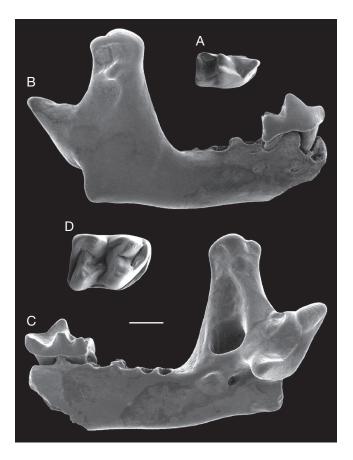


Fig. 7. – Insectivores from Küçükçekmece West, Crusafontina cf. endemica Gibert, 1975: A, right m1 (MNHN.F.TRQ963) in occlusal view; B, C, right mandible with m1 (TRQ962) in lateral (B) and medial (C) views. Schizogalerix sp.: D, right m2 (TRQ961) in occlusal view. Scale bar: 1 mm.

lack of upper dentition prevent a secure assignment, hence its identification as Crusafontina cf. endemica.

Hutchison & Bown (in Bown 1980) described a new genus and two new species of Anourosoricini, Anouroneomys magnus and Anouroneomys minimus, from the Lemoyne Quarry in Nebraska, correlated to the Clarendonian stage. Storch & Qiu (1991) included these species in Crusafontina because of their great similarities in the shape of the mandible and dentition with the European species of Crusafontina. Indeed, A. magnus is similar in size to C. kormosi, while A. minimus is smaller than the smallest species of Crusafontina.

Van Dam (2004) has provided an exhaustive list of all known Anourosoricini occurrences in Eurasia and North America. This list shows that their oldest occurrences in Eurasia start toward the end of middle Miocene (MN8) with poorly documented elements referred to as cf. Crusafontina sp. from Switzerland (Anwil) and Poland (Belchatov A), and *C. exculta* from latest middle Miocene or early late Miocene of Bavaria. The genus Crusafontina is frequent in Vallesian localities of Europe, mainly represented by *C. endemica*, but much less common in Turolian localities, which mainly include C. kormosi in Central and southeastern Europe, and the endemic species C. fastigata and C. vandeweerdi in Spain. A later occurrence is early MN13 at Polgárdi 4 (Hungary) (Van Dam 2004).

CONCLUSIONS

The locality of Küçükçekmece is known since the monograph of Malik & Nafiz (1933) as a late Miocene vertebrate locality near Istanbul. The fossils described in this monograph are found in a sand quarry along the southeastern bank of the Küçükçekmece lagoon. Later on, Father Jean Nicolas collected more material on the western bank of the lagoon and in the nearby cliffs along the Sea of Marmara (Küçükçekmece West). Nicolas (1978) provided a new account on the Küçükçekmece fauna, and mentioned for the first time the presence of small sized mammals at Küçükçekmece, in addition to a castorid that Malik & Nafiz (1933) had recognized from Küçükçekmece East.

The present study describes all available remains of rodents, lagomorphs and insectivores, mostly found at Küçükçekmece West, and also some castorid and spalacid teeth from Küçükçekmece East. The species here described are three species of rodents (*Byzantinia bayraktepensis*, Spalacidae indet. and *Chalicomys jaegeri*), one lagomorph (*Ochotona ozansoyi*) and two insectivores (*Schizogalerix* sp. and *Crusafontina* cf. *endemica*). Such an association is certainly far from reflecting the complete spectrum of small mammals that might have existed in this region. This is due to the fact that this material was collected by hand picking on the outcrops, without using traditional techniques for recovery of small mammals such as screen washing.

Malik & Nafiz (1933) and Nicolas (1978) have already discussed the age of the Küçükçekmece fauna. The first authors used available palaeontological data (molluscs and vertebrates) and the position of the fossiliferous horizon in the local stratigraphy to conclude late Sarmatian age. Nicolas (1978: 457) reached a similar age assignment using the similarities of mammalian taxa, and suggested to include the fossiliferous horizon "dans le Chersonien, equivalent au Vallésien moyen". The presence of *Byzantinia bayraktepensis*, known in Turkey only in localities correlated to MN8 and MN9 (Bayraktepe 1, Yenieskihisar, Dereikebir, Mahmutköy, Pismanköy and Tuğlu see Ünay 1980; Rummel 1998; Joniak & de Bruijn 2015), suggests late Astaracian or early Vallesian correlation. Chalicomys jaegeri and Crusafontina cf. endemica are common in Vallesian localities of Europe. The type locality of the lagomorph Ochotona ozansoyi is Sinap Loc. 84 in Central Anatolia (Sen 2003), dated by magnetostratigraphy as old as 9.37 Ma (Vallesian equivalent, Kappelman *et al.* 2003). From the study of small mammals, it can be concluded that the age of Küçükçekmece fauna should be close to the early/ late Vallesian boundary, or somewhat younger.

