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Micromammals from the late early Miocene of Çapak (western Anatolia) herald a time of change

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Abstract.—The new fossil micromammal assemblage of Çapak represents a mixture of both Anatolian and European faunal elements. The locality is very important for understanding faunal evolution in the less well-known time interval at the end of the early Miocene of western Anatolia. In Çapak, nine species of rodents and one species of ochotonid were encountered: the hamsters *Democricetodon gracilis*, *Megacricetodon primitivus*, *Eumyarion* aff. *E. montanus*, *Cricetodon* cf. *C. aliveriensis*, *Cricetodon* sp., and *Karydomys* cf. *K. strati*, the mole-rat *Debruijnia* sp., the squirrel *Aliveria luteyni*, the dormouse *Myomimus tanjuae* n. sp., and the pika *Albertona balkanica*. The assemblage is referable to Anatolian local zone E or MN unit 4. The relative abundance of the various genera is markedly different from that of the older early Miocene assemblages, suggesting that the environment in Anatolia became drier and had a more open landscape.

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Introduction

The late early Miocene was a period of major changes in the eastern Mediterranean. The collision of the African plate with Eurasia altered both the topography of the region and its climates, offering new migration routes (Rögl, 1999). Anatolia lies right at the center of these events that strongly influenced the distribution of mammals both within the region as well as in other parts of western Eurasia.

The early Miocene of Anatolia shows a high degree of endemicity in taxa of the rodent assemblages between local zones B to D (correlated with MN1-3). While European assemblages are dominated by Eomyidae and Gliridae, Anatolian assemblages are dominated by Muridae. At the beginning of MN4, there was a conspicuous faunal turnover in Europe. After a prolonged absence, known as the cricetid vacuum (Daams and Freudenthal, 1981), muroid rodents entered and immediately took the dominant position they still hold today (De Bruijn et al., 1992). This entrance of the hamsters traditionally marks the transition between the mammal units MN3 and MN4. Notably, earlier research showed that the hamster genera entering Europe at the end of the early Miocene were already present throughout that period in Anatolia (e.g., De Bruijn and Saraç, 1991; Theocharopoulos, 2000; De Bruijn et al., 2006; Wessels, 2009). However, while there are well-studied faunas from the region between zones B–D (correlated with MN1–3), such as Kargı, Kılçak, Harami, Gökler, Gördes, Sabuncubeli, Keseköy (e.g., Van den Hoek Ostende, 1992, 1995, 1997, 2001; Ünay, 1994; Joniak et al., 2017, 2019; Peláez-Campomanes et al., 2019), the younger assemblages are little known, published only as faunal lists or abstracts, such as in the localities of Söke, Dededağ, Belenyenice, Kaplangı, and Horlak (e.g., Sümengen et al., 1990; Ünay and Göktaş 1999; Kaya et al., 2007). As a result, it is not known how the faunas of Anatolia developed at the time major changes took place in the European faunas.

Here, we present the micromammal fauna from the new Anatolian locality of Çapak, which shows a significantly different composition from other early Miocene faunas. The locality was discovered within the framework of the National Geographic Expedition "Palaeogeography of Mammals Following the Collision of the African and Eurasian Plates" in 2015. The locality is situated near the village of Çapak in the northern part of the Torbalı district in the Province of Izmir (Figure 1). Because the rich assemblage of the new site represents a less-known time interval, it provides important information about the evolutionary lineages and migration paths of the Anatolian micromammals in that period. In addition, the presence of some species otherwise known from Europe makes it an important comparison point for interregional correlations. The assemblage shows the first evidence of open woodlands of Anatolia in the early to middle Miocene transition. In this paper, we describe the rodents and the lagomorph from the locality; the small insectivore assemblage will be published elsewhere.

Geological setting

The Neogene Kocaçay Basin (Sözbilir et al., 2011) is one of the NE-SW trending Miocene basins of western Anatolia

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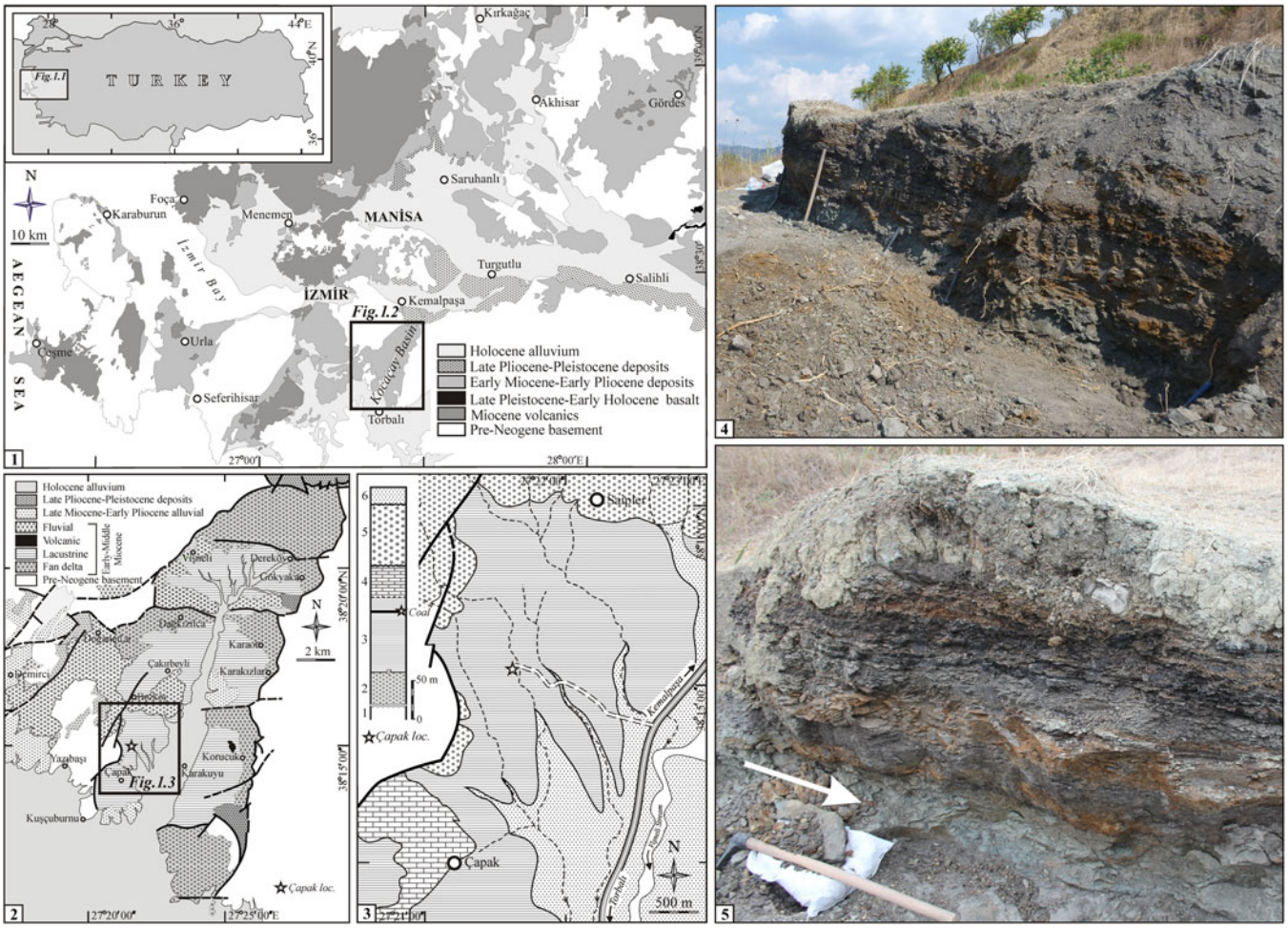


Figure 1. (**1**) Regional geological location of the Kocaçay Neogene basin. (**2**) Simplified geological map of the Kocaçay Neogene basin. (**3**) Early-middle Miocene sequence that crops out around Çapak village: (1) pre-Neogene basement, (2) fan-delta deposits, (3) lacustrine paper-shale deposits, (4) lacustrine limestone, (5) fluvial deposits, (6) Holocene alluvium (modified from Göktaş, 2012). (**4**) Outcrop view of Çapak. (**5**) The fossiliferous layer of Çapak.

(Figure 1.1). Early middle Miocene basin-filling starts with fan delta sediments, continues with lacustrine sediments and ends with fluvial sediments. The late Miocene sequence, which overlies this sequence with an angular unconformity, consists of alluvial fan deposits (Figure 1.2). The lacustrine sequence consists of laminated shales and ends with limestone that includes mudstone, rhyolitic tuff, sandstone and marshy sediments. The Çapak small-mammal fauna was found in the coaly marsh deposits in the lacustrine section that crops out north of the village of Çapak (Figure 1.3)

Materials and methods

Collection.—Approximately 2500 kg of sediment were collected during two fieldwork campaigns (2015 and 2018) and screen-washed with a mesh of 0.5 mm following the method of Daams and Freudenthal (1988b). All concentrate was sorted under the microscope.

Measurements.—Upper cheek teeth are indicated by uppercase and lower cheek teeth by lowercase. Where distinction between first and second molars is questionable, these are indicated as m1/2 or M1/2, respectively. Tooth measurements (maximum length and width) are given in mm and were taken using a Leica MZ16A stereomicroscope and associated software. Terminology used for dental morphology follows Daams and Freudenthal (1988a) and Oliver and Peláez-Campomanes (2013) for Cricetidae, García-Paredes et al. (2010) for Gliridae, Cuenca Bescós (1988) for Sciuridae, Sarıca and Sen (2003) for Spalacidae and López Martínez (1986) for Ochotonidae. SEM photographs were taken at the Slovak Academy of Science in Bratislava. All dental elements have been figured as being left. The letters of inverted photographs have been underlined on the figures.

Repository and institutional abbreviation.—The specimens examined in this study are deposited in the following institution: Ege University Natural History Application and Research Centre (EUNHM), Izmir, Turkey.

