A rodent assemblage from the Eo/Oligocene boundary interval near Süngülü, Lesser Caucasus, Turkey

Una asociación de roedores del tránsito Eoceno/Oligoceno próxima a Süngülü, Lesser Caucasus, Turkey

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Abstract: The assemblage of rodents from Süngülü that will be described below contains two genera and species of Ctenodactylidae, one genus and species of Dipodidae and seven genera representing eight species of Muridae. Three genera and seven species are new. The composition of the assemblage shows that this rodent fauna from Anatolia differs in many respects from that of Europe and Central Asia and is therefore endemic. The age as inferred from the fauna is Latest Eocene or Earliest Oligocene.
Key words: Rodentia, Eo/Oligocene, Lesser Caucasus, West Asia.

Resumen: La asociación de roedores de Süngülü, que será descrita a continuación, contiene dos géneros y especies de Ctenodactylidae, un género y especie de Dipodidae y siete géneros representando ocho especies de Muridae. Tres de los géneros y siete especies son nuevos. La composición de la asociación muestra que esta fauna de roedores de Anatolia difiere en muchos aspectos de las de Europa y Asia central y es por tanto endémica. La edad, inferida a partir de la fauna, es final del Eoceno Superior o principio del Oligoceno inferior.
Palabras clave: Rodentia, Eoceno/Oligoceno, Cáucaso, Turquía

INTRODUCTION

The fossiliferous levels that have yielded the rodent assemblage that will be described below are exposed near the top of a ± 45 m thick section of fluvio-lacustrine deposits situated at about two kilometres north east of the village of Süngülü (fig.1). The contact between this tectonically rather undisturbed south dipping section and the underlying Eocene volcano-clastic rocks cannot be observed because of landslides. The mammal remains have been collected from two subsequent beds: A ± 40 cm thick tuffite with operculae of gastropods, and the overlying ± 30 cm of white silty limestone with silicified nodules. Sample A, taken from the steep west bank of the brook, contains fossils from both levels because these could not be kept separate while undercutting the bank. Samples B and C were taken from the lower and upper fossiliferous bed respectively from a locality on the east bank that is situated at about 60 m east of the original site (A) discovered by the second author (E. Ünay) during the field work in the summer of 1996. The fossil con-

tent and composition of the samples A, B and C is very similar (fig. 2), so the three assemblages, each derived from about 3,5 tons of sediment, will be treated as one sample.

GEOLOGICAL SETTING

The geology of the Lesser Caucasus has been intensively studied during the last decade because of the economical interest of the lignite occurrences in the Oligo/Miocene deposits of the Vale (Georgia) and Balkaya (Oltu basin, Turkey) areas (YILMAZ *et al.*, 1997, ÇAKMAK & ÜNVER, 1994, KOCYIGIT *et al.,* 2001). The belt of the Lesser Caucasus has been formed in a N/S compressional regime that caused intensive large- scale E/W trending folds and NE/SW trending faults. The north dipping overthrusts separate tectonic units that mainly consist of Eocene and older volcanoclastics and shallow marine deposits. The fault zones between these tectonic units cannot be followed at the sur-

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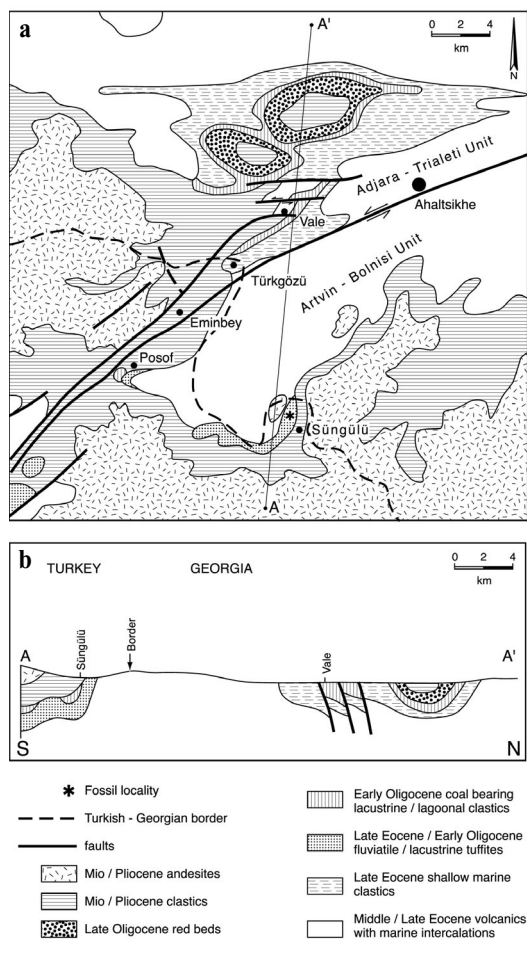[4] Cumhuriyet University, Department of Geology, 58140 Sivas, Turkey

Figure 1.- a. Schematical geological map of the Posov-Vale area after YILMAZ et al. (1997) giving the geographical and stratigraphical position of the fossiliferous bed north of Süngülü. b. Cross section A A¹ after YILMAZ et al. (1997)

Figura 1.- a. Mapa geológico esquemático del área de Posov-Vale, según YILMAZ et al. (1997), indicando la posición geográfica y estratigráfica del nivel fosilífero, al Norte de Süngülü. b. Perfil estratigráfico A A¹, según YILMAZ et al. (1997)

face because of a thick cover of andesites of Mio/Pliocene age. The Oligo/Miocene continental sediments that overly shallow marine Eocene deposits and underlie the andesites are mainly preserved in synclines along the edges of the tectonic units. The lower contact of these continental sections is sometimes concordant (Vale), sometimes discordant (Balkaya), and the sections show great differences in lithology and thickness, which suggests that they were deposited in different basins of tectonic origin (YILMAZ et al. 1997, 2000). Straightforward lithostratigraphical correlation of the different occurrences is therefore impossible. Our

age estimates are based on only three sites producing fossil mammalian remains: The clastics overlying the formation containing the Vale lignite contain in Benara (Ahaltsikhe basin) an assemblage of Late Oligocene age (RUSSELL & ZHAI, 1987, GABUNIA & BENDUKIDZE, 1990), the Balkaya coal has yielded *Spanocricetodon* suggesting a latest Oligocene or earliest Miocene age and the fluvio-lacustrine deposits of Süngülü containing an assemblage of mammalian remains considered to be of latest Eocene or earliest Oligocene age (see below) suggest that the coal occurrences in the area have different ages and were not formed in the same basin.

The assemblage of rodents from the Eo/Oligocene boundary interval of Süngülü is of special interest because it provides the first information on small mammals from this time-slice in west Asia. The nearest occurrences of rodents of similar age are from the Lignite-sandstone Formation of the Ergene basin, Turkey (ÜNAY, 1988), the base of the Ashawq Formation in the Dhofar area, Sultanate of Oman (THOMAS et al., 1999), the lower part of the Jebel el Qatrani Formation, Fayum basin, Egypt (SIMONS, 1968, WOOD, 1968) and the Zaysan basin, E. Kazakhstan. Among these occurrences only the material from the Ergene and the Fayum basins has been studied in sufficient detail to allow a judgement on faunal similarity. The assemblage from the Fayum and Süngülü do not share one single genus, so there must have been a barrier that prevented fauna exchange between the Afro-Arabian and the Anatolian-Pontian landmasses, a configuration that is in accord with the paleogeographical reconstruction of POPOV (2001). Although the rodent fauna of the Eo/Oligocene boundary interval of central Asia is incompletely known it seems to share two genera with the Süngülü assemblage so it seems there has been limited fauna exchange between the two areas during the Late Eocene. The assemblage from Kocayarma (ÜNAY, 1988) in the Ergene basin shows the best fit with that of Süngülü, sharing five genera. In spite of this similarity the groups that are considered to have originated in Europe (Pseudosciuridae, Gliridae) are absent in the assemblage from the Lesser Caucasus,

TAXONOMY

METHODS

The material that will be described below is housed in the collections of the MTA (Mineral Research and Exploration General Directorate), Ankara, Turkey. A selected set of casts is kept in the Faculty of Earth Sciences of the University of Utrecht.

The relative frequency of character variants is given in the descriptions as the quotient of the number of specimens showing a particular character and the number of observations, so 3/5 means that three specimens out of the five available have the feature described.

Samples	I		II	III									N
Süngülü A	1	2	3	4	5	6	7	8	9	10			159
Süngülü B	1	2	3	4	5	6	7	8	9	10			120
Süngülü C	1		3	4		6	7	8	9	10			306

10   20   30   40   50   60   70   80   90   100%

☰ = Ctenodactylidae
▭ = Dipodidae
▨ = Muridae

1. *Ottomania proavita*
2. *Confiniummys sidiki*
3. *Heosminthus minutus*
4. *Paracricetodon wentgesi*
5. *Witenia fusca*

6. *Witenia flava*
7. *Edirnella kempeni*
8. *Pseudocricetodon* aff. *montalbanensis*
9. *Eucricetodon* (*Atavocricetodon*) *kurthi*
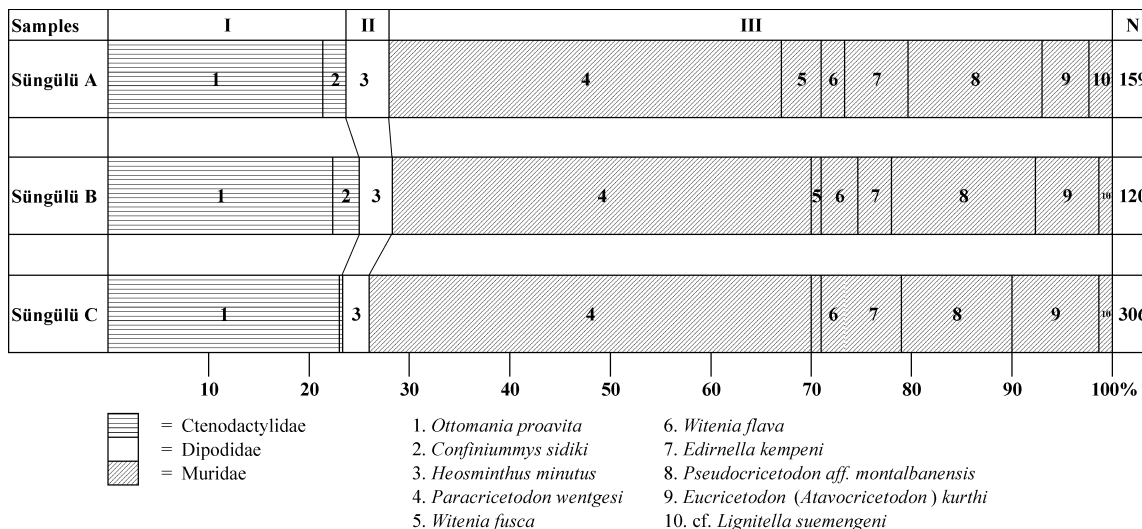10. cf. *Lignitella suemengeni*

Figure 2.- Diagram showing the relative abundance in percentages of the families and species of rodents in the three assemblages from Süngülü. N is the number of complete M1 + M2 + m1 + m2 per sample. In those cases where a species is represented by less than two percent it has been entered as if present in two percent in order to accommodate the number.
Figura 2.- Diagrama mostrando la abundancia relativa, en porcentajes, de las familias y especies de roedores en las tres asociaciones de Süngülü. N es el número de M1 + M2 + m1 + m2 completos por muestra. En el caso en el que una especie no supere el dos por ciento en ninguna de las muestras, ésta ha sido representada como teniendo un dos por ciento, con el fin de poder introducir el número correspondiente.

The measurments of the cheek teeth are given in 0.1mm units. The teeth figured on plates 1-6 are all times16 and from the left side. If the original is from the right side its number on the plate has been underlined.

The nomenclature of cusps and lophs of cheek teeth remains problematical because similar structures occurring in different (super) families may have different origins. We follow FLYNN *et al.,* 1986 in using the term "mesolophule" for the central crest of the upper molars of some baluchimyines and ctenodactilds because we agree that this crest is not homologous with the mesoloph of other rodents. For the second loph of the lower molars of ctenodactylids we prefer the term posterior arm of the protoconid over metalophulid 2 even if this crest connects the posterior side of the protoconid with the posterior side of the metaconid.

SUPERFAMILY CTENODACTYLOIDEA

Introduction: The Paleogene record of the Ctenodactyloidea in Asia has grown explosively during the last two decades showing that the group was already quite diverse in Eocene times. Several major radiation's seem to have occurred in geographically separate areas during different periods, which in some cases led to the development of similar dental patterns in different evolutionary lineages. This circumstance makes identifications based on a few isolated teeth unreliable even at the family level. The quality of

the type material is particularly important for Ctenodactyloidea because the degree of molarisation of the premolars and the dental formula play a decisive role for identification.

While reviewing the literature we counted thirty-nine paleogene genera (including fifteen genera of uncertain status, but excluding obvious synonyms) that we think represent the superfamily. MCKENNA & BELL, 1997 list thirty-three Paleogene genera that we think should be included into the Ctenodactyloidea, a superfamily that they do not recognize. This example shows that there is no consensus among students of the group at the superfamily, family and generic levels. At this stage it is very difficult, if not impossible, to distinguish some of the lophodont genera of the sciurognath Ctenodactyloidea from some of the hystricognath Phiomyidae on the basis of isolated cheek teeth.

In order to solve the taxonomical problems outlined above it would be necessary to restudy all the Asiatic Paleogene type material and to collect more material from many type localities, a task that is obviously far beyond our financial means as well as the scope of this paper that is concerned with the description of the first Eo/Oligocene rodent assemblage to become known from western Asia. However, a general frame is required before we embark on the description of yet new Ctenodactylidae, so we decided to follow DAWSON *et al.,* 1984, recognizing the families Cocomyidae DAWSON *et al,* 1984, Yuomyidae,

DAWSON *et al.,* 1984 and Ctenodactylidae ZITTEL, 1893, although the content of these families in terms of genera may differ. Moreover, we consider the Chapattimyidae HUSSAIN *et al.,* 1978 and the Yuomyidae, two families that show an increase of the degree of molarisation of the premolars through time, as different entities, the Baluchimyinae FLYNN *et al.,* 1986 are regarded as derived Chapattimyidae that remained restricted to South East Asia.

Family Ctenodactylidae ZITTEL, 1893
Genus *Ottomania* n. gen.

Derivatio nominis: Named after the Ottoman Empire.
Type species: Ottomania proavita n. sp.
 Diagnosis: *Ottomania proavita* is a ctenodactylid of medium size with M1 and M2 with five crests and lower molars with four crests and three roots. Cheek teeth brachyodont. Protocone and hypocone sub-equal and connected by a low entoloph in the D4 and M1, rarely so in the M2 and M3. Anteroloph much lower than the protoloph in the D4 and M1, but successively more equal in height from M1 through M3. Permanent premolars non-molariform and very small. P4 with two cusps and one root, p4 with three cusps (lacking the hypoconid and the entoconid) and two roots. D3 with two cusps that are anteriorly and posteriorly connected by short crests. D4 very similar to the M1 in morphology and size, but more bunodont. The dental pattern of the molars becomes more lophodont, and overall less primitive, from D4/d4 through M3/m3.
Differential diagnosis: Among the Paleogene Ctenodactylidae from Central Asia *Protataromys* TONG, 1997 from the Sharamurunian (Middle Eocene) resembles *Ottomania* most in the height, shape and relative size of the molars. The dental pattern of the lower molars of these genera is quite similar, but the upper molars of *Protataromys* have a more primitive pattern in that the metaloph is directed towards the protocone and that the mesolophule is missing. Moreover, the premolars of *Protataromys* are more molariform than in *Ottomania*.

Structurally the poorly documented genus P*rotataromys* is a potential ancestor for *Ottomania*, supposing a trend towards demolarisation of the premolars.The type species *P. mianchiensis* is based on eight isolated teeth and *P. yuanquensis* TONG, 1997, which seems to be a junior synonym of *mianchiensi*s, is based on three teeth only. The genus *Anadianomys* TONG, 1997, type species *Anadianomys declivis* TONG, 1997 from the Sharamurunian seems to have been incorrectly allocated to the Yuomyidae because the molariform tooth described as P4 (TONG, 1997, fig. 51C) seems, judging by the figure, to be a D4. If this interpretation is correct *Anadianomys* probably becomes a junior synonym of *Protataromys* because the dental pattern of the molars of these genera is very similar.

The molar pattern that matches that of the type species of *Ottomania* best is that of the baluchimyines *Hodsahibia azrae* FLYNN *et al.,* 1986 and *H. kayi* FLYNN & CHEEMA, 1994.

The M2 of the species of the two genera are virtually indistinguishable. However, the premolars are molariform in *Hodsahibia,* but not molariform at all in *Ottomania*. *Ottomania* is a good structural ancestor for *Hodsahibia* supposing the lineage would have a strong trend towards molarisation of the premolars.

