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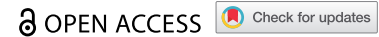


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ARTICLE



New rodents from the late Oligocene site of Gözükızılı in Anatolia (Turkey)

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ABSTRACT

The Oligocene rodent assemblage from Gözükızılı (Anatolia, Turkey) is described. The assemblage is relatively small, but it contains the new large and hypsodont baluchimyine *Daxneria fragilis* nov. gen. nov. sp. In addition, the ctenodactylid *Sayimys*, two new species of *Eucricetodon*: *E. ruber* nov. sp. and *E. oculatus* nov. sp. are present. Rare are the glirids *Bransatoglis* and *Peridyromys/Microdyromys* and a dipodid that could not be classified. The assemblage contains Asian and some European elements and is dated as early part of the late Oligocene (29–26 Ma). The small fauna from Gözükızılı is important because only a few Paleogene rodent faunas are known from Asia Minor.

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Oligocene; Rodentia;
Baluchimyinae;
Ctenodactylinae; *Daxneria*;
Cricetinae

Introduction

Few Paleogene rodent faunas have been described from Asia Minor and south-eastern Europe. Recently several late Eocene and early Oligocene faunas have been reported from southern Serbia (de Bruijn et al. 2018a). Late Oligocene rodent assemblages from Bosnia-Herzegovina and Serbia are Banovići (de Leeuw et al. 2011; de Bruijn et al. 2013), Ugljevik and Paragovo (van de Weerd et al. in prep.). Ünay et al. (2003a) summarized the data on the five known Oligocene rodent faunas from Anatolia (Turkey); two of those, Gözükızılı-1 and Yeniköy, have so far remained undescribed. Despite geographic proximity, the Oligocene faunas from the Balkans and Asia Minor show large compositional differences, underscoring the paleogeographic complexity of the region. In general these assemblages contain limited Western European elements, in contrast, the influence from Asia and the Indian sub-continent is strong. New data is for that reason welcome as we are far from understanding the paleo-biogeography.

Below we study the assemblages from Gözükızılı-1 and nearby Güvendik, both located in the Çankiri-Çorum basin. Although large samples from the Gözükızılı-1 site were screen-washed, the assemblages contain a low number of species. Among these are two new species of the cricetid *Eucricetodon* and a new baluchimyine genus. *Eucricetodon* is a common element in the Oligocene of Europe and fairly common in Asia. Baluchimyinae are initially described as a ctenodactylid rodent subfamily from the Oligocene of the Indian sub-continent, it is now included in the mainly African infraorder of the Hystricognathi. Several studies (Marivaux and Boivin 2019 and references therein) of the Hystricognathi detail the relations between the Asian Baluchimyinae and the several African families. The cheek teeth of the new baluchimyine genus from Turkey are large and show a peculiar type of hypsodonty, this and its dental pattern are unlike any other genus of this subfamily. Several of the Paleogene faunas from Asia Minor contain baluchimyines, suggesting that the subfamily may have been fairly common in the region during that time slice. However, the subfamily is absent in the much better known latest Oligocene and early Miocene of the region.

The Gözükızılı-1 locality

The first rodent teeth from the lower part of the Kızılırmak Formation near Gözükızılı in the Çankiri-Çorum basin were collected by Engin Ünay formerly with the Turkish Geological Survey (MTA) and Nuredtin Kaymakçı (Middle East Technical University) in 1997. Teams of Utrecht University and the MTA made the collection that is described below during 1999 and 2000. Purpose was to date the non-marine Kızılırmak and Güvendik Formations as part of the geological mapping of the region. In total approximately 1200 kg of sediment was washed and sieved from grey silty clays of two levels at the Gözükızılı-1 site (40° 09' 9.0"N, 34° 02' 5.34"E, Figure 1), the lower horizon Gözükızılı-1a and the stratigraphically 1.5 m higher horizon -1b. Specimens from these horizons have been labelled GOZ1a and GOZ1b. Most of the washed sediment was from 1b; the differences between -1a and -1b are not significant and in the systematic descriptions below, the samples are not differentiated. The rodents found suggest a late Oligocene age (Ünay et al. 2003a). During a later visit by a team of the MTA and the Muséum National d'Histoire Naturelle (Paris, France) some fragmentary larger mammal fossils were found near Gözükızılı-1, in a site named Gözükızılı-2 and near Kızılırmak, about 21 km to the north, in the upper member of the formation (Antoine et al. 2008). A detailed map of the area, with Gözükızılı-1 and -2 is in Antoine et al. (2008). Métais et al. (2016) describe a third site, Gözükızılı-3, and positioned the three sites in a stratigraphic section measured near the village Gözükızılı.

The Güvendik site is situated in the Güvendik Formation about 3 km west of Gözükızılı village 40° 09' 13.48"N and 34° 03' 53.32"E (Figure 1). The fossiliferous bed was detected by Engin Ünay, a clay sample of approximately 60 kg was taken in 1999 for screen-washing.

The basin-fill of the Çankiri-Çorum basin has been described by Karadenizli (2011), a summary is in Métais et al. (2016). The non-marine Tertiary sequence starts with about 1150 m coarse-clastics of the Incik Formation interpreted as alluvial fan, braided-river and sandy meandering-river deposits. This is overlain by the Güvendik Formation, which includes bedded gypsum, anhydrite, laminated mudstones, massive mudstones and sandstones. The unit is deposited under evaporitic lake conditions. The Kızılırmak Formation overlies and is partly lateral of the Güvendik Fm. It consists of massive mudstones, sandstones and conglomerates. Interpretations of its



Figure 1. Satellite image of the area near Gözükızıllı village with the two sites where fossil rodents have been collected. Image from Google Earth, date 19/06/2020, copyright 2020 CNES/Airbus, 2020 Google, 2020 Basarsof.

depositional environments range from deep-channel braided-river in its lower parts to floodplains with meandering rivers in its upper part. Kayseri-Özer et al. (2017) reported on the climatic analysis of a few pollen samples from the Güvendik Formation. This analysis suggests a mixed mesophytic forest with elements indicating a dry and warm subtropical climate with low seasonality.

Methods

The material studied has been obtained by wet-screening fossiliferous sediments in the field on a set of fixed sieves, finest mesh is 0.5 mm. Concentrates have been treated with acetic acid to reduce the quantity and sorted to the 0.5 mm fraction under a microscope. Length and width of the teeth were measured with a Leitz Ortholux microscope with mechanical stage and measuring clocks. The measurements are given in millimetre units. Lower case letters refer to the lower dentition, upper case letters refer to the upper dentition. All figured specimens are shown as from the right side, if the original is from the left side the character on the plates has been underlined. Figured specimens from Gözükızıllı-1 are retouched SEM photographs. Other illustrations were prepared from photographic material made available by Laurent Marivaux (Université de Montpellier) or copied from published papers. A description of the method to prepare sections of incisors is available as electronic supplementary material with the online version of de Bruijn et al. (2018b).

Systematic Paleontology

Order Rodentia Bowdich, 1821

Suborder Ctenohystrica Huchon, Catzeflis and Douzery, 2000

Infraorder Hystricognathi Tullberg, 1899

Subfamily Baluchimyinae Flynn et al., 1986

Introduction

The high-crowned cheek teeth described in the following were initially considered to represent a aberrant ctenodactylid (Ünay et al. 2003a). However, the reduction of the posterior side of the

M3 and the presence of a large mesoconule on the DP4 and M1 and M2 point to the Baluchimyinae, a subfamily described from the early Oligocene of Pakistan (Flynn et al. 1986; Flynn and Cheema 1994) with six new genera. Marivaux et al. (2002) and Marivaux and Welcomme (2003) added several species and a new genus of similar age from Baluchistan (Pakistan) to this group of rodents. Marivaux et al. (2000) described a new baluchimyine rodent from the late Eocene from Thailand and Sallam et al. (2009) included *Ottomania* de Bruijn et al. (2003) and *Confiniummys* de Bruijn et al. (2003) into the baluchimyines, thus extending the geographic range of the subfamily from Thailand to Asia Minor.

The large *Ottomania* and the small *Confiniummys* from the latest Eocene of Süngülü (Eastern Anatolia) were initially included by de Bruijn et al. (2003) in the family Ctenodactylidae de Bruijn et al. (2003) noted the resemblance of *Ottomania* with the baluchimyines, but the genera were included in the ctenodactylids because of their supposedly non-molariform P4/p4. However, these P4/p4 were misidentified, the correctly associated P4/p4 are molariform and the two genera belong to the baluchimyines.

A single M1 or M2 from Kavakdere in the Turkish Thrace basin, classified as Ctenodactyloidea indet. by Ünay-Bayraktar (1989), is with its large metaconule a typical baluchimyine. De Bruijn et al. (2003) link the specimen to *Ottomania*, we assign it to *Lindsaya* Flynn et al. (1986), although it is much larger than the single species included in the genus. The half molar illustrated by Gabunia and Bendukize (1990, fig. 7) from Benara (Georgia) is very similar to the specimen of Ünay-Bayraktar and may be included in the same genus. The large M1 or M2 from Benara illustrated in Gabunia and Bendukidze (1990, fig. 6) is possibly a baluchimyine, but it does not seem to resemble any genus known to date.

Phylogenetic studies of Asian and North African hystricognathous rodents including baluchimyines are by Marivaux et al. (2002), Sallam et al. (2011, 2012), Barbière and Marivaux (2015), Sallam and Seiffert (2016) and Marivaux and Boivin (2019). These studies focus on the phylogeny of hystricognathous rodents and the relations between Asian and North African taxa. There is general

agreement that hystricognaths originated from an Asian stock of ctenodactyloids and made the Tethys Ocean crossing to Africa as early as the middle Eocene. Marivaux and Boivin (2019) proposed several models of Tethys crossings (including return trips) that could explain the results of their phylogenetic research. None of the phylogenetic studies cited above formalized the taxonomic relations suggested by the various cladograms. A relevant outcome is that the Asian baluchimyines are polyphyletic, splitted since the middle Eocene. Keeping in mind that rodent cheek teeth are notorious in developing convergent and parallel dental patterns, we refrain from taking a position on the possible phylogenetic subdivisions and continue to indicate the Asian, potentially hystricognathous, taxa as baluchimyines. We include the following genera in this clearly heterogeneous group:

- Baluchimys* Flynn et al., 1986; Pakistan
- Lindsaya* Flynn et al., 1986; Pakistan
- Lophibaluchia* Flynn et al., 1986; Pakistan
- Hodsahibia* Flynn et al., 1986; Pakistan
- Asterattus* Flynn and Cheema, 1994; Pakistan
- Bugtimys* Marivaux et al., 2002; Pakistan
- Ottomania* De Bruijn et al., 2003; Turkey
- Confiniummys* De Bruijn et al., 2003; Turkey
- Daxneria* nov. gen. Gözüükzıllı-1; Turkey

The type locality of *Ottomania* and *Confiniummys* is latest Eocene, whereas the three sites in Pakistan (Y-GSP-417, Z108 and Paali nala C2) have been dated as latest-early Oligocene, slightly older than Gözüükzıllı-1 (see below). *Zindapiria* Flynn and Cheema (1994), originally included in the Baluchimyinae, is considered a 'dipodoid rodent'

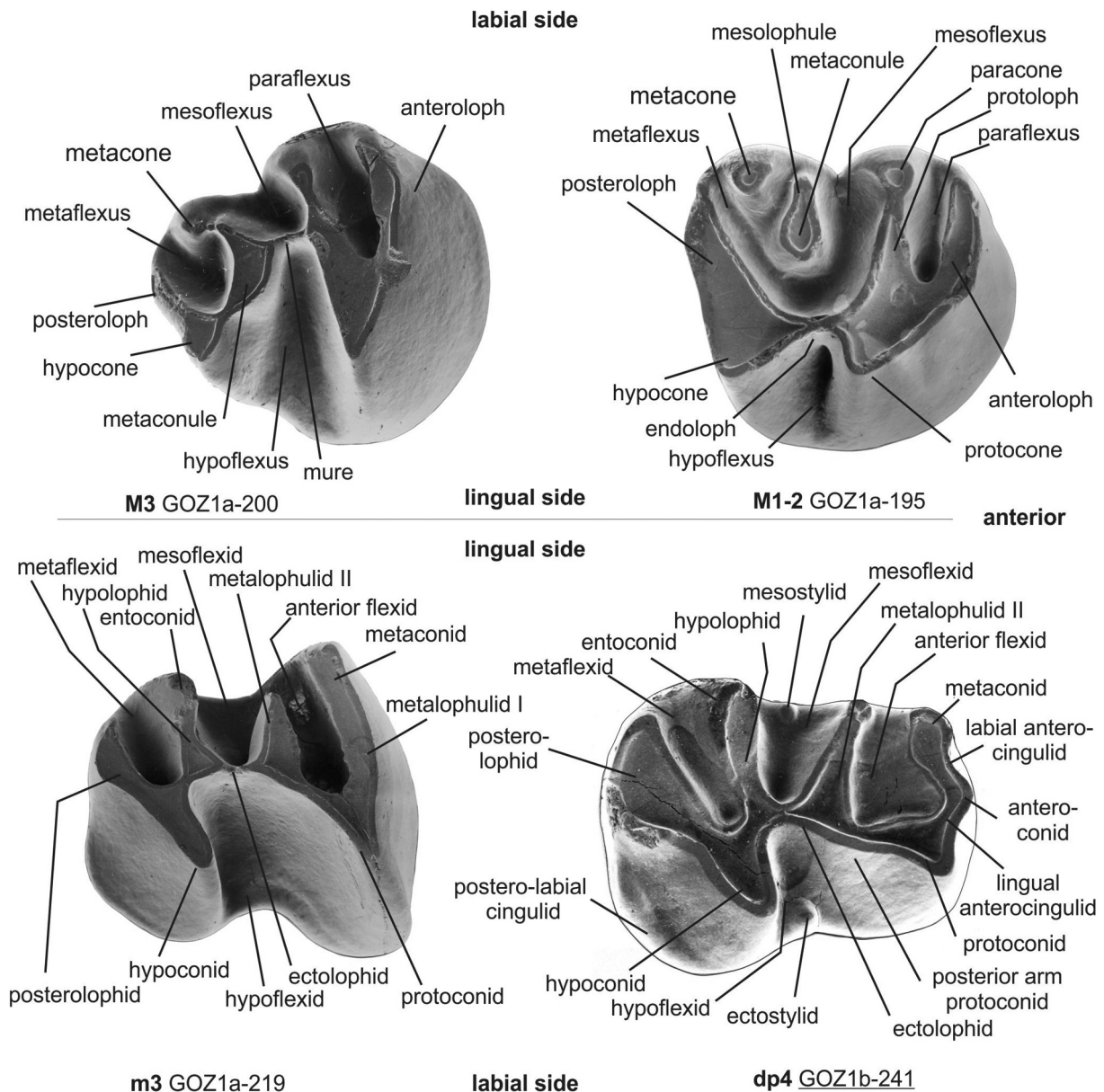


Figure 2. Nomenclature of tooth parts of *Daxneria* nov. gen. described in this paper (adapted after Flynn et al. 1986).

(Marivaux and Welcomme 2003; Marivaux et al. 2004). The terminology used in the description of the dental elements is shown in Figure 2.

Daxneria nov. gen.

Derivatio nominis:

Named after Dr Gudrun Daxner, eminent scientist, in recognition of her studies and management of the Mongolian-Austrian project on the Oligocene of the Valley of Lakes (Mongolia) and Neogene Austrian fossil rodents.

Type species: *Daxneria fragilis* nov. sp.

Diagnosis:

Large baluchimyine with high-crowned molars, thin enamel and without cement. The M3 and m3 are anteriorly higher than posteriorly. DP4 and M1-2 with a large metaconule. M3 with broad anterior side (anteroloph, protocone, protoloph) and reduced narrow posterior side (hypocone-metaloph-posteroloph). Metalophulid II long and well-developed on dp4 and lower molars. The dp4 is relatively short, it has a chevron-shaped transverse anterior lophid formed by the protoconid, the metaconid and the anterocingulids.

Differential diagnosis:

Daxneria fragilis shows some superficial resemblance with high-crowned ctenodactylid species such as the early Miocene *Sayimys giganteus* López-Antoñanzas et al. (2004), but differs from all ctenodactylids in the presence of the large and well-developed metaconule on DP4 and M1-2 and the reduced posterior side of the M3. A similar structure of the M3 and a large metaconule on M1-2 and DP4 occur in baluchimyine species from the Indian subcontinent, hence its allocation to that group. However, crown-height, size and position of the metaconule clearly differentiates *Daxneria* from all the known baluchimyine genera.

Daxneria fragilis nov. sp.

(Figure 2, 3a–j, 4a–l, 5, 7 v–y, 8 t–w)

Derivatio nominis: *fragilis* meaning fragile; its molars are fragile because of their thin enamel.

Synonymy: Ctenodactylidae gen. B. sp. 1 (Ünay et al. 2003a)

Holotype: M1 or M2 sin. GOZ1a-195 (Figure 3(b))

Type locality: Gözükkızıllı-1a, Anatolia Turkey (Figure 1)

Other sites with *Daxneria fragilis*: Gözükkızıllı-1b. The late Oligocene rodent assemblage from Ugljevik (Bosnia-Herzegovina; van de Weerd et al. in prep.) contains three damaged cheek teeth that are close in morphology and size to *Daxneria fragilis*.