As discussed by Lom *et al.* (2016), the Neogene deposits in the vicinity of Küçükçekmece lagoon display a succession of marine and terrestrial deposits. Even the terrestrial deposits, which yielded the Küçükçekmece fauna, include some marine molluscs (Malik & Nafiz 1933; Chaput & Gillet 1939). The vertebrate fauna is mainly composed of terrestrial animals, but also some marine vertebrates such as fishes, turtles, seals and small whales. From these observations Malik & Nafiz (1933: 24) have concluded that "this vertebrate fauna became

fossilized in a bay or estuary that received fluvial input or in a river mouth close to the sea". From the fossils here studied, the abundance of beavers suggests a river environment. The insectivores of this fauna are known as adapted to closed and humid forests.

Acknowledgements

This study was financially supported by CR2P (UMR 7207 CNRS-MNHN). I am grateful to Mehmet Sakınç (Istanbul), who encouraged me to undertake the Küçükçekmece monograph and made available Küçükçekmece fossils for study. Vincent Pernègre (Paris) helped with the use of MNHN collections. Clara Stefen (Dresden) and Jan Van Dam (Utrecht) provided documentation and advice in identifying Küçükçekmece small mammals. Philippe Loubry (Paris) kindly assisted in the study of the ITU collections and executed all photos of this paper.

Constructive comments of the referees Lawrence J. Flynn and Janos Hir greatly improved the present study.

REFERENCES

- ALDANA CARRASCO E. 1992. Los Castoridae (Rodentia, Mammalia) del Neógeno de Cataluña (España). *Treballs del Museu de Geologia de Barcelona* 2: 99-141.
- APOLTSEV D. A. & NEOFITNY S. V. 2015. Location remains of extinct beaver (Castoridae, Rodentia) late Miocene Ukraine. *Prirodnixii almanak* 20: 40-46 (in Russian).
- BACHMAYER F. & WILSON R. W. 1970. Small mammals (Insectivora, Chiroptera, Lagomorpha, Rodentia) from the Kohfidisch fissures of Burgenland, Austria. *Annalen des Naturhistorischen Museums in Wien* 74: 533-583.
- BOWN T. M. 1980. The fossil Insectivora of Lemoyne Quarry (Ash Hollow Formation, Hemphillian), Keith County, Nebraska. *Transactions of the Nebraska Academy of Sciences* 8: 99-121.
- CALVERT F. & NEUMAYR M. 1880. Die Jungen Ablagerungen am Hellespont. Denkschriften der Kaiserlichen Akademie der Wissenschaften / Mathematisch-Naturwissenschaftliche Klasse 40: 357-378.
- CASANOVAS-VILAR I. & ALBA D. M. 2011. The never-ending problem of Miocene beaver taxonomy. Acta Palaeontologica Polonica 56 (1): 217-220. http://dx.doi.org/10.4202/app.2010.0051
- CASANOVAS-VILAR I., ALBA D. M., ALMÉCIJA S., ROBLES J.M., GALINDO J. & MOYÀ-SOLÀ S. 2008. Taxonomy and paleobiology of the genus *Chalicomys* Kaup, 1832 (Rodentia, Castoridae), with the description of a new species from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, Spain). *Journal of Vertebrate Paleontology* 28 (3): 851-862. http://dx.doi.org/10.1671/0272-4634(2008)28[851:TAPOTG]2.0.CO;2
- ČERMÁK S. & REKOVETS L. I. 2010. Early Pliocene ochotonids (Mammalia, Lagomorpha) from Southern Ukraine. *Geodiversitas* 32 (1): 107-120. http://dx.doi.org/10.5252/g2010n1a3
- CHAPUT E. & GILLET S. 1939. Les faunes de mollusques des terrains à *Hipparion gracile* de Küçükçekmece près d'Istanbul (Turquie). *Bulletin de la Société géologique de France*, 5e série, 8: 363-388.
- ENGESSER B. 1980. Insectivora und Chiroptera (Mammalia) aus dem Neogen der Turkei. Schweizerische Paläontologische Abhandlungen 102: 37-363.
- Erbajeva M. A. 1988. [Cenozoic Pikas (Taxonomy, Systematics, Phylogeny)]. Nauka, Moscow, 224 p. (in Russian).
- ErbaJEVA M. A. 2003. Late Miocene ochotonids (Mammalia, Lagomorpha) from Central Mongolia. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 2003: 212-222.