Systematic paleontology

Class Mammalia Linnaeus, 1758
Order Rodentia Bowdich, 1821

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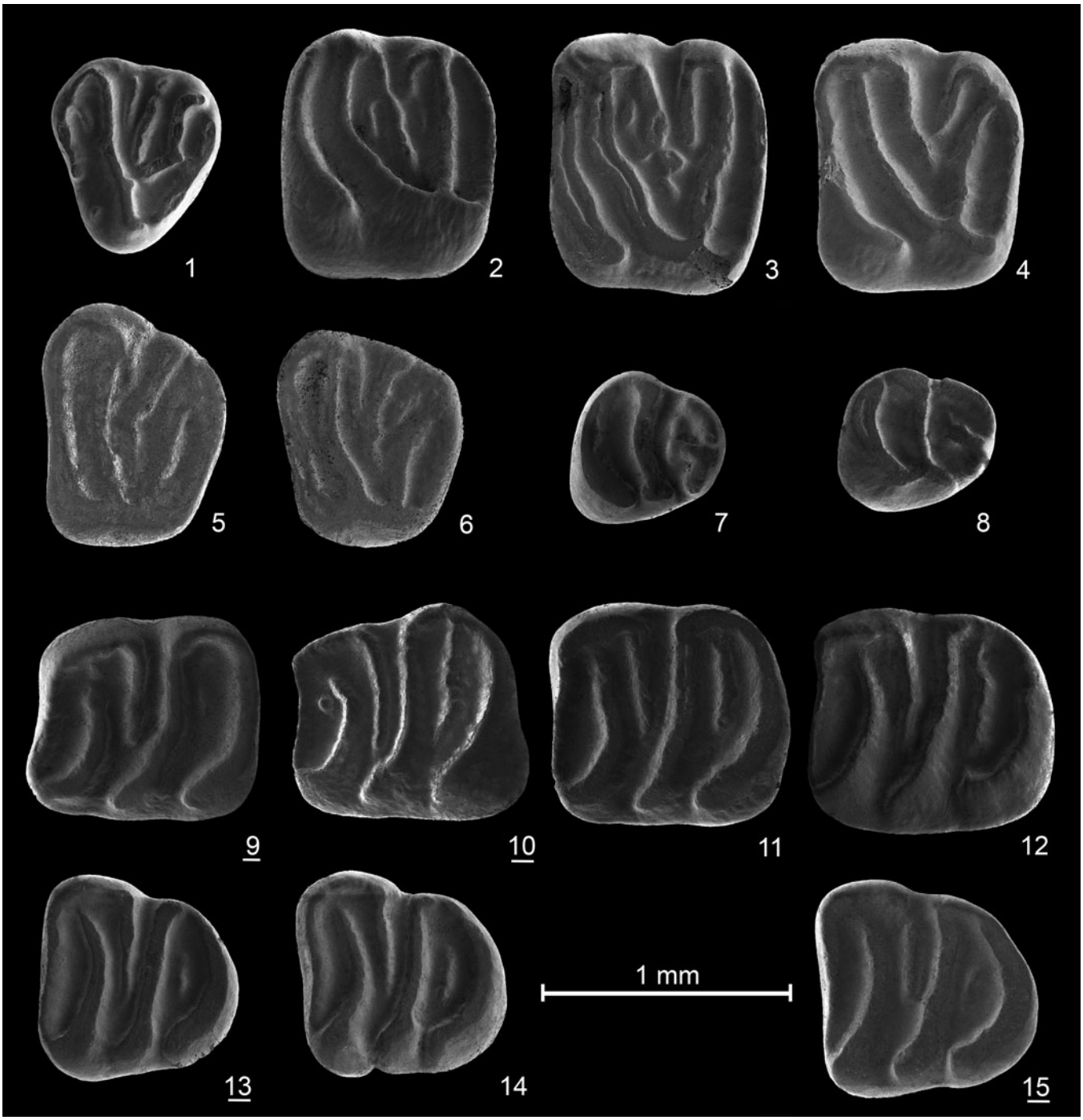


Figure 2. *Myomimus tanjuae* n. sp. (**1**) D4 sin (PV13091), (**2**) M1/2 sin (PV13097; holotype), (**3**) M1/2 sin (PV13094), (**4**) M1/2 sin (PV13093), (**5**) M3 sin (PV13105), (**6**) M3 sin (PV13106), (**7**) p4 sin (PV13134), (**8**) p4 sin (PV13111), (**9**) m1 dex (PV13120), (**10**) m1 dex (PV13124), (**11**) m2 dex (PV13119), (**12**) m2 sin (PV13116), (**13**) m3 sin (PV13129), (**14**) m3 sin (PV13130), (**15**) m3 dex (PV13125).

Family Gliridae Muirhead, 1819
Genus *Myomimus* Ognev, 1924

Type species.—*Myomimus personatus* Ognev, 1924.

Myomimus tanjuae new species
Figure 2

Holotype.—Right M1; PV13097 (length 0.93, width 1.07), Figure 2.2.

Diagnosis.—Small-sized *Myomimus* with an anterior extra ridge in M1 and M2. The ridge pattern in the central valley of the upper molars can be slightly complex. Lower molars are simple, only showing a posterior extra ridge. The m1 and m2 have two roots, while the m3 has three roots.

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Differential diagnosis.—Because the genus *Peridyromys* is sometimes considered a subjective junior synonym of *Myomimus* (see remarks), we include a comparison with the species of *Peridyromys*. *Myomimus tanjuae* n. sp. is smaller than *M. roachi* (Bate, 1937), *M. qafzensis* Haas, 1973, *M. maritsensis* De Bruijn, Dawson, and Mein, 1970; *M. multicristatus* (De Bruijn, 1966), *Peridyromys lavocati* Peláez-Campomanes and Daams, 2002, *P. brailloni* (Thaler, 1966), *P. prosper* (Thaler, 1966), *P. sondaari* Daams, 1999, *P. darocensis* Daams, 1999, *P. jaegeri* Aguilar, 1974, and *P. rex* García-Moreno in Alvarez-Sierra and García-Moreno, 1986.

Myomimus dehmi (De Bruijn, 1966) has a similar size to *Myomimus tanjuae* n. sp., but differs by having simpler dental pattern in the upper molars and having three roots in m1–m2.

Peridyromys aquatilis (De Bruijn and Moltzer, 1974) and *P. obtusangulus* (von Meyer, 1859) have a similar size to *Myomimus tanjuae* n. sp., but differ by the anterior extra ridge on the lower molars.

Myomimus sumbalenwalicus Munthe, 1980 has a similar size to *Myomimus tanjuae* n. sp., but differs by having three roots in m1–m2 and an absence of connection between posterior centroloph and metacone of M1–M2.

Peridyromys murinus (Pomel, 1853) is slightly smaller than *Myomimus tanjuae* n. sp. and differs from it by having no extra ridge on the upper molars.

Peridyromys turbatus Álvarez Sierra et al., 1991 is slightly larger than *Myomimus tanjuae* n. sp. and differs from it by having more complicated lower and upper molar dental patterns.

Occurrence.—Çapak, Izmir, Turkey, late early Miocene, local zone E (MN4).

Description.—

D4.—The outline of the molar is triangular and concave from the labial side (Fig. 2.1). Four main ridges are present (anteroloph, protoloph, metaloph, and posteroloph). The protoloph is higher than the other lophs. The anterior and posterior centrolophs are isolated. The posterior centroloph is longer than the anterior centroloph.

P4.—The protoloph and the metaloph are present, but the molar is broken from the lingual side, which prevents seeing the connections. The specimen is too worn to show any additional features.

M1/2.—The occlusal surfaces of the molars are concave. Four main ridges are present. The protocone is situated on the posterolingual corner, forming a V-shaped trigone. The metaloph and protoloph are connected. The anteroloph is isolated lingually. Both the anterior and posterior centrolophs are present. The central valley ridges have complex patterns in five specimens (Figure 2.3). The anterior centroloph is always longer than the posterior one. The anterior and posterior centrolophs are connected to the paracone and the metacone. There are no extra ridges in two of 12 specimens, while the other 10 specimens have a short anterior extra ridge. The molar has three roots.

M3.—The occlusal surface of the molar is concave. The dental pattern consists of four main ridges accompanied by the anterior and posterior centrolophs. The posterior centroloph is longer than the anterior centroloph. The posterior extra ridge is present in one specimen. The molar has three roots.

p4.—The premolar has a simple pattern and is slightly concave lingually. The posterior part is wider than the anterior part. The anterolophid and the metalophid are not connected to the mesolophid. The posterolophid and mesolophid are connected at the lingual side and end very close to each other at the labial side. The premolar has one root.

m1 and m2.—The m1 and m2 only differ in the outline of the molars. The occlusal surface is slightly concave. The dental pattern consists of four main ridges (anterolophid, metalophid, mesolophid, posterolophid) and centrolophid. The vestigial anterior extra ridge is present in two of 14 specimens. The anterolophid and the metalophid are connected labially in seven of 14 specimens. The lingual connection of the metalophid is variable. It ends free in eight molars and connects to the metaconid in six molars, but it is always directed anteriorly. The posterior extra ridge is present in all specimens; it is connected to the entoconid in three specimens. The molar has two roots.

m3.—The occlusal surface is slightly concave. The anterior part of the molar is wider than the posterior part. The dental pattern consists of four main ridges and centrolophid. The posterior extra ridge is present in all specimens. The molar has three roots.

Etymology.—The species is named in honor of Prof. Dr. Tanju Kaya, in recognition of her work on the fossil mammals of Turkey and her continuous support of micromammal research in the region.

Material.—2 D4 (PV13090, 13091), 1 P4 (PV13112), 13 M1/2 (PV13092–13104), 3 M3 (PV13105, 13106, 13141), 3 p4 (PV13110, 13111, 13134), 8 m1 (PV13118–13120, 13123, 13124, 13132, 13133, 13140), 6 m2 (PV13114–13117, 13121, 13122), 7 m3 (PV13125–13131).

Measurements.—Measurements of isolated cheek teeth are in Table 1.

Remarks.—The genus *Myomimus* is known from several Anatolian localities. The locality Keseköy yielded *Myomimus* sp. (Ünay, 1994), Çandır provided *Myomimus* n. sp. (De Bruijn et al., 2003), the Tuğlu and Sinap localities recorded *M. dehmi* (Sen, 1990; Joniak and De Bruijn, 2015; The NOW Community, 2020), and the locality of Hayranlı yielded *M. maritsensis* (Kaya and Kaymakçı, 2013). The genus *Peridyromys* is only recorded from three Anatolia localities. The localities of Hancılı 2 and Sofça yielded *Peridyromys* indet. (The NOW Community, 2020) and the locality of Paşalar provided *P. lavocati* Peláez-Campomanes and Daams, 2002.

Table 1. Measurements of *Myomimus tanjuae* n. sp. from Çapak.