Age: late Oligocene

Paratypes: Incomplete specimens have numbers between brackets, s = sinistral, d = dextral. Gözükkızıllı-1a: **DP3:** 191d, 192d, 198?; **DP4:** 193s, 194s; **M1** or **M2:** 195s, 196d, 197d; **M3:** 200d; **dp4:** 201s, 202s, (205d), 206d, (207d), 208d; **m1-2:** 211d, (212s), (213d), (214d), (215d), (216d); **m3:** 219d, (220d).

Gözükkızıllı-1b: **DP3:** 221d, 222d, 223d, 224d, 225d, 226d; **DP3 & DP4:** 227d; **DP4:** 228s; **M1-2:** (231d), 233s, (236d); **M3:** 237s; **dp4:** 241s, 242s, (243s), (244d), 245d, (246d); **M1** or **M2:** 247d, 248d, (249s), (250s).

Measurements: see Table 1

Diagnosis: as for the genus

Differential diagnosis: as for the genus

Description

DP3 (Figure 3d, maxilla fragment). The ten specimens (seven left, three right) have an oval outline and a single root. A transverse ridge is present in the middle, posteriorly a low cingulum connects to the ridge at the lingual tooth margin. A few specimens have a trace of an anterior cingulum.

DP4 (Figures 3d, 3f–g, 7y). is low-crowned and molariform, four complete specimens are in the sample. A broad lingual and two smaller labial roots are preserved on one specimen. The oblique anteroloph and protoloph are smoothly curved; the protoloph ends in a cuspidate paracone. The flexus between metaconule and metacone is shallow. Two specimens have a rounded metaconule without mesolophule. On two others the metaconule extends into a mesolophule, together half-moon shaped, one of these has a low connection to the metacone (Figure 3d). The metacone is rounded. The hypoflexus is short, the endoloph is close to the lingual border of the occlusal surface.

M1-2 (Figures 2, 3b–c 7w–x). Four complete and two incomplete M1 or M2 are available, these are higher crowned than the DP4. The M1 or M2 has four roots, the lingual two roots are either closely together or fused. The anteroloph and protoloph are smoothly curved, but less oblique than on DP4. The protoloph ends in the cuspidate paracone. The paraflexus is transverse; the mesoflexus is deep and curved backwards. The posteroloph is isolated from the metacone on all four M1-2, it has a low connection to the metaconule in one specimen (Figure 3c). The metaconule has a short mesolophule. The metacone is rounded, it is slightly higher and separated from the lower metaconule by a shallow flexus and from the posteroloph by the deeper metaflexus. The posteroloph is very wide near the hypocone, the anterior arm of the hypocone is connected to the protocone forming a short, high and narrow endoloph on all specimens.

M3 (Figures 2, 3a, 3e, 3i–j, 7v). Two complete specimens are in the sample. Characteristic are the high anterior sides. The anterior side is wide, the posterior side is narrow and reduced. The protocone, its anterior arm and the anteroloph form a smoothly curved anterior tooth margin; the paraflexus is long. The protoloph ends in a cuspidate paracone. The hypoflexus is very long, resulting in a sharp V-shaped and pinched protocone. The posterior side of the molar is strongly reduced; the homology of the dental elements is shown in Figure 2. The hypocone is reduced and shifted labially, it is fused with the metaconule; in one specimen it is narrow (Figure 3a), on the other it is larger (Figure 3j). The hypoflexus and metaflexus are separated by a thin and high mure, a connection between metaconule and protoloph. The metacone is small and attached to the metaconule, the metaflexus forms a small basin.

dp4 (Figures 2, 4d–g, 4j–k). Twelve specimens are in the two samples, of which five have the anterior part damaged. The dp4 is low-crowned. The metaconid and protoconid are connected by a transverse ridge incorporating the labial and lingual anterocingulid and the anteroconid. The anteroconid is only slightly protruding, with wear it disappears as a separate element. The protoconid is triangular. The metaconid of one specimen (Figure 4k) has a short labially-directed spur. All specimens have a well-developed and long cristid, slightly curved forward, and reaching the lingual tooth margin, named here the metalophulid II. The connection to the posterior arm of the protoconid is broad. The metalophulid II separates a large anterior flexid from the mesoflexid, the mesoflexid is deeper than the anterior flexid. A low ectostylid is present in the hypoflexid of six out of ten teeth; in two out of twelve teeth a minor mesostylid is present in the mesoflexid. The posterolophid is broad with a relatively narrow connection to the hypoconid. An unworn specimen shows that the posterolophid is higher than the cuspid.

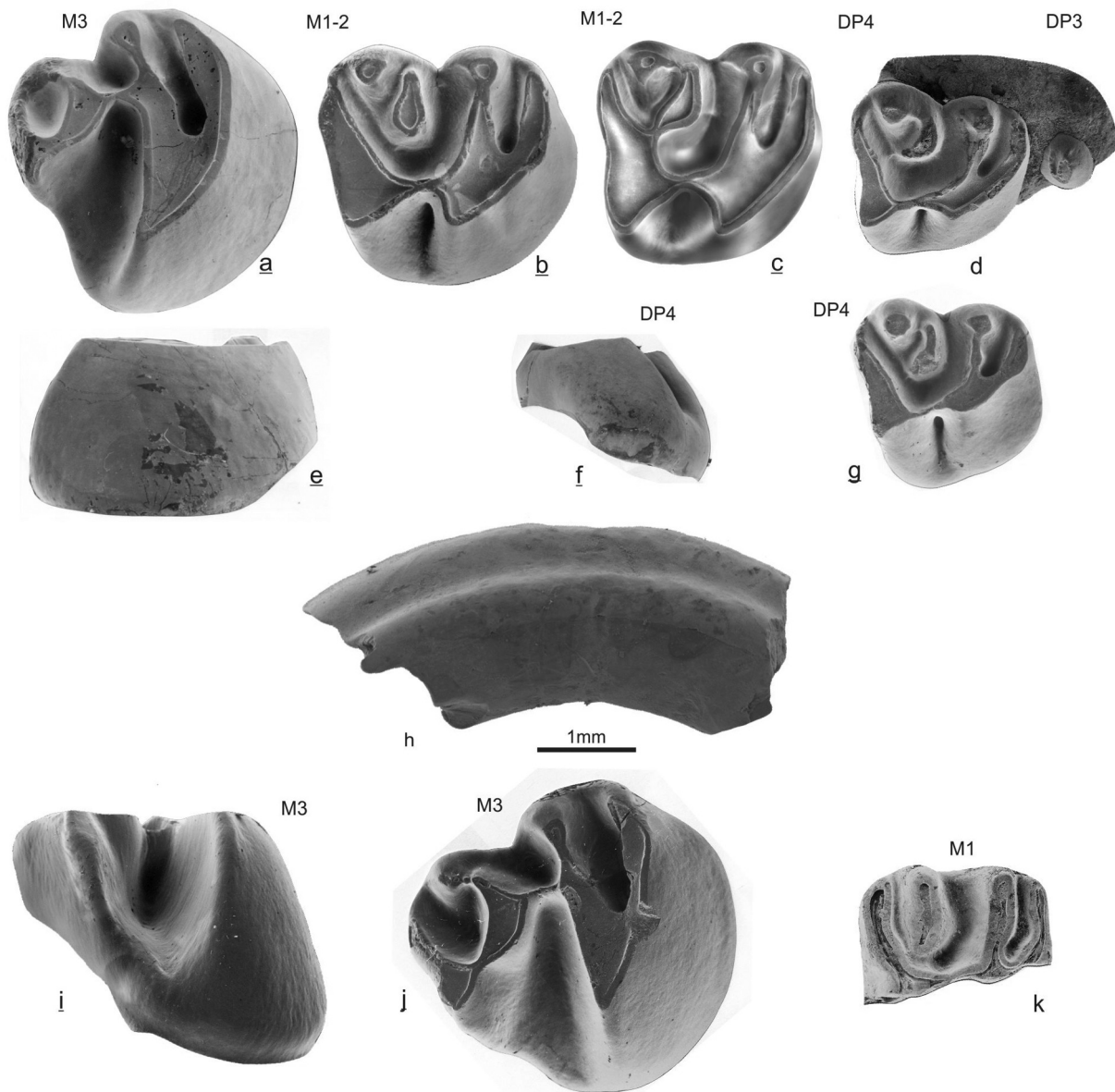


Figure 3. Upper cheek teeth of *Daxneria fragilis* nov. gen. nov. sp. (a–j) and *Sayimys* sp. (k) from Gözükkızıllı-1, occlusal, lingual or antero-lingual view. *Daxneria fragilis*: a & e GOZ1b-237, b GOZ1a-195, c GOZ1b-233, d GOZ1b-277, f & g GOZ1b-228, h upper incisor, no number, i & j GOZ1a-199. *Sayimys* sp.: k GOZ1b-251.

Table 1. Measurements of *Daxneria fragilis* nov. gen. nov. sp. from Gözükkızıllı-1a and 1b; shown are minimum, maximum, mean, number of observations and standard deviation.

<i>D. fragilis</i>	Length					Width				
	min	max	mean	N	SD	min	max	mean	N	SD
GOZ1a & 1b	0.5	0.70	0.63	10	0.059	0.71	0.88	0.806	10	0.067
D3	1.76	1.90	1.843	4	0.060	1.93	2.15	2.045	4	0.090
DP4	2.35	2.71	2.518	4	0.152	2.47	2.63	2.550	5	0.060
M3	2.98	3.54	3.260	2	–	3.12	3.20	3.160	2	–
dp4	2.05	2.30	2.160	7	0.094	1.45	1.77	1.600	11	0.093
m1-2	2.45	2.85	2.608	5	0.147	1.99	2.69	2.401	10	0.235
m3	–	–	3.430	1	–	–	–	3.190	1	–

The postero-labial cingulid is well-developed, with a well-developed stylid on one specimen (Figure 4j–k).

m1-2 (Figure 4b–c, f). There are two complete m1 or m2, seven are incomplete with the anterolophulid broken. Metaconid and entoconid are merged into the relatively narrow lophids.

Protoconid and hypoconid are strongly pinched and have an antero-labial direction. The metalophulid I is about straight and transverse, with wear it will become slightly curved. In slightly worn and worn specimens the metalophulid II is long, reaching the tooth border. The posterolophid shows an obtuse angle at its posterior side reflecting the merged hypoconulid. The posterolophid narrows toward the hypoconid, in about half of the specimens, it reaches the entoconid. A strong postero-labial cingulid is present on all ten specimens.

m3 (Figure 4a,e, 4h–i). There are two m3; one is complete, one has a damaged anterior side. Both have a strongly-pinched protoconid, jutting out far more in antero-labial direction than the hypoconid, resulting in a wide anterior side of the molar. Similar to the m1-2, the outline of the molar is at its base indented between protoconid and hypoconid. The metalophulid II is well developed and long, the anterior flexid is narrow and longer than the mesoflexid. The posterolophid narrows toward the hypoconid. An obtuse angle at its posterior side

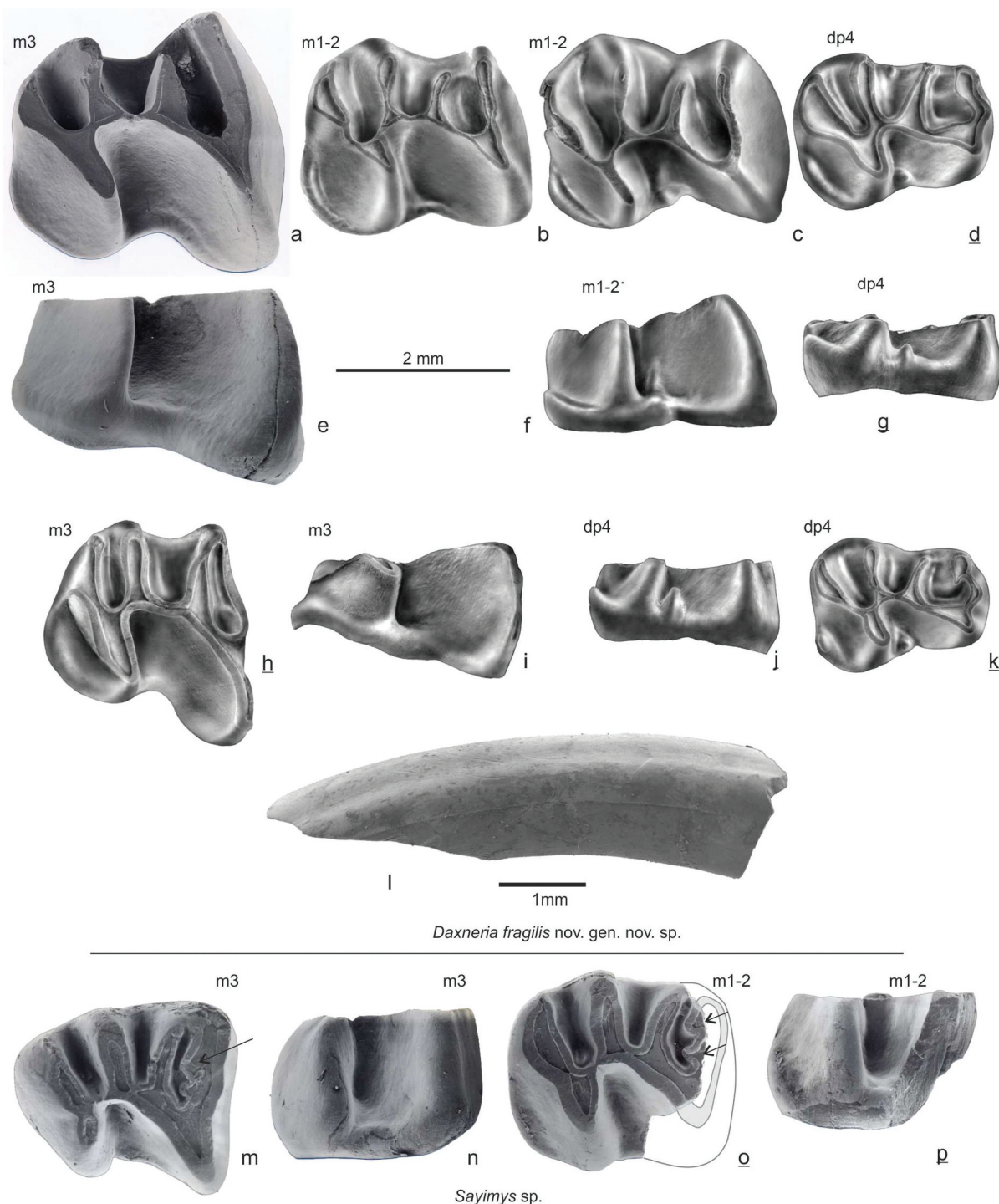


Figure 4. Lower cheek teeth *Daxneria fragilis* nov. gen. nov. sp. and *Sayimys* sp. (lower row) from Gözükkızıllı-1, occlusal and labial views. *Daxneria fragilis*: a & e GOZ1a-219, b GOZ1b-247, c & f GOZ1b-248, d & g GOZ1b-241, h & i GOZ1a-220, j & k GOZ1a-202, l lower incisor no number. *Sayimys* sp.: m & n GOZ1b-253, o & p GOZ1b-252.

marks the hypoconulid. A postero-labial cingulum is present on one (Figure 4a) but almost absent on the other specimen (Figure 4h).

Incisor enamel

The broad upper incisor has a sulcus (Figure 3h). The relatively slender lower incisor has a faint sulcus (Figure 4l) and a smooth slightly crenulated surface. The enamel thickness is approximately 250 μm (Figure 5). The portio externa (PE) is

thin (~5% of the total), it consists of radial enamel (Figure 5f), with prisms bending upward and very thin IPM (inter prismatic matrix). The portio interna (PI) is very thick (~95%) consisting of transverse multiserial Hunter-Schreger bands (HSB). The bands contain ~ three to four prisms (Figure 5e, f), these make an angle with the normal on the enamel-dentine junction (EDJ) of about 35°. Thin plates of IPM are present in the bands (5f arrowed), the crystallites of the IPM plates are orthogonal to the prisms. A PLEX (prisma-less external layer) is not observed.