Ottomania proavita n. sp.
(Plate 1, figs. 1-11. Plate 2, figs. 1-9 and text fig. 3)

Derivatio nominis: Proavitus meaning hereditary suggests that this species is structurally a good ancestor for a number of later species in the *Tataromys* group.
Type locality: Süngülü C.
Holotype: Fragment of a maxilla with D4-M2, Süngülü C, nr. 552, (fig 3).
Type level: Eo/Oligocene boundary interval
Diagnosis: As for the genus *Ottomania*.
Differential diagnosis: As for the genus *Ottomania*.

Material and measurements (samples A, B and C)

	Length		Width		
	Range	Mean	N	Mean	Range
D3	9,6 – 12,7	11,3	4	13,1	10,6 – 15,3
D4	15,8 – 19,4	18,14	24/30	21,19	19,4 – 22,6
P4	11,0 – 13,3	12,19	38/37	13,43	12,6 – 15,2
M1	17,4 – 21,6	19,29	38/37	22,34	20,9 – 24,9
M2	18,8 – 22,5	20,66	35/32	24,14	20,9 – 25,3
M3	18,2 – 22,0	19,49	21/21	22,66	20,6 – 24,2
d4	22,3 – 24,5	23,64	18/20	15,67	14,9 – 16,8
p4	11,2 – 11,6	11,4	2	13,6	13,2 – 13,9
m1	20,2 – 24,0	21,63	32/31	17,61	16,5 – 20,1
m2	21,1 – 25,2	23,05	20/21	20,70	18,9 – 22,6
m3	22,3 – 24,6	23,38	16/14	20,12	18,6 – 21,1

Description:
D3. (Plate 1, fig. 7). The occlusal surface of the D3 is round, bearing two cusps near the centre that are connected by two crests. The posterior crest is usually higher than the anterior one.If our allocation of specimens is correct this element shows a wide size range.
D4. (Plate 1, figs. 10 and 11) The occlusal surface of the D4 is somewhat shorter lingually than labially because the protocone has a more labial position than the hypocone. The shape of the protocone and the hypocone of unworn teeth is quite different: The protocone is incorporated into the protoloph and entoloph, but the hypocone is antero-posteriorly compressed. The anteroloph is much lower than the protoloph, lingually separate from the protocone, but labially connected by a thin crest to the paracone. The paracone and metacone are situated near to one another and may be weakly connected by a posterior spur of the paracone and/or an anterior spur of the metacone. These spurs show a great deal of variation and may be absent (9/18). Some specimens have a small mesostyle close to the labial edge

Figure 3.- Fragment of a left maxillary with D4, M1, M2 of *Ottomania proavita* from Süngülü C (nr. 552 Holotype).
Figura 3.- Fragmento de maxilar izquierdo con D4, M1, M2 de Ottomania proavita *de Süngülü (nr. 552 Holotipo).*

1mm

of the occlusal surface. The strong metaconule, that usually has a postero-labial as well as an antero-labial arm, has a central position on the line between the protocone and the metacone. The metaconule sometimes shows weak connections to the entoloph (12/28) and/or the paracone (3/28) and/or the posteroloph (1/28), or is isolated (3/28). The posteroloph descends from the tip of the hypocone in order to ascend as a narrow ridge to halfway the height of the metacone. The D4 has, just as the molars, three strong not diverging roots.

P4. The occlusal surface of the P4 is oval. Its dental pattern with one lingual cusp and one labial cusp (presumably the protocone and the paracone) that are posteriorly connected is very similar to that of Miocene *Sayimys*. The P4 has one root.

M1. (Plate 1, figs. 1 and 2) The occlusal surface of the M1 is more nearly square than that of the D4, because the paracone and the metacone are further apart and the hypocone is situated posteriorly of the protocone. The dental pattern of the M1 is similar to that of the D4, but more lophodont and the arms of the metaconule are longer, better defined and stronger. The metaconule of the M1 is always firmly connected to the metacone. In most specimens the anterior arm of the metaconule is long, passes in between the paracone and the metacone and reaches the labial edge of the occlusal surface (24/31).

M2. (Plate 1, figs. 3 and 4) The occlusal surface of the M2 is sub-rectangular (wider than long). The dental pattern is much more lophodont than that of the D4 and M1 (fig. 3). In contrast to the configuration in the M1, the protocone is always connected to the anteroloph by a high crest, the entoloph is missing, and the hypocone, lingual half of the metaloph, metaconule and mesolophule form a strong crest that is parallel to the protoloph. The mesolophule part of this crest is usually narrower and lower than the metalophule part and may be missing (1/35). The labial part of the metaloph connects the metacone to the metaconule that is

incorporated into the third crest.

M3. (Plate 1, figs. 5 and 6) The shape of the occlusal surface of the M3 is rounded. The dental pattern differs from that of the M1 and M2 in having basically four lophs only. Remnants of the metacone and the labial part of the metaloph are preserved in some specimens (10/19), but this crest is never complete (plate 1, fig. 6). The pattern of the anterior half of the M3 is similar to that of the M2, but the posterior half is reduced.

d4. (Plate 2, figs. 8 and 9). The shape of the occlusal surface of the d4 is elongate and resembles that of the m1 of cricetids. The dental pattern is bunodont. The sub-equal protoconid and metaconid are higher than the anteroconid and the talonid. The anteroconid has a somewhat labial position and is usually connected to the protoconid by a low anterolophulid (18/23). This anterolophulid has a more labial position than the ectolophid. The posterior arm of the protoconid is an almost straight transverse ridge that reaches the lingual edge of the occlusal surface. The metaconid is connected to this ridge by a posterior spur. The long straight ectolophid is narrow and low and situated more or less on the central longitudinal axis of the occlusal surface. The hypoconid is antero-posteriorly compressed and the hypolophid reaches the ectolophid antero-lingually of the hypoconid. The hypoconulid is large. Some of the d4 have a weak: "mesolophid" (3/16), plate 2, figs. 8 and 9) that disappears in an early stage of wear. The d4 has two strong roots that do not diverge.

p4. (Plate 2, fig. 7). The occlusal surface of the p4, an element that is represented in our collection by two specimens only, is rounded. Its dental pattern consists of two conicle main cusps that are tentatively considered to be the protoconid and the metaconid, a weak posterior cingulum and a low anteroconid. The position of this tooth in the mandible cannot be reconstructed on the basis of the specimen figured, because that has neither roots nor a wear facet of the m1. However, a second, slightly damaged, specimen from sam-

ple C has the two roots preserved and shows an indistinct facet. It is suggested that the third weak cusp is situated in front of the protoconid and is an anteroconid.

m1. (Plate 2, figs. 1 and 2). The occlusal surface of the m1 is sub-rectangular (longer than wide). The very short trigonid, formed by a protoconid and metaconid that are anteriorly connected by the metalophid and posteriorly by the posterior arm of the protoconid, is higher than the talonid. The anterior cingulum is very weak and low and disappears at an early stage through interdental wear. In some m1 the posterior arm of the protoconid continues as a weak ridge on the posterior slope of the metaconid all the way to the lingual border of the occlusal surface (13/28). The straight ectolophid is situated slightly labially of the central longitudinal axis of the occlusal surface. The hypoconid is antero-posteriorly compressed. The transverse hypolophid connects to the ectolophid in front of the hypoconid. The large hypoconulid is more incorporated into the posterolophid than in the d4. A weak «mesolophid» is present in some specimens (4/23) (plate 2. fig. 1). The m1 has three roots.

m2. (Plate 2, figs. 3 and 4). The occlusal surface of the m2 is sub-rectangular. Its dental pattern is generally similar to that of the m1, but the posterior arm of the protoconid is more variable in length, more posteriorly directed and therefore not connected to the metaconid. The m2 is also more lophodont than the m1 and its trigonid and talonid are more equal in height. The m2 has three roots.

m3. (Plate 2, figs. 5 and 6). The occlusal surface of the m3 is somewhat rounded posteriorly. Its dental pattern is similar to that of the m2, but the posterior arm of the protoconid is more oblique and always long. The hypoconulid is even more incorporated into the posterolophid than in the m2. The m3 has three roots.

Remarks: The differences in dental pattern between the D4 and M1 on the one hand and the M2 and M3 on the other hand are very pronounced in Ottomania. Summarizing: D4, M1 bunodont, entoloph present, lingual sinus directed posteriorly, anteroloph not connected to protocone, mesolophule weak or absent. M2, M3 lophodont, ectoloph absent, lingual sinus directed anteriorly, anteroloph connected to protocone, mesolophule long and reaching the labial border of the occlusal surface. These differences are of the same order of magnitude as those that have been used in the literature to distinguish genera of primitive ctenodactylids, so the necessity to have good material in order to adequately characterise genera in the family becomes apparent. It is particularly intriguing that the difference, between the anterior and posterior upper cheek teeth are not reflected in the occluding lower cheek teeth.

The M2 of *Ottomania* have a dental pattern that is identical to the M2 of the baluchimyine *Hodsahibia* FLYNN *et al.*, 1986. If we had known the M2 of *Ottomania* only we would not have hesitated to allocate that tooth to *Hodsahibia*. However, the deciduous teeth and the premolars are completely different in the two genera which makes it clear that they represent different (sub)families.

The under-representation of the p4 of *Ottomania proavita* in all the three samples from Süngülü is not understood. This even more so because that small round tooth may be expected to survive rough handeling while screenwashing better than for instance its long fragile predecessor the d4. Can it be that retarded replacement of the deciduous teeth occurred in the lower dentition, but not in the upper dentition of the same species? The relatively large number of not very worn d4 in our collection (19/25) contradicts this hypothesis.

The enigmatic upper tooth of an indeterminate ctenodactyloid described from Kocayarma (Ergene basin) by the second author (ÜNAY, 1988 Pl.7, fig.8) as a P4 or M1 shows a similar mophology as the D4 of *Ottomania* (Pl.1, figs. 10, 11).Its relatively narrow anterior part, posteriorly directed sinus and double centrally placed metaconule leave little doubt that this tooth represents a D4 of an otherwise unknown species of *Ottomania*.

Genus *Confiniummys* n. gen.

Derivatio nominis: *Confinium* in Latin means border area. This name has been chosen because the Lesser Caucasus separates countries as well as cultures.

Type species: *Confiniummys siddiki* n. sp.

Diagnosis: Confiniummys is a small ctenodactylid with five-crested M1 M2 and four-crested and three-rooted m1, m2 and m3. The hypocone of the upper molars is smaller than the protocone. The anteroloph of the upper molars has about the same height as the protoloph and is connected to the protocone. The premolars are not molariform. P4 with two cusps and one root, p4 with three cusps and one root. Cheek teeth brachyodont. Upper cheek teeth more lophodont than lower cheek teeth. The relative size and the shape of the molars is as in the Phiomyidae and Chapattimyidae.

Differential diagnosis: The shape, relative size and dental morphology of the molars of *Confiniummys* is very similar to *Protophiomys* JAEGER *et al.*, 1985 from the Late Eocene of Algeria, *Baluchimys krabiense* MARIVAUX *et al.*, 2000 from the Late Eocene of Thailand and *Baluchimys*

Plate 1. - *Ottomania proavita* n. gen. n. sp., **1,2**, M1; **3**, **4**, M2; **5**, **6**, M3; **7**, D3; **8**, **9**, P4; **10**, **11**, D4. *Confiniummys sidiki* n. gen. n. sp., **12**, P4; **13**, **14**, M1-2; **15**, M3.

1mm
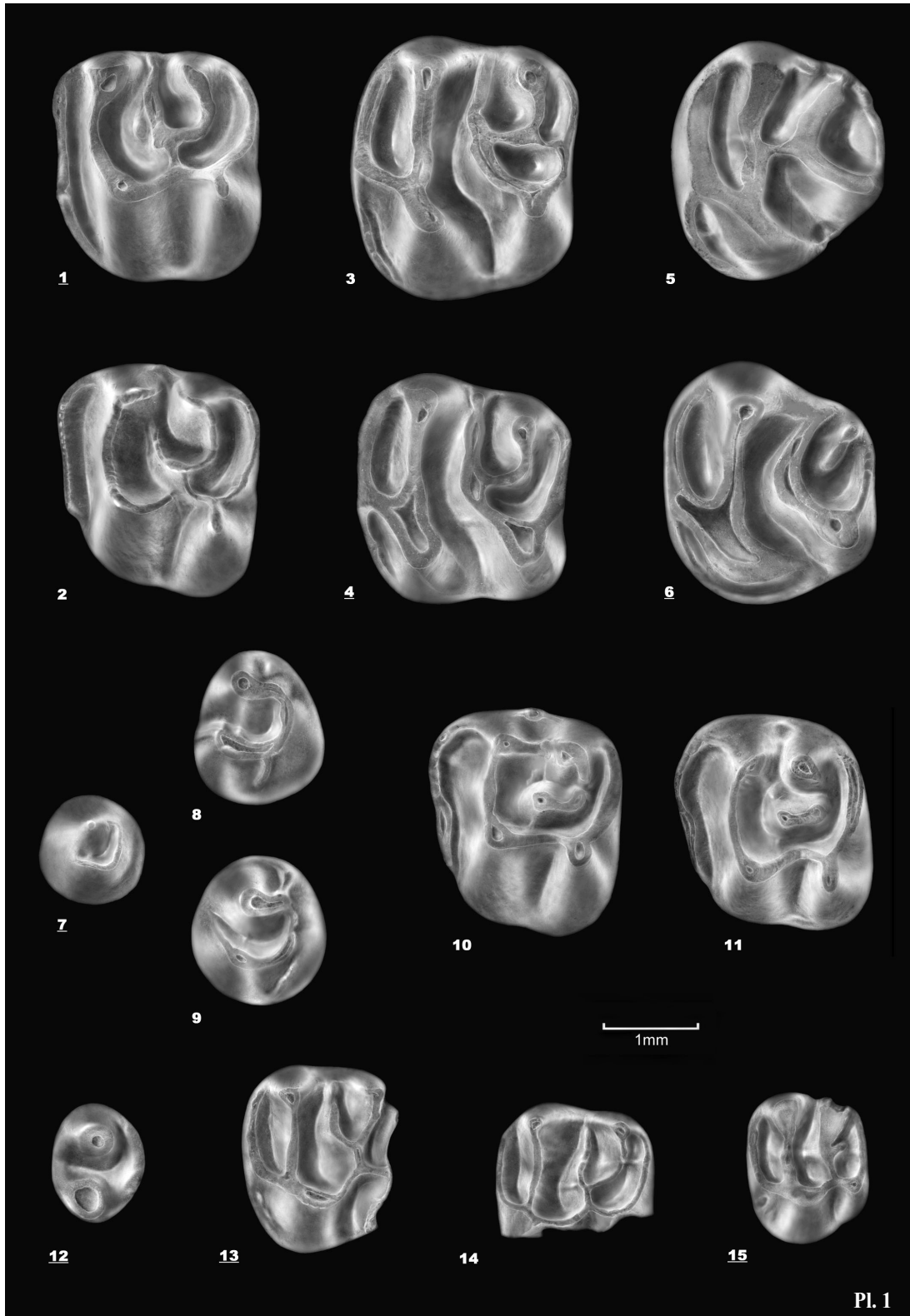
Pl. 1

FLYNN *et al*., 1986 from the Early Miocene of Pakistan. However, the premolars of *Confiniummys* are not molariform. It is the morphology of the premolar that makes *Confiniummys* a typical ctenodactylid and not a member of the probably ctenodactyloid derived Chapattimyidae (Baluchimyinae) or *Phiomyidae.Confiniummys* shows similarities with *Ottomania* in having five-crested M1 and M2 and four-crested m1, m2 and m3 and in having three-rooted lower molars. However, the differences in the shape and the relative size of the lower molars,and the differences in the morphology of the P4 and the p4 (plate 1, figs. 8, 9 and 12, plate 2 ,figs. 7 and 10) are considered to be of sufficient importance to classify the two ctenodactylid species from Süngülü in different genera.

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Confiniummys siddiki n. sp.
(Plate 1, figs. 12-15, Plate 2, figs. 10-15)

</div>

Derivatio nominis: This species is named after Mr. SIDDIK AÞIK in recognition of his contribution to the success of our collecting campaigns.

Type locality: Süngülü A

Holotype: m1 dext. Sample A, nr. 323, (Plate 2, fig. 13)

Type level: Eo/Oligocene boundary interval

Diagnosis: As for the genus *Confiniummys*

Differential diagnosis: As for the genus *Confiniummys*

Material and measurements samples A, B en C

	Length			Width	
	Range	Mean	N	Mean	Range
P4		8,5	1	10,5	
M1-2		14,8	1	17,8	
M3		11,3	1	14,1	
d4	13,0 – 14,5	13,8	2/1	10,5	
p4		10,5	1	7,9	
m1		15,9	1	14,3	
m2	14,1 – 17,0	15,9	4/2	14,3	14,0 – 14,5
m3	14,2 – 16,6	15,2	4	14,0	13,3 – 14,3

Description:

D3 and D4 not known.