	Length				Width		
	min	mean	max	N	min	mean	max
D4	0.77	0.78	0.79	2/2	0.84	0.85	0.86
M1/2	0.89	0.93	0.97	11/12	0.99	1.07	1.14
M3	0.78	0.80	0.81	3/3	0.93	0.97	1.00
p4	0.58	0.63	0.67	3/3	0.64	0.68	0.72
m1/2	0.82	0.98	1.05	14/14	0.75	0.93	1.04
m3	0.85	0.93	1.01	7/7	0.85	0.88	0.92

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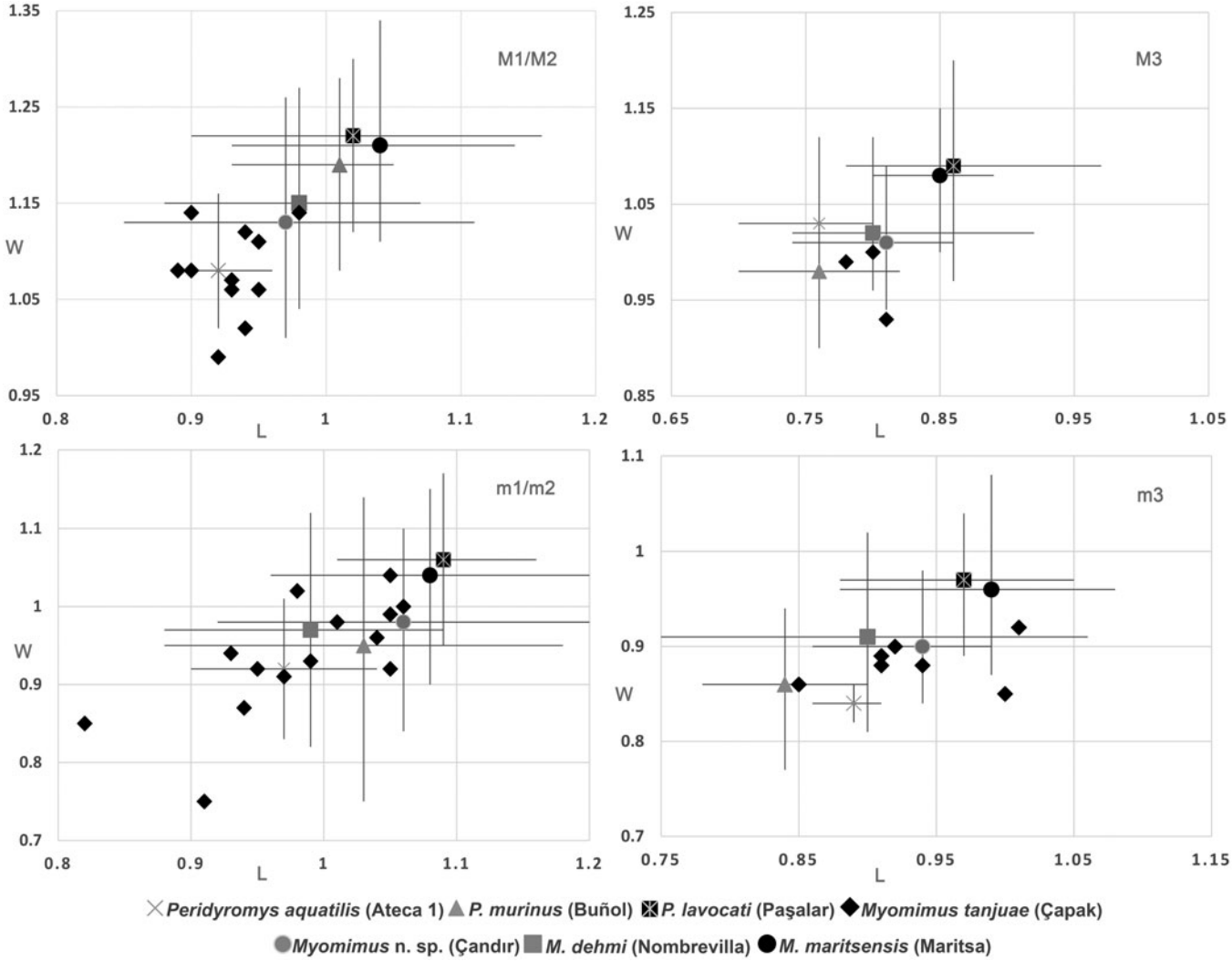


Figure 3. Scatter diagram of the upper and lower molars of *Myomimus* and *Peridyromys* from Anatolia and Europ (data after Daams, 1981; Peláez-Campomanes and Daams, 2002; De Bruijn et al., 2003).

The relationship between the genera *Peridyromys* and *Myomimus* has been cause of debate. De Bruijn et al. (1970) synonymized these two genera because of the similarity of the dental patterns. According to them, the only difference is the size of lower p4, which is relatively large in *Peridyromys* and small in *Myomimus*. By contrast, Daams (1981) preferred to keep both genera, based on the different number of the roots. Species of *Myomimus* have three roots while *Peridyromys* has two roots for lower m1, m2 and m3, with some exceptions (Daams, 1981). In addition, a major argument was the time gap between their respective stratigraphic ranges—*Peridyromys* being recorded up to MN4 and *Myomimus* appearing in Europe from MN9 onwards. Therefore, there was no *Peridyromys*/*Myomimus* record from MN4 to MN9. This situation changed when De Bruijn et al. (2003) published a new species of *Myomimus* from the middle Miocene hominoid site of Çandır in Turkey. They considered this species unique because of the number of roots (the m1 and m2 have two roots, the m3 has three roots). Because the age of the locality is considered MN5/6, this would close the gap in the record of *Myomimus*/*Peridyromys*. A full revision of the two genera is needed to clarify the proposed synonymy, which is outside the scope of the current paper. We do note that, as yet, there do not seem to be clear differences between *Myomimus* and *Peridyromys*.

Myomimus from Çapak falls metrically in the lower range of *Myomimus* n. sp. from Çandır (Figure 3) and is very similar morphologically. Moreover, both *Myomimus tanjuae* n. sp. and the Çandır *Myomimus* are characterized by having two roots in m1–m2 and three roots in m3. However, we have not studied the *Myomimus* material from Çandır, therefore we do not deem it opportune to change its current classification.

Family Muridae Illiger, 1811
Genus *Democricetodon* Fahlbusch, 1964

Type species.—*Democricetodon crassus* Freudenthal in Freudenthal and Fahlbusch, 1969 (=*Cricetodon minor* Lartet, 1851 sensu Fahlbusch 1964).

Democricetodon gracilis Fahlbusch, 1964
Figure 4

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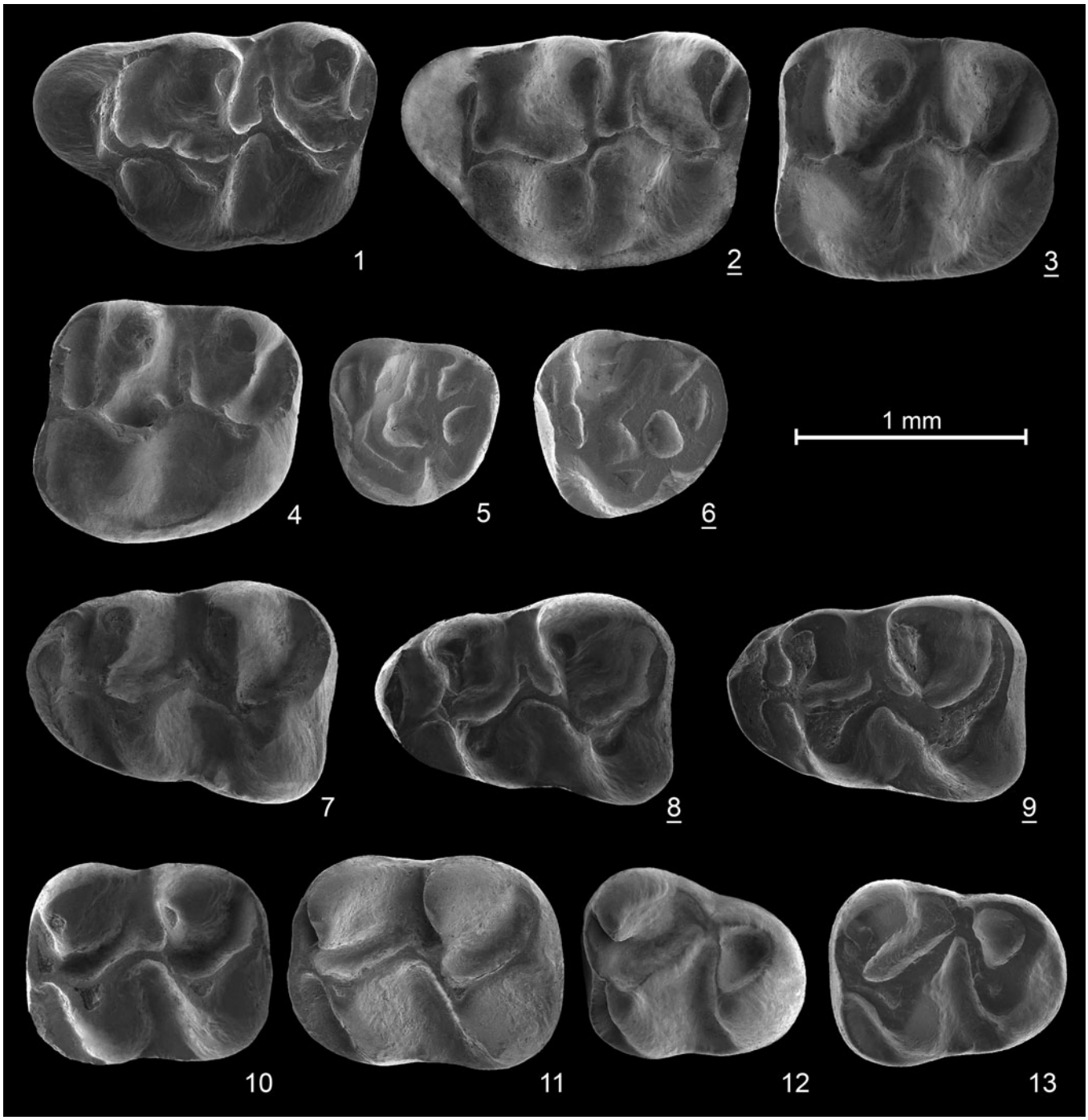


Figure 4. *Democricetodon gracilis* Fahlbusch, 1964. (**1**) M1 sin (PV13001), (**2**) M1 dex (PV13008), (**3**) M2 dex (PV13015), (**4**) M2 sin (PV13011), (**5**) M3 sin (PV13026), (**6**) M3 dex (PV13028), (**7**) m1 sin (PV13037), (**8**) m1 dex (PV13032), (**9**) m1 dex (PV13030), (**10**) m2 dex (PV13045), (**11**) m2 sin (PV13048), (**12**) m3 sin (PV13054), (**13**) m3 sin (PV13057).

Holotype.—Right M1 (BSPG 1959 II 247), Sandelzhausen, Germany. The specimen is stored in Bayerische Staatssammlung für Paläontologie und Geologie, Munich.

Description.—

M1.—The anterocone is simple. The lingual anteroloph is comma-shaped and connected to the base of the protocone. The labial anteroloph is connected to the base of the paracone. It is transverse in seven and curved in three molars. The anterolophule is strong and connected to the protocone. The labial spur of the anterolophule is weak and only present in three out of 10 specimens. The protolophule is double in four and only the posterior one is present in the remaining five molars (one of the 10 M1 specimens is missing the posterior part). The posterior paracone spur is absent. The mesoloph is of medium length in eight and short in one specimen. The metalophule is directed posteriorly; it is connected to the posteroloph in seven and fused to the posteroloph in two molars. A weak mesostyle

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is present in two specimens. The lingual mesocingulum is, at most, weakly developed. The sinus is transverse. The molar has three roots.

M2.—The lingual anteroloph is short and connected to the base of the protocone. The labial anteroloph is long and connected to the base of the paracone. The protolophule is double in 12 (only the anterior protolophule is present in one specimen), it is not visible in three specimens due to wear. The posterior paracone spur is absent. The metalophule is transverse in four specimens and directed anteriorly in 11 specimens. The mesoloph is always long and connected to the labial border in five molars. The mesostyle is present in seven out of 15 specimens. The lingual mesocingulum is present. The sinus is transverse. The molar has three roots.