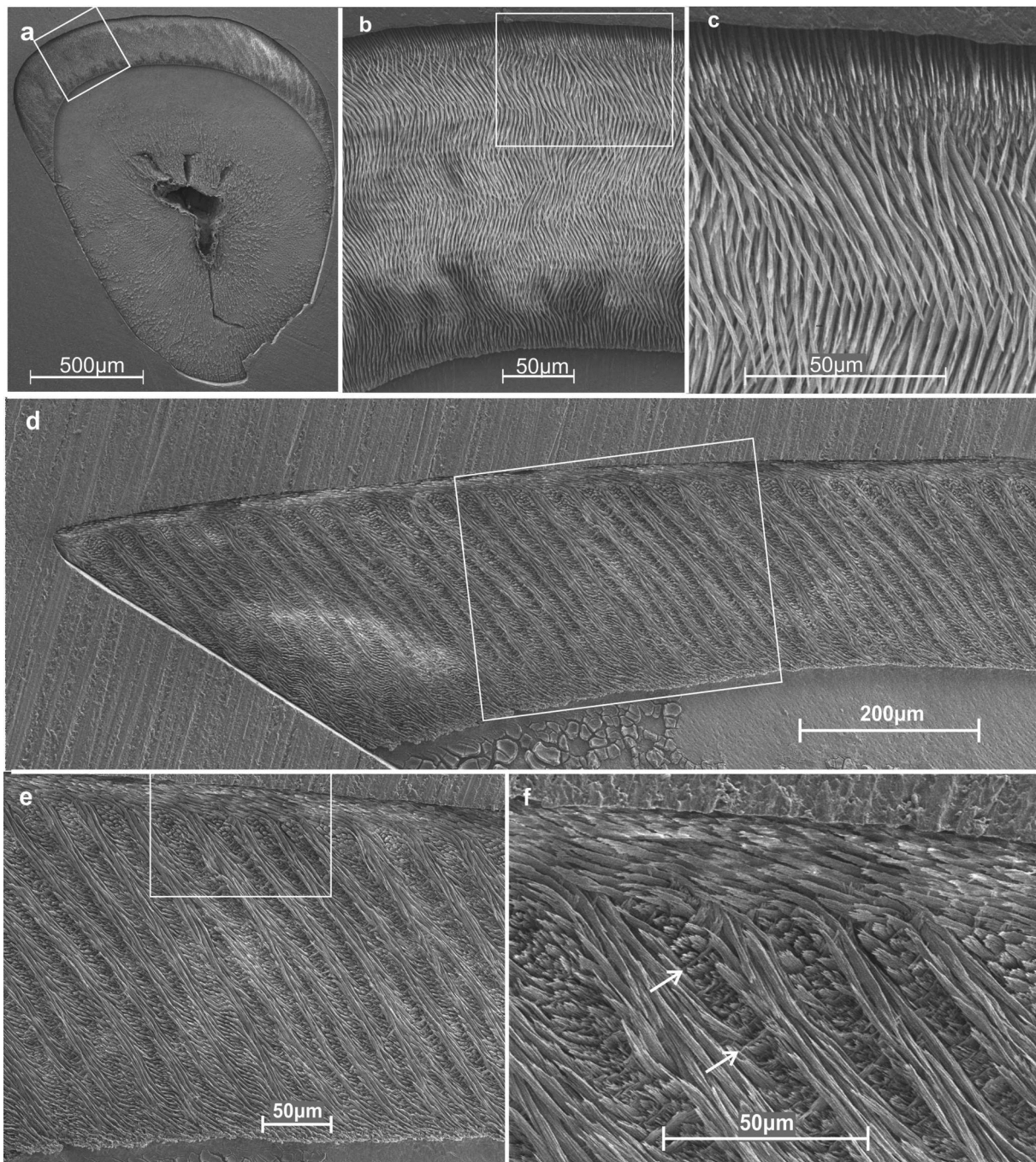


Figure 5. Sections of the lower incisor of *Daxneria fragilis* nov. gen. nov. sp. a-c transverse sections; b enlargement of square in a, c enlargement of square in b. d-f sagittal sections: e enlargement of square in d, f enlargement of square in e.

Comparisons

Flynn et al. (1986) described four sectioned baluchimyine incisors from site Y-GSP417 (Oligocene, Pakistan); genus and species have not been identified. Martin (1992) shows two details of the longitudinal sections of one of these specimens. Relative thickness of the PE is about 20%, the PI shows multiserial HSB, IPM is thick and anastomosing making a sharp angle with the prisms. Marivaux et al. (2000) illustrate the structure of the *Baluchimys krabiensis* (late Eocene, Thailand). The PI is ~20% of total enamel thickness. The longitudinal sections show multiserial HSB with thick IPM. The PI in cross-section shows reticulate IPM in a wavy pattern. *Daxneria* shares the multiserial HSB pattern with the baluchimyids from

Pakistan and Thailand, but differs from these in the relative thickness of the PE and in the thickness, morphology and crystallite direction of the IPM.

Although the dental morphology of *Daxneria* is unique, the cheek teeth suggest affinities with the Baluchimyinae. In order to facilitate comparison we reduce the array of these Asian rodents into two groups of species and illustrate and compare these with *Daxneria*.

The first group that may be recognized consists of the very similar *Baluchimys* and *Lindsaya* (Figure 6). Like *Daxneria*, permanent premolars are not known for this group and we posit that these taxa retain their dp4 and DP4. Upper molars of this group are characterized by a relatively well developed metaconule without,

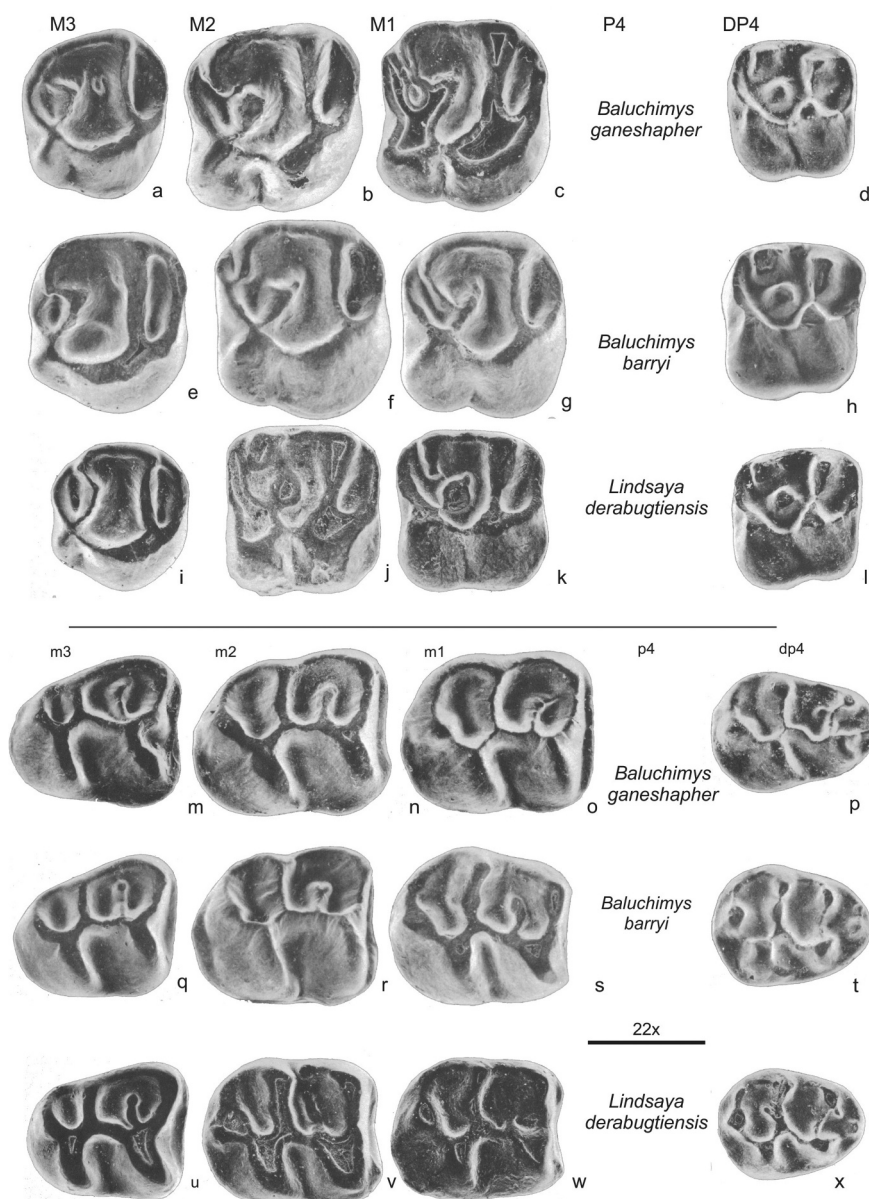


Figure 6. Upper and lower cheek teeth of *Baluchimys ganeshapher* (a, b, c, d, m, n, o, p), *Baluchimys barryi* (l, f, g, h, q, r, s, t) and *Lindsaya derabugtiensis*, all three from site Y-GSP417 (Flynn et al., 1986). The bar represents 1 mm; the approx. enlargement has been added.

or with a short mesolophule, the metaconule is connected to the hypocone, an endoloph is present. The upper molars of *Daxneria*, share the endoloph and the tendency to isolate the metaconule with *Baluchimys* and *Lindsaya*, but the metaconule of *Daxneria* has a much more labial position. Major structural differences between *Daxneria* and this group are observed in the M3. The posterior side of the M3 of *Daxneria* is strongly reduced, hypocone and metacone are tiny, but the metaconule is relatively large. The hypoflexus is very deep and a mure is present. The anterior side of the M3 of *Daxneria* is wide, considerably wider than that of the M1 or M2. The M3 of *Baluchimys* and *Lindsaya* is slightly smaller than the M2, its posterior side shows some reduction. The M3 of *Baluchimys* and *Lindsaya* shows a protocone that is expanded in posterior direction, hypocone and metacone are small, a hypoflexus is nearly absent. Lower molars of *Baluchimys* and *Lindsaya* show a short or weak metalophulid II, that of *Daxneria* is strong, long and ends free. In *Daxneria* protoconid and hypoconid are long and narrow.

The second group of species is composed of *Bugtimys*, *Hodsahibia*, *Lophibaluchia* and *Ottomania* (Figures 7 and 8). *Confiniummys* resembles *Ottomania* in most dental characteristics, it is neither illustrated here nor further discussed because it is poorly documented. *Lophibaluchia*, *Ottomania* and *Daxneria* retained their dp4 and DP4, while *Bugtimys* and *Hodsahibia* have a p4 and P4. Three genera of this group have no endoloph on M1-3 (*Bugtimys*, *Hodsahibia*, *Lophibaluchia*; Figure 7). On *Ottomania* the protoconid and hypoconid of the DP4 and most M1 are connected, but not on the M2 (Figure 7s). The endoloph is present on all upper cheek teeth of *Daxneria* (Figure 7v-y). Upper molars of the four genera in this group are more or less lophodont with three curved lophs. The third loph of the M1 and M2 connects the hypocone through the metaconule and mesolophule to the labial tooth margin (Figure 7). In *Hodsahibia*, *Bugtimys* and *Ottomania* the metacone is connected to metaconule through the labial part of the metaloph resulting in an Y-shaped configuration of these lophs. The Y-configuration is poorly

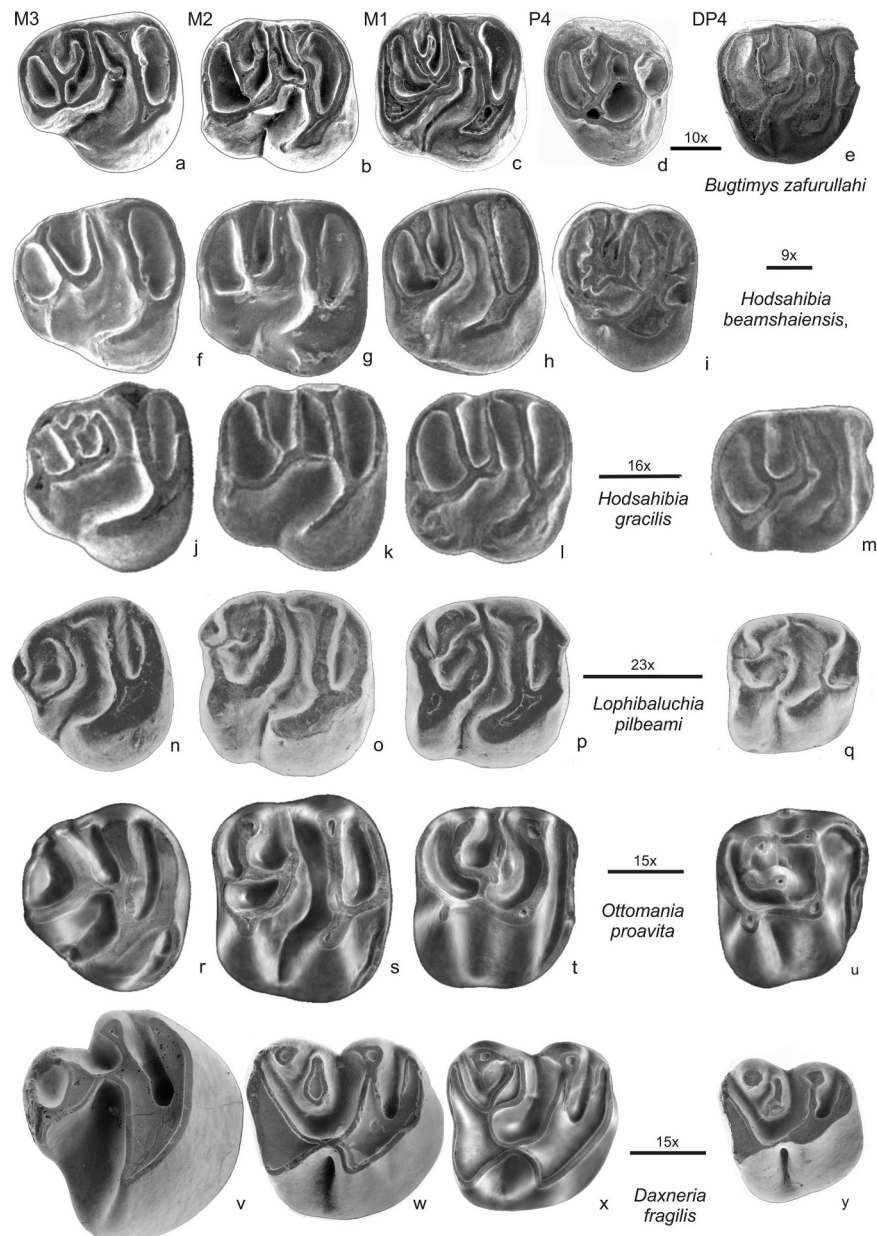


Figure 7. Comparison of upper cheek teeth of *Daxneria fragilis* (v-y) with *Bugtimys* Marivaux et al., 2002 site Paali nala C2 (a-e), *Hodsahibia* Marivaux & Welcomme 2003 site Paali nala C2 (f-h), *H. gracilis* Paali nala C2 (j-m), *Lophibaluchia* Flynn et al., 1986 site Y-GSP417 (n-q) and *Ottomania* de Bruijn et al., 2003 site Süngülü. *Daxneria*, *Ottomania* and *Lophibaluchia* retained their DP4 and have no P4. The bar represents 1 mm; the approx. enlargements have been added, these are not the same.

developed in *Lophibaluchia* because of absence of the metacone-metaconule connection (Figure 7o-p). The M3 shows a reduced posterior region, in particular in *Lophibaluchia* and *Ottomania*. The M3 of *Ottomania* illustrated in Figure 7r has a mure, metacone and labial metaloph are absent. Other specimens (de Bruijn et al. 2003, plate 1 Fig. 6) have no mure and a tiny metacone and labial metaloph are present. Compared to this group of four genera, the tooth pattern of the posterior side of upper molars of *Daxneria* is rather different. There is no metaloph, metacone and metaconule are isolated or nearly isolated and the metaconule has a labial position. There is an endoloph on the M1-2 of *Daxneria* and the hypoflexus is sharp and short. The M3 of *Daxneria* is strongly reduced, it resembles that of *Ottomania*, but in *Ottomania* the third loph of the M3 incorporates

hypocone, lingual part of the metaloph, metaconule and mesolophule; the metacone and its connection to the metaconule has completely disappeared on the specimen in Figure 7r. In *Daxneria* the third loph is composed of hypocone, an enlarged metaconule and a tiny metacone.

The lower molars of *Baluchimys* and *Lindsaya* (Figure 7) have a short metalophulid II that mostly ends free. *Bugtimys*, *Hodsahibia*, *Lophibaluchia* and *Ottomania* (Figure 8) have a long metalophulid II that may end free near the lingual border or is connected to the posterior side of the metaconid. The metalophulid II of *Daxneria* is long and ends free in all preserved specimens.