P4. (Plate 1, fig. 12) The occlusal surface of the P4 is oval. The dental pattern consists of two round plump cusps (presumably the protocone and the paracone) and a weak posterior cingulum. Its structure is even more simple than in such primitive ctenodactyloid rodents as *Tamquammys* SHEVYREVA, 1971, *Sharomys* DASHZEVEG, 1990 and *Karomys* DASHZEVEG, 1990.

M1-2. (Plate 1, figs. 13 and 14) The shape of the occlusal surface is sub-rectangular. The protocone is connected to the somewhat smaller hypocone by a complete

entoloph. The anteroloph runs from the tip of the protocone to the base of the paracone. The transverse protoloph connects to the anteroloph just in front of the protocone. The metaloph connects lingually to the ectoloph in front of the hypocone. The metaloph bifurcates, at the place where the metaconule of more bunodont ctenodactylids is situated, into a mesolophule branch and the labial part of the metaloph that connects to the metacone. The well-developed posteroloph runs from the tip of the hypocone to the base of the metacone.

M3. (Plate 1, fig. 15). This four-crested tooth has a protocone that is much larger than the hypocone. The transverse protoloph and metaloph connect slightly in front of the protocone, respectively, the hypocone. The entoloph is well developed. The mesoloph is absent in the M3, but there is a weak metaconule.

d4. (Plate 2, figs. 11 and 12). The d4 has a very small anteroconid that, in contrast to the configuration seen in many other ctenodactylids, is situated more or less in between the isolated protoconid and metaconid as in *Birbalomys* and *Chapattimys.* The ectolophid, connecting the protoconid and the hypoconid, is low. The hypolophid is interrupted and does not reach the hypoconid. The hypoconulid is large and isolated in one specimen, but seems to have been smaller in the other.

p4. (Plate 2, fig. 10). The occlusal surface of this one-rooted tooth that is tentatively identified as p4, is oval. Since there is no wear facet of an adjoining tooth, the position of this tooth in the dentition remains questionable, so it cannot be excluded that we are dealing with an upper premolar. Our interpretation of the dental pattern, is for the time being, that the largest of the three cusps is the homologue of the fused protoconid and metaconid. The second largest cusp would than be the entoconid and the smallest cusp the hypoconid.

m1. (Plate 2, fig. 13). The shape of the occlusal surface of the m1 is sub-rectangular. The dental pattern shows a remnant of the low anterior cingulum on the antero-labial side, a straight transverse metalophid, a well developed posterior arm of the protoconid that does not reach the metaconid, a hypolophid that connects to the ectolophid in front of the hypoconid and a rather strong hypoconulid on the posterolophid.

m2, m3.(Plate 2, figs. 14 and 15). The m2 and the m3 differ from the m1 in the shape of their occlusal surfaces only. These lower molars resemble the ones of *Protophiomys, Baluchimys, Chapattimys, Advenimus* and even *Phiomys* in shape and dental pattern. In other words, these genera share a large number of characteristics that are probably inherited from their primitive ctenodactyloid ancestors.

Plate 2. - *Ottomania proavita* n. gen. n. sp., **1**, **2**, m1; **3**, **4**, m2; **5**, **6** m3; **7**, p4; **8**, **9**, d4. *Confiniummys sidiki n*. gen. n. sp., **10**, p4; **11**, **12**, d4; **13**, m1; **14**, m2; **15**, m3.

1mm

Pl. 2
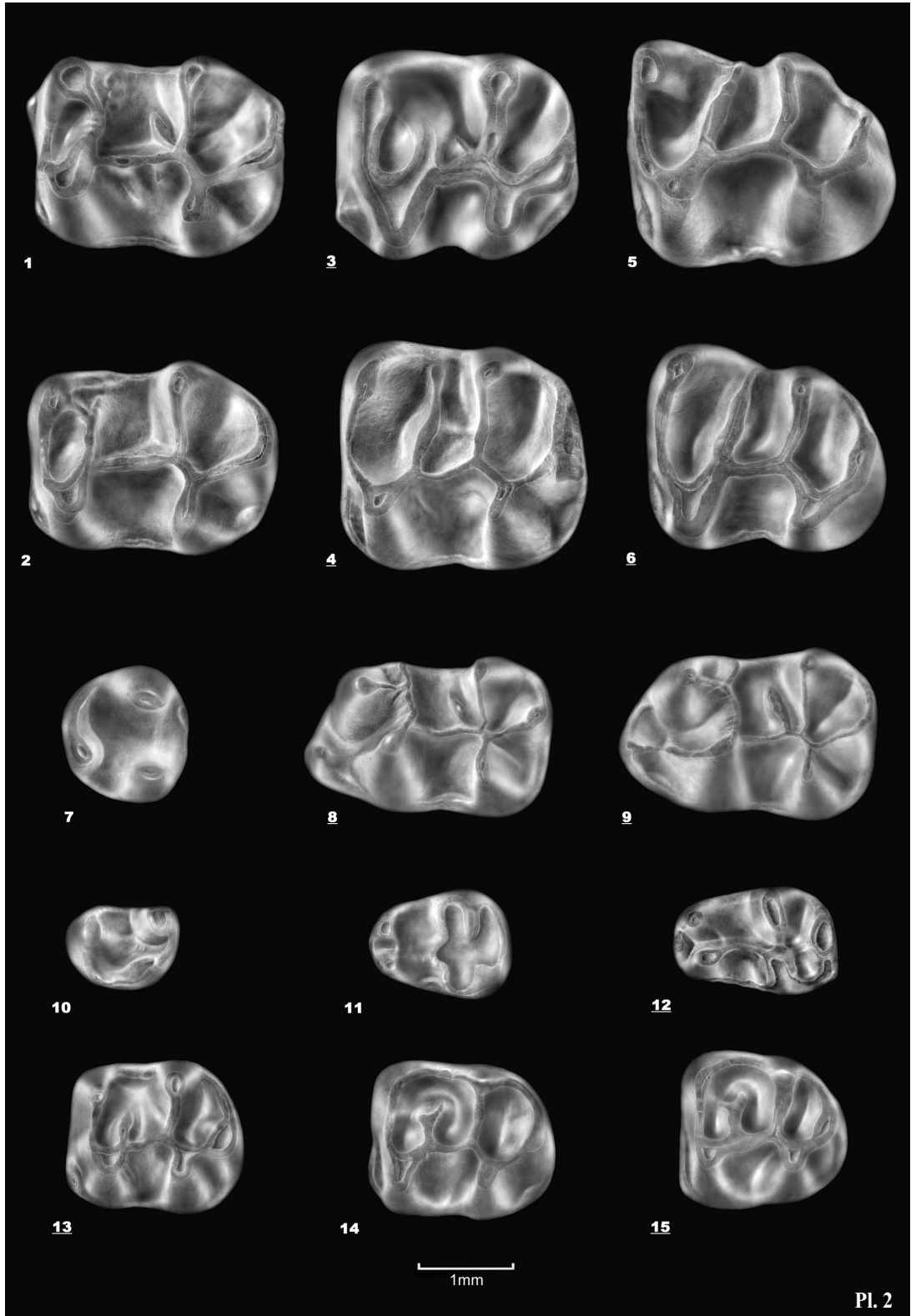
Remarks: If our allocation of the material described above to one species *Confiniummys siddiki* is correct, the contrast between the bunodont non-molariform premolars and the lophodont molars is remarkable. The species is of special interest because its presence in west Asia, in beds that are presumably of Eo/Oligocene age, contributes to the reconstruction of the geographical dispersal and phylogenetical coherence of ctenodactyloid derivates during the Eocene (Hussain *et al.*, 1978, Jaeger *et al.* 1985, Flynn *et al.* 1986, Peláez-Campomanes & López Martínez, 1996) and touches the unresolved problem of the origin of the hystricognaths. Unfortunately the groups that play a key role in this discussion (Chapattimyidae, Baluchimyinae, *Protophiomys, Zamoramys* and *Confiniummys* are almost exclusively known by isolated teeth. More material from the Lesser Caucasus would help, but the known localities, yielding about one isolated tooth of *Confiniummys* per ton of matrix, are not promising.

Superfamily MUROIDEA Illiger,1811

Introduction: The contents of this superfamily has traditionally been restricted to rodents with a myomorph skull morphology and three molars as cheek teeth. This "definition" is strictly not tenable since it was shown that *Cricetops dormitor* has a hystricomorph skull and that *Pappocricetodon antiquus* has a P4. Now that the Eocene record in central Asia and North America of rodents that are assigned to either the Muroidea or the Dipodoidea is improving, the difference between the earliest representatives of these two superfamilies has become diffuse (i.e. the dental morphology of *Palasiomys conulus* Tong, 1997 and *Primisminthus yuenus* Tong, 1997 is essentially the same, but the first is considered, for reasons that are beyond our comprehension, to be a muroid while the second has been considered a dipodoid. Since there is now strong evidence that the Dipodidae and the Muridae s.l. are more closely related than either one is to any other group of rodents we consider it justified to use the superfamily Muroidea here to group the two families.

Family Dipodidae Fischer von Waldheim, 1817

Introduction: The subdivision of the extant Dipodidae into the subfamilies Sicistinae, Zapodinae, Allactaginae, Dipodinae, Paradipodinae and Euchoreutinae is based on the degree of specialisation of the zygoma, dentition, hind feet, cervical vertebrae etc. to a wide variety of life-styles. Since the range of ecological niches occupied by Dipodidae is wide it has become the most diverse of all rodent families. Unspecialised Paleogene Dipodidae are usually referred to the Zapodinae, the subfamily that contains the generalised extant members of the family, on the basis of dental similarity. This procedure is in our opinion unsatisfactory because this arrangement does not reflect the phylogenetical relationships. We therefore prefer not to allocate the Paleogene members to

subfamily.

While reviewing the literature on the Paleogene Dipodidae of Eurasia we gained the impression that this group has been over-split on the genus level. McKenna & Bell (1997) reached a similar conclusion and formally synonymised *Parasminthus* Bohlin, 1946, *Sinosminthus* Wang, 1985, *Heosminthus* Wang, 1985, *Gobiosminthus* Huang, 1992 and *Shamosminthus* Huang, 1992 with *Plesiosminthus* Viret, 1926. We do not follow this decision because the differences in crown height, relative size and proportions of the cheek teeth and the external shape of the upper incisors between the type species of most of these genera seems too great to include them into one single genus. Awaiting a revision of the Asiatic Paleogene Dipodidae we tentatively maintain all generic names.

Genus *Heosminthus* Wang, 1985

Type species: *H. primiverus* Wang, 1985 from the Lower Oligocene of Cajichong, Yunnan, China.

Heosminthus minutus Daxner-Höck, 2001.
(Plate 3, figs. 1- 9)

Type locality: Hsanda Gol. Central Mongolia.
Type level: Hsanda Gol Formation above basalt 1, Lower Oligocene
Locality: Süngülü

Material and measurements

	Length			Width	
	Range	Mean	N	Mean	Range
M1-2	9,3 – 10,5	9,98	10	8,73	8,1 – 9,7
M3		6,7	1	5,9	
m1	8,7 – 10,4	9,52	6/7	7,10	6,1 – 8,4
m2	9,7 – 11,1	10,47	3	8,17	7,8 – 8,4
m3	7,8 – 8,6	8,2	2	6,7	6,1 – 7,2

Description

M1-2. (Plate 3, figs. 1-3).One M1 is sitting in a fragment of a maxilla with the alveole of the P4 preserved, so the position of this tooth is certain. Some of the M1-2 from Süngülü have a slightly more rectangular shape than the M1 that is still sitting in the maxilla and may therefore be M2. However, none of these has such a strong lingual branch of the anteroloph as the M2 in the type material, so we are unable to separate the M1 from the M2 with certainty. The occlusal surface of all M1-2 is somewhat longer than wide. The anterior cingulum is weak. The strong anterior arm of the protocone reaches the paracone in some M1-2 (3/10), in the others there is no connection. The slightly backwards directed protoloph connects the paracone to the posterior arm of the protocone. The metaloph is sometimes interrupted (3/10), sometimes connected to the hypocone (3/10) and sometimes connected to the posteroloph just behind the hypocone (4/10). The long pos-

teroloph reaches the posterior side of the metacone. The mesoloph is either short or of medium length. The M1-2 have three roots.

M3. (Plate 3, fig 4). The only available M3 is damaged and does not show much detail. It shows four transverse crests (the mesoloph is absent) and two longitudinal crests that connect the protocone to the very small hypocone.

m1. (Plate 3, figs. 5 and 6). The m1 is narrow anteriorly and its anteroconid is small. The protoconid and the metaconid are connected by the posterior arm of the protoconid (metalophulid 2).The protoconid and the metaconid are situated opposite each other, but the hypoconid and the entoconid are alternating. The transverse hypolophid is connected to the rather oblique ectolophid just in front of the hypoconid. The mesolophid is short or of medium length and directed antero-lingually. The mesoconid and hypoconulid are either weak or absent. The posterolophid extends all the way to the base of the entoconid.

m2. (Plate 3, fig. 7). The lingual branch of the anterolophid is narrow and straight, its labial branch descends from the anteroconid to the base of the protoconid. The protoconid and metaconid ,and the hypoconid and entoconid have alternating positions. The short and weak metalophid is either transverse (2/3) or directed forwards (1/3). The transverse hypolophid connects to the ectolophid anteriorly of the hypoconid. The mesolophid is variable in length and may be almost absent (2/3).

m3. (Plate 3, figs. 8 and 9). The anterior part of the m3 is similar to the m2 and has the lingual as well as the labial branch of the anteroloph well developed. The entoconid is small (2/3) or incorporated into the posterolophid (1/3). The hypolophid is weak or absent and the mesolophid is absent.

Remarks: The morphology of the *Heosminthus* cheek teeth from Süngülü and that of the type material of *Heosminthus minutus* from Hsanda Gol, Central Mongolia is, with the exception of the greater similarity of the M1 and M2 in the Turkish material, virtually identical. The sum of the mean lengths of the upper as well as the lower cheek teeth is 11% longer in the *H. minutus* material from Süngülü, but since the number of specimens is limited and the teeth from the two areas were measured by using different types of measuring microscopes the size difference between the two samples may well be an artifact.

The occurrence of *H. minutus* in the rodent assemblages from Hsanda Gol and Süngülü is unexpected because these diverse faunas do not share other species and are completely different in composition. The Aplodontidae, Cylindro-dontidae and Eomyidae, present in Central Asia, are not known to occur in Turkey. Moreover, the Ctenodactylidae and the Muroidea are, with the exception of *Eucricetodon* s. l., represented by different genera in the two areas. The peculiar westwards extension of the geographical range of *Heosminthus* during the Eo/Oligocene boundary interval has its compeer in its possible descendant *Heterosminthus*.

Family Muridae ILLIGER, 1811

The family Muridae as used here embraces all true murids from the primitive Pappocricetodontinae to the highly specialised Oligo/Miocene Melissiodontinae and the extant Murinae, Arvicolinae, Gerbillinae. Other than in the chapters on the Ctenodactylidae and the Dipodidae (in which the genera were not grouped into subfamilies) we shall group the muridae on the basis of dental morphology. All these groups will be given subfamilial status provided that such a name is available.

Paracricetodontinae MEIN & FREUDENTHAL, 1971

Genera included: *Paracricetodon* SCHAUB, 1925, *Trakymys* ÜNAY, 1989, ? *Mirabella* DE BRUIJN *et al*. 1987.

Original diagnosis: Foramen incisivum ends in front of the anterior border of the M1.Mandible plump with shallow diastema (translated from French)

ÜNAY (1989) regarded the Paracricetodontinae as a subfamily of the Melissiodontidae, a point of view that has been correctly contested by KRISTKOIZ (1992), FREUDENTHAL *et al*. (1992) and MÖDDEN (1999). She diagnosed the subfamily as follows: "Large sized Melissiodontids. Main cusps of upper as well as lower cheek teeth shaped as in most cricetids. Sinusid of the m3 inclined obliquely backwards". FREUDENTHAL, *et al*. (1992) in their "Classification of European Oligocene cricetids" give an emended diagnosis of the paracricetodontinae: «Medium sized to large cricetids. Ectolophid poorly developed. Metaconid and entoconid connected by a high cingulum-ridge along the border of the lower molars. m1 and m2 with free hypoconid hind arm Anteroconid of m1 poorly developed and anterior metalophulid absent. M3 with free anterior arm of protocone. Posterior part of M3 little reduced. Mandible almost vertical with respect to the occlusal surface, diasteme flat.»