M3.—The lingual anteroloph is connected to the base of the protocone in two, absent in two molars. The labial anteroloph is connected to the paracone. The metacone is developed only in one specimen. The metacone and the hypocone are connected by the posteroloph and the metalophule. The ridge between the paracone and metalophule is incomplete. The mesoloph is present in one specimen. The sinus is very shallow and narrow. The molar has three roots.

m1.—The anteroconid is elliptical. The labial anterolophid is longer than the lingual anterolophid. The labial anterolophid is connected to the base of the protoconid; the lingual anterolophid is connected to the base of the metaconid. The metalophulid is anterior in 12, weak and short in four specimens, absent in one specimen. The hypolophulid is anterior in all specimens. The posterolophid is strong and long, connected to the base of the entoconid. A weak labial posterolophid is present in two molars. A posterior sulcus is present in five m1. The mesolophid is short in two, of medium length in four, long and connected to the lingual border in four m1. The ectostylid is present in two and the mesostylid is present in one specimen. The labial mesocingulid is weak or absent. The sinus is wide and directed anteriorly. The molar has two roots.

m2.—The lingual anterolophid is weakly present in four molars. The labial anterolophid is connected to the base of the protoconid. It is short in five, long in four specimens. The metalophid is present in four, fused to the lingual anterolophid in five m2. The hypolophulid is always directed anteriorly. The mesolophid is of medium length in two, long and reaching to the lingual side of the molar in four, and reaching to the metaconid in three specimens. The posterolophid is long, connected to the base of the entoconid. A weak posterior sulcus is present. The ectostylid is present in one molar. The labial mesocingulid is present. The sinusid is transverse. The molar has two roots.

m3.—The lingual anterolophid is very short. The labial anterolophid is connected to the base of the protoconid. It is strong in five and weak in four specimens. The metalophulid is present in five, absent in one, and fused to the lingual anterolophid in three molars. The mesolophid is connected to the labial ridge. The posterior arm of the protoconid is long. The posterolophid is long and connected to the reduced entoconid. The sinusid is transverse. The molar has two roots.

Material.—10 M1 (PV-13000–13009), 15 M2 (PV-13010–13024), 4 M3 (PV-13025–13028), 15 m1 (PV-13030–13044), 9 m2 (PV-13045–13053), 9 m3 (PV-13054–13062).

Table 2. Measurements of *Democricetodon gracilis* from Çapak.

	Length				Width		
	min	mean	max	N	min	mean	max
M1	1.41	1.50	1.63	8/9	0.95	1.02	1.10
M2	0.95	1.12	1.27	14/14	0.90	1.01	1.15
M3	0.69	0.78	0.85	4//4	0.67	0.78	0.86
m1	1.26	1.32	1.41	10/10	0.87	0.93	0.98
m2	1.12	1.17	1.23	8/8	0.81	0.92	0.97
m3	0.86	0.99	1.05	9/9	0.72	0.80	0.86

Measurements.—Measurements of cheek teeth are given in Table 2.

Remarks.—*Democricetodon* first appeared in Anatolia in the early part of the early Miocene, in the Kılçak section (local zone B), much earlier than its first occurrence in Europe (Theocharopoulos, 2000). *Democricetodon* developed in Anatolia before it dispersed throughout Europe at the beginning of MN4 (e.g., Fahlbusch, 1964; Aguilar, 1982; Klein Hofmeijer and De Bruijn, 1988).

In the early Miocene of Anatolia, the genus *Democricetodon* is represented by various species: *Democricetodon anatolicus* Theocharopoulos, 2000 from Harami 3, *D. haltmari* Theocharopoulos, 2000 from Gökler and *D. doukasi* Joniak et al., 2017 from Keseköy (Theocharopoulos, 2000; Joniak et al., 2017). The specimens from Çapak are bigger than those of *D. haltmari* and *D. anatolicus*, and fall in the same size range as *D. doukasi* (Figure 5). However, *Democricetodon* from Çapak differs from *D. doukasi* in having higher crowned molars, a posteriorly directed metalophule in the M1 and the absence of a posterior paracone spur in M1–M2.

During the middle Miocene of Anatolia, *Democricetodon* is represented by European forms only. *Democricetodon* aff. *D. gaillardi* (Schaub, 1925) is known from the locality of Çandır (De Bruijn et al., 2003) and *Democricetodon brevis* (Schaub, 1925) is known from the locality of Paşalar (Peláez-Campomanes and Daams, 2002). Both species are larger than the *Democricetodon* from Çapak.

Democricetodon gracilis is a very common species in the MN4 to MN6 assemblages from central Europe (e.g., Fahlbusch, 1964; Daxner-Höck, 1998; Wessels and Reumer, 2009). It rarely occurs in the Iberian Peninsula but is known in late MN4/early MN5 sites in the Ebro Basin (Suárez Hernando, 2017) and the Vallès-Penedès Basin (Agustí, 1981; Jovells-Vaqué and Casanovas-Vilar, 2018) as well. It is also known from the eastern Mediterranean localities of Aliveri (MN4), Karydia (MN4) and Thymiana A (MN5) (Theocharopoulos, 2000; Koufos, 2006). The species is also tentatively listed from two Anatolian localities, Yeniliman and Belenyenice (Saraç, 2003). The Çapak specimens fall metrically and morphologically within the variation of the type material of *D. gracilis* from Sandelzhausen (MN5) (Wessels and Reumer, 2009) (Figure 5). However, the bottom of the sinuses is situated higher above the enamel-dentine junction in the Sandelzhausen specimens. In this respect, the molars from Çapak are more similar to those of *D. gracilis* from Forsthart (MN4) (Ziegler and Fahlbusch, 1986) in having a lower crown. As yet, it is unclear

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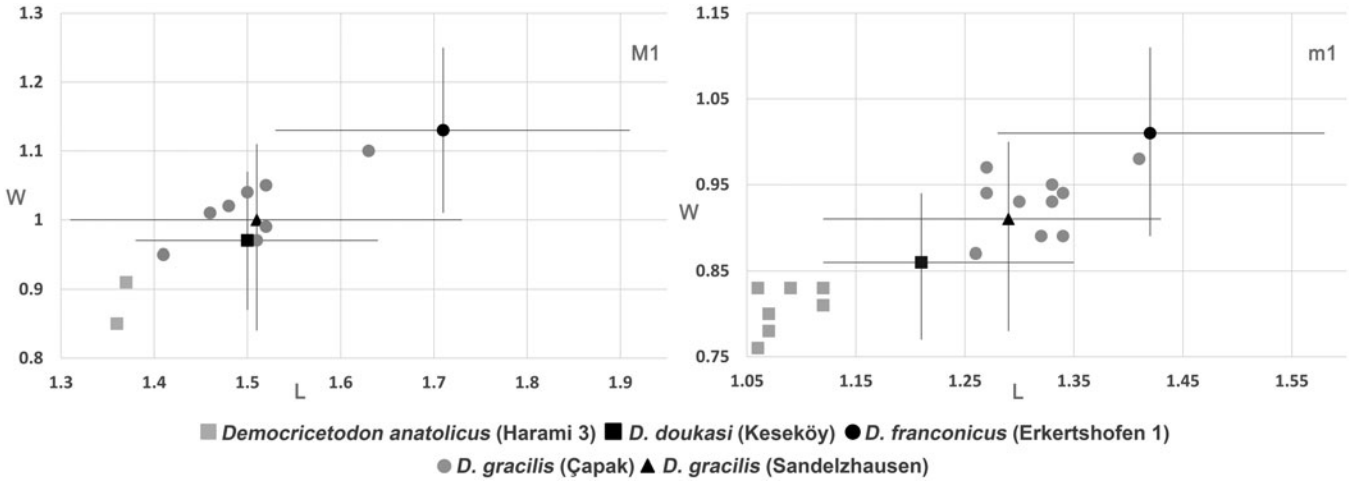


Figure 5. Scatter diagram of the upper and lower first molars of small sized *Democricetodon* from Anatolia and adjacent area (data are after Klein Hofmeijer and De Bruijn, 1988; Theocharopoulos, 2000; Wessels and Reumer, 2009).

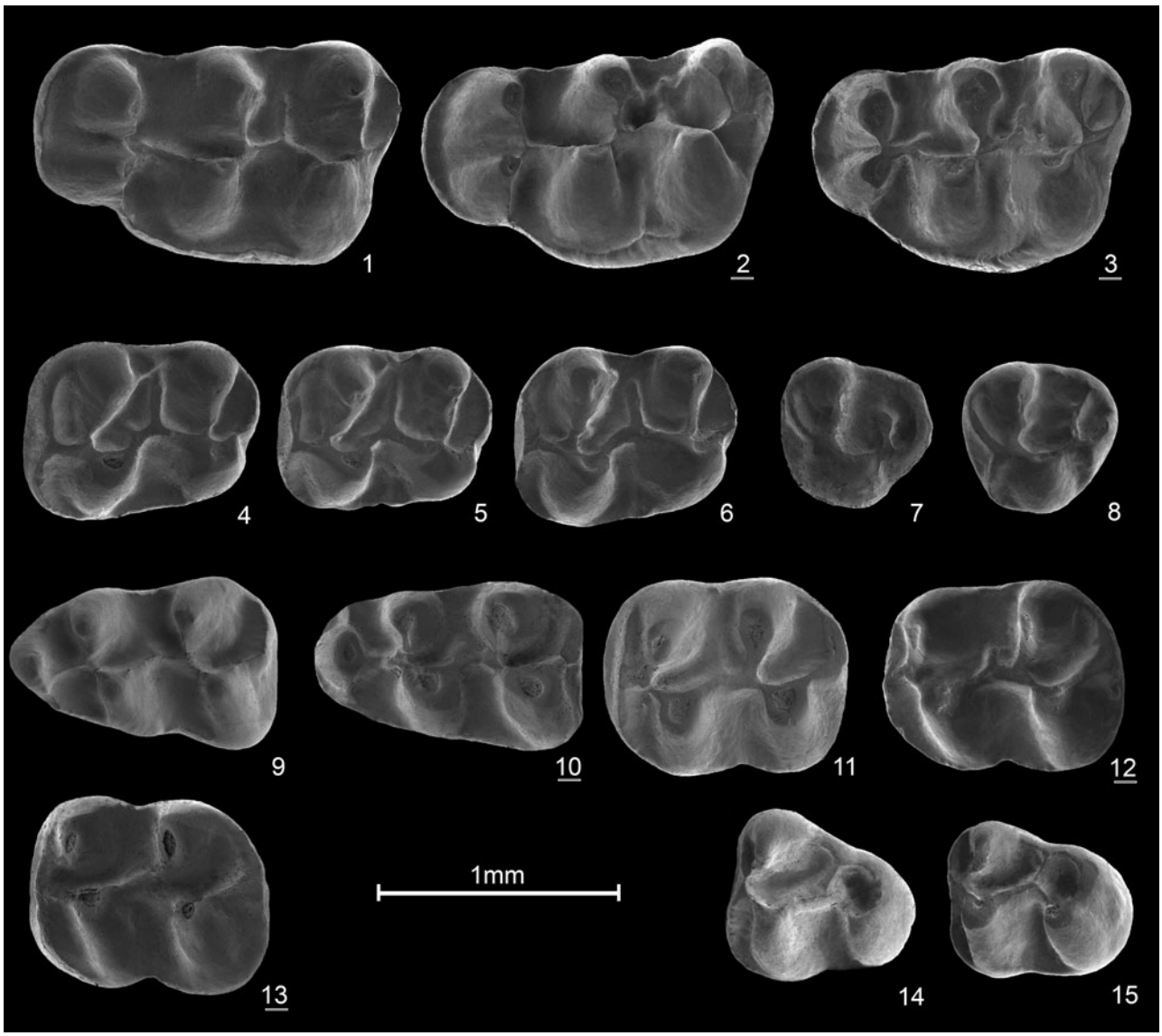


Figure 6. *Megacricetodon primitivus* (Freudenthal, 1963). (**1**) M1 sin (PV13237), (**2**) M1 dex (PV13238), (**3**) M1 dex (PV13239), (**4**) M2 sin (PV13264), (**5**) M2 sin (PV13266), (**6**) M2 sin (PV13269), (**7**) M3 sin (PV13281), (**8**) M3 sin (PV13282), (**9**) m1 sin (PV13301), (**10**) m1 dex (PV13312), (**11**) m2 sin (PV13324), (**12**) m2 dex (PV13335), (**13**) m2 dex (PV13333), (**14**) m3 sin (PV13341), (**15**) m3 sin (PV13339).