In addition to the tooth pattern, it is the partial hypsodonty that characterizes the molars of *Daxneria* and differentiate it from all other

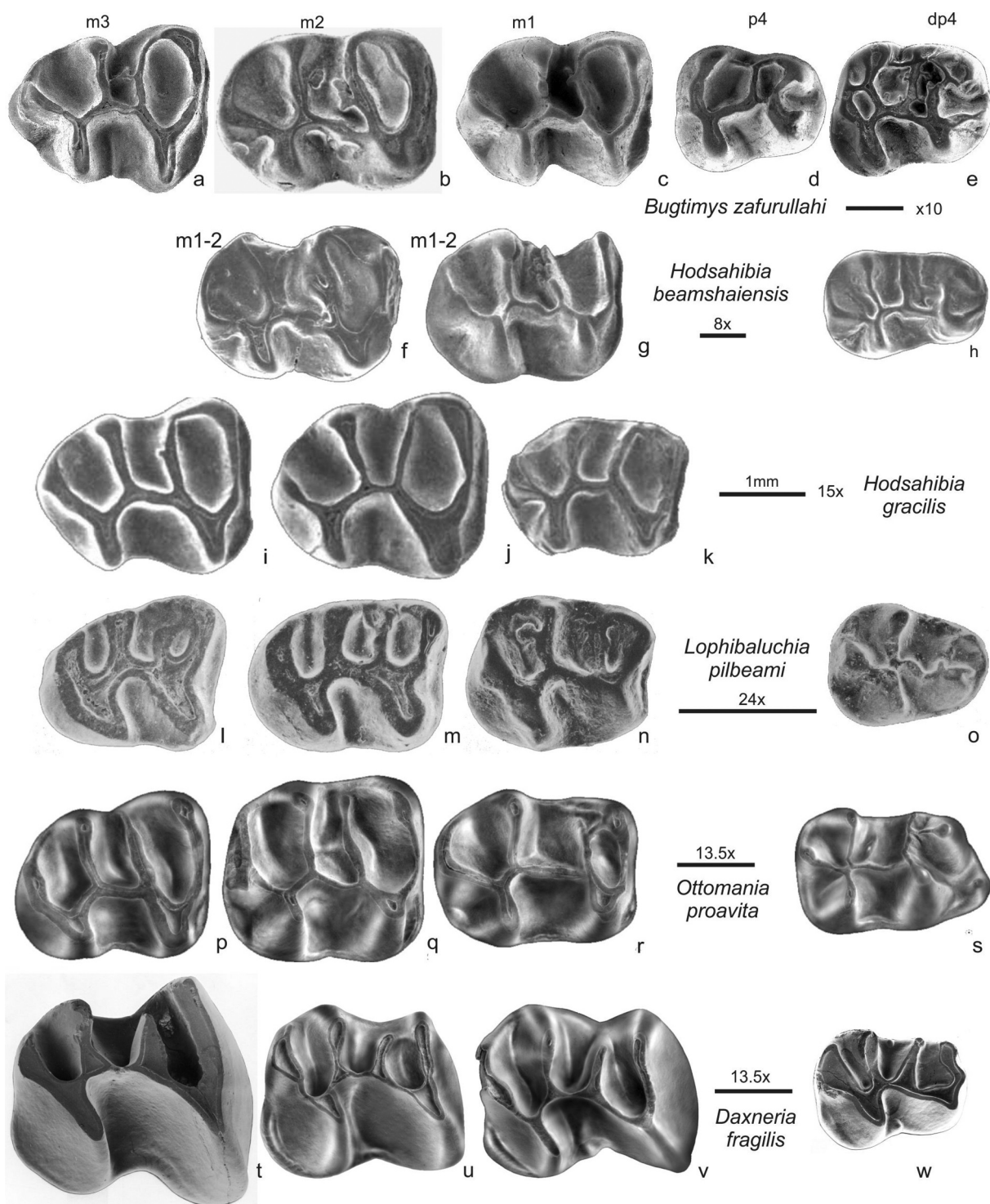


Figure 8. Comparison of lower cheek teeth of *Daxneria fragilis* with *Bugtimys* Marivaux et al. (2002) site Paali nala C2, (a-e); *Hodshahibia beamshaiensis* Marivaux and Welcomme (2003) site Paali nala C2, (f-h); *H. gracilis* Marivaux and Welcomme (2003) site Paali nala C2, (i-k); *Lophibaluchia* Flynn et al. (1986) site Y-GSP417, (l-o) and *Ottomania* de Bruijn et al. (2003), site Süngülü, (p-s). *Daxneria*, *Ottomania* and *Lophibaluchia* retained their DP4 and have no P4. The bar represents 1 mm; the approx. enlargements have been added, these are not the same.

genera included in the Baluchimyinae. *Daxneria* clearly represents a separate branch within this Asian subfamily that was already supposed to be polyphyletic.

Premolars

In assemblages consisting of isolated molars the determination of dental positions can be difficult. To associate isolated molars in

assemblages containing several related species is even more challenging, certainly so when collections are small. The recognition of permanent and deciduous molars is often problematic, see the discussion in Flynn and Cheema (1994). Retention of the deciduous premolars is fairly common among the Ctenohystrica. In order to establish whether this is the case in the Asian baluchimyines the morphology of the deciduous and the permanent premolars has to be established. We compared first the cheek teeth of all well-

illustrated Asian baluchimyine genera (Flynn et al. 1986; Flynn and Cheema 1994; Marivaux and Welcomme 2003) and some North African Ctenohystrica. In baluchimyines the P4, if present, is more or less triangular or heart-shaped, with an insignificant hypocone. In contrast, the hypocone of the DP4 is sturdy, resulting in a more or less square-outline of the occlusal surface, the anteroloph is well developed. This P4/DP4 morphology is illustrated in *Hodsahibia* and *Bugtimys* (Figures 7d,f) and is seen as well in *Dianomys* (Eocene Wang 1984, 2001) and African genera included in the late Eocene “protophiomyines” (sensu Marivaux and Boivin 2019). The p4 of baluchimyines has the four main cuspids (protoconid, hypoconid, metaconid and entoconid) well-developed and is posteriorly wider than anteriorly, the anteroconid is absent (Figure 8d). In contrast, the dp4 is long and the anteroconid may be present. P4/p4 with this morphology have not been found in the assemblages of *Daxneria*, *Ottomania* and *Lophibaluchia*, so the P4 and p4 positions in the composed tooth-rows remains vacant in Figures 6, 7 and 8. In small assemblages of isolated teeth the absence of the permanent fourth premolar may be accidental, but for *Ottomania*, *Baluchimys*, *Lindsaya* and *Lophibaluchia* there is enough material to suggest that the absence of P4 and p4 is not accidental. Our working hypothesis is that within the Asian baluchimyines the genera *Hodsahibia* and *Bugtimys* have a P4 and p4, but *Baluchimys*, *Lindsaya*, *Lophibaluchia*, *Ottomania* and *Daxneria* have no permanent fourth premolar, but retained their deciduous cheek teeth.

Family Ctenodactylidae Gervais, 1853
Subfamily Ctenodactylinae Hinton, 1933

Introduction

Ctenodactylidae radiated in Central Asia during the Oligocene, where some eight genera have been described from several basins (Wang 1997). Extensive studies of the rodents from the Valley of Lakes (Mongolia, see Oliver et al. 2017 and references therein) and from Ulanatal in neighbouring Chinese Inner Mongolia (see Gomes Rodrigues et al. 2014 and references therein) document the details of Oligocene ctenodactylid expansion. Most species become extinct during the late Oligocene, only the hypsodont *Distylomys* Wang (1988), *Prodistylomys* Wang (1988), *Sayimys* Wood (1937) and a species of *Yindirtemys* Bohlin (1946) survived into the early Miocene. The ctenodactylid *Sayimys* Wood (1937) is present in the early and middle Miocene of China (Bohlin 1946), Kazakhstan (Kordikova and de Bruijn 2001), Anatolia (López-Antoñanzas et al. 2004; Hartman et al. 2019), Greece (López-Antoñanzas et al. 2005) and the early Oligocene and Miocene of the Indian subcontinent (see Hartman et al. 2019 and references therein). With the formation of a land connection between Turkey and Arabia during the early Miocene, Ctenodactylidae migrated into Arabia and beyond, into northern Africa (Wessels et al. 2003; López-Antoñanzas, 2015). Middle and late Miocene African genera are *Sayimys* (including *Proafricanomys* López-Antoñanzas et al. 2015), *Metasayimys* Lavocat (1961), and *Africanomys* Lavocat (1961). Giant ctenodactylids have been found on Sardinia, these are part of a Miocene insular fauna (de Bruijn and Rümke 1974); a Pleistocene insular fauna with the ctenodactylid *Pellegrinia* De Gregorio (1887) is known from Sicily. Today four genera survive in northern Africa. The three specimens described below from Gözükkızıllı are included in *Sayimys*, this means that these are the so far the oldest known record of the genus.

Sayimys Wood 1937

Sayimys sp.

Figures 3k, 4m-p, 9a-d

Localities: GOZ1b

Synonymy: aff. *Sayimys* sp. (Ünay et al. 2003a)

Materials and measurements: GOZ1b-251d, damaged M1 (Figure 6(k); length 2.04 mm); GOZ1b-252s, incomplete m1-2 (Figures 4o,p; length 2.33 mm, width 2.34 mm); GOZ1b-253s, m3 (Figures 4m,n; length 2.62 mm, width 2.38 mm).

Description

The damaged upper molar is possibly a M1 (Figures 3k, 9a), because it is relatively small, compared to the associated lower molars. The molar shows the four lophs typical for *Sayimys*, the metaloph is isolated, that is, not connected to the posteroloph.

The high-crowned m1 or m2 is incomplete. Judging by its width, it is probably a m2. The anterior side of the anterolophid is missing (Figures 4o and 9d), so it was a bit longer than the measured length. The posterior side of the anterolophid shows two crenulations (arrowed in Figures 4o, 9d). The metalophulid II is long, bending slightly forward, reaching the lingual tooth border. A well-developed postero-labial cingulid is present.

The high-crowned m3 is complete. The posterior side of the anterolophid shows two crenulations (arrowed in Figure 4m), similar to the m1 or m2. The metalophulid II is long reaching the lingual tooth border. The hypolophid is not in line with the oblique ectolophid, but these form an obtuse angle. The protoconid is long and narrow, jutting out in labial direction. The hypoconid is relatively small, a minor constriction is present between this cuspid and the posterolophid.

Comparisons

The three molars from Gözükkızıllı-1 have been compared with the Oligocene ctenodactylids from the well-known basins in Mongolia and Chinese nei Mongol (Wang 1997; Vianey-Liaud et al. 2006 & 2010; Gomes Rodrigues et al. 2014; Oliver et al. 2017) but they do not fit any of the Oligocene genera. Instead, the molars resemble *Sayimys*. Figure 9 shows the molars from Gözükkızıllı and *Sayimys* specimens from the early Miocene of the Aktau Mountains (Kazakhstan; Kordikova and de Bruijn 2001) and from Z113 in the Zinda Pir Dome (Pakistan). The Z113 site was originally described as early Miocene, but placed in the late Oligocene by Métais et al. (2009). Unfortunately, not all tooth positions are represented in the Gözükkızıllı-1 material and in the compared assemblages. The well-developed and long metalophulid II in the Gözükkızıllı lower molars is also present in *Sayimys* from Aktau and in *S. flynni* (Baskin, 1996) from Z113, but it is absent in *S. minor* de Bruijn et al. (1981) and *S. giganteus* López-Antoñanzas et al. (2004). The narrow protoconid protruding in labial direction is also present in *Sayimys* from Aktau and in *S. giganteus*. The Gözükkızıllı-1 material seems closest to that from the Aktau mountains described as *Sayimys* aff. *obliquidens*. *Sayimys obliquidens* from its type area Taben Buluk is larger. Moreover, there are doubts about the homogeneity of its type assemblage and about the location and age of the type locality (Hartman et al. 2019); therefore, classification as *Sayimys* sp. is preferred.

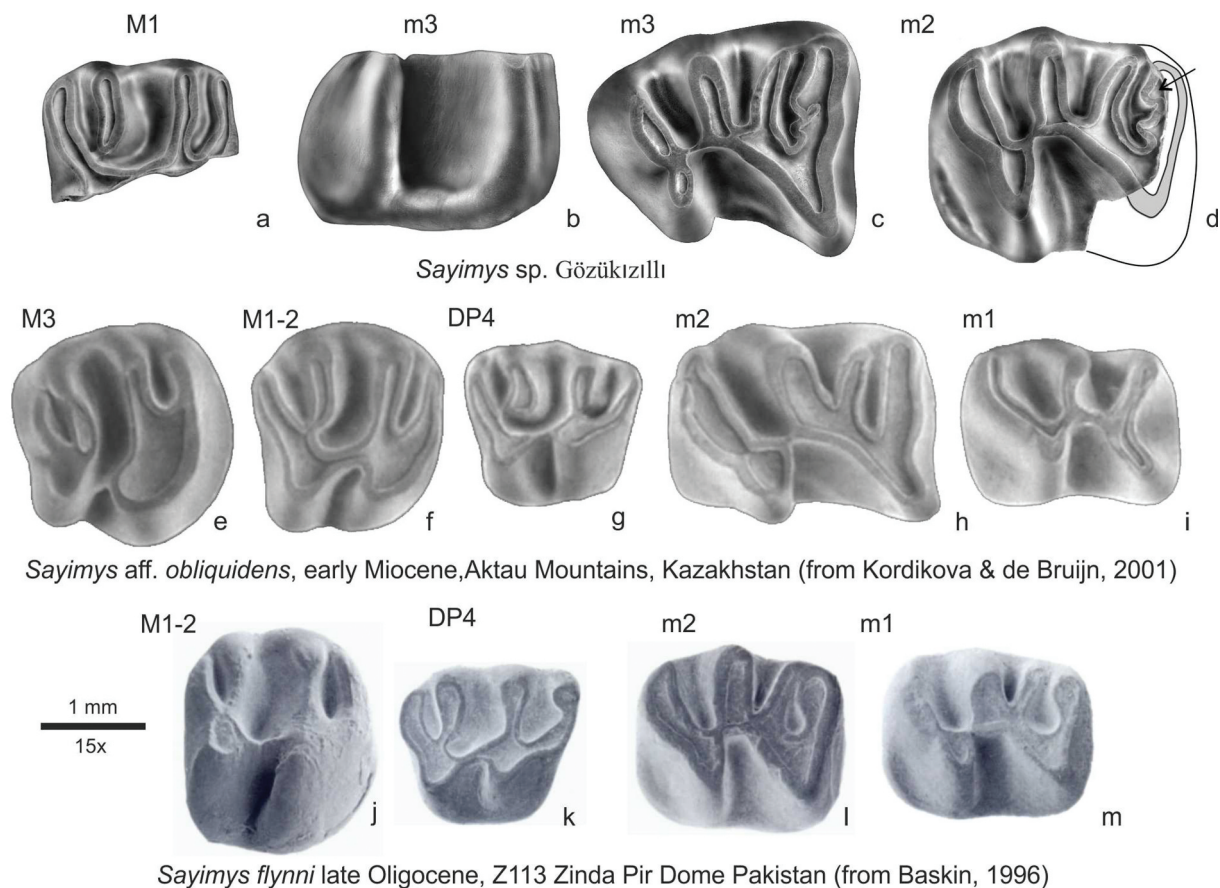


Figure 9. Comparison of *Sayimys* sp. from Gözükkızıllı with *Sayimys* aff. *obliquidens* from the middle member of the Chul'adyr Formation Aktau Mountains, Kazakhstan (e-i) and *S. flynni* from Z113, Zinda Pir, Pakistan (j-m).

Suborder Supramyomorpha D'Elia, Fabre
and Lessa, 2019
Family Muridae, Illiger 1811
Subfamily Eucricetodontinae Mein and
Freudenthal, 1971a
Eucricetodon Thaler, 1966

Type species: *Cricetodon collatum* Schaub, 1925
Type locality: Küttigen Germany, age late Oligocene

Introduction

The subfamily Eucricetodontinae was originally meant to contain all European 'Oligocene' hamster-like rodents except the Paracricetodontinae Mein and Freudenthal, 1971a and the Melissiodontinae Schaub, 1925. Freudenthal et al. (1992) restricted the subfamily basically to the genus *Eucricetodon*, while the genera *Mirabella* de Bruijn et al., 1987 (now *Mirabella* de Bruijn et al., 2007) and *Eumyarion* Thaler, 1966 were added with a question mark. In the meantime a large number of new species of *Eucricetodon* s.l. all over Eurasia have been described.

Table 2 lists the species included in *Eucricetodon* (including *Atavocricetodon*) from Europe with type locality and age using the Paleogene mammalian MP zones (Schmidt-Kittler 1987; Aguilar et al. 1997) and the Neogene MN zones (de Bruijn et al. 1992). The listing is approximately from old to young.

Several of the Western European species included in *Eucricetodon* are based on limited type material, on holotypes from unknown locality and age, or on an incomplete and worn

tooth row. Notorious in this respect are the holotypes from the Quercy in France in old museum collections. Mainly because of this Vianey-Liaud (1972) considered these species 'inutilisable' (translation unusable). These are listed in Table 3. To declare these species 'inutilisable' was entirely correct. Unfortunately, Comte (1985) and Freudenthal (1994) revived *Eucricetodon dubius* while Dienemann (1987) revived *E. murinus* and *E. incertus*. Freudenthal (1994) rejected the holotype selected by Mayo (1982) for *E. dubius* (Mont-de-Doury) and stated that Schaub (implicitly) designated a mandibula from the Quercy. Next Freudenthal classified a large collection of isolated molars from Vivel del Rio (Spain, early Oligocene, MP28) under that name. Earlier, Freudenthal et al. (1992) considered *Eucricetodon praecursor* a synonym of *E. dubius*, a view maintained by Freudenthal and Suarez (2016).