- Erbajeva M. A., Flynn J. L., Li C.-K. & Marcus L. 2006. New Late Cenozoic Ochotonids from China. Beiträge zur Paläontologie 30: 133-141.
- FLYNN L. J.& JACOBS L. L. 1990. Preliminary analysis of Miocene small mammals from Paşalar, Turkey. Journal of Human Evolution 19: 423-436.
- Franzen J. L. & Storch G. 1975. Die unterpliozäne (turolische) Wirbeltierfauna von Dorn-Dürkheim, Rheinhessen (SW-Deutschland). 1. Entdeckung, Geologie, Mammalia: Carnivora, Proboscidea, Rodentia. Grabungsergebnisse 1972-1973. Senckenbergiana lethaea 56 (4/5): 233-303.
- GERVAIS P. M. 1859. Zoologie et Paléontologie française. (Animaux vertébrés), Première partie: Mammifères. 2. Arthur Bertrand, Paris, 544 p.
- GIBERT J. 1975. New insectivores from the Miocene of Spain. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B 78: 108-133.
- HOEK OSTENDE L. W. VAN DEN & DOUKAS C. S. 2003. Distribution and evolutionary history of the early Miocene erinaceid Galerix symeonidisi Doukas, 1986, in REUMER J. W. F. & WES-SELS W. (eds), Distribution and Migration of Tertiary Mammals in Eurasia. A Volume in Honour of Hans de Bruijn. Natuurmuseum Rotterdam (DEINSEA 10): 287-303.
- HUGUENEY M. 1999. Family Castoridae, in RÖSSNER G. E. & HEISSIG K. (eds), The Miocene Land Mammals of Europe. Verlag Friedrich Pfeil, Munich: 281-300.
- HUGUENEY M. & DURANTON F. 2012. Les Castoridae de Sansan. in Peigné S. & Sen S. (eds), Mammifères de Sansan. Muséum national d'Histoire naturelle, Paris: 95-118 (Mémoires du Muséum national d'Histoire naturelle; 203).
- JONIAK P. & DE BRUIJN H. 2015. Rodents from the Upper Miocene Tuğlu Formation (Çankırı Basin, Central Anatolia, Turkey). Paläontologische Zeitschrift 89:1039-1056. http://dx.doi. org/10.1007/s12542-015-0257-
- Kappelman J., Duncan A., Feseha M., Lunkka J.-P., Ú D., McDow-ELL F., RYAN T. M. & SWISHER III C. C. 2003. — Chronology, in Fortelius M., Kappelman J., Sen S. & Bernor R. L. (eds), Geology and Paleontology of the Miocene Sinap Formation, Turkey. Columbia University Press, New York: 41-66.
- KORMOS T. 1926. Ámblycoptus oligodon n.g. & n. sp. Eine neue Spitzmaus aus dem ungarischen Pliozän. Annales Historic-naturales Musei Nationalis Hungarici 24: 352-370.
- LARTET E. 1851. Notice sur la colline de Sansan. J.-A. Portes, Auch, 45 p.
- Lom N., Ülgen S. C., Sakinç M. & Şengör A. M. C. 2016. Geology and stratigraphy of Istanbul region, in SEN S. (ed.), Late Miocene mammal locality of Küçükçekmece, European Turkey. Geodiversitas 38 (2): 175-195 (this volume). http:// dx.doi.org/10.5252/g2016n2a3
- LUNGU A. N. 1981. [Hipparion Fauna of Middle Sarmatian of Moldavia (Insectivora, Lagomorpha and Rodentia)]. Shtiintsa Press, Kishinev, 138 p. (in Russian).
- Malik A. & Nafiz H. 1933. -– Vertébrés fossiles de Küçük Çekmece. Bulletin de la Faculté des Sciences de l'Université d'Istanbul 8: 1-119.
- Mayr H. & Fahlbusch V. 1975. Eine unterpliozäne Kleinsäugerfauna aus der Oberen Süsswasser-Molasse Bayerns. Mitteilungen der Bayerischen Staatssammlungen für Paläontologie und historische Geologie 15: 91-111.
- Mazzini I., Hudá kova N., Joniak P., Ková ová M., Lucifora S., MIKES T., MULCH A., ROJAY B., ESU D. & SOULIÉ-MÄRSCHE I. 2013. — Palaeoenvironmental and chronological constraints on the Tuğlu Formation (Çankırı Basin, Central Anatolia, Turkey). Turkish Journal of Earth Sciences 22: 747-777. http://dx.doi. org/10.3906/yer-1207-10
- MEIN P. & FREUDENTHAL M. 1971. Une nouvelle classification des Cricetidae (Mammalia, Rodentia) du Tertiaire de l'Europe. Scripta Geologica 2: 1-37.