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whether this is part of an overall trend within the species or if it is a feature that is an ecophenotypical variation.

Genus *Megacricetodon* Fahlbusch, 1964

Type species.—*Cricetodon gregarius* Schaub, 1925.

Megacricetodon primitivus (Freudenthal, 1963)
Figure 6

Holotype.—Ramus with m1–m3 56-142, Valtorres, Calatayud-Montalbán Basin, Spain. The specimen is stored in Institut Català de Paleontologia Miquel Crusafont, Barcelona.

Description.—

M1.—The anterocone is slightly divided in three and deeply split in 19 specimens. There is a cingulum in front of the anterior furrow of the anterocone in all of the specimens. The labial cusp of the anterocone is larger than the lingual cusp. The anterolophule is connected to the lingual anterocone in 12 specimens, it is connected between the two cones in two, in which it is divaricated into two lophules, and it is connected to the labial and the lingual anterocone in two M1. The labial spur of the anterolophule is present in three specimens. The protolophule is directed posteriorly in all specimens. An indistinct posterior paracone spur is present in three specimens. The lingual mesocingulum is generally strong and it is barely visible or absent in worn specimens. The mesoloph is long (it is connected to the labial edge) in 19 and of medium length in three specimens. The metalophule is transverse in four and directed posteriorly in 17 molars. The sinus is transverse. The molar has three roots.

M2.—The labial anteroloph is longer than the lingual anteroloph. The labial anteroloph is connected to the paracone and the lingual anteroloph continues to the cingulum; it is not connected to the protocone. The lingual mesocingulum is present in all specimens except for one molar. The protolophule is directed anteriorly in 17, transverse in seven, double in four, and directed posteriorly in one specimen. The protolophule II is incomplete in two out of four specimens. The entoloph is angular. The posterior arm of the protocone is longer than the anterior arm of the hypocone in a high proportion of the M2. The ectoloph is present in 11 M2. The development of the mesoloph is variable—it is short in one, of middle length in 10, long in nine and long and connected with the labial border in eight specimens. The ectoloph is connected with the mesoloph in seven of the M2. The metalophule is directed anteriorly in 15, transverse in 11, and directed posteriorly in one specimen. The molar has three roots.

M3.—The labial anteroloph is connected to the paracone. The lingual anteroloph is present in four molars; it is connected to the base of the protocone in two specimens. The protolophule is transverse. The metalophule is connected to the anterior arm of the reduced hypocone. The neo-entoloph is present only in two M3. The weak metacone is present in three molars. The hypocone is present in four specimens. The molar has three roots.

m1.—The anteroconid is rounded. The anterolophulid is long. The metalophulid is always single, short and directed anteriorly. The mesolophid is absent in seven specimens, of medium length in 24 specimens. The ectomesolophid is only present in one specimen. The hypolophulid is directed anteriorly. The sinusid is directed slightly anteriorly. The lingual and labial mesocingulid are present. The cusps are slender. The molar has two roots.

m2.—The labial anterolophulid is longer than the lingual anterolophulid and is connected to the protoconid. The labial anterolophid continues to the mesocingulid and is not connected to the protoconid in one specimen. The lingual mesocingulid is connected with the entoconid in 11, free in five and absent in five molars. The labial mesocingulid is always connected to the hypoconid; it is well developed in five specimens. The mesolophid is generally short, but long in one and absent in one molar. The hypolophulid is directed anteriorly. The cusps are slender. The molar has two roots.

m3.—The lingual anterolophulid is short, and the labial anterolophid is long and connected with the protoconid in ten specimens. The labial mesocingulid is well developed in five and weak in nine molars. The mesolophid is of medium length and present only in one m3. The cusps are slender. The molar has two roots.

Material.—22 M1 (PV13230–13250, 13318), 30 M2 (PV13252–13280, 13319), 10 M3 (PV13281–13289, 13084), 31 m1 (PV13290–13317, 13080, 13081, 13083), 19 m2 (PV13320–13337, 13082), 14 m3 (PV13338–133449, 13086, 13087).

Measurements.—Measurements of cheek teeth are given in Table 3.

Remarks.—The story of *Megacricetodon* is not as well known as that of the other hamsters in the early Miocene of Anatolia. The earliest records are from the local zone D localities of Keseköy and Kınık 1 and are assigned to *Megacricetodon* sp. and *M.* cf. *M. primitivus*, respectively (Ünay and Göktaş, 2000; Wessels et al., 2001). The records from Söke and Dededağ (local zone E) are assigned *M.* cf. *M. primitivus* and *M. primitivus* (Ünay and Göktaş, 1999), but as a preliminary list with a short description only. Kaya et al. (2007) also indicated several *Megacricetodon* from early Miocene assemblages, but only in faunal lists.

Megacricetodon first appears in Europe in MN4, with occurrences such as *M. hellenicus* Oliver and Peláez-Campomanes, 2016 from Aliveri (Greece), *M.* aff. *M. collongensis* (Mein, 1958) from Langenau 1 (Germany), *M. primitivus* from Artesilla (Spain) and *M. bezianensis* Bulot, 1980 from Bézian (France) (Bulot, 1980; Sach and Heizmann, 2001; Oliver

Table 3. Measurements of *Megacricetodon primitivus* from Çapak.

	Length				Width		
	min	mean	max	N	min	mean	max
M1	1.30	1.36	1.56	22/21	0.80	0.90	1.00
M2	0.92	0.98	1.16	29/29	0.76	0.83	0.95
M3	0.64	0.72	0.79	10/10	0.63	0.71	0.85
m1	1.15	1.26	1.34	22/23	0.70	0.81	0.87
m2	0.88	1.05	1.15	17/17	0.76	0.85	0.91
m3	0.77	0.85	0.90	14/14	0.66	0.71	0.76

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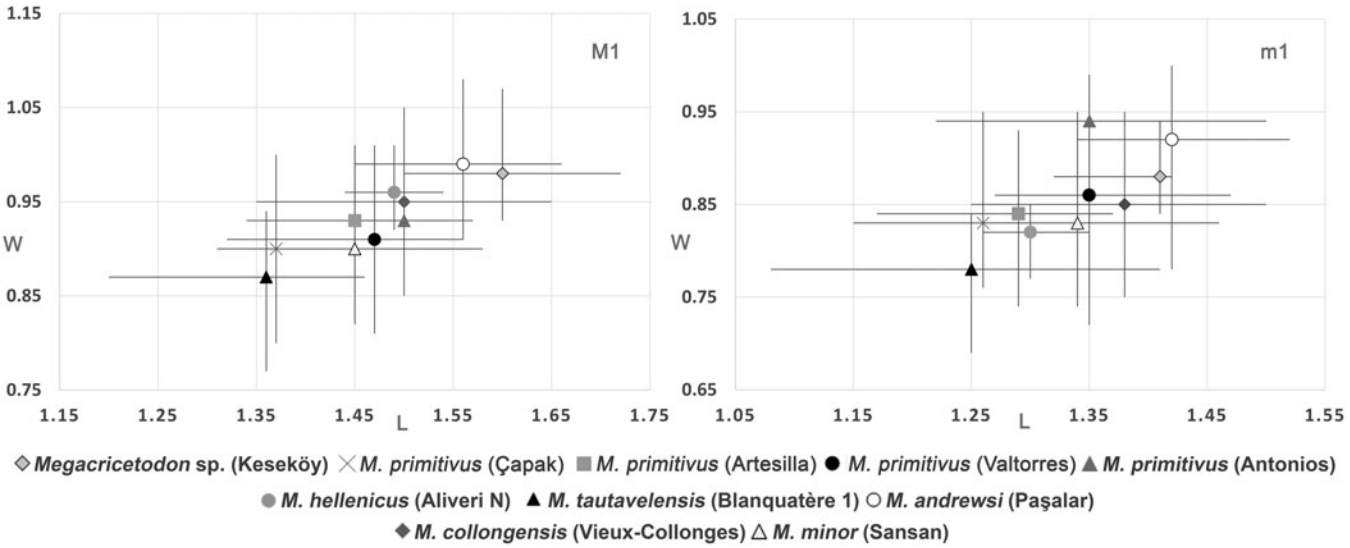


Figure 7. Scatter diagram of the upper and lower first molars of small and medium-sized *Megacricetodon* from Anatolia, Europe, and Asia (data are after Mein, 1958; Freudenthal, 1963; Wessels et al., 2001; Peláez-Campomanes and Daams, 2002; Lazzari and Aguilar, 2007; Bi et al., 2008; Oliver Pérez et al., 2008; Oliver and Peláez-Campomanes; 2014, 2016; Oliver, 2015).

and Peláez-Campomanes, 2014, 2016). It then continues as a very common element in the European faunas with an array of different species until MN10.

Somewhat surprisingly, *Megacricetodon primitivus* is known from southwestern and southeastern Europe, but was never encountered in central Europe. The *Megacricetodon* assemblage from the Greek locality Antonios (MN5) was assigned to *M. primitivus* by Vasileiadou and Koufos (2005). However, Oliver and Peláez-Campomanes (2014) argued against this designation, based on the stronger cingulum in front of the anterocone and the presence of an ectoloph in M1 and short or absent mesolophid in m1. Notably, all these character states seem to apply to the Çapak material as well. Nevertheless, all the individual characters fall within the variation of *M. primitivus* from Spain (Oliver, 2015). The mean value of *M. primitivus* from Çapak is among the lower values of *M. primitivus* from Artesilla and Valtorres (Figure 7).

A comprehensive study of all early Miocene *Megacricetodon* material from Asia minor and southeastern Europe is needed to clarify the relation with the assemblages from the Spanish localities. Until that time, the Çapak material is best assigned to *M. primitivus*.

Genus *Eumyarion* Thaler, 1966

Type species.—*Cricetodon medius* Lartet, 1851 (=*Cricetodon helveticus* Schaub, 1925).