Eucricetodon gerandianus (Gervais, 1848–1852) is another problematic species. Its type locality is Langy near St-Gérard-le-Puy (France). Daams (1976) reported that the holotype of Gervais is lost and that further collection at that site is impossible. He proposed a "hypotypoid", three upper molars figured in Schaub (1925; plate 3, figure 14) from la Chaux near St. Croix in Switzerland and described a good collection from Cetina de Aragon (Spain) as *E. gerandianus*. The holotype selected by Daams was rejected by Huguency (1999) because a 'hypotypoid has no nomenclatural value' and she designated a neotype, a lower tooth row, from St-Gérard-le-Puy figured in Schaub, a site close to the original type locality. Many pages have been printed concerning uncharacteristic and incomplete holotypes without paratypes, originating from unknown localities and of imprecisely known ages. The best and easiest solution to solve these problems is to ring-fence or

Table 2. List of species of *Eucrietodon* from Europe. The allocation into groups is after Freudenthal & Martin-Suarez (2016).

Species	Type locality; age; group; remarks
<i>E. atavus</i> (Misonne, 1957)	Hoogbutsel, Belgium; early Oligocene, MP21; <i>Atavocricetodon</i> grp
<i>E. atavoides</i> Freudenthal, 1996	Ollalla 4, Spain; early Oligocene, MP22; <i>Atavocricetodon</i> grp
<i>E. nanooides</i> Freudenthal, 1996	Ollalla 4, Spain; early Oligocene, MP22; <i>Atavocricetodon</i> grp
<i>E. minusculus</i> Freudenthal, 1996	Ollalla 4, Spain; early Oligocene, MP22; <i>Atavocricetodon</i> grp
<i>E. nanus</i> Peláez-Campomanes, 1995	Valdecollares, Spain; early Oligocene, MP23; <i>Atavocricetodon</i> grp
<i>E. hugueneyae</i> Freudenthal, 1996	Montalbán 1D, Spain; early Oligocene, MP23; <i>Atavocricetodon</i> grp
<i>E. huberi</i> (Schaub, 1925)	Mümliswil, Switzerland; late Oligocene, MP26; <i>huerzeleri</i> grp
<i>E. martinensis</i> Freudenthal, 1994	Mirambueno 4D, Spain; late Oligocene, MP26; <i>huerzeleri</i> grp
<i>E. margaritae</i> Daams et al. 1989	Pareja, Spain; late Oligocene, MP26; <i>huerzeleri</i> grp
<i>E. huerzeleri</i> Vianey-Liaud, 1972	Oensingen, Switzerland; late Oligocene, MP26; <i>huerzeleri</i> grp
<i>E. robustus</i> Augusti & Arbiol, 1989	Fraga 4, Spain; late Oligocene, MP27; <i>dubius</i> grp
<i>E. quercyi</i> Vianey-Liaud, 1972	Pech-du-Fraysse, France; late Oligocene, MP28; <i>dubius</i> grp
<i>E. liber</i> Ziegler 1994	Herlingen 9, Germany; late Oligocene, MP29; <i>dubius</i> grp
<i>E. thezelensis</i> Comte, 1985	Thézels, France; late Oligocene, MP30; <i>dubius</i> grp
<i>E. collatus</i> (Schaub, 1925)	Küttigen, Switzerland; latest Oligocene, MP30; <i>collatus</i> grp; holotype by Thaler 1966
<i>E. longidens</i> Hugueneu, 1969	Coderet, France; latest Oligocene, MP30; <i>collatus</i> grp; originally subspecies of <i>E. collatus</i>
<i>E. hesperius</i> Engesser, 1985	Paulhiac, France; earliest Miocene, MN1; <i>collatus</i> grp
<i>E. cetinensis</i> Daams, 1976	Cetina de Aragon, Spain; early Miocene, MN2; <i>collatus</i> grp
<i>E. gerandianus</i> (Gervais, 1848-1852)	Langy, France; early Miocene; <i>collatus</i> grp; see Daams 1976
<i>E. aquitanicus</i> Baudelot & de Bonis, 1968	Laugnac, France; early Miocene, MN2; <i>collatus</i> grp
<i>E. hochheimensis</i> (Schaub, 1925)	Hochheim, Germany; early Mioc.; <i>collatus</i> grp; known from a single m2 only (Hugueneu 1999)
<i>E. haslachensis</i> (Schaub, 1925)	Haslach/Ulm, Germany; early Mioc.; MN2?; <i>collatus</i> grp; holotype by Dienemann 1987
<i>E. infralactorensis</i> (Viret, 1930)	Estrepouy, France; early Miocene, MN3; <i>collatus</i> grp; see Hugueneu & Bulot 2011
<i>E. quadratus</i> (Viret, 1930)	Estrepouy, France; early Miocene, MN3; <i>collatus</i> grp; see Hugueneu & Bulot 2011

Table 3. *Eucrietodon* species based on limited type material from unknown type localities and of uncertain age.

Species	Type locality
<i>E. gergovianum</i> (Schaub, 1925)	Quercy, France; Oligocene
<i>E. murinus</i> (Schlosser, 1884)	Quercy, France; Oligocene
<i>E. praecursor</i> (Schaub, 1925)	Quercy, France; Oligocene
<i>E. incertus</i> (Schlosser, 1884)	Quercy, France; Oligocene
<i>E. dubius</i> (Schaub, 1925) *	Quercy, France; Oligocene

*included in *Heterocricetodon* by Hugueneu (1980) and Engesser (1987)

quarantine these species, that is, restrict these species to their holotypes and ignore these names in future studies.

Problematic, but for different reasons, are *Eucrietodon infralactorensis* and *E. quadratus* both from Estrepouy (France). The size range of *Eucrietodon* from Estrepouy is very large and therefore Viret et al. (1930) recognized two species, the smaller *E. infralactorensis* and the larger *E. quadratus*. However, later collecting at Estrepouy suggested that *E. quadratus* falls within the size range of *E. infralactorensis* and is thus its junior synonym, while there is as yet an unnamed much smaller species in the sample (see for a discussion Hugueneu and Bulot 2011).

Freudenthal (1996) described the subgenus genus *Atavocricetodon* (type species *A. atavoides*) and included *atavus*, *murinus*, *huberi*, *nanus*, *nanooides*, *hugueneyae*, *nanooides* and *minusculus*. In this way he subdivided *Eucrietodon* into an early Oligocene and a late Oligocene-early Miocene group. *Eucrietodon* species described from Asia and Asia Minor are in Table 4. Marivaux et al. (1999) described a new *Atavocricetodon* species from the Oligocene of Pakistan extending the geographic range of the genus to the Indian subcontinent. de Bruijn et al. (2003) maintained the subgenus *Atavocricetodon*, but considered it a 'morpho-subgenus' with a 'primitive' dental pattern and included some Asian species. Gomes Rodrigues et al. (2013) showed that the outline of the M1 cannot be used to distinguish *Atavocricetodon* from *Eucrietodon* and argued that the distinction of the two genera is not meaningful. Maridet et al. (2009) described a late Oligocene *Eucrietodon* assemblage from the Junggar basin (northern China) and noted its resemblance to the latest Oligocene *E. longidens* from Europe. Lopez-Guerrero et al. (2017) studied *Eucrietodon* from the early Oligocene to early late Oligocene

Table 4. List of Asian *Eucrietodon* species.

Species	locality; age
<i>E. kurthi</i> de Bruijn et al., 2003	Süngülü, Turkey; latest Eocene
<i>E. wangae</i> Li et al., 2016	Red Beds, Erden Obo, China; latest Eocene
<i>E. caducus</i> (Shevyreva, 1967)	Zayzan depression, Kazakhstan; early Oligocene
<i>E. deploratus</i> (Shevyreva, 1967)	Zayzan depression, Kazakhstan; early Oligocene
<i>E. paaliensis</i> (Marivaux et al., 1999)	Paali Nala C2, Pakistan; early Oligocene
<i>E. asiaticus</i> (Matthew and Granger, 1925)	Hsanda Gol, China; middle Oligocene
<i>E. bagus</i> Gomes Rodrigues et al., 2012	Ulantatal UTL4, China; late Oligocene
<i>E. jilantaiensis</i> Gomes Rodrigues et al., 2012	Ulantatal UTL4, China; late Oligocene
<i>E. occasionalis</i> Lopatin, 1996	Altyn Shokysu bone bed 4, Kazakhstan; late Oligocene
<i>E. sajakensis</i> Bendukidze, 1993	Sayaken, Kazakhstan; late Oligocene
<i>E. youngi</i> Li & Qiu, 1980	site IVPP#78027, near Tianjiazhai, Xining basin, China; early Mioc.

succession in the Valley of Lakes and linked the observed trends in dental morphology to environmental change.

Freudenthal and Martin-Suarez (2016) reviewed European *Atavocricetodon-Eucrietodon* and recognized a chronological sequence of an *Atavocricetodon* group and four groups in *Eucrietodon*.

- the *Atavocricetodon* group occurring in MP21-23 (early part early Oligocene)
- the *huerzeleri* group occurring in MP24-27 ('middle' Oligocene)
- the *dubius* group occurring in MP27-29 (late Oligocene)
- the '*praecursor*' group occurring in MP 29 (late Oligocene)
- the *collatus* group occurring in MP29-MN3 (latest Oligocene – earliest Miocene)

The groups of Freudenthal and Martin-Suarez have been added to the species in Table 2. Confusing is the name *praecursor* group when the holotype of *E. praecursor* is a synonym of *E. dubius*. The differences between the five groups as defined by Freudenthal and Martín-Suárez (2016) are subtle, such as size of the cusps (difficult

to grasp on illustrations) and frequencies of dental characters. Further, Freudenthal and Martin-Suarez claimed presence of morphological breaks between the groups, implying that each of the groups immigrated into the European realm and that ‘ancestor-descendant relationships’ cannot be demonstrated except within the *collatus* group. For a discussion on late Oligocene-early Miocene *Eucricetodon* (the *collatus* group) see Huguency (1999) and Berthet et al. (2005).

Eucricetodon from Gözükızıllı-1

Fairly large assemblages of isolated molars of *Eucricetodon* have been collected from the two horizons in Gözükızıllı-1. The size distribution of the molars, in particular of the third molars, shows the presence of two species (Figure 10). The separation into two groups of the first and second molars is uncertain because the large and the small specimens have the same morphology and cluster metrically. Thus, some small specimens of the large species and large specimens of the small species may have been wrongly assigned.

The lengths of the Gözükızıllı-1 M1 has been compared with that of the late Oligocene and early Miocene species from Europe (Figure 11). Similar to Gözükızıllı several European sites have two species of *Eucricetodon*. Figure 11 shows that many sites show large ranges in the length of the M1.

We were hesitant to name new species because in the list of formally named species of *Eucricetodon* that we compiled are already over 40 species, of which 12 described from sites in Asia and Asia Minor. However, the split anterocone on the M1 of large and small *Eucricetodon* from Gözükızıllı-1 restricted the playing field to a few late Oligocene and early Miocene species from western Europe that are included in the *huerzeleri* and *collatus* groups of Freudenthal & Suarez (2016). The small species is described as *Eucricetodon ruber* nov. sp. and the large species as *E. oculatus* nov. sp. The nomenclature of parts of *Eucricetodon* molars is shown in Figure 12.

Eucricetodon ruber nov. sp.
(Figures 13g-l and 14 g-l)

Derivatio nominis: based on the name of the type locality Gözükızıllı-1 which means red eyes in Turkish. We included the word red in the name of this small species (*ruber* means red) and include eye (*oculus*) in the name of the large species.

Holotype: M1 dext. GOZ1b-105 (Figure 13l)

Type locality: Gözükızıllı-1b, about 21 km south of Kızıllırmak, Anatolia Turkey.

Other sites with *Eucricetodon ruber*: Gözükızıllı-1a, Güvendik
Age: late Oligocene

Paratypes:

Gözükızıllı-1a: **M1:** 101s*, 102s, 103s, 104s, 105s, 113d, 115d, 116d, 117d, 118d; **M2:** 101s*, 121s, 123s, 124s, 133d, 135d, 136d; **M3:** 141s, 142s, 143s, 151d, 153d, 154d, 155d, 156d;

m1: 161s, 165s; **m2:** 171s, 172s, 174d, 175d, (176d), 177d, 178d; **m3:** 184s, 185s, 186s.

Gözükızıllı-1b: **M1:** 105s, 106s, 107s, 108s, 109s, (110s), (112d), 114d; **M2:** 123s, 124s, 125s, 126s, 127s, 128s, 129s, 134d, 135d, 136d, 137d, 140d; **M3:** 143s, 144s, 145s, 146s, 147s, 148s, 155d, 156d, 157d, 158d. **m1:** 163s, 165s, 166s, 167s, 168s, 171d, 172d, 173d, 174d, 175d, 176d, 177d, 178d; **m2:** 185s, 186s, 187s, 188s, 193d, (194d), (195d), 196d; **m3:** 204s, 205s, 214d, -215d, 216d.

The molars indicated with * are from the same individual, s = sinistral, d = dextral, incomplete specimens between brackets.

Synonymy: *Eucricetodon* sp. 2 (Ünay et al. 2003a)

Measurements: see Table 5

Diagnosis: Small *Eucricetodon* with a split anterocone on M1 and without posterior spur (the anterolophule). Cusps high and well-developed, ridges low to very low. Low ectoloph on M1 and M2. The m1 with a cuspidate anteroconid and pointed anterior outline.

Comparisons: the comparisons of *E. ruber* with other species is given below in combination with *E. oculatus*.

Description: apart from the size *E. ruber* and *E. oculatus* are identical in dental morphology, therefore see below for the combined description of the species.

Eucricetodon oculatus nov. sp.
(Figure 13a-f and 14a-f)

Derivatio nominis: based on the name of the type locality Gözükızıllı which means red eyes in Turkish. We included the word eye in the name of the larger species (*oculatus* means with eyes) and include red (*ruber*) in the name of the small species.

Holotype: M1 dext. GOZ1b-102 (Figure 13c)

Type locality: Gözükızıllı-1b, 20 km south of Kızıllırmak, Anatolia Turkey

Other sites with *Eucricetodon oculatus*: Gözükızıllı-1a and Güvendik-1

Age: late Oligocene

Paratypes:

Gözükızıllı-1a: **M1:** 111d, (112d); **M2:** 131d; **m3:** 181s.

Gözükızıllı-1b: **M1:** (101s), 102s, (103s), (104s), 111d, 115d, (120s); **M2:** 121s, 122s, 130s, 131d, 132d; **M3:** 141s, 142s, 149d, 150d, 151d. **m1:** 161s, 162s; **m2:** 181s, 182s, 183s, 189d, 191d; **m3:** 201s, 202s, 211d, 212d.

Synonymy: *Eucricetodon* sp. 3 (Ünay et al. 2003a).

Measurements: see Table 6

Diagnosis: Larger than *Eucricetodon ruber*, but with identical dental morphology. Anterocone on M1 with two cusps and without anterolophule. Cusps high and well-developed, ridges low to very low. Low ectoloph on M1 and M2 or spurs on the paracone and metacone may be present. The cusp-like anteroconid on the m1 gives it a pointed anterior outline.

Description of *Eucricetodon ruber* and *E. oculatus*

Lower Incisor (Figure 15). The material consists of isolated and broken specimens; we have therefore not been able to differentiate the incisors of the two species. We assume that the enamel of the lower incisor of both species have the same microstructure. The external surface of the lower incisor is smooth with two parallel longitudinal ridges, enamel thickness is 200 µm. Portio interna (PI) is very thick (~80%), portio externa (PE) is reduced. The PI consists of longitudinal uniserial Hunter-Schreger Bands (HSB). The intra-prismatic matrix (IPM) of the internal part of the PI makes an angle of about 45 degrees to the HSB; in the external part of the PI the IPM is parallel to the prisms. An anticline in the prisms of the PI is present below the mesial ridge. The PE consists of tangential enamel, the prisms disappear toward the outer surface into the prisma-less external layer (PLEX). Schmelzmuster is type 10 (Kalthoff 2000).