- MÉSZÁROS L. G. 1998. Crusafontina (Mammalia, Soricidae) from late Miocene localities in Hungary. Senckenbergiana lethaea 77:
- MÉSZÁROS L. G. 1999. An exceptionally rich Soricidae (Mammalia) fauna from the upper Miocene localities of Polgárdi (Hungary). Annales Universitatis Scientiarom Budapestinensis, Sectio Geologica 32: 5-34.
- MÉSZÁROS L. G. 2000. New results for the late Miocene Soricidae stratigraphy in the Pannonian Basin. Newsletters on Stratigraphy 38: 1-11.
- MONTUIRE S., SEN S. & MICHAUX J. 1994. The middle Pleistocene mammalian fauna from Emirkaya-2, Central Anatolia (Turkey): Systematics and paleoenvironment. Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen 193 (1): 107-144.
- MÖRS T. & STEFEN C. 2010. The castorid Steneofiber from NW Germany and its implications for the taxonomy of Miocene beavers. Acta Palaeontologica Polonica 55 (2): 189-198. http:// dx.doi.org/10.4202/app.2009.0013
- NICOLAS J. 1978. Un nouveau gisement de vertébrés dans le Chersonien: Kutchuk-Tchekmedje Ouest (Thrace turque). Comptes rendus de l'Académie de Sciences 287D: 455-458.
- OZANSOY F. 1961. Sur quelques mammifères fossiles (Deinotherium, Serridentinus, Dipoides) du Tertiaire d'Anatolie occidentale-Turquie. Bulletin of the Mineral Research and Exploration Institute 56: 85-93.
- PRIETO J. & VAN DAM J. A. 2012. Primitive Anourosoricini and Allosoricinae from the Miocene of Germany. Geobios 45: 581-589.
- REUMER J. W. F. 1984. Ruscinian and early Pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (The Netherlands) and Hungary. Scripta Geologica 73: 1-173.
- RUMMEL M. 1998. Die Cricetiden aus dem Mittel- und Obermiozän der Türkei. Documenta Naturae 123: 1-300.
- RZEBIK-KOWALSKA B. 1975. The Pliocene and Pleistocene Insectivores (Mammalia) of Poland. II. Soricidae: Paranourosorex and Amblycoptus. Acta Zoologica Cracoviensa 20: 167-182.
- SARAÇ G. 2003. Türkiye omurgali fosil yataklari (Fossil vertebrate localities of Turkey). MTA Report No 10609, 218 p. (unpublished).
- SARICA N. & SEN S. 2003. Spalacidae (Rodentia), in FORTEL-IUS M., KAPPELMAN J., SEN S. & BERNOR R. L. (eds), Geology and Paleontology of the Miocene Sinap Formation, Turkey. Columbia University Press, New York: 141-162.
- SEN S. 1990. Stratigraphie, faunes de mammifères et magnétostratigraphie du Néogène de Sinap Tepe, Province d'Ankara, Turquie. Bulletin du Muséum national d'Histoire naturelle, Paris, série C 12 (3/4): 243-277.
- SEN S. 1998. Rodentia and Lagomorpha, in SEN S. (ed.), Pliocene vertebrate locality of Çalta, Ankara, Turkey. Geodiversitas 20 (3): 359-378.
- SEN S. 2003. Lagomorpha, in FORTELIUS M., KAPPELMAN J., SEN S. & BERNOR R. L. (eds), Geology and Paleontology of the Miocene Sinap Formation, Turkey, Columbia University Press, New York: 163-178.
- SEN S. 2016. Historical background, in SEN S. (ed.), Late Miocene mammal locality of Küçükçekmece, European Turkey. Geodiversitas 38 (2): 153-173 (this volume). http://dx.doi. org/10.5252/g2016n2a2
- SEN S. & SARICA N. 2011. Middle-Late Miocene Spalacidae (Mammalia) from Western Anatolia, and the phylogeny of the family. Yerbilimleri-Bulletin of the Earth Sciences 32: 21-50.
- SICKENBERG O., BECKER-PLATEN J. D., BENDA L., BERG D., ENGESSER B., Gaziry W., Heissig K., Hünermann K.A., Sondaar P. Y., SCHMIDT-KITTLER N., STAESCHE U., STEFFENS P. & TOBIEN H. 1975. — Die Gliederung des höheren Jungtertiars und Altquartars in der Turkei nach vertebraten und ihre Bedeutung für die Internationale Neogene-Stratigraphie. Geologische Jahrbuch B15: 1-167.
- STEFEN C. 2009. The European Tertiary beaver *Chalicomys jaegeri* (Rodentia, Castoridae) revisited. Kaupia 16: 161-175.