These diagnoses show that it is difficult, if not impossible, to define a cricetid subfamily on the basis of tooth mophology even if specialists agree on its validity. In our opinion formal diagnoses are therefore better avoided. The case of the Paracricetodontinae serves to demonstrate this view: Of the three characteristics, given by ÜNAY (1989) the first has become irrelevant now that we have a small *Paracricetodon* species, the second and third are not characteristic because they occur in many other cricetids. FREUDENTHAL *et al*. (1992) give eight characteristics (see above).Of these 1) is irrelevant, 2 & 3) occur in many primitive cricetids, 4)occurs in some species of *Eucricetodon* (*Atavocricetodon*) and *Pseudocricetodon* (*Allocricetodon*) also, 5 & 6) occur in many primitive cricetids, 7) is not true for all species assigned to the subfamily by the authors and 8) is correct for the western European species only.

Genus *Paracricetodon* Schaub, 1925

Type species: *Cricetodon spectabilis* Schlosser, 1884
Other species included: *P. cadurcensis* (Schlosser, 1884), *P. confluens* Schaub, 1925, *P. dehmi* Hrubesch, 1957, *P. walgeri* Bahlo, 1975, *P. kavakderensis* Ünay, 1989, *P. kodjayarmensis* Ünay, 1989, *P. wentgesi* n. sp., The species *confluens* seems to be a junior synonym of *spectabilis*

Geographical range: Europe including European Turkey, Lesser Caucasus.
Stratigraphical range: Oligocene
Introduction: Schaub (1925) defined the genus Paracricetodon as follows: "Cricetodontids" with lengthened m3 and free-ending posterior arm of the hypoconid. Upper molars with free-ending anterior arm of the protocone in M2 and M3,without endoloph, with shallow sinus and well-marked connection between the lingual cusps"(translated from German).

Bahlo (1975)"emended" Schaubs diagnosis as follows: "Medium to large Cricetidae with the following characteristics: Lower cheek teeth with free-ending posterior arm of the hypoconid, at least in the m1 and m2. m3 relatively lengthened. Upper cheek teeth with free-ending anterior arm of the protocone in the M2 and M3. Endoloph absent or weakly developed. Lingual cusps with clear connection. Sinus shallow"(translated from German).

Neither of these diagnoses recognises some features that are in our opinion characterising *Paracricetodon*, so the genus will be re-defined below.

Emended diagnosis: Lower cheek teeth: Anteroconid of m1 weak and in many specimens developed as a low cingulum only. Metalophulid 1 usually missing in the m1, but present in the m2 and m3 (as in *Pappocricetodon* Tong, 1992 and *Ulaancricetodon* Daxner-Höck, 2000). Endolophid complete and posterior arm of the protoconid strong in all molars. A free-ending posterior arm of the hypoconid is present in the m1 and m2 of all species and may be indicated in the m3 of some. The m3 is about as long as the m1, or longer.

Upper cheek teeth: Anterocone of the M1 rather strong and blade-shaped. The anterior arms of the protocone and hypocone are well developed in the M1 and M2 of all species, but absent in the M3 of some. The ectoloph sinuous as in many Miocene cricetid species from western Asia.

The sinus of the M1 and M2 is, in contrast to the configuration in most other cicetids, posteriorly directed.

The M1 is much longer than the m1.

The M3 of the eastern Mediterranean *Paracricetodon* species *kodjayarmensis*, *kavakderensis* and *wentgesi* are relatively small with hypocones absent or small, but the M3 of the central and western European *Paracricetodon* species *spectabilis*, *walgeri* and *dehmi* are relatively large and have well developed hypocones. Since the oldest cricetid *Pappocricetodon* has small M3 that lack the hypocone, we consider this to be the primitive character state. This implies that the western species are more derived in this respect than the eastern ones.

Paracricetodon wentgesi n. sp.
(Pl.6, figs. 1-15)

Derivatio nominis: The species is named in honour of Mr. W.O. Wentges, acknowledging his support of the paleontology of small mammals.
Type locality: Süngülü B
Holotype: Isolated M1, nr.529 from Süngülü B, Plate 6, fig. 1
*Type level*: Eo/Oligocene boundary interval
Diagnosis: *Paracricetodon wentgesi* is a small species of *Paracricetodon* .M3 sub-triangular with a weak lingual branch of the anteroloph, shallow sinus and tiny hypocone. Anterior arm of the protocone strong in the M1 and M2, rarely developed in the M3. Posterior spur of the paracone of the M1 and M2 burgee-shaped and connected to the anterior spur of the metacone. Anteroconid of the m1 retracted and much lower than the protoconid and the metaconid. Mesolophid of lower molars variable in length and directed forwards. m3 on average slightly shorter than the m1. Endolophids of lower molars complete.

Differential diagnosis: The cheek teeth of *Paracricetodon wentgesi* are about twenty-five percent smaller than those of the second smallest species of the genus (*P. walgeri*). The hypocone of the M3 is smaller and more labially situated than in the western European species of the genus. In contrast to the situation in other species of the genus the m3 of P. *wentgesi* is on average somewhat shorter than the m1.

Material and measurements samples A and B

	Length			Width	
	Range	Mean	N	Mean	Range
M1	17.0 - 20.9	19.79	14/21	13.50	12.3 - 14.9
M2	13.4 - 15.5	14.68	26/25	13.00	12.0 - 14.3
M3	11.2 - 14.0	12.98	17/19	12.22	10.8 - 13.3
m1	13.9 - 17.5	15.99	33/32	10.98	9.4 - 12.0
m2	14.7 - 17.3	15.69	28/31	12.35	11.3 - 13.4
m3	14.4 - 16.9	15.83	20/19	12.01	11.0 - 12.9

Plate 3. - *Heosminthus minutus* Daxner-Höck 2001. **1,** M1; **2**, **3**, M1-2; **4**, M3; **5**, **6**, m1; **7**, m2; **8**, **9**, m3. Witenia fusca n. gen. n. sp. **10**, **11**, M1; **12**, **13**, M2; **14**, **15**, M3; **16**, m1; **17**, m2; **18**, m3.

Pl. 3

1mm
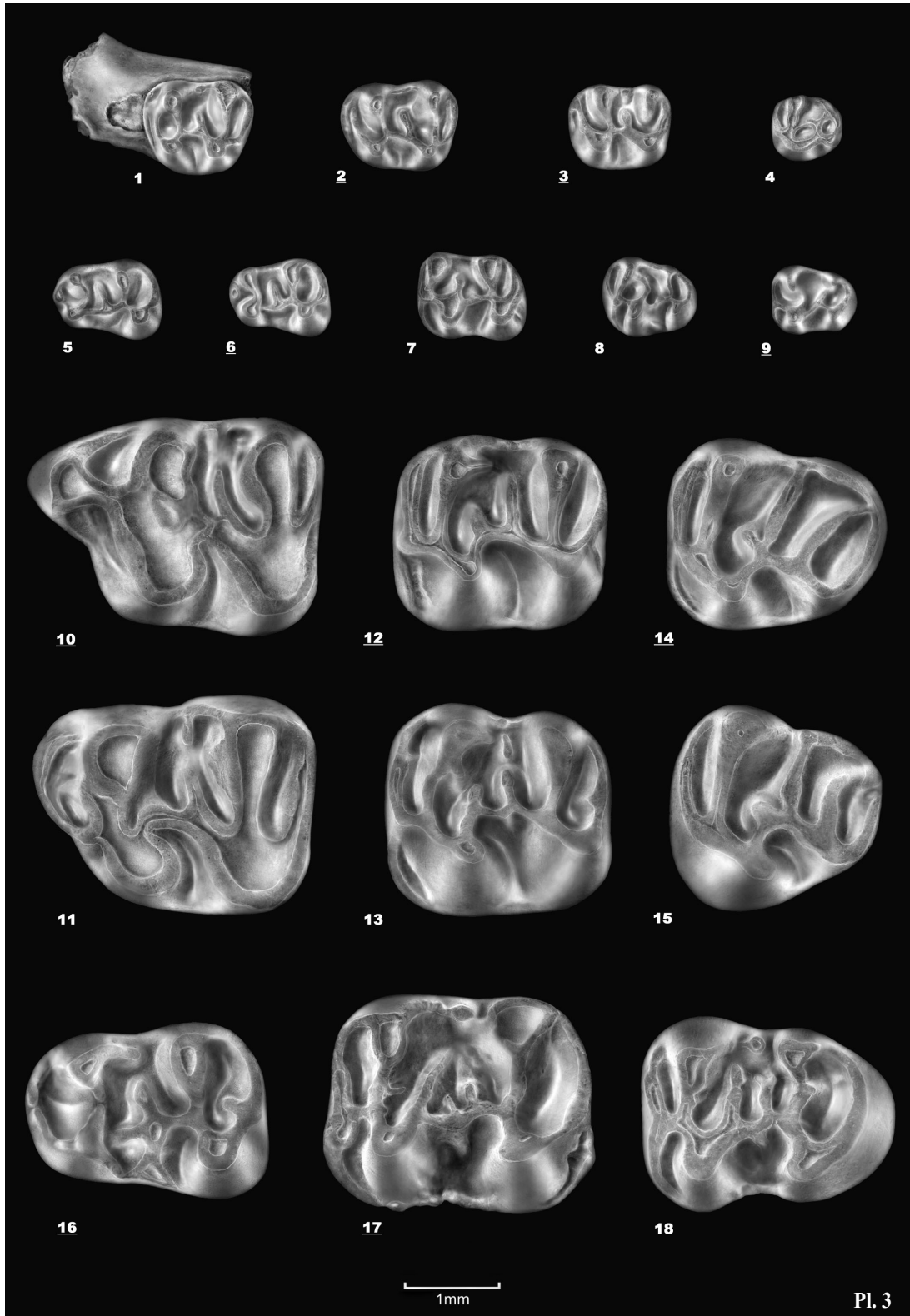
Description:

M1. (Plate 6, figs. 1, 2, 13).The well-developed blade-shaped anterocone has about the same height as the protocone and the paracone. The width of the anterocone, that is connected to the protocone and paracone, shows considerable individual variation. The anterior arm of the protocone is usually long, reaching the labial arm of the anterocone (38/47). The narrow protoloph is sometimes transverse and connected to the protocone(16/51), but more often curving forwards and connected to the anterior arm of the protocone (Pl. 6 figs. 1, 2) as in other Paracricetodon species. The burgee-shaped posterior spur of the paracone is almost invariably connected to the anterior spur of the metacone, forming a continuous ectoloph. The anterior arm of the hypocone is parallel to the anterior arm of the protocone, but does not reach the ectoloph in the majority of the specimens (38/52). The forwards curving metaloph connects the metacone to the hypocone. The posteroloph connects the metacone and hypocone.

M2. (Plate 6, figs. 3, 4). The long straight anteroloph is divided into a shorter lingual part and a longer labial part by the weak anterolophule. The strong anterior arm of the protocone connects to the paracone in the majority of the M2 (48/67). In the others this ridge ends either free or connects to the labial part of the anteroloph. The anterior arm of the protocone and the short forwards curving protoloph usually enclose a pit. In some specimens there is a short mesoloph between the protoloph and the anterior arm of the hypocone (6/67).The anterior arm of the hypocone is parallel to the anterior arm of the protocone and of medium length (ending freely). In some M2 this ridge is long and thin and connects to the ectoloph (9/67).The transverse or slightly forwards directed metaloph connects the metacone to the antero-labial side of the hypocone. The posterior spur of the paracone is burgee-shaped and connects to the anterior spur of the metacone forming a continuous ectoloph. The rather short posteroloph connects invariably to the posterior slope of the metacone.

M3. (Pl. 6, figs. 5, 6). The anteroloph is divided into a long labial branch and a shorter lingual branch by a weak anterolophule. The anterior arm of the protocone is present in a few M3 only (5/45).The protoloph is more or less transverse in all the M3.The sinus separating the rather large protocone from the tiny indistinct hypocone is shallow. The metacone is incorporated into the posteroloph. The short metaloph and the posteroloph enclose a small pit. The structures within the trigone basin show considerable individual variation and are, with the exception of the remnants of the labially situated anterior arm of the hypocone, not easy to homologise.

m1. (Plate 6, figs. 7, 8, 14). The anteroconid of the m1 is basically developed as a crest that starts at the tip of the metaconid and descends to meet the base of the protoconid. The central part of this crest may, or may not, be slightly elevated suggesting an incipient anteroconid. A short anterolophulid, connecting the protoconid to the antero-

conid, is present in a minority of the specimens (19/61). The metalophulid 1 is almost always absent (28/31). The lingual part of the posterior arm of the protoconid usually curves forwards forming a metalophulid 2. A forwards directed low mesolophid, initiating from the longitudinal ridge close to where the hypolophid meets that ridge, is present in most specimens (47/59). The posterior arm of the hypoconid ends freely in the posterior basin.

m2. (Pl. 6, figs. 9, 10, 15). The anterolophid is well developed and continues in some specimens along the labial margin of the occlusal surface to the hypoconid. A short anterolophulid connects the protoconid to the anterolophid. The metalophid 1 (which is absent in the m1) is complete in most m2 (50/60) and connects to the anterolophid in front of the protoconid. The posterior arm of the protoconid is variable in length. This ridge forms a metalophulid 2 in some specimens, but ends freely in the main basin in others. A weak mesolophid is present in most m2 (34/48). The hypolophid is directed slightly forwards and reaches the longitudinal ridge in front of the hypocone. The ectomesolophid shows considerable individual variation and may be absent. The posterior arm of the hypoconid is always well developed, but on average shorter than the posterior arm of the protoconid. The posterolophid smoothly curves from the hypoconid to the posterior crest of the entoconid.

m3. (Pl. 6, figs. 11, 12). The anterolophid of the m3 is long and connected to the protoconid by a short anterolophulid. The metalophid is complete in all specimens and connects in the majority of the m3 to the anterolophulid. In some this crest is directed somewhat more forwards and connects to the anterolophid. The strong posterior arm of the protoconid is invariably directed postero-lingually and ends freely in the main basin. The mesolophid is weak or absent. The hypolophid is transverse or directed slightly forwards and inserts in front of the hypoconid. The ectomesolophid shows a great deal of individual variation in length and can be absent. Traces of the posterior arm of the hypoconid occur rarely (3/44). The posterolophid curves smoothly from the hypoconid to the tip of the well-developed entoconid.

Remarks: Paracricetodon wentgesi is of special interest because this primitive cricetid, that presumably is the oldest representative of the genus, shows a sinus in the upper molars which shape is determined by the strong posterior arm of the protocone. Surprisingly this, at least theoretically, primitive configuration is rare in cricetids as well as in rodents in general.

Assuming that the quadritubercular molar pattern derives from a tritubercular configuration, it seems logical to homologise the strong posterior arm of the protocone with the lingual part of the original metaloph. However, this interpretation is contradicted by the dental pattern of the earliest cricetids *Palasiomys conulus* Tong, 1997 and *Pappocricetodon antiquus* Wang & Dawson, 1994 from

the Middle Eocene of China. In these the shape of the sinus of the M1 and M2 is determined by the strong anterior arm of the hypocone, and is thus directed forwards. Whether or not the strong posterior arm of the protocone in *Paracricetodon* is to be interpreted as primitive remains therefore uncertain. This the more so because this rare characteristic occurs also in the M1 and M2 of *Meteamys* DE BRUIJN *et al.*, 1992 from the Late Oligocene of Anatolia and in *Byzantinia* DE BRUIJN, 1967 from the Late Miocene of the eastern Mediterranen area, two cricetids that are certainly quite specialised. Since it can be demonstrated that the posteriorly directed sinus in *Byzantinia* developed secondarily during the Late Miocene it may well be that this condition has developed in parallel in *Paracricetodon*.

Comparison of the dental pattern of *Paracricetodon wentgesi* with that of the earliest cricetids suggest that it shows the following primitive characteristics:

M1 larger than m1.

m3 about as long as the m1.

Anterior arm of the protocone of the M1 long.

Posterior arm of the protoconid of the lower molars posteriorly directed and long.

Metalophulid 1 almost always absent in the m1.

Metalophulid of the m2 and m3 transverse and inserting directly in front of the protoconid.

The occurrence of a species of *Paracricetodon* that is much smaller than all other species of that genus in deposits of Eo/Oligocene age shows that size is not a valid criterium for defining cricetid genera, as has been suggested by FREUDENTHAL (1994, 1996) and by FREUDENTHAL *et al.* (1992).