M1 (Figure 13c, f, i, l). The cusps are high and pointed, ridges are low and thin. The anterocone is subdivided into two conules and shows an anterior groove; the labial conule is distinctly higher and is better developed than the lingual one. A low anterior cingulum is present at both sides of the anterocone, connecting low to the proto- and paracone. There are no other connections between the

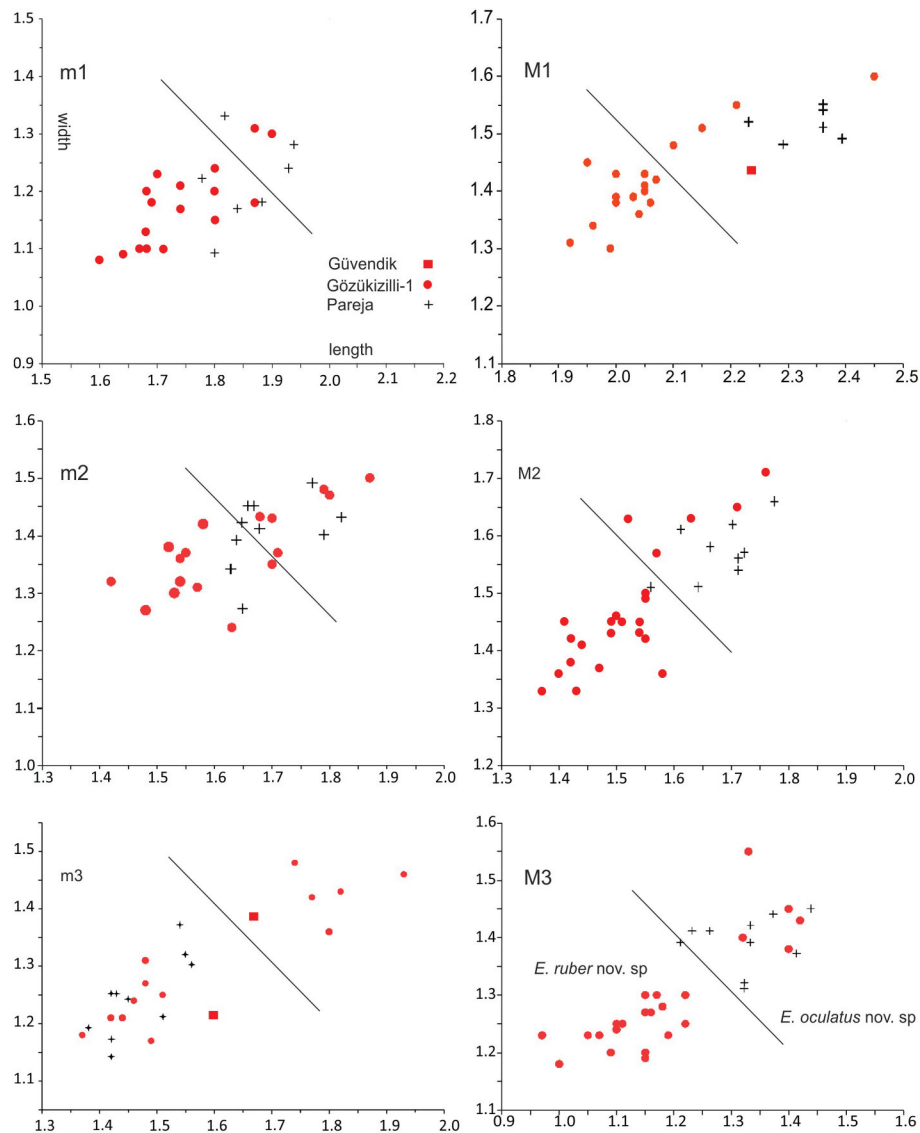


Figure 10. Length-width scatter diagrams of the molars of the two species of *Eucricetodon* from Gözükızılli-1 (red points) and *E. margaritae* (black crosses) from Pareja. The line separates the Gözükızılli points into *E. oculatus* nov. sp. and *E. ruber* nov. sp. The measurements of *E. margaritae* from Pareja have been digitised from Daams et al. (1989, Figure 3).

anterocone and proto- and paracone. The anterior arm of the protocone is short, it either reaches the base of the paracone, or it ends free (Table 7). The posterior arm of the protocone continues into the mure, a protolophule-2 is attached to the mure. The mesoloph is low and variable in length, it is confluent with the anterior arm of the hypocone (Table 7). One of the molars has a short ectomesoloph. Spurs on paracone or metacone are either absent, short or are long and developed into low ectolophs (Table 7). The short metaloph is poorly developed and may be incomplete, it mostly connects to the posterior arm of the hypocone (Table 7). The posteroloph is low and connects to the base of the metacone.

M2 (Figure 13b, e, h, k). The lingual anteroloph is short. The labial anteroloph is low, it connects to the base of the paracone. The lingual sinus is strongly curved in anterior direction. The protolophule-1 connects to the anterior arm of the protocone. The posterior arm of the protocone and the anterior arm of the hypocone form the curved mure. The mesoloph may be short, of medium length or long; on specimens where it is of medium length it may reach the base of the metacone (Table 7).

The curved metalophule inserts on the hypocone anterior of its apex. The posterior arm of the hypocone is confluent with the posteroloph; the low posteroloph inserts at the base of the postero-labial side of the metacone. The paracone spur may be absent, short or long and forms a complete but low ectoloph (Table 7). A few specimens of both species have a low cingulum, labial of the spurs or ectoloph. One specimen of *E. oculatus* (Figure 13e) has a short spur attached to the mure anterior of the mesolophule.

M3 (Figure 13a, d, g, j). The metacone is the highest cusp in used specimens. All specimens tend to close the lingual sinus by means of spurs on protocone and hypocone (Table 7) but the closure is incomplete on some. The lingual anteroloph is short, the labial one is long. The protolophule-1 inserts on the anterior arm of the protocone. The metacone and hypocone are incorporated into a posterior loph that connects hypocone, metacone and paracone. It is lowest and weakest between metacone and paracone. Irregular ridges possibly homologous to the metalophule, anterior arm of the hypocone and mure are present in the central basin. The mesoloph can be long and connected to the posteroloph, of medium length or

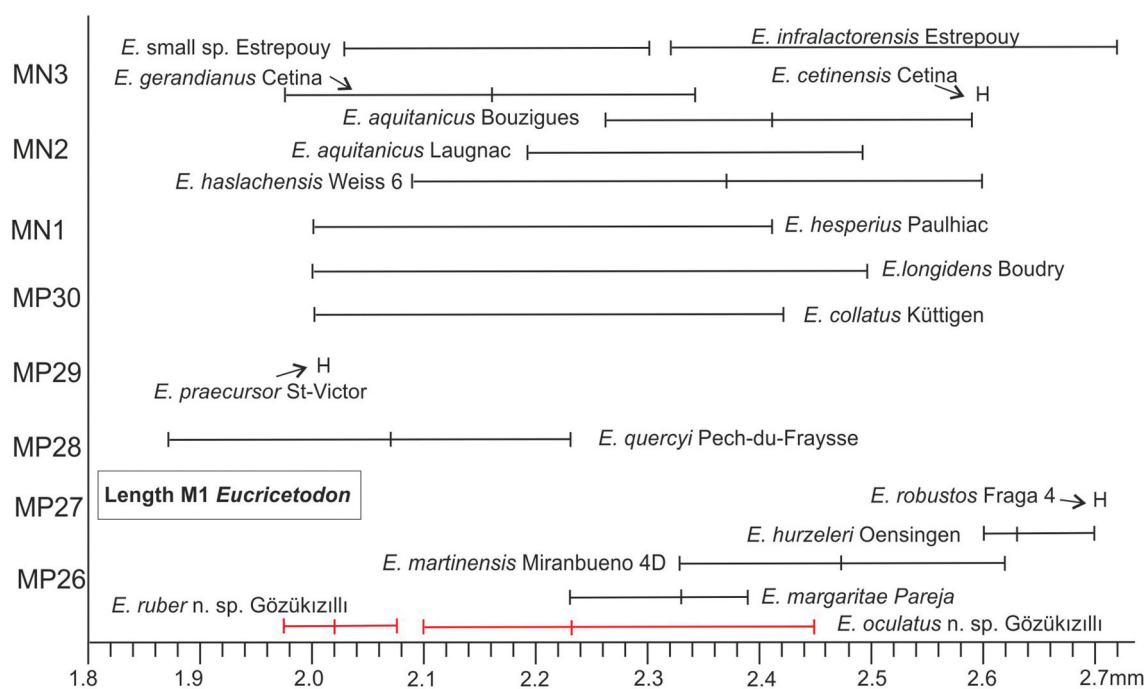


Figure 11. The length of M1 (range and average) of *Eurycetodon* from Gözükkızıllı compared with that of late Oligocene and early Miocene species of *Eurycetodon* from Europe. For Bouzigues see Aguilar (1974); for Cetina (de Aragon) see Daams (1976); for Estrepouy see Huguene & Bulot; for Fraga 4 see Augusti & Arbiol 1989; for Laugnac see Daams (1976); for Mirambueno 4D see Freudenthal (1994). for Oensing, St-Victor-la-Coste and Pech-du-Fraysse see Vianey-Liaud (1972); for Paulhiac, Boudry and Küttigen see Engesser 1985; for Pareja see Daams et al. (1989); for Ulm & Weiss-6 see Dienemann (1987).

absent (Table 7). The curved mure inserts on the proto-loph. One small specimen has no connection between protocone and proto-lophule. Some molars of both species have a faint very low second mesolophule.

m1 (Figure 14c,f,i,l). The cusps are high and pointed, the ridges are low to very low. The pointed anterior side of the molar bears a rounded anteroconid. An anterior cingulid descends at both sides from the anteroconid; the distance between anteroconid and metaconid is short, resulting in a high lingual anterior cingulid. The anterior arm of the protoconid may end free or can be connected low to the anteroconid. The metalophulid I is absent, the metalophulid II and posterior arm of the protoconid form together a “<”-shaped ridge. The hypolophid connects to the anterior arm of the hypoconid or to the ectolophid. The posterolophid comes down from the hypoconid, rounds the posterior side of the molar and ascends the entoconid. Some m1 have a well-developed free-ending posterior arm of the hypoconid. On others this ridge is short or absent. All specimens have a spur on the metaconid, some on the entoconid as well, but these do not develop into a complete ridge. The mesolophid can be absent, rudimentary, of medium length or long, many specimens have a rudimentary ectomesolophid.

m2 (Figure 14b,e,h,k). The ridges of the m2 are better developed and higher than in the m1. Unworn teeth have pointed cusps. The labial anterolophid descends sharply to the antero-labial corner of the protoconid. The lingual anterolophid is short; on slightly worn specimens it is situated at the anterior side of the metaconid. A short and weak metalophulid I connects to the anterior tooth border between the lingual and labial anterolophid. It is absent in one molar of *Eurycetodon ruber*. The posterior arm of the protoconid ends free halfway the lingual tooth border; on some specimens it reaches the posterior side of the metaconid, in particular in the m2 of *E. ruber*. It is absent in one m2 of *E. oculus*. The ectolophid shows a minor thickening, indicating an incipient mesoconid with lingually as well as labially short spurs. Similar to the m1, the posterolophid descends from the hypoconid, rounds the

posterior side of the molar and ascends the entoconid. A hypoconulid is present on some specimens; these have a minuscule remnant of the free-ending posterior hypoconid arm. A very low cingulid is present in the labial sinus of most m2.

m3 (Figure 14a,d,g,j). The m3 of *E. oculus* is long and slender with relatively high and strong ridges. The m3 of *E. ruber* is more reduced. The posterolophid is sturdy, well developed, it rounds the posterior side of the m3, connects to the entoconid, and continues as a lingual ridge along the border to the metaconid. The entoconid of the smaller species, *E. ruber*, is small and incorporated into the posterolophid. In *E. oculus* the ridge along the lingual border is less well-developed and the entoconid stands out as a separate cusp. The anterior side of the m3 is similar to that of the m2. The posterior arm of the protoconid is long, has an oblique posterolingual orientation and ends free. On one specimen of *E. oculus* it touches the lingual border; on one m3 of *E. ruber* it bends forward and connects low to the metaconid. The hypoconid is smaller than the protoconid. The ectolophid is well developed; a hypolophid connects to the entoconid. One m3 of *E. ruber* (Figure 14d) has a low ridge at the posterior side of the metaconid, connecting metalophulid 1 to the posterior arm of the protoconid.

Comparisons and discussion

Eurycetodon oculus is very close in dental morphology to *E. ruber*, but it is slightly larger (Figure 10), the differences in the frequencies of character states are not significant. The m3 of *E. oculus* is long and slender with relatively high and strong ridges. The m3 of *E. ruber* is more reduced. The few molars from Güvendik match with those of *E. ruber* and *E. oculus*. The size of one of the two m3 is closer to those of *E. ruber* (Figure 10), the other is closer to *E. oculus* and so is the single complete M1.

The two Gözükkızıllı species have been compared with Oligocene species that have a bicuspidate anterocone on M1: *Eurycetodon*

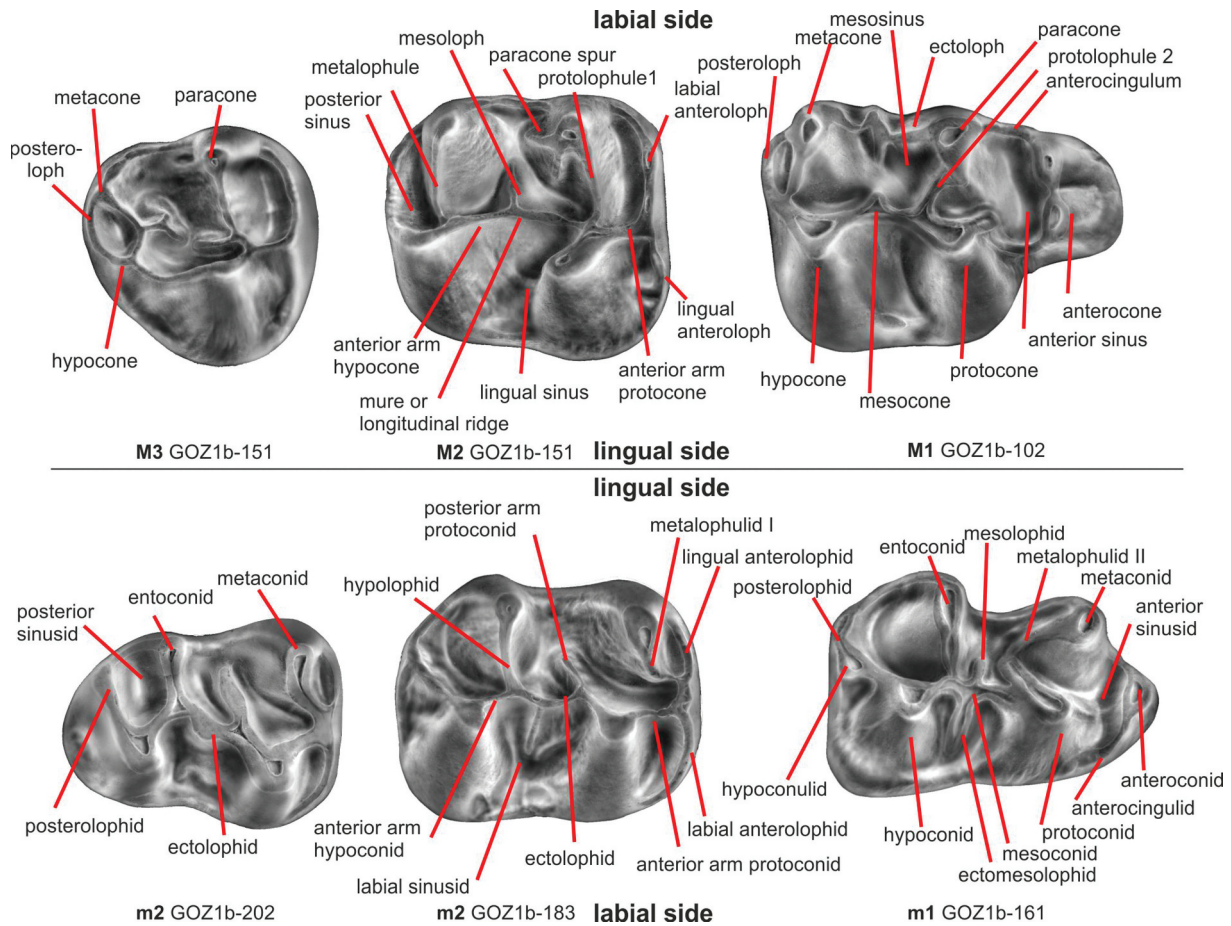


Figure 12. Nomenclature of parts of *Eucricetodon* molars (adapted after Mein and Freudenthal 1971b).

martinensis, *E. margaritae*, *E. huberi* and *E. huerzeleri*. These species form the fairly homogenous *huerzeleri* group of Freudenthal and Martín-Suárez (2016). *E. martinensis* Freudenthal (1994) is larger than *E. ruber* and *E. oculus* (Figure 11), its anterocone in a part of the specimens is bicuspidate. All six M1 of *E. margaritae* from the type locality have an anterocone divided into two cusps; this species shows a complete overlap in size with *Eucricetodon* from Gözükızıllı (Figure 10). All molars except the m3 of *E. margaritae* are comparable in size to *E. oculus*, but the m3 of *E. margaritae* is equal in size to *E. ruber* (Figure 10). The published figures of the M1 of *E. huerzeleri* (Vianey-Liaud 1972; Dienemann 1987) show a bicuspidate anterocone, however, this species is much larger than the two Gözükızıllı species.

Figures 13 and 14 compares the dental morphology of *E. margaritae* with that of *E. ruber* and *E. oculus*. *Eucricetodon margaritae* and the two Gözükızıllı species share the split anterocone on M1, but compared to *E. margaritae*, the anterocone that of *E. ruber* and *E. oculus* is narrower. *E. margaritae* may have a backward spur (an anterolophule) on the anterocone. The metalophule on M1 is directed backwards or absent in *E. ruber* and *E. oculus*, but it is slightly directed forward in *E. margaritae*. The posterior sinus is lingually open in *E. margaritae*, closed in *E. ruber* and *E. oculus*. The M1 of *E. ruber* and *E. oculus* has ectolophes or spurs on paracone/metacone, these are absent in *E. margaritae*. On M2 the lingual sinus of *E. ruber* and *E. oculus* is much stronger curved forward than in *E. margaritae*. On m1 the anterolophulid is missing in *E. ruber* and *E. oculus*, but can be present in *E. margaritae*. The m1 of *E. margaritae* always has the metalophulid I and often the

metalophulid II; in *E. ruber* and *E. oculus*, the metalophid I is always absent.