Eumyarion aff. *E. montanus* De Bruijn and Saraç, 1991
Figure 8.1–8.4

Description.—

M2.—The labial anteroloph is well developed. The lingual anteroloph is vestigial. The protolophule is slightly directed anteriorly and connected to the posterior arm of the protocone. The posterior paracone spur is well developed and connects to the long mesoloph. The metalophule is parallel with the protolophule and connected to the entoloph just in front of the hypocone. The sinus is narrow and directed anteriorly. The roots are not preserved.

M3.—The labial anteroloph is connected to the base of the paracone. The lingual anteroloph is very weak. The paracone spur is absent. The protolophule is very short. A short mesoloph starts at the middle of the longitudinal crest connecting the protolophule and metalophule. The posterior part of the molar is broken. The roots are not preserved.

m1.—The outline of the molar is very narrow. The cusps are slender. The labial and lingual anterolophids are comma-shaped and connected to the base of the protoconid and to the metaconid, respectively. The labial anterolophid is longer than the lingual anterolophid. The anterolophulid is low and relatively short. The metalophid is connected to the anterior arm of the protoconid. The postero-lingual crest is very distinctive and connects to the base of the entoconid. The mesolophid is of medium length and directed anteriorly. The ectomesolophid is absent. The posterior arm of the hypoconid is strong and is not connected to the posterolophid. The sinusid is wide. The roots are not preserved.

m3.—The lingual anterolophid is connected to the base of the metaconid. The labial anterolophid is short and descends to the base of protoconid. A narrow protosinus is present. The metalophid is short and connects to the anterior arm of the protoconid. The mesolophid is of medium length and directed posteriorly. The hypolophulid is connected to the ectolophid, just in front of the hypoconid. The roots are not preserved.

Material and measurements.—1 M2 (PV13210, 1.47 x 1.38), 1 M3 (PV13211, — x 1.20), 1 m1 (PV13212, 1.94 x 1.04), 2 m3 (PV13214, 1.29 x 0.91; PV13215, 1.31 x 1.06).

Remarks.—The genus *Eumyarion* is dominant in the early Miocene of Anatolia with a large number of species

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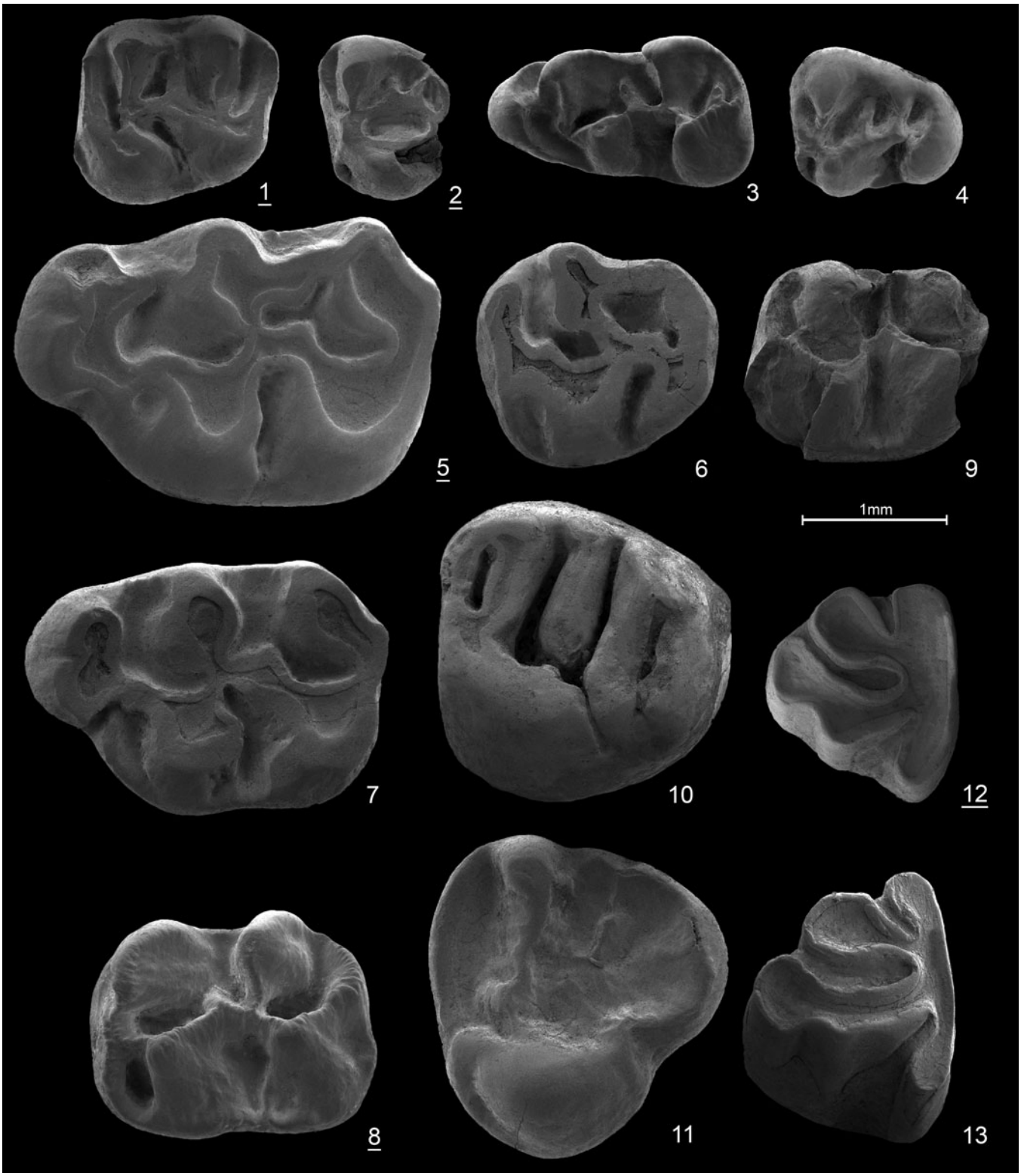


Figure 8. *Eumyarion* aff. *E. montanus* De Bruijn and Saraç, 1991. (**1**) M2 dex (PV13210), (**2**) M3 dex (PV13211), (**3**) m1 sin (PV13212), (**4**) m3 sin (PV13215). *Cricetodon* sp. (**5**) M1 dex (PV13203), (**6**) M3 sin (PV13204). *Cricetodon* cf. *C. aliveriensis* Klein Hofmeijer and De Bruijn, 1988. (**7**) M1 sin (PV13201), (**8**) m2 dex (PV13200). *Karydomys* cf. *K. strati* López-Antoñanzas et al., 2018. (**9**) M2 sin (PV13216). *Debruijnia* sp. (**10**) M3 dex (PV13220). *Aliveria luteyni* De Bruijn, Van der Meulen, and Katsikatsos, 1980. (**11**) M3 sin (PV13217). *Albertona balkanica* López Martínez, 1986. (**12**) p3 dex (PV13223), (**13**) p3 sin (PV13224).

(*E. intercentralis* De Bruijn and Saraç, 1991, *E. microps* De Bruijn and Saraç, 1991, *E. carbonicus* De Bruijn and Saraç, 1991, *E. montanus*, *E. orhani* De Bruijn et al., 2006, *E. gordesensis* Peláez-Campomanes et al., 2019 and *E. lukasi* Peláez-Campomanes et al., 2017) and up to three species may occur together in a single assemblage (De Bruijn and Saraç,

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1991; De Bruijn et al., 2006; Joniak et al., 2017; Peláez-Campomanes et al., 2019). By contrast, the *Eumyarion* from Çapak is one of the least common taxa in the fauna.

The m1 from Çapak is metrically almost in the same range, but narrower than *Eumyarion* aff. *E. carbonicus* from Harami 3 and *E. montanus* from its type locality Keseköy and from Sabuncubeli (De Bruijn and Saraç, 1991; De Bruijn et al., 2006). In morphology, Çapak specimens are closest to *E. montanus*, but there are some notable differences. The lingual anteroloph is present in the M3 from Çapak, but it never occurs in *E. montanus*. The metalophulid is single and the ectomesolophid is absent in the m1 from Çapak, but the metalophulid is double and ectomesolophid is present in *E. montanus*. We classify the Çapak material therefore as *E.* aff. *E. montanus*, indicating that the scarcity of the material does not allow a formal species definition, even though it is clearly different than any *Eumyarion* known so far.

Genus *Cricetodon* Lartet, 1851

Type species.—*Cricetodon sansaniensis* Lartet, 1851.

Cricetodon sp.
Figure 8.5–8.6

Description.—

M1.—The labial outline of the molar is sinuous. The cusps are robust and the enamel is thick. The molar is worn. The anterocone is slightly divided. The labial cusp of the anterocone is partly damaged. The lingual anteroloph is connected to the protocone. The anterior ectoloph is slender and reaches the paracone. The posterior ectoloph is well developed and complete, connected to the metacone. The protolophule is short and directed posteriorly. The metalophule is fused to the posteroloph. The mesoloph is short and directed posteriorly. The sinus is narrow and transverse. The roots are not preserved.

M3.—The outline of the molar is rounded. The lingual anteroloph is short, connected to the protocone, enclosing a narrow protosinus. The labial anteroloph is long and strong and does not reach the paracone. The anterolophule is well developed and there is a small lingual spur. The posterior ectoloph is complete and connected to the metacone. The mesoloph is absent. The neo-entoloph is absent. The metacone is fused with the posteroloph. The metalophule is absent. The sinus is deep, narrow, and directed posteriorly. The roots are not preserved.

Material and measurements.—1 M1 (PV13203, 2.93 x 2.00), 1 M3 (PV13204, 1.70 x 1.56).

Remarks.—The genus *Cricetodon* is represented in Anatolia by several species during the early and middle Miocene (Tobien, 1978; Sen and Ünay, 1979; Ünay, 1990; De Bruijn et al., 1993; Çınar Durgut and Ünay, 2016; Joniak et. al., 2019). The Çapak assemblage comprises two different species of *Cricetodon*; the larger *Cricetodon* sp. and the smaller *Cricetodon* cf. *C. aliveriensis*.

The M1 of *Cricetodon* sp. from Çapak is morphologically very similar to the M1 of *Cricetodon candirensis* from its type locality Çandır described by Tobien (1978). The size also is among the upper range of *C. candirensis* (Figure 9). However, M3 from Çapak is morphologically more similar to *C. pasalarensis* (Tobien, 1978) because of the incomplete anterior ectoloph, complete posterior ectoloph and single protolophule. *Cricetodon candirensis* typically has an elongated M3, whereas *C. pasalarensis* and the *Cricetodon* from Çapak have rounded M3. However, there are also some other differences: the M3 of *C. pasalarensis* has a mesoloph in 86% of the specimens, but the M3 from Çapak has no mesoloph. While the sinus is directed posteriorly in Çapak specimen, it is directed forward in *C. pasalarensis*. In that respect, and because of the limited material, we prefer to leave the large Çapak *Cricetodon* in open nomenclature.