Pseudocricetodontinae ENGESSER, 1987

Genera included: Pseudocricetodon THALER, 1969 (=*Allocricetodon* FREUDENTHAL, 1994), *Lignitella* ÜNAY, 1989, *Cincamyarion* AGUSTI & ARBIOL 1989, *Adelomyarion* HUGUENEY, 1969

Diagnosis (as re-phrased by FREUDENTHAL *et al.*, 1992 after ENGESSER, 1987): "Small to large Oligocene and Lower Miocene cricetids with rather lophodont molars. M1 with large prelobe, straight or concave labial edge, and with long anterior arm of protocone. M2 with double protolophule. m1 mostly with a strong ridge descending from the metaconid, along the border of the tooth, into the mesosinusid, without reaching the entoconid. In the m1 the mesolophid is frequently double, m1 and m2 nearly always without the posterior arm of the hypoconid. Mandible transversely inclined with respect to the occlusal surface, diasteme concave».

The subfamily Pseudocricetodontinae was created to embrace the lophodont European Oligocene cricetid genera *Pseudocricetodon* and *Heterocricetodon* Schaub, 1925. This concept was basically maintained in the classification

presented by FREUDENTHAL *et al.* (1992) who recognise the tribes Pseudocricetodontini (with *Pseudocricetodon, Lignitella* and *Kerosinia*) and Heterocricetodontini (with *Heterocricetodon* and *Cincamyarion*) within the subfamily. An essential discrepancy between the classifications of FREUDENTHAL et al, 1992, ÜNAY, 1989, ALVAREZ SIERRA *et al.*, 1999 and the one presented here concerns the genus *Adelomyarion*. FREUDENTHAL & CUENCA BESCOS (1984) doubt whether or not *Adelomyarion* is a cricetid and FREUDENTHAL *et al.*, 1992 consider it very far away from the *Pseudocricetodontinae* and state: "There seems little doubt that the subfamily Adelomyarioninae will have to be raised to a higher taxonomic level in the future". ÜNAY (1989) recognises a subfamily Adelomyarioninae within Pseudocricetodontidae while ALVAREZ SIERRA *et al.*, (1990) see *Allocricetodon* (an established Pseudocricetodontine) as a junior synonym of *Adelomyarion*. We prefer to synonymize *Allocricetodon* with *Pseudocricetodon* (see below).

KRISTKOIZ (1992), in his revision of the Late Oligocene rodents from Gaimersheim, analysed the cranial and dental characteristics of *Heterocricetodon* and *Pseudocricetodon* and reached the conclusion that the two genera belong to different groups. A point of view that we share.

FREUDENTHAL (1994) in his descriptions of new material from the province of Teruel defines the genus *Allocricetodon* (type: *cornelii*) in which some species that were previously classified in *Pseudocricetodon* are included. We do not follow this arrangement and consider *Allocricetodon* a junior synonym of *Pseudocricetodon* because the morphological differences between the species grouped in these 'genera' are considered to be trivial and because size difference is considered not to be characteristic at the genus level (see above). The differential diagnosis for *Allocricetodon* given by FREUDENTHAL (1994) reads: "Larger than *Pseudocricetodon* and *Kerosinia*, smaller than *Heterocricetodon* and *Cincamyarion*. Cingulum ridges closing the valleys of the lower molars are better developed than in *Pseudocricetodon*. The metalophulid of m3 is anterior, and there is a well-developed posterior branch of the protoconid; in *Kerosinia* this branch forms the posterior metalophulid, and the anterior metalophulid is absent». Comparison of the dentitions of the type species of *Pseudocricetodon* and *Allocricetodon* shows that these differ in the degree of reduction of the M3, m3 only.

Genus *Pseudocricetodon* THALER, 1969

Type species: *P. montalbanensis* THALER, 1969 Other species included: *P. thaleri* HUGUENEY, 1969, *P. philippi* HUGUENEY, 1971, *P. moguntiacus* (BAHLO, 1975), *P. moguntiacus orientalis* ÜNAY, 1989, *P. simplex* FREUDENTHAL *et al.*, 1994, *P. adroveri* FREUDENTHAL *et al.*, 1994, *P. nawabi* MARIVAUX *et al.*, 1999, *P. cornelii* FREUDENTHAL, 1994 (type of *Allocricetodon*), *P. incertus* (SCHLOSSER, 1884), *P. landroveri* (DAAMS *et al.*, 1989)

Diagnosis (DIENEMANN, 1987): "Small to medium sized cricetids with 'lophodontish' dental pattern. The main cusps and crests are separated by valleys with a flat bottom The well-defined gracile ridges are usually straight, rarely irregular due to small folds in the enamel" (translated from German).

Geographical range: Europe including European Turkey, Lesser Caucasus, Pakistan (Bugti area)

Stratigraphical range: Oligocene – Early Miocene

Introduction: While reviewing the literature on *Pseudocricetodon* we were struck by the similarity in morphology of the eleven species here allocated to the genus, a similarity that contrasts to the rather wide variation per sample. Since there seems to be no general evolutionary trend and since samples from widely separate areas such as Pakistan, Eastern Turkey and Spain do not show essential differences, we think the genus has been over-split. This the more so because a number of named species have roughly the same age and geographical origin. In the assemblage of Süngülü *Pseudocricetodon* is represented by a species of average size which will be, pending a revision of the genus, allocated to the European species *P. montalbanensis*.

<div align="center">

Pseudocricetodon aff *montalbanensis*
(Plate 5, figs 8-20)

</div>

Material and measurements samples A, B en C

	Length			Width	
	Range	Mean	N	Mean	Range
M1	12.7 - 15.1	14.18	15/19	9.65	8.1 - 10.6
M2	9.5 - 12.6	11.12	34/35	10.41	9.0 - 11.9
M3	9.3 - 9.8	9.6	2	9.9	9.8 - 9.9
m1	11.2 - 12.7	12.32	10/11	9.12	8.2 - 10.4
m2	11.0 - 12.2	10.87	11	9.84	8.4 - 10.3
m3	10.3 - 12.1	9.49	7	9.53	8.9 - 10.0

Description:

M1. (Plate 5, figs. 8, 9, 10) The labially situated anterocone is blade - shaped and has its tip almost on the straight line connecting the paracone and metacone. The lingual branch of the anteroloph continues as a cingulum to the base of the protocone. The protocone and hypocone are sub-equal in size, but the protocone is lower. The strong anterior arm of the protocone ends freely in the anterior basin. (13/15). The protoloph is somewhat posteriorly directed inserting on the posterior arm of the protocone (11/16), or its lingual part curves forwards and connects with the anterior arm of the protocone (4/16). This last con-

figuration is unusual in *Pseudocricetodon*, but common in *Kerosinia*. The short mesoloph is weak and sometimes bifurcates. The long metaloph inserts on the antero-labial side of the hypocone. The long thin posteroloph ends against the base of the metacone.

M2. (Plate 5, figs. 11, 12, 13) The thin anteroloph is divided by the anterolophule into a short lingual branch and a long labial branch. The protoloph is confluent with the anterior arm of the protocone. There are usually two weak mesoloph-like ridges (17/20). The anterior one of these, which is developed as the continuation of the posterior arm of the protocone, is always shorter than the posterior one and can be absent. Two M2 have a fully developed new endoloph. In these specimens the original endoloph is preserved. The straight metaloph is confluent with the anterior arm of the hypocone. The long thin posteroloph ends against the base of the metacone.

M3. (Plate 5, fig. 14) This element is represented by two specimens with very simple dental pattern. The anteroloph has a short lingual branch and a very long labial branch. The long protoloph is confluent with the anterior arm of the protocone. The metaloph is shorter than the protoloph and confluent with the posterior arm of the protocone. There is an indistinct low structure in the main basin that cannot be homologised. The sinus is almost non- existent. A lingual cingulum encloses the protocone. The posteroloph and metaloph enclose a shallow basin.

m1. (Plate 5, figs. 15 and 16) The anteroconid is small and situated near the protoconid/metaconid complex, so it hardly influences the length of the m1. The protoconid and anteroconid are connected by an anterolophule that is in line with the longitudinal crest. The metalophule 1 is missing. The metalophule 2 connects the metaconid to the postero-lingual side of the protoconid. The mesolophid is weak or absent. The length of the ecotomesolohid is variable. A long hypolophid connects the entoconid to the antero-lingual part of the hypoconid. The long thin posterolophid connects the tip of the hypoconid to the base of the entoconid.

m2. (Plate 5, figs. 17, 18) The occlusal surface of the m2 is sub-rectangular. The straight anterolophid is divided into a long lingual branch and a short labial branch. The short anterolophulid is situated lingually of the protoconid. The long transverse metalophid and hypolophid are confluent with the anterior arms of the protoconid and hypoconid. The posterior arm of the protoconid is variable in length and ends freely in the main basin. The mesolophid is rather weak and may be absent (2/6). The long thin posterolophid descends from the tip of the hypoconid lingually and ascends steeply to the tip of the entoconid.

m3. (Plate 5, figs. 19, 20) The long anterolophid connects the base of the protoconid and the metaconid. The

Plate 4. - *Witenia flava* n. gen. n. sp.; **1**, **2**, M1; **3**, M2; **4**, M3; **5**, m1; **6**, m2; **7**, m3.
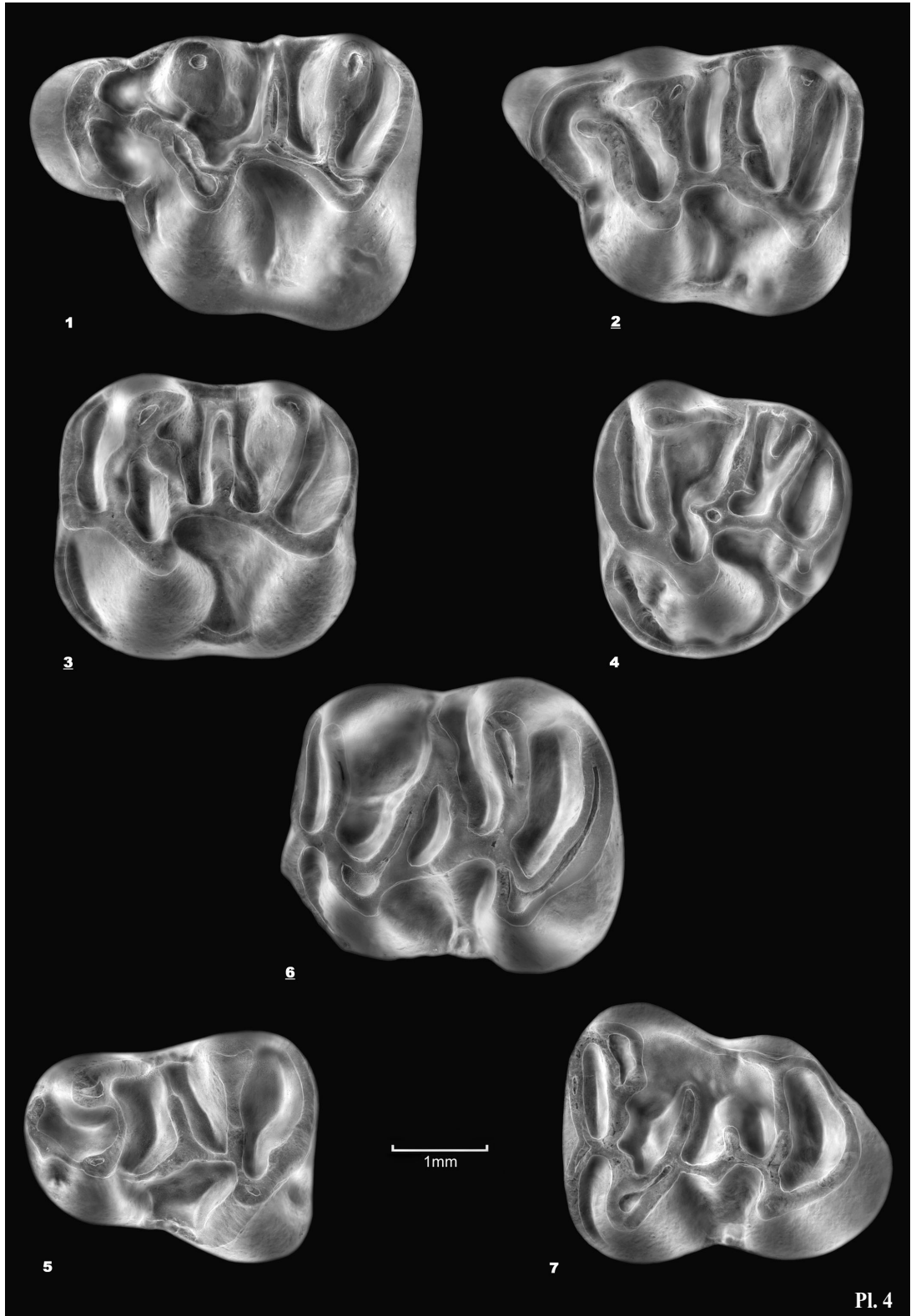
short anterolophulid, that is situated slightly lingually of the protoconid, divides the anterolophid into a long lingual branch and a short labial branch. The transverse metalophulid and hypolophulid are confluent with the anterior arms of the protoconid and hypoconid. The posterior arm of the protoconid is rather long and transverse, ending freely in the main basin. The mesolophid is weak or absent and the ectomesolophid is strong. The posterolophid descends lingually from the tip of the hypoconid and ascends steeply to the tip of the entoconid.

Remarks: The *Pseudocricetodon* material from Süngülü is of interest because it is, judging by the composition of the assemblage, the oldest record of the genus. The anterocone of the M1 and the anteroconid of the m1 are more retracted and blade-shaped than in most other assemblages. Moreover, the strong anterior arm of the protocone of the M1 is not connected to the anterocone as is often the case in other assemblages (including that of *P. moguntiacus orientalis* from Turkish Thrace). These characteristics suggest that the species from Süngülü is a shade more primitive *P. montalbanensis*. The differences relative to *montalbanensis* are subtle, so we assign our material to *P.* aff. *montalbanensis.*

Genus *Lignitella* ÜNAY, 1989

cf. *Lignitella suemengeni* ÜNAY, 1989
(Plate 5, figs. 21-24)

Introduction: Five very small cricetid teeth from Süngülü are tentatively assigned to this poorly known monospecific genus. The only tooth position that is known from the type locality Kocayarma (E. Oligocene, Thrace) as well as from Süngülü is M2. The teeth from both localities have the longitudinal crest in an unusually lingual position. The m1 that are tentatively allocated to *Lignitella* have the longitudinal crest in a labial position. Identification remains uncertain, until more material will be available.

Material and measurements:
1 M2 (8.8 x 8.0), 2 M3 (7.0 – 7.3 x 7.2 – 7.3), 2 m1 (9.8 –10.0 x 7.0 – 7.4)

Description:
M2. (Plate 5, fig. 23) The anteroloph consists almost exclusively of the long labial branch. The lingual branch is nothing but a vague ledge on the anterior surface of the protocone. The protoloph and metaloph are straight, parallel and forwards directed. The posterior spur of the paracone is long and reaches the metacone. There are two oblique mesolophs. The anterior one of these is shorter than the posterior one. The sinus is shallow and directed slightly forwards. The thin posteroloph connects the hypocone to the base of the metacone.

M3. (Plate 5, fig. 24) The two M3 allocated to L. suemengeni on the basis of size are rather different from each other and may not belong here both. The figured specimen has a well-developed lingual branch of the anteroloph, which is absent in the other specimen as well as in the M2 (see above), so the anteroloph shows either great variation or the two teeth represent different taxa. The two specimens are also different in that the figured one has no mesoloph, while the mesoloph in the other is long and reaches the labial border of the occlusal surface. Since the M3 is not available from the type locality assignment of the specimens from Süngülü remains speculative.

m1. (Plate 5, figs. 21,22) The 'anteroconid' is just a low ridge directly in front of the protoconid/metaconid complex. Both m1 have a short thin transverse metalophulid 1 that inserts labially on the anterolophulid. The posterior arm of the small protoconid connects the protoconid and metaconid also, so the two metalophulids enclose a small pit between the protoconid and metaconid. The longitudinal ridge is straight and low. The mesolophid is weak in one, absent in the other specimen. The transverse hypolophid inserts labially just in front of the small hypoconid or on the hypoconid proper. The long posterolophid descends from the tip of the hypoconid to the base of the entorconid.

Remarks: If our identification of the five teeth described above is correct, the m1 of *Lignitella* differs from that tooth in *Pseudocricetodon* by having a metalophulid 1. However, one m1 of *P. cf. montalbanensis* (Plate 5, fig. 15) from Süngülü shows a similar structure. Another difference between the m1 of the two genera is that the anteroconid is weaker, and developed as a ridge, in *Lignitella*.