The early Miocene of Spain and France has yielded some other species that may show a bicuspidate anterocone of the M1, these species are in the *collatus* group of Freudenthal and Martín-Suárez (2016). An assemblage from Cetina de Aragon (Spain) included in *E. gerandianus* by Daams (1976), has a double anterocone in 13 out of 27 M1. It is of similar size as *Eucricetodon* from Gözükızıllı (Figure 11), but differs because of its relatively broad M1 and m1. *E. infralactorensis* from Estrepouy also has a split anterocone, but similar to the material from Cetina de Aragon, its M1 is relatively wide. After compiling the list containing 41 formally described species of *Eucricetodon* species it was a surprise that only *E. margaritae* from the early part of the late Oligocene of Spain resembles the two sibling species from Gözükızıllı in size and morphology.

Table 8 lists the eleven samples for which the microstructure of the lower incisor is available. Early Oligocene *Eucricetodon* samples (included in the *atavus* group) have a type 1 microstructure, the latest Oligocene and Miocene species (included in the *collatus* group) have type 4. In between is a mixed bag from the early part of the late Oligocene with various 'groups' and schmelzmuster types. Much more microstructure data is needed and the allocation to group of the various species needs to be reviewed. But, it seems to us that Gomes Rodrigues et al. (2013) are unduly pessimistic on the merits of the enamel microstructure. The schmelzmuster data adds to our suspicion that *Eucricetodon* is polyphyletic.

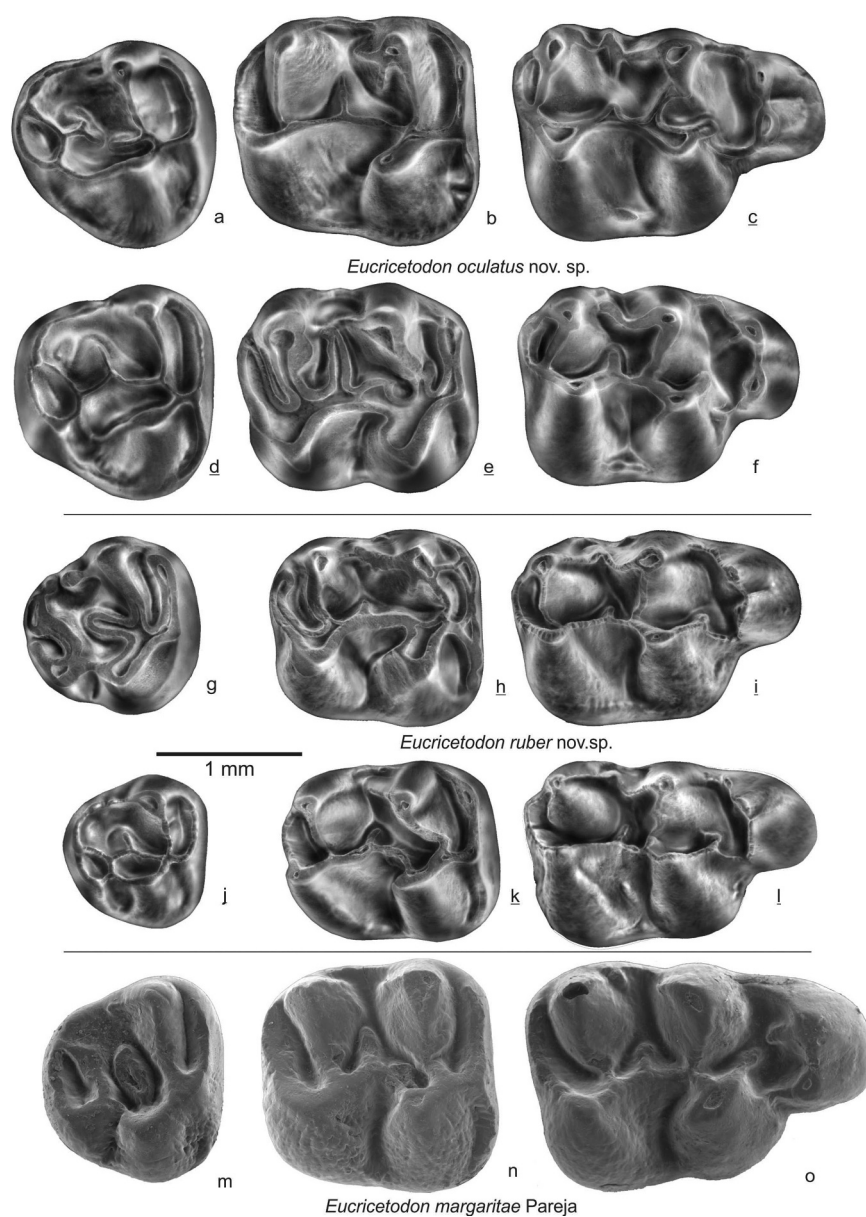


Figure 13. Upper molars of *Eucricetodon oculatus*, *E. ruber* from Gözükızıllı-1 and *E. margaritae* from Pareja (Spain). *E. oculatus*: a GOZ1b-151, b GOZ1b-131, c GOZ1b-102 holotype, d GOZ1b-141, e GOZ1b-121, f GOZ1b-111; *E. ruber*: g GOZ1b-156, h GOZ1b-126, i GOZ1b-106, j GOZ1b-144, k GOZ1b-128, l GOZ1b-105 holotype; *E. margaritae*: m-o.

Suborder Eusciurida Flynn et al., 2019
Family: Gliridae Muirhead, 1819

The three glirid teeth from Gözükızıllı are the oldest record of the family in Anatolia.

Subfamily: Bransatoglirinae Daams and de Bruijn, 1995

Bransatoglis cf. *sjeni* Ünay-Bayraktar, 1989
(Figure 16bc)

Materials & measurements: P4 dext. GOZ1b-258, length 0.64, width 0.86 mm; M1 sin. GOZ1b-255; length 1.34 mm, width 1.45 mm.

Synonymy: *Bransatoglis* cf. *complicatus* (Ünay et al. 2003a)

Description and comparisons

The P4 (Figure 16c) does not have an interdental facet on its anterior side, so this species did not have a DP3. There are narrow notches separating the lingual ends of the proto-loph and posteroloph from the protocone. The long anterior centroloph is not connected to the paracone. The posterior centroloph is absent. There is an indistinct low extra ridge in the valley between the metaloph and the posteroloph.

The occlusal surface of the M1 (Figure 16b) is narrower anteriorly than posteriorly. The endoloph is complete. The anterior centroloph is longer than the posterior one, but does not reach the endoloph. There is a well-developed extra-ridge between the proto-loph and the anterior centroloph and an indistinct incipient extra-ridge between the proto-loph and the anteroloph.

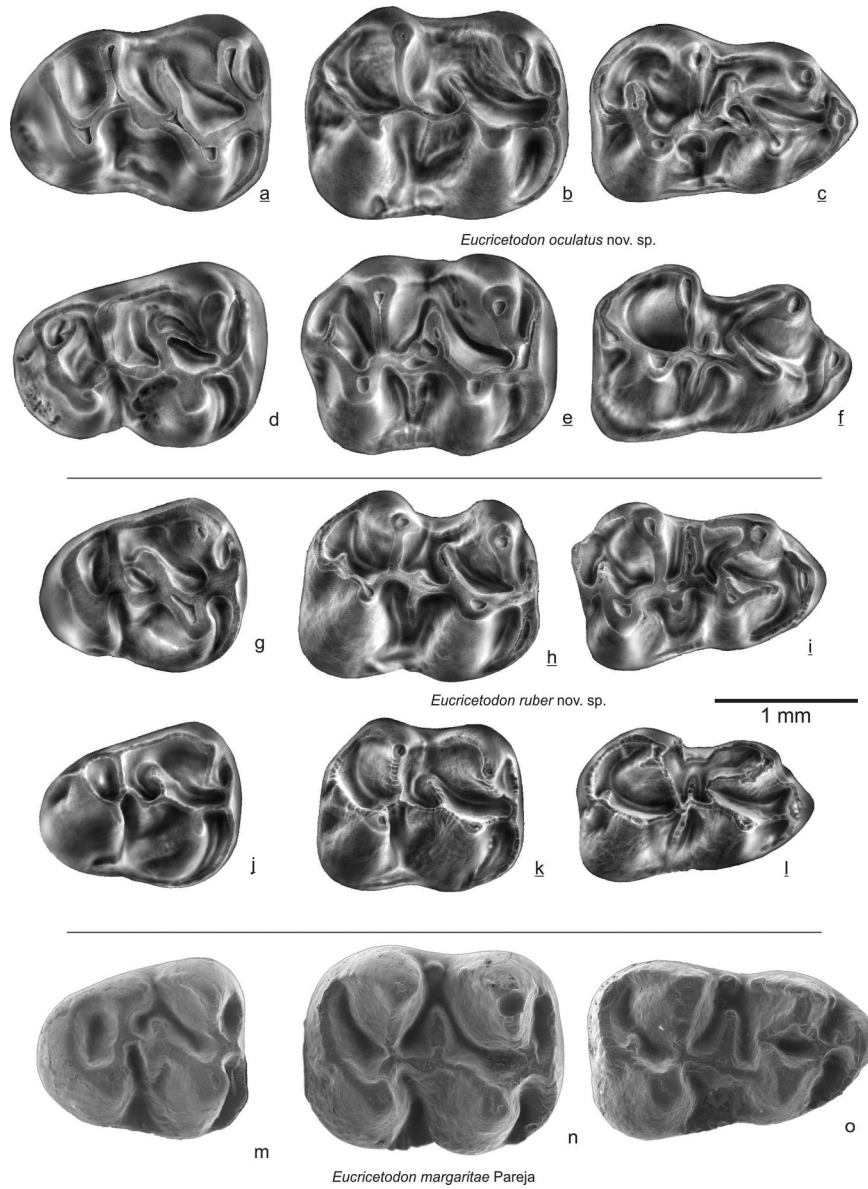


Figure 14. Lower molars of *Eucricetodon oculatus*, *Eucricetodon oculatus*, *E. ruber* from Gözükızıllı-1 *E. ruber* from Gözükızıllı-1 and *E. margaritae* from Pareja (Spain). *E. oculatus*: a GOZ1b-202, b GOZ1b-183, c GOZ1b-162, d GOZ1b-211, e GOZ1b-182, f GOZ1b-161; *E. ruber*: g GOZ1b-216, h GOZ1b-186, i GOZ1b-166, j GOZ1b-204, k GOZ1b-188, l GOZ1b-167; *E. margaritae*: m-o.

Table 5. Measurements of *Eucricetodon ruber* nov. sp. from Gözükızıllı-1 and Güvendik.

<i>E. ruber</i>	Length					Width				
	min	max	mean	N	SD	min	max	mean	N	SD
Gözükızıllı-1										
M1	1.92	2.07	2.016	16	0.044	1.30	1.45	1.388	17	0.044
M2	1.37	1.58	1.479	20	0.062	1.33	1.50	1.419	20	0.049
M3	0.97	1.22	1.124	18	0.069	1.18	1.30	1.244	18	0.037
m1	1.60	1.87	1.720	15	0.072	1.08	1.24	1.157	15	0.054
m2	1.42	1.69	1.561	12	0.078	1.24	1.42	1.335	12	0.052
m3	1.37	1.51	1.456	8	0.045	1.17	1.31	1.230	8	0.047
Güvendik										
m1	–	–	–	–	–	–	–	1.140	1	–
m3	–	–	1.600	1	–	–	–	1.220	1	–

Table 6. Measurements of *Eucricetodon oculatus* nov. sp. from Gözükızıllı-1 and Güvendik.

<i>E. oculatus</i>	Length					Width				
	min	max	mean	N	SD	min	max	mean	N	SD
Gözükızıllı-1										
M1	2.10	2.45	2.228	4	0.155	1.48	1.66	1.546	8	0.062
M2	1.52	1.76	1.647	6	0.090	1.57	1.71	1.638	5	0.050
M3	1.32	1.42	1.374	5	0.046	1.38	1.55	1.442	5	0.066
m1	1.87	1.90	1.885	2	0.021	1.30	1.31	1.305	2	0.007
m2	1.68	1.87	1.774	5	0.07	1.37	1.5	1.45	5	0.051
m3	1.74	1.93	1.812	5	0.073	1.36	1.48	1.430	5	0.046
Güvendik										
M1	–	–	2.240	1	–	–	–	1.430	2	–
m3	1.66	1.67	1.635	2	–	1.22	1.38	1.300	2	–

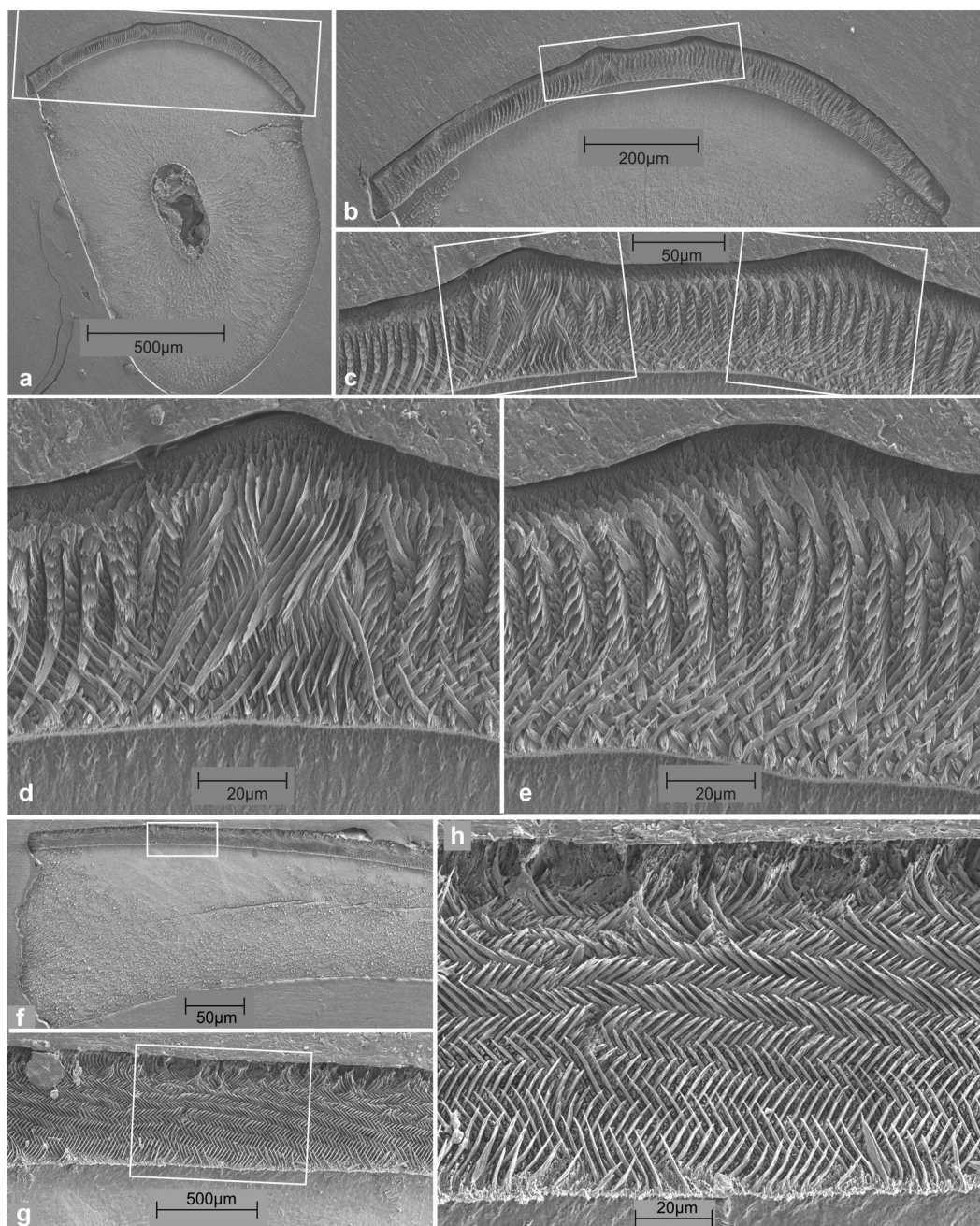


Figure 15. Transverse sections (a-e) and sagittal sections (f-h) of the lower incisor of *Eucricetodon* from Gözükızıllı-1.

The two *Bransatoglis* cheek teeth from Gözükızıllı-1 are the same size as those of *B. sjeni* from Kocayarma (Thrace basin; Ünay-Bayraktar 1989). The P4 from Gözükızıllı-1 differs from the type material of that species in lacking the posterior centroloph. The endoloph of the M1 from Gözükızıllı-1 is complete whereas the lingual ends of the anteroloph and posteroloph are separated from the protocone by a notch on the specimens from Kocayarma. The morphology of the specimens from Gözükızıllı is interpreted as more advanced than the material from Kocayarma.

Subfamily indet.

cf. *Peridyromys*/*Microdyromys* sp. (Figure 16d)

Material and measurements: m1sin. GOZ1b-258; length 0.90 mm, width 0.82 mm.

Synonymy: *Glirulus* sp. (Ünay et al. 2003a).