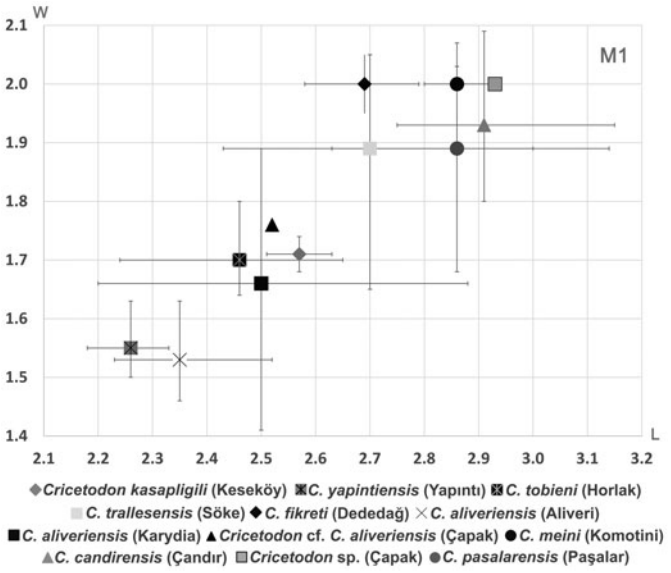


Figure 9. Scatter diagram of the upper first molar of medium and large sized *Cricetodon* from Anatolia and adjacent area (data after Klein Hofmeijer and De Bruijn, 1988; Ünay, 1990; De Bruijn et al., 1993, 2003; Vasileiadou and Koufos, 2005; Çınar Durgut and Ünay, 2016; Skandalos, 2017).

Cricetodon cf. *C. aliveriensis* Klein Hofmeijer and De Bruijn, 1988
Figure 8.7, 8.8

Holotype.—M1 sin, no. 542, Aliveri, Greece. The specimen is stored at Utrecht University, Department of Earth Sciences, Utrecht, The Netherlands.

Description.—

M1.—The anterocone is slightly divided into two equal cusps. The lingual spur of the anterolophule joins to the base of the protocone. The labial anteroloph connects to the base of the paracone. The anterolophule is connected to the lingual cusp of the anterocone. The protolophule is very short and directed posteriorly. The mesoloph is short and directed posteriorly. The metalophule is strong, posteriorly oriented and connects to the weak posteroloph. The molar has no ectolophs. The sinus is narrow and directed anteriorly. The molar has four roots.

m2.—The labial anterolophid is strong and connects to the base of the protoconid. The lingual anterolophid is almost

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absent. The metalophulid is short and connected to the anterolophule. The mesolophid is short and directed anteriorly. The hypolophulid is short, directed anteriorly and connects to the ectolophid. The posterolophid is strong and joins to the base of the entoconid. The sinusid is wide and transverse. Inside the sinusid there is a short, low, but distinctive crest originating from the anterior wall of the hypoconid towards the labial mesocingulid. The roots are not preserved.

Material and measurements.—1 M1 (PV13201, 2.52 × 1.79), 1 m2 (PV13200, 2.04 × 1.56).

Remarks.—The M1 falls metrically within the variation of the type material of *Cricetodon tobieni* from Horlak and is just outside the range of the small collection of the type material of *Cricetodon kasapligili* from Keseköy (De Bruijn et al., 1993). However, *Cricetodon tobieni* De Bruijn et al., 1993 and *C. kasapligili* De Bruijn et al., 1993 differ from the *Cricetodon* from Çapak by having slender cusps and three roots in M1. In addition, *C. tobieni* has a paracone spur that is absent in the Çapak specimen.

The Çapak material resembles *C. aliveriensis* in many respects. However, the size of M1 is outside the range of the type locality of *C. aliveriensis* (Aliveri), although it is similar in size to the larger specimens from Karydia (Skandalos, 2017). *Cricetodon* cf. *C. aliveriensis* is also known from the Anatolia locality of Hacibekirli (Akgün et al., 2021). However, the limited material from Hacibekirli does not allow comparison with the Çapak material. Morphologically, the Çapak material fits well with *C. aliveriensis*, but since we have only two specimens, which, moreover, are larger than those from the type locality, we prefer to classify it as *C.* cf. *C. aliveriensis*.

Genus *Karydomys* Theocharopoulos, 2000

Type species.—*Karydomys symeonidisi* Theocharopoulos, 2000.

Karydomys cf. *K. strati* López-Antoñanzas et al., 2018
Figure 8.9

Holotype.—UM Thy 0-30, a left M2, Thymiana, Chios, Greece. The specimen is stored at the paleontological collections of the University of Montpellier, France.

Description.—

M2.—The anterolingual part of the molar is broken. The labial anteroloph is long. The protolophule is double. Protolophule II is somewhat stronger than protolophule I. The posterior paracone spur is well developed and connects to the long mesoloph at the labial border of the molar. The metalophules are double, but weak and situated lower than the protolophules. The sinus is directed slightly anteriorly. The posterolingual part is damaged, but a small postero-sinus is present. The roots are not preserved.

Material and measurements.—1 M2 (PV13216, 1.82 × 1.41).

Remarks.—The rare hamster *Karydomys* is represented by six different species between MN3 and MN6 in central Europe, the eastern Mediterranean, Kazakhstan, and China (Mein and Freudenthal, 1981; Theocharopoulos, 2000; Kordikova and De Bruijn, 2001; Mörs and Kalthoff, 2004; Maridet et al., 2011; López-Antoñanzas et al., 2018). In Karydia 1, from which the genus was originally described, it is represented by *Karydomys symeonidisi* Theocharopoulos, 2000, which is morphologically and metrically similar to our specimen. However, *K. symeonidisi* has a stronger metaloph and it is not double. *Karydomys strati* López-Antoñanzas et al., 2018 from the Island of Chios resembles our specimen in having double protolophules and metalophules, a long mesoloph, and in the connections with the posterior paracone spur. It also falls within the size range of the Chios species. However, our specimen is partly broken and does not preserve the lingual anteroloph. In that respect, we prefer to classify it as *Karydomys* cf. *K. strati*.

Family Spalacidae Gray, 1821
Genus *Debruijnia* Ünay, 1996

Type species.—*Debruijnia arpati* Ünay, 1996.

Debruijnia sp.
Figure 8.10

Description.—

M3.—The outline of the M3 is semicircular. The occlusal pattern consists of five lophs. The labial anteroloph is connected to the paracone. The lingual anteroloph is absent. The protolophule reaches the paracone area, but a true paracone is not defined. The mesoloph is strong and isolated by two valleys on the labial side; it does not reach the endoloph. The posterosinus is enclosed by the posteroloph and the metalophule. The sinus is deep and very narrow.

Material and measurements.—1 M3 (PV13220, 2.25 x 2.35).

Remarks.—The Çapak specimen metrically only fits with *Debruijnia kostakii* De Bruijn, 2017 from Karydia 2. A morphological comparison with this and other species, however, is hampered by the ontogenetic stage of our specimen. It represents a very young individual with only a little wear on the anterior part of the tooth. This makes it difficult to compare with other specimens because they generally represent more advanced stages of wear. Therefore, we prefer to leave its classification in open nomenclature.

Family Sciuridae Fischer, 1817
Genus *Aliveria* De Bruijn, van der Meulen, and Katsikatsos, 1980

Type species.—*Aliveria brinkerinki* De Bruijn, van der Meulen, and Katsikatsos, 1980.

Aliveria luteyni De Bruijn, van der Meulen, and Katsikatsos, 1980
Figure 8.11

Holotype.—M1 dext. no. 171. Aliveri, Greece. The specimen is stored at Utrecht University, Department of Earth Sciences, Utrecht, The Netherlands.

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Description.—

M3.—The anteroconule is weak. The protoloph is transverse with an irregular course and bears a small protoconule. The paracone and protocone are well developed. The remnant of the metaloph is low and incomplete. The metacone is fused with the posteroloph. The hypocone is absent, but there is a small notch. The surface of the posterior valley is slightly crenulated.

Material and measurements.—M3 (PV13217, 2.12 x 2.14).

Remarks.—The flying squirrel, *Aliveria luteyni*, is known from the Greek localities of Aliveri and Karydia and the Turkish localities of Kaplangi 1 and Kaplangi 2 (de Bruijn et al., 1980; Koufos, 2006; Bosma et al., 2018). The *Aliveria* specimen from Çapak is morphologically identical to the type material from Aliveri and metrically it is among the upper values of the measurements of the type material.

Order Lagomorpha Brandt, 1855
Family Ochotonidae Thomas, 1897
Genus *Albertona* López Martínez, 1986

Type species.—*Albertona balkanica* López Martínez, 1986.

Albertona balkanica López Martínez, 1986
Figure 8.12, 8.13s

Holotype.—Left lower jaw with p3–4 and m2, no. 1. Aliveri, Greece. The specimen is stored at Utrecht University, Department of Earth Sciences, Utrecht, The Netherlands.

Description.—

p3.—The talonid is separated by two flexids: the labial hypoflexid and the lingual metaflexid. The metaflexid is well developed. The hypoflexid is longer than the metaflexid. The anterostylid is well developed and does not connect to the metaconid. The protoconid is triangular in one specimen and rounded in the other. The metaconid is well developed. The anterior part of the centroflexid is directed lingually. The protoflexid is present as a shallow sulcus.

Material and measurements.—2 p3 (PV13223, 1.48 x 1.23; PV13224, 1.47 x 1.56).

Remarks.—*Albertona* comprises only two species: *A. balkanica* from Aliveri (López Martínez, 1986) and *A. aegeensis* Ünay and Göktaş, 1999 from Söke, in addition to *Albertona* cf. *A. aegeensis* from Dededağ (Ünay and Göktaş, 1999). *Albertona balkanica* is otherwise known from Snegotin (MN4) in Serbia (Marković, 2010). The Çapak specimens are metrically among the upper values of *A. balkanica* from Aliveri and identical morphologically. Our material is also close metrically and morphologically to *A.* cf. *A. aegeensis* from Dededağ as described by Ünay and Göktaş (1999). Based on the measurements and illustrations in Ünay and Göktaş (1999), the Dededağ material shows strong similarities with *A. balkanica* as well.

Table 4. The rodent composition of the Çapak assemblage. The entry "0(1)" is used in those instances in which the last molars and, for some taxa, premolars are excluded from the count because these elements are generally small and may have been lost while processing (which would give a bias towards larger species). If a species is only represented by premolars or M3s, it is counted as 1, because otherwise the data would falsely suggest an absence of that species.