Eucricetodontinae MEIN & FREUDENTHAL, 1971

Introduction: The Eucricetodontinae were originally defined in a restricted sense, just containing the genus Eucricetodon. The five species included in that genus by MEIN & FREUDENTHAL are: The type species *E. collatus* (SCHAUB, 1925) and the late Oligocene to Early Miocene *E. gerandianus, e. infralactorensis* (VIRET, 1930), *E. aquitanicus* BAUDELOT & DE BONIS, 1968 and *E. longidens* HUGUENEY, 1970. This restricted concept of the genus had the disadvantage that another ten "*Eucricetodon*" species had to be listed as Eucricetodontinae incertae sedis.

Plate 5. - *Edirnella kempeni* n. sp.; **1**, M1; **2**, M2; **3**, M3; **4**, m1; **5**, m2; **6**, m3. ? *Zhungaromys* sp., **7**, M1 damaged; *Pseudocricetodon* aff. *montalbanensis* THALER, 1969; **8-10**, M1; **11-13**, M2; **14**, M3; **15**, **16**, m1; **17**, **18**, m2; **19**, **20**, m3; *cf. Lignitella suemengeni* ÜNAY, 1989; **21**, **22**, m1; **23**, M2; **24**, M3.
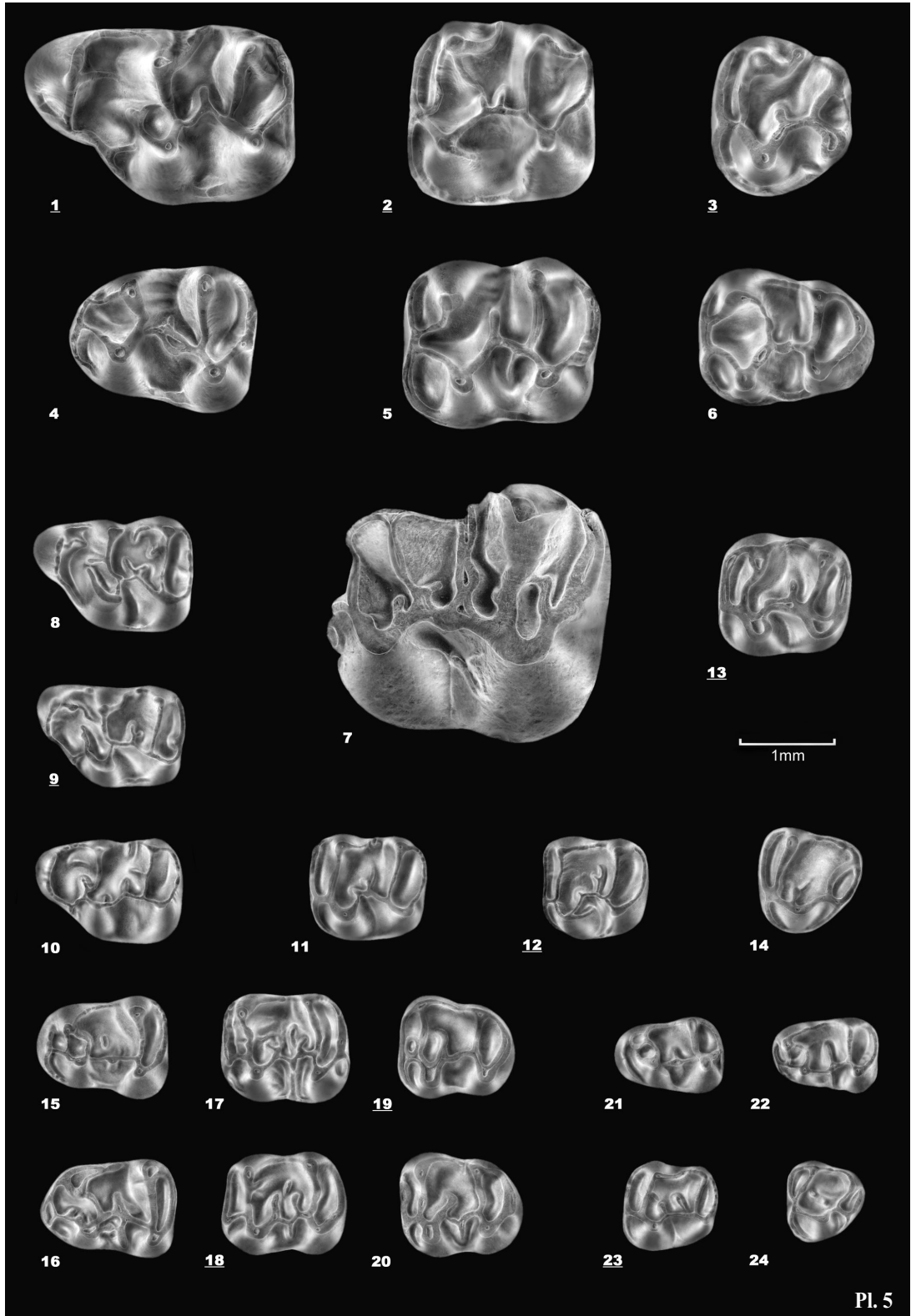
Pl. 5

Other authors, using the genus to house a wide variety of unspecialised as well as derived cricetid species from Europe and Asia, included many more species in the genus. ÜNAY (1989) lists, apart from the five species included by MEIN & FREUDENTHAL (1971), another nineteen species. This list contains some species of uncertain status, but there have been at least another ten species described since ÜNAY (1989).

In order to clarify the situation FREUDENTHAL *et al.* (1992) redefined the Eucricetodontinae, in which they include next to *Eucricetodon* the genera *Eumyarion* THALER, 1966 and *Mirabella* DE BRUIJN *et al.* (1987) with a question mark, as follows: "Small to large cricetids, dentition with rather bunodont cusps. Mandible transversally inclined with respect to the occlusal surface, diasteme concave with steep posterior border. Maxilla with short foramen incisivum, not – or only slightly – entering between the M1. Lower molars: m3 smaller than m1. Posterior part of m3 generally reduced. Protoconid hind arm in m1 and m3 frequently present, in m1 it may be connected to the metaconid. Anterior metalophulid in m1 frequently present. Posterolophid of m1 often forms a wide curve. In m2 and m3 the metalophulid is generally placed far forward, and the anterosinusid reduced. Upper molars: Lingual border of M1 straight or convex, forming an angle of less than 90º with the posterior border. The prelobe of M1 may be set off from the rest of the molar, but more frequently the lingual border between anterocone and protocone is smooth."

The problem of classifying these generalised cricetids is that they occur all over Eurasia from the Late Eocene onward into the Early Miocene showing a mozaic of minor differences that do not define discrete groups. In order to overcome this problem FREUDENTHAL (1996) defined the genus *Atavocricetodon* (type species *A. atavoides* FREUDENTHAL, 1996 from the Early Oligocene of Olalla 4a, Spain) to house the small Oligocene European members of the subfamily that have a primitive dental pattern. The definition of the genus *Atavocricetodon* has the practical advantage that it unites the primitive small Eucricetodontines into what seems to be a "morpho-subgenus". However, there is no reason to assume that its members are more closely related among them than they are to the more evolved later *Eucricetodon* species. In other words *Atavocricetodon* is a grade rather than a clade. We nevertheless maintain *Atavocricetodon* as a subgenus of *Eucricetodon* for pragmatical reasons.

Genus *Atavocricetodon* FREUDENTHAL 1996

Type species: *Atavocricetodon atavoides* FREUDENTHAL, 1996

Other species included: *A. murinus* (SCHLOSSER, 1884), *A. huberi* (SCHAUB, 1925), *A. atavus* (MISONNE, 1957), *A. meridionalis* (WANG & MENG, 1986), *A. leptaleos* (WANG & MENG, 1986), *A. nanus* (PELÁEZ-CAMPOMANES, 1995), *A. nanoides* FREUDENTHAL, 1996, *A. hugueneyae* FREUDENTHAL, 1996, *A. minusculus* FREUDENTHAL, 1996, *A. paaliensis* MARIVAUX, VIANEY-LIAUD & WELCOMME, 1999, *A. kurthi* n. sp.

Geographical range: Europe, Lesser Caucasus, Pakistan (Bugti area) and China

Stratigraphical range: Late Eocene and Early Oligocene

All these cricetids have approximately the same dental morphology, but differ somewhat in size and/or subtle details of the dental pattern. FREUDENTHAL (1996) diagnosed *Atavocricetodon* as follows: "Eucricetondontinae of very small to medium size, with relatively low-crowned cheek teeth with thin enamel, relatively small cusps, and long crests. Lower molars with or without hypoconid hind arm. m1 with protoconid hind arm frequently connected to the metaconid. Upper molars generally with a posterior protolophule and an anterior metalophule. M1 generally without a complete anterolophule. Old entoloph on M3 frequently present, or even complete, neo-entoloph fully developed."

The Eucricetodon material from Süngülü shows all the dental characterises of *Atavocricetodon*, so we shall restrict comparisons to the members of that subgenus.

Eucricetodon (Atavocricetodon) kurthi n. sp.
(Plate 6, figs. 16-27)

Derivatio nominis: The species is named in honour of Prof. Dr. K.H. Kurth. The first author (H.d.B.) expresses his gratitude for restoring his good health.

Type Locality: Süngülü B

*Holotype*: Isolated M1, Süngülü B, nr. 1104 (Pl. 6, fig. 17)

Type level: Eocene/Oligocene boundary interval

Diagnosis: Small *Atavocricetodon* of roughly similar size as *A. minusculus* from Spain, *A. leptaleos* from China and *A. paaliensis* from Pakistan.

M1 plump with simple somewhat medially placed single anterocone. Anterior arm of protocone ending freely and protoloph confluent with the posterior arm of the protocone. Mesoloph (= anterior arm of hypocone) of medium length or long. Metaloph anteriorly directed and inserting on the antero-labial corner of the hypocone.

M2 with parallel, slightly forward directed protoloph

Plate 6. - *Paracricetodon wentgesi* n. sp.; **1, 2, 13**, M1; **3, 4**, M2; **5, 6**, M3; **7, 8, 14**, m1; **9, 10, 15**, m2; **11, 12**, m3. *Eucricetodon* (*Atavocriceton*) *kurthi* n. sp.; **16, 17**, M1; **18, 19**, M2; **20, 21**, M3; **22, 23**, m1; **24, 25**, m2; **26, 27**, m3.

1mm

Pl. 6
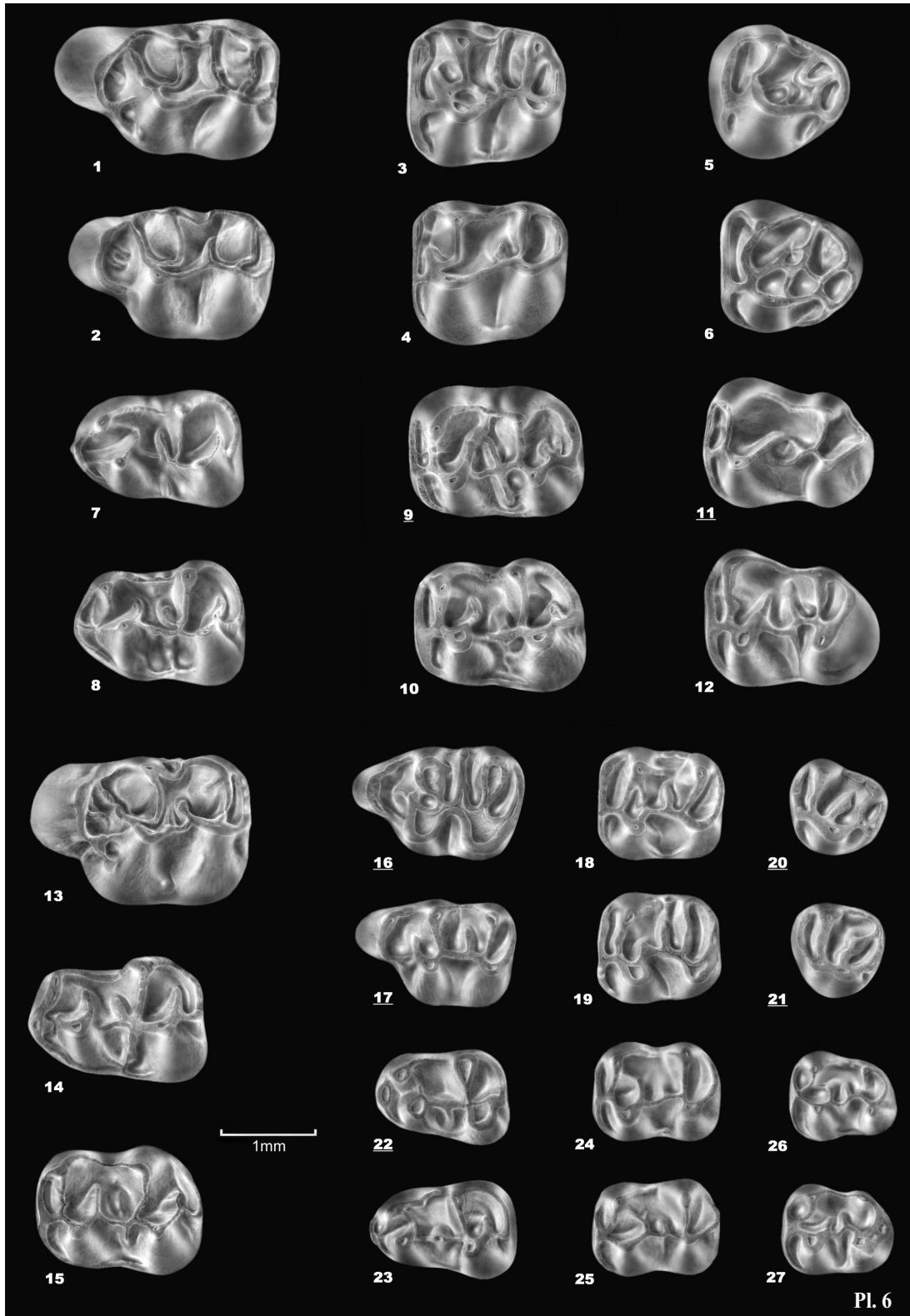
and metaloph that connect lingually to the anterior arms of the protocone and hypocone. Mesoloph short or absent. Some specimens show an incipient protolophule 2.

m1 with a very low, small retracted anteroconid. Metalophulid 1 incomplete or absent, metalophulid 2 formed by the posterior arm of the protoconid. Mesoconid often present, freely ending posterior arm of the hypoconid present in m1, absent in m2 and m3. Hypolophid missing in the m3.

Differential diagnosis: Atavocricetodon kurthi n. sp. is smaller than all other species of the genus except *A. minusculus, A. leptaleos* and *A . paaliensis. A . kurthi* differs form A. minusculus in having a plumper M1 and m1, a low anteroconid and a free-ending posterior arm of the hypoconid in the m1 and a medium to long mesoloph in the M1. *A. kurthi* n. sp. differs from *A. leptaleos* in having a much less developed anteroconid in the m1, which makes that tooth proportionally shorter. The protoloph connects to the posterior arm of the protocone and not via the anterior arm as in leptaleos. The mesoloph of the M1 is longer. *A. kurthi* teeth are less lophodont and plumper and shorter than those of *A. paaliensis* and the mesoloph is longer. Moreover, the cingulum that closes the lingual sinus of the M1, M2 of *A. paaliensis* is absent in *A. kurthi.*

Material and measurements samples A, B en C

	Length			Width	
	Range	Mean	N	Mean	Range
M1	15.1 – 16.7	16.0	6/7	10.9	10.0 – 11.5
M2	10.6 – 12.4	11.6	13/10	10.9	9.9 – 11.5
M3	8.6 – 9.3	8.9	4	8.9	8.6 – 9.4
m1	11.9 – 13.1	12.4	4/5	8.8	8.6 – 8.9
m2	10.6 – 12.4	12.0	12	9.8	9.2 – 11.0
m3	10.2 – 11.8	10.8	9	8.9	8.3 – 9.7

Description

M1. (Plate 6, figs. 16, 17) The anterocone is somewhat medially placed and narrow. Its lingual arm reaches the base of the protocone and the labial arm the base of the paracone. In one specimen (nr. 823) there is a very distinct comma-shaped cusp between the anterocone and the protocone. The anterior arm of the protocone is variable in length, directed forwards and ending freely, or directed towards the paracone. The protoloph and the metaloph converge lingually, the protoloph inserts on the posterior arm of the protocone, the metaloph on the anterior arm of the hypocone. The mesoloph is either long (3/6) or of medium length. The posteroloph descends from the tip of the hypocone to the base of the metacone. The sinus is more or less transverse.

M2. (Plate 6, figs. 18, 19) The well-developed long anteroloph is divided into a shorter lingual part and a longer labial part by the anterolophule. The parallel protoloph and metaloph insert on the anterior arm of the protocone and metacone respectively. In some specimens

(3/12) there is an incipiant protolophule 2. The mesoloph is short. The posteroloph descends from the tip of the hypocone to the base of the metacone. The sinus is directed obliquely forwards.