Description and comparisons

This small m1 probably has a somewhat aberrant morphology in showing a connection between the incomplete metalophid

Table 7. Character states in upper molars of *Eucricetodon ruber* nov. sp. and *E. oculatus* nov. sp. from Gözükızıllı-1.

	M1		M2		M3	
	<i>E. ruber</i>	<i>E. oculatus</i>	<i>E. ruber</i>	<i>E. oculatus</i>	<i>E. ruber</i>	<i>E. oculatus</i>
Anterior arm protocone to paracone	5/19	2/6	–	–	–	–
Anterior arm protocone free ending	14/19	4/6	–	–	–	–
Mesoloph absent to very small	9/19	2/7	7/18	1/6	5/20	0/2
Mesoloph medium long	8/19	4/7	12/8	2/6	13/20	1/2
Mesoloph long	2/19	1/7	1/19	3/6	2/20	1/2
Para- and metacone spurs absent	4/17	2/8	7/19	4/6	–	–
Para- and metacone spurs present	5/17	2/8	11/19	2/6	–	–
Ectolophs present	8/17	4/8	2/19	0/6	–	–
Metaloph interrupted	4/17	1/7	–	–	–	–
Metaloph complete	13/17	6/7	–	–	–	–
Sinus incompletely closed	–	–	–	–	11/18	4/5
Sinus closed	–	–	–	–	7/18	1/5

Table 8. Schmelzmuster types of lower incisors in *Eucricetodon* samples. The allocation to group (grp) is after Freudenthal and Martín-Suárez (2016).

Species, locality, (group)	Type	Age	References
<i>E. infralactorensis</i> , Estrepouy, (collatus grp)	Type 4	MN3, early Mioc.	Kalthoff 2000
<i>E. gerandianus</i> , La Chauz 7, (collatus grp)	Type 4	MN2a, early Mioc.	Kalthoff 2000
<i>E. longidens</i> , Coderet, (collatus grp)	Type 4	MP30, late Oligoc.	Kalthoff 2000
<i>E. liber</i> , Herrlingen 9, (dubius grp)	Type 4	MP29, late Oligoc.	Kalthoff 2000
<i>E. dubius</i> , Herrlingen 8, (dubius grp)	Type 4	MP28, late Oligoc.	Kalthoff 2000
<i>Eucricetodon</i> sp., Ugljevik 10	Type 10	MP 27–28, late Oligoc.	van de Weerd et al. in prep.
<i>E. huerzeleri</i> , Mas de Pauffié, (huerz. grp)	Type 1	MP26, late Oligoc.	Gomes Rodrigues et al. 2013
<i>Eucricetodon</i> , Gözükızıllı-1 10	Type 10	MP25–26, late Oligoc.	This paper
<i>E. cf. huberi</i> , Belgaric-1, (huerz. grp)	Type 8	MP25, late Oligoc.	Gomes Rodrigues et al. 2013
<i>E. atavus</i> , Itardies, (Atavocr. grp)	Type 1	MP23, early Oligoc.	Kalthoff 2000, Gomes Rodrigues et al. 2013
<i>E. aff. nanus</i> , Cavalé, (Atavocr. grp)	Type 1	MP22, early Oligoc.	Gomes Rodrigues et al. 2013

and the centrolophid. This configuration is unusual but the tooth has the common basic dental pattern of a glirid m1 with a rather long centrolophid, an anterior extra-ridge and a posterior extra-ridge. This basic morphology and its small size are shared by a number of species of the genera *Peridyromys* and *Microdyromys*. This small m1 shows the presence of a second genus and species of Gliridae in Gözükızıllı and documents fauna exchange between Europe and Anatolia.

cf. *Dipodidae* gen. et sp. indet.
(Figure 16a)

Materials and measurements: m3sin GOZ1b-259, length 0.89 mm, width 0.72 mm and m3 dex GOZ1b-260, length 0.87 mm, width 0.72 mm.

Remarks

The two m3 with a cricetid pattern do not show characteristic features to ascertain whether they represent a cricetid or a dipodid. Possible options in this size group are in the pseudocricetodontinae and the dipodines. The only records of the Pseudocricetodontinae in the Palaeogene of Anatolia are from Yeniköy and Süngülü (de Bruijn et al. 2003). Since Dipodidae occur in several late Oligocene assemblages from the area we tentatively allocate the two m3 to cf. *Dipodidae* gen. et sp. indet.

Biogeography and Chronology

Table 9 shows the distribution and numbers of first and second molars and the minimum numbers of individuals in the two Gözükızıllı horizons. Striking is the relatively low number of species considering the large samples that have been taken. *Daxneria* teeth are rather fragile and break easily during the washing and screening process. The minimum number of individuals of *Daxneria* is based on four right m1 in Gözükızıllı-1a and three left d4 in Gözükızıllı-1b. *Daxneria* and *Sayimys* are Asian elements, the glirids *Bransatoglis* and cf. *Peridyromys/Microdyromys* have an European origin.

Figure 17 summarises the chronostratigraphic position of Gözükızıllı with respect to the Eocene and Oligocene rodent faunas described from the wider region, including the Balkans, Thrace basin, Anatolian basins, Georgia, Kazakhstan and Pakistan. *Eucricetodon* is the first cricetid to arrive in Central and Western Europe, marking the ‘Grande Coupure’. It is present in Anatolia in Süngülü (latest Eocene), Yeniköy and Gözükızıllı-1. The two species of *Eucricetodon* from Gözükızıllı resemble *E. margaritae* from the late Oligocene of Spain (MP26). Krijgsman et al. (1996) suggested that the sites in Anatolia with *Eucricetodon* are older than the faunas dominated by *Meteamys* and *Muhsinia* (Inkonak, Kargı), giving the Gözükızıllı-1 fauna a range between approx. 29 and 26 Ma (Figure 17). Métais et al. (2016) presented a preliminary age of approx. 28 Ma for Gözükızıllı-2 and –3 based on unpublished magneto-stratigraphic data. If correct, Gözükızıllı-1 (stratigraphically ~35 m above Gözükızıllı-2) could be about 28–27 Ma.

The faunas from Yeniköy and Gözükızıllı have a low diversity. Ünay et al. (2003a) therefore suggested the possibility of insularity for Anatolia during the Oligocene. Palaeogeographic maps lend some support for this hypothesis, but the published maps covering the Oligocene differ in details. Jones (1999, Figures 14.6–14.8) assumes a marine connection between the Indian Ocean and the Caspian region, thus isolating Anatolia from the east. However, Meulenkamp and Sissingh (2003, Figure 5) and Métais et al. (2015) showed a corridor between Anatolia and the Iranian block. Whatever the geography may have been, migration was possible, perhaps the corridor area functioned as a filter-bridge. A marine barrier existed between Anatolia and the Thrace basin during the late Eocene-early Oligocene (Meulenkamp and Sissingh 2003, Figure 5) explaining the large difference between the Oligocene rodent faunas from the Thrace basin and Anatolia. This barrier disappeared after 30 Ma (Okay et al. 2019), but the difference between the rodent faunas from the Thrace basin and Anatolian persisted for some time. During the late Oligocene high-diversity faunas with ‘balanced pan-Anatolian character’ appear in Inkonak and Kargı (Ünay et al. 2003a).

Only a few Eocene and early Oligocene rodent faunas are known from the great swathe of country formed by the southern rim of Asia, the Indian continental block, Asia Minor and areas in between (a palaeogeographic map is Figure 8 in Gomes Rodrigues et al. 2012). The age of most cluster near 29–28 Ma (Figure 17).

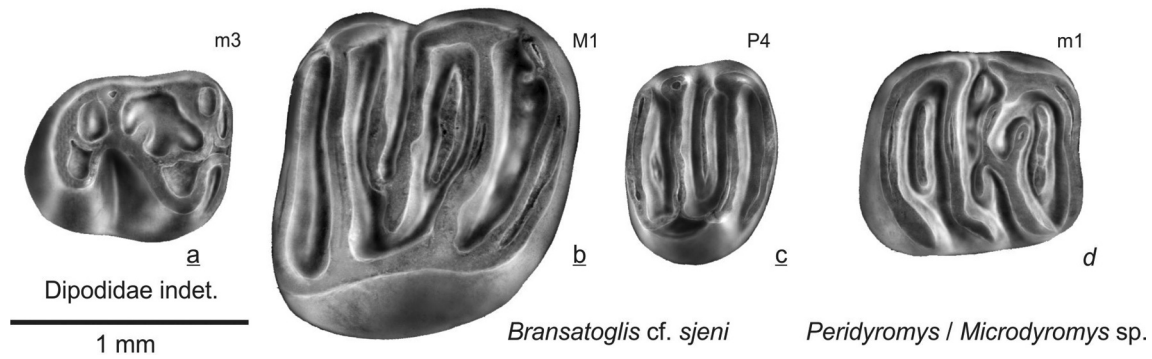


Figure 16. The Dipodidae and Gliridae from Gözükişilli: a Dipodidae gen. et sp. indet. GOZ1b-260; *Bransatoglis cf. sjeni*: b GOZ1b-255, c GOZ1b-258; *Peridyromys* or *Microdyromys*: d GOZ1b-257.

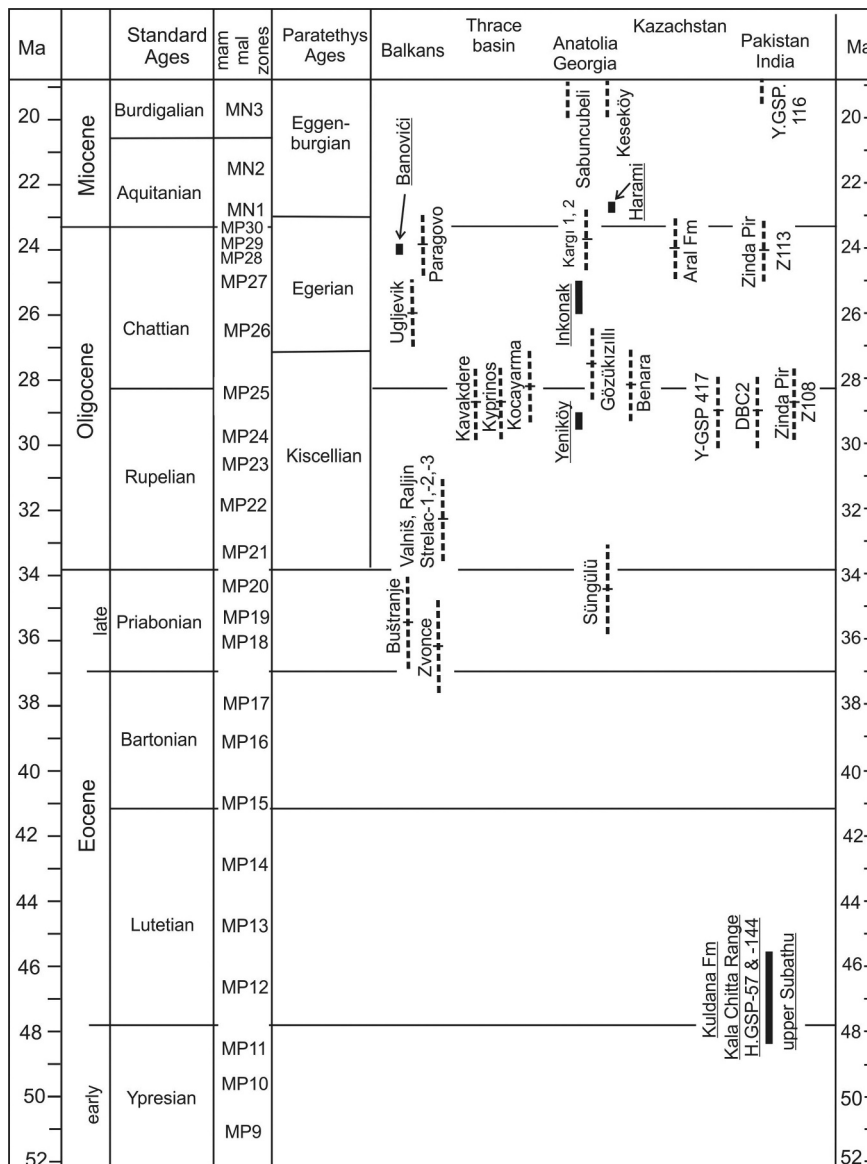


Figure 17. Chronostratigraphic scheme of Palaeogene faunas from Anatolia and the wider region of the Balkans and Southern Asia. Broken lines indicate uncertainty ranges, duration of these are arbitrarily set at 8% of the estimated age. Locations with a magneto-stratigraphic or chronostratigraphic age estimate have a solid range and names are underlined. References on the sites are: Aral Fm (Lucas et al. 1998; Bendukidze et al. 2009), Banovice (de Bruijn et al. 2013), Benara (Métais et al. 2016), Buštranje, Strelac, Valniş, Zvonce (de Bruijn et al. 2018ab), Harami, Inkonak, Kargı, Yeniköy, Keseköy (Krijgsman et al. 1996; Ünay et al. 2003a), Kala Chitta Range/upper Subathu Grp. (Hussain et al. 1978; Gingerich 2003), Kavakdere, Kocayarma (Ünay-Bayraktar 1989), Kyprinos (Doukas and Theodoropoulos 1999), Paragovo, Ugljevik (Marković et al. 2019; van de Weerd et al. in prep), Sabuncubeli (de Bruijn et al. 2006), Süngülü (de Bruijn et al. 2003), Y-GSP417, DBC2, Z108 (Métais et al. 2009), Y-GSP116 (Hartman et al. 2019), Z113 (Lindsay and Flynn 2016).

Table 9. Composition of the faunas found in Gözükızılı-1a, -1b and Güvendik. Shown are the total number of first and second molars (M1/2) and the minimum number of individuals (N) as determined from the largest number of one of the dental elements. The cross indicates that no first or second molar has been found, but that the taxon is represented by another dental element.

	GOZ-1a		GOZ-1b		Güvendik	
	M1/2	N	M1/2	N	M1/2	N
<i>Daxneria fragilis</i>	9	4	7	3		
<i>Sayimys</i> sp.			2	1		
<i>Eucrietodon</i>	28	7	60	10	3	2
<i>Bransatoglis</i> cf. <i>sjeni</i>			1	1		
<i>Peridyromys</i> / <i>Microdyromys</i> sp.			1	1		
cf. <i>Dipodidae</i> gen. et sp. indet.			X	1		
totals	37	11	71	17	3	2

Baluchimyines have been found in most of these, in the larger assemblages of the late-early Oligocene of Pakistan with up to six species. They thus form an important part of the rodent faunas in this poorly sampled region. However, baluchimyines are completely absent in the late Eocene and early Oligocene faunas of the Balkans. Baluchimyines are believed to have evolved from an Eocene ancestor close to the chapattimyids found in the Kuldana Formation (Flynn 1986; Marivaux and Boivin 2019), but an enormous gap in the fossil record separate these groups (Figure 17).

The three glirid teeth from Gözükızılı are the oldest record of the family from Anatolia. The glirids (being of European origin) in Gözükızılı show that migration from Europe to Anatolia was possible. This seems supported by the similarity of Gözükızılı *Eucrietodon* to a late Oligocene Spanish species.

Antoine et al. (2008) and Métais et al. (2016) reported on the age of the finds of larger mammals in Gözükızılı-2 and -3 in the lower Kızılırmak Formation. In contrast to the rodent faunas, Antoine et al. (op. cit.) and Métais et al. (op. cit.) do not see evidence for geographic isolation in the larger mammals. They indicate that the large mammals are late Oligocene, probably slightly younger than those of Benara (Georgia). Gabunia and Bendukidze (1990) illustrated the cricetids *Eucrietodon*, *Paracricetodon*, *Pseudocricetodon* and the glirid *Peridyromys* from Benara with simple line drawings. Comparison with good illustrations confirm their identifications. The worn half molar of Figure 3 in Gabunia and Bendukidze may be included in the baluchimyine *Lindsaya*. The Benara rodent faunule may thus be close in age to those from Gözükızılı and the Thrace basin (Ünay-Bayraktar 1989).

Conclusions

The Gözükızılı-1 rodent faunas are of low diversity and contain Asian and European elements. *Eucrietodon* is dominant, two new species *E. ruber* and *E. oculatus* are described. These are morphologically very similar, but differ in size. The two *Eucrietodon* species are morphologically close to the late Oligocene *E. margaritae* from Spain. The new genus *Daxneria*, an Asian element in the assemblage, is well represented in Gözükızılı-1. It is included in the Baluchimyinae, a subfamily known from the latest Eocene of Thailand, the “middle” Oligocene of the Indian sub-continent and the latest Eocene of Süngülu (Asia Minor). *Daxneria fragilis* has a specialised dentition with high-crowned teeth, strong roots and thin enamel. Similar to several other baluchimyine genera *Daxneria fragilis* has no permanent fourth premolar, but retains its deciduous premolar. The M3 of *Daxneria* resembles those of *Ottomania* and *Lophibaluchia* in having a reduced posterior part. The ctenodactyl *Sayimys* sp. is another Asian

element in Gözükızılı-1. It is the oldest record of this genus so far. The two glirid species in Gözükızılı-1 are European elements. The possible dipodid completes the faunal list. Our age estimate of this fauna is 29–26 Ma, that is in the early part of the late Oligocene.

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