	Total		M1+M2 +m1+m2		MNI	
Rodent species	N	%	N	%	N	%
Myomimus tanjuae n. sp.	43	17.6	27	14.6	13	19.8
Democricetodon gracilis	62	25.6	49	26.2	15	22.7
Megacricetodon primitivus	127	52.0	103	55.0	31	47.0
Eumyarion aff. *E. montanus*	5	2.0	2	1.1	2	3.0
Cricetodon cf. *C. aliveriensis*	2	0.8	2	1.1	1	1.5
Cricetodon sp.	2	0.8	1	0.5	1	1.5
Karydomys cf. *K. strati*	1	0.4	0(1)	0.5	1	1.5
Debruijnia sp.	1	0.4	0(1)	0.5	1	1.5
Aliveria luteyni	1	0.4	1	0.5	1	1.5
Σ	244	100	187	100	66	100

Discussion

The composition of the assemblage and paleoenvironmental considerations.—The rodent assemblage of Çapak consists of 244 molars representing nine species belonging to four different families (Table 4). The hamsters are the most dominant group in the assemblage (81.6% of all specimens and 84.4% of M1 + M2 + m1 + m2). They are represented by six species belonging to five genera. The fauna is strongly dominated by *Megacricetodon primitivus*, which comprises more than half of the assemblage. *Democricetodon gracilis* is the second most dominant species in the assemblage with ~25.6%, signifying one of the first occurrences of this well-known species from the early and middle Miocene of Europe. The genus *Cricetodon* is represented by two species with two molars of each: the small species *Cricetodon* cf. *C. aliveriensis* and the larger *Cricetodon* sp. The presence of two species of *Cricetodon* in one assemblage is uncommon during the early and middle Miocene in Anatolia, known previously only from the localities of Kınık and Yapıntı (Çınar Durgut and Ünay, 2016). *Eumyarion* is one of the most common hamsters of the early Miocene in Anatolia. However, *Eumyarion* aff. *E. montanus* is represented by just five molars in the Çapak assemblage, which is a~2% of the rodents. The rare genus *Karydomys* completes the range of hamsters in the assemblage, with *Karydomys* cf. *K. strati* being represented by a single molar. Gliridae is the second most dominant family in the assemblage and is represented by a new species *Myomimus tanjuae* n. sp., comprising 17.6% of all rodent specimens. Representatives of the Spalacidae (*Debruijnia* sp.) and Sciuridae (*Aliveria luteyni*) are the rarest taxa in the assemblage. They are each represented by just one molar.

The majority of the assemblage consists of only three species (*Megacricetodon primitivus*, *Democricetodon gracilis*, and *Myomimus tanjuae* n. sp.). The general composition of the assemblage is very different from known early and middle Miocene assemblages of Anatolia. *Megacricetodon* prefers a relatively dry and warm environment, but it can rarely be present in wet conditions (Daams and Freudenthal, 1988a). Its

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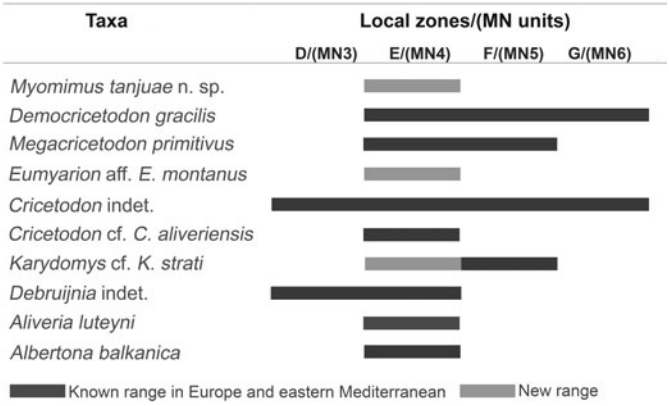


Figure 10. The biochronological ranges of the taxa from Çapak assemblage based on the Anatolian local zones and MN units.

abundance in the Çapak assemblage, therefore, suggests a change towards a drier environment. *Myomimus tanjuae* n. sp. from Çapak is the third most abundant species and the only glirid in the fauna. Following the morphotype classification of van der Meulen and De Bruijn (1982), *Myomimus* from Çapak is classified as part of the asymmetrical molar group (i.e., ground dwellers that prefer an open country biotope). The flying squirrel *Aliveria* is rare, but surprisingly present in the assemblage and, as an arboreal animal, suggests that part of the environment was woodland. During the early Miocene of Anatolia, *Eumyarion* was one of the most diverse and dominant genera and is considered to have preferred humid conditions, such as those inferred for the localities of Keseköy, Sabuncubeli, Harami, and Gördes (e.g., De Bruijn and Saraç, 1991; De Bruijn et al., 2006; Bilgin et al., 2019; Joniak et al., 2019; Peláez-Campomanes et al., 2019). By contrast, Çapak has a very limited presence of *Eumyarion*, while *Megacricetodon* and *Democricetodon* become the most dominant genera at that time. These changes are clearly seen when comparing faunal compositions and appear to be the result of a transition from a moist and close environment in the early Miocene to a dry and more open environment in the middle Miocene in Anatolia.

The age of the assemblage.—The Çapak assemblage yielded an interesting mixture of Anatolian and European species that is unlike any other rodent assemblage in Anatolia. Its elements occur between local zone D–G or MN3–MN6 (Figure 10). Unfortunately, some rarer elements could not be identified at the species level, but the overall distribution of fauna provides sufficient clues to the age of the locality.

The most abundant species, *Megacricetodon primitivus*, is very well known and characteristic for MN4–5 of Spain. It is also known from the Greek locality of Antonios (MN5) (Vasileiadou and Koufos, 2005) and was listed from several Turkish localities (Saraç, 2003). Surprisingly, *M. primitivus* is not known from central Europe, and therefore seems to have a disjunct distribution. Even though this may cast some doubts on the relationship between Iberian populations and those from the eastern Mediterranean, there are no clear differences between the Spanish and the Çapak material.

Democricetodon gracilis shows similar characters with *D. gracilis* from Forsthart (MN4) and the type locality of Sandelzhausen (MN5), being more like the former in having a somewhat lower crown. *Democricetodon gracilis* was mentioned as one of the typical taxa for local zone E by Ünay et al. (2003), a zone that the authors correlated to Unit MN4.

Eumyarion is the most abundant genus in Anatolian faunas from the local zones C and D (MN2–MN3) (e.g., De Bruijn et al., 1993; Joniak et al., 2019) *Eumyarion* is only represented in Anatolia by very limited material from local zone E (MN4) (e.g., Ünay et al., 2001) and from the local zones E–H, there is no record of *Eumyarion* at all. However, in local zone H (MN7–8), a single specimen was reported from Sarıçay (Rummel, 1998). *Eumyarion* from Çapak is represented by just a few elements, and these are clearly different from any other species known so far, being most similar to *E. montanus* from Keseköy (local zone D, MN3), but with more advanced characteristics.

Cricetodon sp. shares several characters with *C. pasalarensis* from Paşalar (local zone F/G, MN5/6) and with *C. candirensis* from Çandır (local zone G, MN6), but the limited material does not allow its assignation to either species. The second *Cricetodon* shares similarities with *C. aliveriensis* from Karydia (MN4).

The rare taxon *Karydomys* ranges from MN3 to MN6 (e.g., Mörs and Kalthoff, 2004; Maridet et al., 2011). The single specimen from Çapak is metrically and morphologically very close to *K. strati* from the island of Chios (MN5) (López-Antoñanzas et al., 2018).

The first occurrence of *Debruijnia* is from local zone D (MN3), from the localities of Keseköy and Sabuncubeli, and the genus has its last occurrence in MN4 from the locality of Karydia (De Bruijn, 2017). *Debruijnia* sp. from Çapak is metrically within the range *D. kostakii* from Karydia, but the morphological comparison is hampered by it being unworn.

The flying squirrel, *Aliveria luteyni*, is known from the localities of Aliveri and Karydia in Greece and Kaplangı 1 and Kaplangı 2 in Turkey. All these localities are correlated to MN4.

The Ochotonidae *Albertona* is very characteristic for the late early Miocene lagomorphs from the eastern Mediterranean and Serbia (López Martínez, 1986; Ünay and Göktaş, 1999; Marković, 2010). The specimens from Çapak fall metrically and morphologically within the variation of the type material of *Albertona balkanica* from Aliveri.

The Çapak assemblage shares similarities with the locality of Aliveri in many respects. *Cricetodon aliveriensis*, *Democricetodon gracilis*, *Aliveria luteyni*, and *Albertona balkanica* are known from both localities, but the stage of evolution of *Cricetodon* cf. *C. aliveriensis* from Çapak seems more advanced than *C. aliveriensis* from Aliveri and closer to the assemblage from Karydia. Even though the localities of Çapak and Aliveri share some species, they clearly represent different environments. Because both faunas were collected from lignitic lacustrine deposits, we assume this represents a different ecosystem in the surrounding landscape. The locality of Aliveri shows a large diversity of rodents and the presence of the eomyids *Pseudotheridomys* and *Ligerimys*, as well as three species of flying squirrel, points to a forested environment. However, the locality of Çapak has less diversity than Aliveri, and the dominance of *Megacricetodon primitivus* (52%) followed by 17.6% for *Myomimus tanjuae* n. sp. indicates a dry and open environment.

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Based on our current state of knowledge, the Çapak assemblage seems to be best placed in the uppermost part of zone E, younger than Aliveri and correlated with late MN4.

Biogeographic implications.—Because of the diachronicity of the MN-system (van der Meulen et al., 2011, 2012), the exact temporal relation of Çapak to the central European MN4 localities remains unclear. Generally, this diachronicity implies that localities in the east can be older than those from the same zone in the west. This is clear for the locality of Aliveri, which, as an MN4 locality, contains the eomyid *Pseudotheridomys*, a taxon that is mainly known from MN3 sites in the rest of Europe. Van den Hoek Ostende et al. (2015) followed Koufos (2006) in estimating the age of Aliveri between 18.0–17.5 Ma, stressing, however, that this is just an estimate. In the Daroca-Calamocha area in Spain, the lower boundary of MN4 is placed at 17.0 Ma (van der Meulen et al., 2012).

Van den Hoek Ostende et al. (2015) suggested that a drying trend from the east may have been the cause behind the migrations of *Megacricetodon*, *Democricetodon*, and *Eumyarion* from Anatolia to Europe. However, it is unlikely that such a trend affected the migration of *Eumyarion* because this genus favors humid circumstances. Nevertheless, it is clear that the genus must have migrated into Europe before it was extirpated in Anatolia and, as we now know, Çapak represents the last Anatolian occurrence before that extirpation. *Megacricetodon* and *Democricetodon*, on the other hand, seem to have favored the dryer condition at Çapak, and may well have expanded their distribution as drier conditions also developed in Europe. As we noted, the chronology is still unclear and finding a point of comparison for dating the changes heralded by the Çapak fauna remains an important challenge for the future.

Conclusions

Çapak is an exciting location having both European and Anatolian elements in its faunal assemblage. This provides us with a view of the evolution of micromammals from a little-known period in western Anatolia. The assemblage yielded nine rodents and one lagomorph species: *Myomimus tanjuae* n. sp., *Democricetodon gracilis*, *Megacricetodon primitivus*, *Eumyarion* aff. *E. montanus*, *Cricetodon* sp., *Cricetodon* cf. *C. aliveriensis*, *Karydomys* cf. *K. strati*, *Debruijnia* sp., *Aliveria luteyni*, and *Albertona balkanica*. Judged on the basis of a faunal comparison, the locality of Çapak would seem to be younger than Aliveri and close to that of Karydia, best located in the uppermost part of local zone E, which is correlated with MN4. The dominance of *Megacricetodon primitivus* and *Myomimus tanjuae* n. sp. and the presence of a small number of *Aliveria luteyni* and *Eumyarion* aff. *E. montanus* indicate a transition from a humid and forest environment in the early Miocene to an open and dry environment in the middle Miocene.

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