M3. (Plate 6, figs. 20, 21) The occlusal surface of the M3 is rounded. The anteroloph may be short and weak. The protoloph and the metaloph converge towards the protocone. In some M3 the main basin is smooth, but in others there are irregular crests. The hypocone is very weak and the sinus is shallow.

m1. (Plate 6, figs. 22 and 23) The retracted anteroconid is much lower than the protoconid and metaconid and is situated on the longitudinal median axis of the occlusal surface. The metalophulid 1 is present in some m1 (2/5), but absent in others. The posterior arm of the conicle protoconid forms the metalophulid 2. The low straight ectolophid is short and may bear an indistict mesoconid. The mesolophid is weak or absent. The posterior arm of the hypoconid is variable in length and directed towards the entoconid. The posterolophid is detached from the hypoconid and ascends lingually to the tip of the entoconid.

m2. (Plate 6, figs. 24, 25) The lingual and labial branch of the anterolophid are almost the same length. The metalophulid 1 is incomplete in some m2 (4/10), in the others its is somewhat forwards directed and inserts on the anterolophulid or on the anterolophid. The posterior arm of the protoconid is shorter in m2 than in the m1 and usually does not reach the base of the metaconid. The low and straight ectolophid may bear a small mesoconid. The mesolophid is absent (4/10), weak and indistinct (5/10) or of medium length (1/10). The labial part of the transverse hypolophid is low and narrow and inserts on the antero-lingual corner of the hypoconid. The posterior arm of the hypoconid is absent (8/10) or weak (2/10). Other than in the m1, the posterolophid is confluent with the posterior arm of the hypoconid and descends towards the base of the entoconid.

m3. (Plate 6, figs. 26, 27) The lingual and labial branch of the anterolophid are equal in length. The slightly forwards directed metalophulid 1 inserts on the anterolophulid (6/9), on the anteroconid (1/9) or on the anterolophid (2/9). The posterior arm of the protoconid is rather short and ends freely except in one m3 (Plate 6, fig. 26). The mesolophid is short or absent. A peculiar characteristic of *A. kurthi* is that although the entoconid of the m3 is usually rather well developed, the hypolophid of that tooth is missing. The posterolophid is strong, incorporates the entoconid and continues as an endolophid along the lingual edge of the occlusal surface till the tip of the metaconid.

Remarks: The subgenus *Atavocricetodon* has an unusually large geographical range that is, among cricetids, matched by *Democricetodon* only. Since *Atavocricetodon* as well as *Democricetodon* are having very unspecialised cricetid dentitions it is conceivable that we have reached the limits of paleontological classification based on dentitions and unite taxa in the same (sub)genus that belong biologically to different groups.

Comparison of the dentition of *A. kurthi* n. sp. with that of the enigmatic genus and species *Primus microps* from the Lower Miocene Murree Formation of northern Pakistan reveals some striking similarities. The unusual absence of the hypolophid in the m3 of both these taxa makes one wonder whether or not the overall similarity of their dentition is the result of close phylogenetical ties or is yet another example of parallel evolution.

Pappocricetodontinae Tong, 1997

Type genus: *Pappocricetodon* Tong, 1992 (= *Raricricetodon*, Tong, 1997)
Other genera included: ? *Palasiomys* Tong, 1997; *Witenia* n. gen.

Introduction: The assemblage from Süngülü contains two large cricetid species that obviously represent the same genus. Apart from their unusually large size the cheek teeth of these species match the primitive pattern seen in *Pappocricetodon* and *Raricricetodon* Tong, 1997. Judging by the figures and measurements in Tong (1997) the type species of these "genera": *P. rencunensis* and *R. zhongtiaensis* from the lower, respectively the upper, fossiliferous beds of the Rencun member of the Hedi Formation are very similar and do not warrant the recognition of the two genera. We therefore consider *Raricricetodon* a junior synonym of *Pappocricetodon* and maintain the species *R. zhongtaensis* in *Pappocricetodon*. Tong (1997) gives the following diagnosis for the Pappocricetodontinae: "Primitive cricetids, with lower-crowned cheek teeth. P4 present in the Irdinmanhan genus, *Palasiomys* and *'Pappocricetodon' antiquus*, lost in the later taxa; M1 more or less enlarged, parastyle crescentic, cuspate or a swelling, anterolobe small or absent, preprotocrista extending anterolabially and usually connected with parastyle, protoconule minute when present, generally anterior connection between protocone and paracone, sometimes double connection present; m1 smaller than m2 in size, anteroconid weak or absent; M2-3 and m2-3 anterocone(id) low, precingulum continuous, but less elevated; m2-3 with incipient premetacristid and ectomesolophid developed in the later species; m3 ectolophid curved". We consider this elaborate diagnosis to be the diagnosis of *Pappocricetodon* also.

Genus *Witenia* n. gen.

Derivatio nominis: Named in honour of L.W.L.de Bruijn (blond Wiet) and L. de Bruijn (dark Wiet) in recognition of their sponsoring of research on fossil small mammals at the University of Utrecht.
Type species: *Witenia flava* n. sp.
Other species included: *Witenia fusca* n. sp., ? *Leidymys azybaevi* Shevyreva, 1994. We have not seen the specimens of *Leidymys azybaevi* from the Lower Oligocene of the Zaisan basin, so generic allocation is uncertain.

Diagnosis: Anterocone of the M1 narrow, crescentic and situated somewhat more lingually then the paracone. Metaloph single and sometimes incomplete in the M1, double or incipiently double in the M2. M3 with a deep, anteriorly directed, sinus. Anteroconid of the m1 developed as a narrow antero-lingually directed crest of the protoconid. m3 larger than m1. The sinus of the lower cheek teeth is large and lingually bounded by an antero-labially posterolingually directed oblique crest.
Differential diagnosis: *Witenia* differs from *Pappocricetodon* in having the anterocone of the M1, more lingually placed. The metalophule of the M2 is always double or incipiently double in *Witenia*, rarely so in *Pappocricetodon*. The sinus of the M3 of *Witenia* is deep and delimited by the original longitudinal crest, in *Pappocricetodon* this sinus is shallow and delimited by the new protocone-hypocone connection. The sinusid of the lower cheek teeth of *Witenia* is larger than in *Pappocricetodon* and *Palasiomys* and lingually delimited by an oblique longitudinal crest. *Witenia* differs from *Palasiomys conulus* (type species) in having more lophodent cheek teeth. The endoloph of the M1, M2 is incomplete in *Palasiomys*, but complete in *Witenia*.

<center>

Witenia flava n. sp.
(Plate 4, figs. 1-7)

</center>

Derivatio nominis: " Flavus" in Latin means blond
Type locality: Süngülü A
Type level: Eo/Oligocene boundary interval
Holotype: M1 sin. Süngülü A, nr 371 (Pl. 4, fig. 1)
Diagnosis: Large species of *Witenia*. Upper molars with long mesoloph (= anterior arm of hypocone) reaching the labial border of the occlusal surface. Protolophule 1 and 2 well developed in M2. Lingual branch of the anteroloph of the M3 well developed.
Differential diagnosis: Witenia flava cheek teeth are about 20% larger than those of *W. fusca* n.sp. The mesoloph of the M1, M2, the protolophule 2 of the M2 and the lingual branch of the anteroloph of the M2, M3 are stronger in *W. flava* than in *W. fusca*.

Material and measurements samples A, B and C.

	Length			Width	
	Range	Mean	N	Mean	Range
M1	31.0 – 36.4	33.1	7/9	25.3	23.5 – 27.7
M2	26.0 – 28.0	27.3	4	26.1	25.7 – 26.5
M3	21.5 – 24.2	23.2	4	24.0	22.7 – 25.2
m1	27.1 – 27.5	27.3	2	20.8	20.3 – 21.2
m2	28.1 – 31.6	29.9	2	25.7	27.4 – 23.9
m3	29.8 – 30.9	30.4	2	23.2	22.4 – 24.0

Description:
M1. (Plate 4, figs. 1,2) The narrow anterocone is blade-shaped (6/7), or developed as a low cusp (1/7). The strong lingual part of the anterior arm of the protocone is directed

antero-labially. The labial part of this crest is much weaker and connected to the anterocone (6/7). The voluminous paracone is connected to the posterior arm of the protocone by the protoloph (7/9), or more or less isolated and weakly connected to the anterior arm of the protocone (2/9). The mesoloph (=anterior arm of hypocone) is usually long and reaches the labial border of the occlusal surface (9/10). The strong somewhat forwards directed metaloph inserts on the antero-labial side of the hypocone. The posteroloph descends from the tip of the hypocone to the base of the metacone from which it is separated by a weak notch

M2. (Plate 4, fig. 3) The labial part of the anteroloph is somewhat longer than the lingual part. The protolophule 1 connects the paracone to the anterior arm of the protocone and seems to be the homologue of the anterior arm of the protocone in the M1. The protolophule 2 is incomplete (1/5) or connects the posterior arm of the protocone to the base of the paracone (4/5). The mesoloph is long and the metaloph is somewhat directed forwards inserting on the anterior side of the hypocone. The posteroloph descends from the tip of the hypocone to the base of the metacone.

M3. (Plate 4, fig. 4) The anteroloph of the M3 is very strong. Its lingual branch continues as a lingual cingulum to the hypocone, while its labial branch is developed as in the M2. The transverse straight single protoloph connects the paracone to the anterior arm of the protocone. The long thin mesoloph and metaloph are parallel and insert separately on the original endoloph. The hypocone is situated postero-labially of the protcone. The deep sinus is lingually open and strongly directed forwards.

m1 (Plate 4, fig. 5) The anteroconid of the m1 is, as such, absent, but there is a low antero-lingually directed spur of the protoconid. The metalophulid 1 is absent, but the rather small protoconid and metaconid are connected by the posterior arm of the protoconid as in all other Pappocricetodontinae. The large sinusid is lingually bounded by an oblique crest that connects the postero-labial part of the protoconid to the transverse hypolophid. The mesolophid is long and reaches the lingual border of the occlusal surface. The posterolophid descends from the tip of the hypoconid and ascends again to the tip of the entoconid.

m2. (Plate 4, fig. 6) The labial branch of the anterolophid is slightly shorter than the lingual branch. The parallel metalophid and hypolophid are somewhat anteriorly directed and insert on the anterior arms of the protoconid and the hypoconid respectively. The posterior arm of the protoconid is exceptionally strong and meets the long mesolophid near the lingual edge of the occlusal surface. The longitudinal crest is oblique as in the m1. The posterolophid descends from the hypoconid and ascends again to the tip of the entoconid.

m3. (plate 4, fig. 7) The m3 is much longer than the m1. The lingual and labial branches of the anterolophid are equal in length. The parallel metalophid and hypolophid are directed somewhat forwards and insert on the antero-lophulid and the longitudinal ridge respectively. The posterior arm of the

protoconid ends freely in the main basin. The mesolophid is short and does not connect to the posterior arm of the protoconid. The smoothly curving posterolophid is much higher than in the m1 and m2 and connects the hypoconid to the entoconid.

Witenia fusca n. sp.
(Plate 3, figs. 10-18)

Derivatio nominis: "*Fuscus*" means dark in Latin
Type locality: Süngülü A
Type level: Eo/Oligocene boundary interval
Holotype: M1 dext. Süngülü A, nr. 351 (Pl. 3, fig. 10).
Diagnosis: W. *fusca* cheek teeth are of medium size. Mesoloph of M1 and M2 usually incomplete. Metalophule 2 of M2 incomplete. Lingual branch of the anteroloph of the M3 weak or absent.

Differential diagnosis: The cheek teeth of *W. fusca* are about 20% smaller than the ones of *W. flava*. The anterocone is more retracted in *W. fusca* than in W. flava and less clearly set off from the protocone. The mesolophs of the M1 and M2 are not complete as in *W. flava* and the protolophule 2 of the M2 is shorter than in that species. The M3 differs from that tooth in *W. flava* in having a posteriorly expanded occlusal surface and in the weaker development of the lingual branch of the anteroloph.

Material and measurements. Samples A, B and C.

	Length			Width	
	Range	Mean	N	Mean	Range
M1	26.5 – 27.6	27.1	2	21.8	21.7 – 21.9
M2	20.0 – 23.0	21.6	4	20.7	18.8 – 22.1
M3	19.9 – 20.7	20.3	2	19.0	18.6 – 19.4
m1	21.2 – 21.6	21.4	2	16.7	16.5 – 16.8
m2	24.8 – 25.5	25.2	2	20.8	20.6 – 20.9
m3		23.9	1	18.1	

Description:

M1. (Plate 3, figs. 10, 11) The anterocone is situated close to the protocone/paracone complex and not clearly set-off from the protocone. The anterior arm of the protocone is strong and connected to the anterocone. The voluminous paracone is isolated until a late stage of wear. The mesoloph (= anterior arm of the hypocone) is of medium length and does not connect with the mesostyle. The transverse metaloph connects the metacone to the hypocone. The posteroloph is narrow and separated from the metacone by a notch.

M2. (Plate 3, figs. 12, 13) The lingual branch of the anteroloph is only slightly shorter than the labial branch. The strong transverse protolophule 1 is lingually confluent with the anterior arm of the protocone. The protolophule 2 is short and does not connect to the paracone in early wear stages. The mesoloph is longer than the protolophule 2, but does not reach the edge of the occlusal surface. The transverse metaloph inserts on the anterior arm of the hypocone. The posteroloph descends form the tip of the hypocone to

the base of the metacone and is separated from that cusp by a narrow notch.

M3. (plate 3, figs. 14 and 15) The labial branch of the anterloph is long, but the lingual branch is weak or absent. The strong transverse protolophule 1 is confluent with the anterior arm of the protocone. The potolophule 2 is developed as a short antero-labially directed spur. The mesoloph is long and reaches the labial edge of the occlusal surface where it inserts on the ectoloph. The long oblique metaloph is narrow. The posteroloph continues from the "hypocone" along the edge of the occlusal surface to the paracone. The hypocone and metacone are entirely incorporated into this ridge and not recognisable as cusps.

m1. (Plate 3, fig. 16) The anteroconid is absent, but there is a lingually directed spur of the protoconid in front of the protoconid/metaconid complex that hardly contributes to the length of the m1. The protoconid and metaconid are situated near to one another and connected by the posterior arm of the protoconid. The longitudinal ridge is oblique relative to the median longitudinal axis of the occlusal surface and connects the posterior part of the proto-cone to the hypolophid. The longitudinal ridge and the mesolophid/ectomesolophid make right angles (cross-configuration). The hypolophid inserts on the longitudinal ridge just in front of the hypoconid. The posterolophid (bearing a small hypoconulid) descends from the tip of the hypoconid and ascends lingually to the tip of the entoconid.

m2. (Plate 3, fig. 17) The lingual and labial branch of the anterolophid are approximately the same length. The transverse metalophid is either confluent with the anterior arm of the protoconid or inserts on the anterolophulid. The long posterior arm of the protoconid ends freely in the main basin. The longitudinal ridge is oblique relative to the median longitudinal axis of the occlusal surface. The mesolophid/ectomesolophid and the longitudinal ridge make right angles. The posterolophid is rather wide because there is a poorly delimited hypoconulid. One of the two m2 has a peculiar cingulum along the postero-labial base of the hypoconid.

m3. (Plate 3, fig. 18) The lingual and labial branch of the anterolophid are the same length. The parallel metalophid and hypolophid are directed somewhat anteriorly and insert on the anterior arms of the protoconid and hypoconid. The long posterior arm of the protoconid is almost transverse and reaches the base of the metaconid. The mesolophid is of medium length. There is a welldelimited round mesostylid between the metaconid and the entoconid. The wide strong posterolohid is constricted just posteriorly of the entoconid.

Muridae incertae sedis

Genus ? *Zhungaromys* Emry, Tyutkova, Lucas & Wang, 1998

cf. *Zhungaromys* sp.
(Plate 5, fig. 7)

Remarks: One broken M1 from Süngülü B (width 24.3) of about the same size as the M1 of *W. fusca* shows a, for a cricetid, very unusual dental pattern. The only animal we could find in the literature that has a somewhat similar morphology is the poorly documented questionable cricetid *Zhungaromys gromovi* Emry *et al.*, 1998 from the Middle Eocene Kalpak Formation of the Zaisan basin (eastern Kazakhstan). Unfortunately the M1 of that species is not known yet, so the posterior part of our specimen has to be compared to the M2. The two specimens share a strongly forwards directed sinus, a very strong anterior arm of the protocone, a dental pattern consisting of voluminous cusps and crests separated by narrow valleys and above all the presence of a ridge between the metaloph and the postero-loph, a structure that, to our knowledge, is unique. If our allocation of the specimen from Süngülü B (nr. 391) to *Zhungaromys* is correct, it represents a species that is much larger than *Z. gromovi*.