- STEFEN C. 2011. A brief overview of the evolution of European Tertiary beavers. *Baltic Forestry* 17: 148-153.
- STORCH G. & QIU Z. D. 1991. Insectivores (Mammalia, Erinaceidae, Soricidae, Talpidae) from the Lufeng Hominoid locality, late Miocene of China. *Geobios* 24: 601-621.
- STORCH G. & ZAZHIGIN V. S. 1996. Taxonomy and phylogeny of the *Paranourosorex* lineage, Neogene of Eurasia (Mammalia: Soricidae: Anourosoricini). *Paläontologische Zeitschrift* 170: 257-268.
- STROMER E. 1928. Wirbeltiere im obermiocänen Flinz Münchens. Abhandlungen der Bayerischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Abteilung 32 (1): 1-71.
- SUATA-ALPASLAN F. 2009. Ochotona mediterranensis nov. sp. (Lagomorpha-Mammalia) from early Pliocene of Iğdeli (Anatolia-Turkey). International Multidisciplinary Scientific GeoConference SGEM 2009: 99-103.
- ÜNAY E. 1976. The remains of *Steneofiber jaegeri* Kaup (Rodentia, Mammalia) found in the Çanakkale region. *Bulletin of Mineral Research and Exploration Institute of Turkey* 86: 95-100.
- ÜNAY E. 1977. The Upper Miocene steneofibers (Rodentia, Mammalia) of Çatakbağyaka. Bulletin of the Geological Society of Turkey 20: 69-72.
- ÜNAY E. 1980. The Cricetodontini (Rodentia) from the Bayraktepe section (Çanakkale, Turkey). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* B 83: 399-418.
- ÜNAY E. 1981. Middle and Upper Miocene rodents from the

- Bayraktepe section (Çanakkale, Turkey). Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B 84: 217-238.
- ÜNAY E. 1996. On fossil Spalacidae. *in Bernor R. L.*, Fahlbusch V. & Mittman H. W. (eds), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York: 246-252.
- ÜNAY E., DE BRUIJN H. & SARAÇ G. 2003. A preliminary zonation of the continental Neogene of Anatolia based on rodents, in REUMER J. W. F. & WESSELS W. (eds), Distribution and Migration of Tertiary Mammals in Eurasia. A Volume in Honour of Hans de Bruijn. Natuurmuseum Rotterdam (DEINSEA 10): 539-547.
- VAN DAM J. A. 2004. Anourosoricini (Mammalia: Soricidae) from the Mediterranean region: a pre-Quaternary example of recurrent climate-controlled north-south range shifting. *Journal of Paleontology* 78 (4): 741-764.
- VAN DAM J. A. 2010. Anourosoricini (Soricidae, Mammalia): new taxa and systematic position in the light of molecular phylogenetics. *Journal of Vertebrate Paleontology* 30: 1221-1228.
- ZIEGLER R. 2005. The insectivores (Erinaceomorpha and Soricomorpha, Mammalia) from the Late Miocene hominoid locality Rudabánya. *Palaeontographia Italica* 90: 53-81.
- ZIEGLER R. 2006. Insectivores (Lipotyphla) and bats (Chiroptera) from the late Miocene of Austria. Annalen des Naturhistorischen Museums Wien 107 A: 93-106.

Submitted on 3rd March 2016; accepted on 15 May 2016; published on 24 June 2016.