Melissiodontinae Schaub, 1925

Type species: *M quercyi* Schaub, 1920
Genera included : *Edirnella* Ünay, 1989

Schaub (1925) gave the following diagnosis for *Melissiodon*. "Molars with four cusps and of about the same length. Cusps not voluminous. Occlusal surface divided by high enamel ridges into deep enclosed valleys. The connections between the cusps show a strongly modified cricetid pattern. The single or double anteroconid of the m1 does not add to the length of this tooth. The M1 with its wide bicuspid anterocone is much longer than M2. The alveole of the lower incisor is situated below the m2" (free translation from German).

Schaub did not give a formal diagnosis for his Melissiodontinae, but since all later students of the group with the exception of Ünay (1989), have restricted the (sub)family to the genus *Melissiodon* proper it seems safe to apply Schaub's generic diagnosis to the (sub) family. The inclusion of the Melissiodontinae and Paracricetodontinae into a single family Melissiodontidae as suggested by the second author (Ünay, 1989) on the basis of dental similarity has been shown to be incorrect (Kristkoiz, 1992). The morphology of the skull (?Hystricomorphous) and the mandible of *Melissiodon* are so different from all other cricetids that there was good reason to maintain the subfamily as monogeneric (Freudenthal *et al.*, 1992, Mödden, 1999). However, the new material of the genus *Edirnella* that will be described below supports the conclusion of Ünay (1989) that *Edirnella* and *Melissiodon* are related. It is our working hypothesis that *Edirnella* is in the ancestry of *Melissiodon,* so the dental characteristics of the Melissiodontinae (sensu Ünay, 1989) do not apply

because neither *Melissiodon* nor *Edirnella* has a posterior arm of the hypoconid in the m2.

Genus *Edirnella* ÜNAY, 1989

Type species: *Edirnella sinani* ÜNAY, 1989
Other species included: *E. kempeni* n.sp.

Edirnella kempeni
(Plate 5, figs. 1-6)

Derivatio nominis: The species is named after Kempen & Co merchant bank, acknowledging the financial support of the research of the first author (H.d.B.).
Type locality: Süngülü A
Holotype: Isolated M1 dext, Süngülü A nr. 401 (Plate 5, fig. 1)
Type level: Eo/Oligocene boundary interval.
Diagnosis and differential diagnosis: E. kempeni teeth are about 20% smaller than those of *E. sinani* and there is no overlap between the size ranges of the two species. The sinus of the upper molars is less deep in *kempeni* than in *sinani* and the protoloph of the M3 is transverse in *E. kempeni*, but forwards directed in *E. sinani*. The general dental pattern of the upper cheek teeth is similar in the two species, but the ones of *kempeni* are deviating less from the basic cricetid type than those of *sinani*.

Material and measurements Samples A, B and C.

	Length			Width	
	Range	Mean	N	Mean	Range
M1	24.5 – 25.3	24.9	2	17.1	16.0 – 18.1
M2	13.7 – 18.5	16.88	13	16.67	13.4 – 18.2 *
M3	12.0 – 14.0	12.85	20	14.94	13.9 – 16.5
m1	17.7 – 20.5	19.0	6	14.68	13.0 – 16.0
m2	16.7 – 18.6	17.67	7	15.49	14.2 – 16.6
m3	16.5 – 19.9	18.25	8/9	14.10	12.9 – 15.3

*The range of length and width of the M2 is unusually large because of one specimen nr. 412. It can not be excluded that this specimen (13.7 x 13.4) with the morphology of M2 is either a M3, or represents a smaller species.

Description:
M1. (plate 5, fig. 1) The single blade-shaped anterocone is narrower and more labially placed in the specimen figured than in the other one. The labial branch of the anterocone connects to the base of the paracone, the lingual branch bears a *Melissiodon* cusp of variable size, but is otherwise developed as a narrow cingulum that may continue all the way to the hypocone (1/4) as in *E. sinani*. The other specimens do not show an antero-lingual crest on the hypocone. The anterior arm of the protocone ends either freely or is connected to the paracone. All three specimens have a low ridge con-

necting the anterior arm of the protocone to the *Melissiodon* cusp. The protoloph is somewhat posteriorly directed and inserts on the low longitudinal ridge behind the protocone. The paracone has a postero-labially directed burgee-shaped spur. The mesoloph (=anterior arm of hypocone) is short or of medium length. In one specimen this ridge reaches the metacone. The narrow metaloph descends from the tip of the metacone to the base of the hypocone (or the anterior arm of the hypocone). The narrow posteroloph continues around the metacone to half way its labial side. Some specimens have a sharp posterior crest on the metacone (3/4) that connects to the posteroloph.

M2. (Plate 5, fig. 2) The anteroloph is divided by a short anterolophule into a more or less equal labial and lingual part. The lingual branch of the anteroloph continues as a lingual cingulum that reaches the hypocone. The thin transverse protolophule 1 descends from the tip of the paracone to the base of the anterior arm of the protocone. The metalophule 2 is usually an indistinct connection between the posterior arm of the protocone and the paracone. The paracone has a brugee-shaped posterior spur that ends on the labial edge of the occlusal surface. The notch between the paracone spur and the metacone is deep. The thin metalophule descends from the tip of the metacone to the base of the anterior arm of the hypocone. The burgee-shaped posterior crest of the metacone connects that cusp to the thin posteroloph that descends from the tip of the hypocone to the labial side of the metacone.

M3. (Plate 5, fig. 3). The shape of the occlusal surface of the M3 shows much variation. Some M3 are antero-posteriorly compressed and very short, others are more square and simular to the M2 but without posteroloph. The labial branch of the anteroloph is usually longer than the lingual branch, but in some M3 the lingual branch continues as a lingual cingulum all the way to the small hypocone. The protolophule 1 is usually transverse (13/15) and inserts on the anterior arm of the protocone, but in the two others it is forwards directed and connected to the labial branch of the anteroloph. The short mesoloph is directed towards the paracone, but never forms a protolophule 2. The sub-equal hypocone and metacone are situated on the posterior border of the occlusal surface. The posteroloph is absent (9/17) or poorly developed.

m1. (plate 5, fig. 4) The anterolophid of the m1 is a low smoothly curving ridge that is situated very closely to the protoconid and metaconid which gives the tooth an unnatural short plump appearance. A strong anterolophulid that descends from the tip of the protoconid reaches the anterolophid near its middle. The spot where the anterolophulid meets the anterolophid is somewhat more elevated than the rest of the anterolophid suggesting a tiny anteroconid. The long posterior arm of the protoconid is confluent with the short metalophid. The part of the sinus in front of the mesoconid is much deeper than the part behind the mesoconid just like in *Melissiodon*. This means that the longitudinal ridge makes an angle with the central longitudinal axis of

the occlusal surface. The short hypolophid descends from the tip of the very high voluminous entoconid to the anterior arm of the hypoconid. The posterolophid descends form the tip of the hypoconid lingually and then ascends to the tip of the entoconid. The hyopconulid is small and indistinct (4/5). A short mesolophid is present in two out of five m1.

m2. (Plate 5, fig. 5) The lingual and labial arm of the anterolophid are of about the same length. The antero-lophulid and the strongly forwards directed metalophulid 1 insert on the anterolophid separately (as in Melissiodon). The labial arm of the anterolophid, the protoconid and the anterolophulid enclose an oval basin. The strong posterior arm of the protoconid ends freely (2/6) or forms a meta-lophulid 2 that connects the metaconid to the protoconid. The ectomesolophid is weak or absent. The slightly forwards curving hypolophid descends steeply from the tip of the entoconid to the base of the longitudinal ridge in front of the hypoconid. The longitudinal ridge proper is strongly oblique, connecting the antero-lingual part of the hypoconid to the posterior arm of the protoconid near the centre of the occlusal surface. The narrow posterolophid descends from the tip of the hypoconid and connects with the weak postero-lingual spur of the entoconid.

m3. (Plate 5, fig. 6) The labial branch of the anterolophid is longer than its lingual branch. The long anterolophulid and the forwards directed metalophulid reach the anterolophid separately. The anterolophulid, labial arm of the anterolophid and the protoconid enclose an oval basin. The strong poste-rior arm of the protoconid either connects to the metaconid (7/9) or ends freely in the main basin (2/9). The hypolophid descends form the rather small-conicle entoconid and con-nects congluently with the anterior arm of the hypoconid. The smoothly curving posterolophid usually connects the hypoconid to the entoconid (5/6), but is separated from the entoconid by a notch in one specimen.

Remarks: ÜNAY (1989 Plate 7, fig. 5) excluded a worn lophodont second molar from *Edirnella sinani* and identified it as *Heterocricetodon* cf. *schlosseri* SCHAUB, 1925. We agree with MEIN (pers. comm, 1989) that this tooth is not the m2 sin of *Heterocricetodon*, but the M2 dext of *E. sinani*.

The material of *E. kempeni* is of special interest because it contains the first incontestable information on the lower dentition of *Edirnella*. This new material leaves, in our opinion, no doubt that *Melissiodon* stems from *Edirnella*, because these genera share a large number of derived den-tal characteristics. These are:

Upper dentition; The shape of the anterocone of the M1. The presence of the *Melissiodon* cusp in the M1. The V-shaped protocone and hypocone and the absence of the posteroloph in the M3.

Lower dentition; The strong anterolophulids in the m1-m3. The presence of the oval basin in front of the proto-conid in m2, m3. The oblique ectolophids in m1-3. The V-shaped protoconid and hypoconid. The presence of thin ridges with steep walls.

COMPOSITION OF THE ASSEMBLAGE

The Süngülü mammal assemblage is dominated by rodents, but there are some insectivore and artiodactyle remains also. Lagomorpha are absent.

The eleven rodent species recognised represent three families only: the Ctenodactylidae, Dipodidae and Muridae. The Ctenodactylidae (± 22%) are represented by two species, the Dipodidae (± 3%) by one species and the Muridae (± 75 %) by seven species (not counting cf. *Zhungaromys* which is represented by one broken molar only). This dominance of the Muridae in number of specimens as well as species seems to be characteristic for Anatolian assemblages from the Eocene to the Pliocene. The Late Eocene/Early Oligocene assemblages of Central Asia differ in that the diversity of the Ctenodactyloidea is larger and that of the Muridae smaller. Moreover, these assemblages contain as a rule some Ischyromyidae and Cylindrodontidae, families that are not known from Anatolia. So far there is no Paleo-gene record of the Lagomorpha from Anatolia while the Gliridae seem to appear in the Late Oligocene, the Sciuri-dae in the Early Miocene and the Eomyidae in the Middle Miocene. The composition of the Paleogene Anatolian rodent assemblages differs sharply form the European ones in the absence of Theridomyidae, Pseudosciuridae, Gliridae and Sciuridae. The Early Oligocene assemblages from the Ergene basin (Thrace) contain an interesting mixture of taxa from the Western European and the Anatolian fauna province (Ünay, 1989). Typical European elements in these faunas are the Pseudosciuridae and Gliridae while the Eomyidae, a family that is supposedly of North American origin, is shared with the European as well as the Central Asiatic faunas. The fauna from Süngülü shares the murid genera *Pseudocricetodon* and *Paracricetodon* with Europe and the genus *Eucricetodon* with Europe and Central Asia. The affinity of the associations from Anatolia and Thrace is documented by the exclusive presence of the murid genera *Edirnella* and *Lignitella* in Süngülü and Kocayarma.

Comparison of the assemblage from Süngülü with faunas of similar age from Central Asia and Europe shows that the Late Eocene/Early Oligocene rodent fauna of Anatolia has endemic characteristics. This suggest that fauna exchange between Anatolia and Central Asia, and between Anatolia and Europe was limited by physical and/or ecological barriers during that period.

THE AGE OF THE ASSEMBLAGE

The biostratigraphical correlation of the Süngülü association of rodents is difficult because the nearest well documented Paleogene sequences from Europe and Central Asia hardly contain taxa that occur in Süngülü. Our age estimate has therefore to be based on the, per definition inaccurate, comparison of stage –of – evolution of the representatives of the three families present.

Ctenodactylidae: The species *Ottomania proavita* shows a similar stage of evolution in molar structure as P*rotataromys mianchiensis* from the Late Middle Eocene of Shange (China), but its premolars are less molariform. Whether or not this should be interpreted as archaic or derived is uncertain, but since the premolars of *Ottomania* are even less molariform than in the oldest ctenodactyloids (Tamquammyinae) we assume that trends towards de-molarisation as well as towards molarisation of the pre-molars occur in different lineages. We are thus inclined to consider *Ottomania* to be younger than *Protataromys*.

The structure of the molars of *Confiniummys sidiki* is almost identical to that in *Protophiomys algeriensis* from the Late Eocene of Nementcha (Algeria), but its pre-molars are not molariform as in this last species. Basically the molars of most Paleogene phiomyids are similar to those of the early ctenodactyloids, but the premolars seem to have become molariform at a very early stage in the evolution of this African sister group, so the age relationship of *Confiniummys* and *Protophiomys* is uncertain.

Dipodidae: *Heosminthus minutus* from Süngülü is about identical to the type material from the Early Oligocene of Hsanda Gol, (Mongolia), a locality that is situated between two basalts that have been radiometrically dated at 31.5 and 28 Ma. The only difference between the material from the two localities seems to be that the M1 and M2 are more similar to each other in our material than in the types, a characteristic than we are inclined to interpret as primitive. This means that Süngülü is probably somewhat older than Hsanda Gol.

Muridae: The two species of *Witenia* from Süngülü have very similar dentitions that differ primarily in size. These species are both reminiscent of *Pappocriceton* in many respects, but have a larger M3 and an anteroconid in the m1 that is developed as an antero-lingually directed crest of the protoconid. Since the oldest known species *Pappocricetodon antiquus* has a small triangular M3 and a tiny centrally placed anteroconid in the m1, the situation in *Witenia* seems more derived. This idea is supported by the greater similarity of *Witenia* to *P. schaubi* from the Late Eocene of Zhaili (China) than to the older species *P. antiquus, P. zhongtiaensis* and *P. rencunensis*. Since our species are much larger than any *Pappocricetodon* they suggest a latest Eocene or earliest Oligocene age.

Edirnella kempeni is somewhat smaller and more primitive than *Edirnella sinani* from Kocayarma, a locality that is situated above a volcanic tuff that has been given a fission track date of 33.2 Ma (ÜNAY, 1989). Since *Edirnella* is a highly specialised cricetid there is good reason to suppose that the species *E. kempeni* and *E. sinani* have an ancestor descendent relationship, so Süngülü is considered to be older than Kocayarma, a locality that has been correlated with MP 25.

Pseudocricetodon aff. *montalbanensis* from Süngülü seems to be somewhat more primitive than the type material of *P. montalbanensis* from the Lower Oligocene of Montal-ban (Spain), a locality that is currently correlated with MP 23. Unfortunately we have been unable to detect a well defined evolutionary trend in *Pseudocricetodon*. Although the later species appear to have a somewhat more complex dental pattern than the early Oligocene ones we hesitate to use the group for biostratigraphy.

Paracricetodon wentgesi is, among the European species of the genus, morphologically most similar to *P. dehmi* from the Lower Oligocene (MP 23) locality Bern-loch (Germany), but much smaller. The very small size of *P. wengesi* suggest that it may be the oldest record of the genus, but it should be kept in mind that there seems to be a consis-tent difference in the development of the M3 between the western European and the eastern European/western Asiat-ic representatives of the genus, so these may well have had independent phylogenetical histories.

Eucricetodon (Atavocricetodon) kurthi from Süngülü is small and matches *A. minusculus* from the Lower Oligocene of Olalla 4A (Spain) and *A. leptaleos* from the Lower Oligocene of Caijiachong (China) best. This, however, may not be a strong reason to consider the Süngülü fauna to have an early Oligocene age because all *Atavocricetodon* just have the basic cricetid dental pattern. All considered, the rodent assemblage from Süngülü strongly suggests a Late Eocene to Early Oligocene age. The presence of an indeterminate glyptosaure in the assemblage (Böhme, pers comm) seems to be in favour a Late Eocene age because these reptiles have so far never been found in beds that are younger than Eocene.

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APPENDIX

List of the families, genera and species of rodents in the assemblage from Süngülü

Ctenodactylidae
        Ottomania proavita n. gen. n. sp.
        Confiniummys sidiki n. gen. n. sp.
Dipodidae
        Heosminthus minutus Daxner-Höck, 2001
Muridae
        Witenia fusca n. gen. n. sp.
        Witenia flava n. gen. n. sp.
        Edirnella kempeni n. sp.
        cf. *Zhungaromys* sp.
        Pseudocricetodon aff P. montalbanensis Thaler, 1969
        cf. *Lignitella suemengeni* Ünay, 1989
        P*aracricetodon wentgesi* n. sp.
        Eucricetodon (Atavocricetodon) kurthi n. sp.