Deperetomys (Rodentia, Muridae) from the Oligocene of Serbia and Bosnia and Herzegovina

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Abstract

Two new late Oligocene species of *Deperetomys*: *D. calefactus* and *D. saltensis*, are described and the affinities between the various species are discussed. The new records extend the stratigraphic range of *Deperetomys* into the Oligocene, making it the first European Miocene murid that can be traced across the “Cricetid vacuum”. A single M1 of a large early Oligocene murid that may represent the oldest record of *Deperetomys* is described. The classification problems that arise as a result of the fast increase of information of the Paleogene Muridae from Asia and the Middle East are addressed and the need to recognise and define clades above the genus level is demonstrated. Our conclusion is that the *Deperetomys* clade contains at least three different evolutionary lineages.

Keywords Muridae · *Deperetomys* · Oligocene · Balkans · Systematics · New species

Introduction

The first teeth of a large Oligocene cricetine from the Balkans were collected by one of us (ZM) in 1997 from the coal used for heating the Natural History Museum in Belgrade. This remarkable find, which could be traced to the coal mine of Bugotovo Selo near Ugljevik in Bosnia and Herzegovina, triggered the collaboration of the vertebrate palaeontology

sections of the Natural History Museum in Belgrade and the Department of Earth Sciences of Utrecht University. The sites that yielded the material that will be described and discussed resulted from collecting campaigns in Ugljevik in 2004 and 2005, Banovići in 2007 and 2008 (sites in Bosnia and Herzegovina), Paragovo in 2016 and 2017 and Raljin in 2015 and 2017 (sites in Serbia).

The Bugotovo Selo mine near Ugljevik is an open pit in Bosnia and Herzegovina with late Oligocene coals. The majority of the material has been collected from the main coal seam in 2005 (see below).

Banovići (Turija) is an open pit mine in Bosnia and Herzegovina with latest Oligocene coals. Its magnetostratigraphy and palaeontology was described in de Leeuw et al. (2011) and de Bruijn et al. (2013). The site and geological setting of Paragovo (late Oligocene, Serbia) and Ugljevik will be described in the near future. Raljin is an early Oligocene site in SE Serbia and has been described by de Bruijn et al. (2018). The location of these sites is shown in Fig. 1, the relative stratigraphic position is in Fig. 2 and the composition of the rodent associations in Fig. 3.

Recognition of entities on the species level within the material described below presented no problem, but the generic allocation of these closely related species, which are considered to represent one clade, posed problems because the dentitions of a number of genotypes of Paleogene cricetids are similar (Figs. 4, 5 and 6). The three species that will be

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Fig. 1 Map showing the location of Raljin, Ugljevik, Banovići and Paragovo together with other sites discussed in this paper

described and discussed below are assigned to *Deperetomys* Mein and Freudenthal, 1971 because they share with the type species the presence of an ectoloph in the upper molars, a lower incisor with two longitudinal ridges and a type 10 enamel schmelzmuster (Kalthoff 2000). *Deperetomys* species are compared in Figs. 7 and 8. Two of the three species described below are new, one of these, *Deperetomys magnus* de Bruijn et al. (2003) from Banovići was described earlier (Figs. 9 and 10).

During the course of our studies of the Paleogene rodents from the Balkans, it became clear that these assemblages contain numerous Asian components (de Bruijn et al. 2018; Marković et al. 2018b; Wessels et al. 2018). This circumstance led to the comparison of our material with genera from all over Eurasia containing large species with a double anterocone in the M1 and a deep forward directed sinus in the M3. Unfortunately, the schmelzmuster of the lower incisor could not be used as a selection criterion for this comparison because this characteristic is not known in a number of genera that qualify otherwise.

Methods

The teeth from the mine near Ugljevik originate mostly from the main coal seam. These were partly collected by splitting

the matrix with a chisel and partly by treating the coal debris several times with a mixture of caustic soda, peroxide and warm water in the laboratory. The treated matrix was subsequently “gold-panned” in order to separate the heavier teeth from the coal. A few remains of large mammals from the Ugljevik coal have been published by Laskarev (1925) and Malez and Thenius (1985), but small mammal remains have so far passed unnoticed (Marković et al. 2018a).

The material from Banovići, Paragovo and Raljin has been collected by wet-screening large amounts of fossiliferous matrix on a set of stable sieves in the field. Concentrates have been sorted to the 0.65-mm fraction under a microscope. Length and width of the teeth were measured with a Leitz Ortholux microscope with mechanical stage and measuring clocks. The measurements are given in millimeter units. The pictures were made using a table-top SEM and a high-resolution SEM. All specimens are figured as left ones, if the original is from the right side; this is indicated by underlining its number on the figure. Lower case letters refer to the lower dentition, upper case letters refer to the upper dentition. Abbreviations for measurements and descriptions are as follows: N, number of specimens; R, range of measurements; L, length; W, width; sin, sinistral; dext, dextral. Abbreviations and terminology used in the description of the microstructure of enamel are as follows: HSB = Hunter Schreger band, IPM = inter prismatic matrix, PE = portio

Fig. 2 Scheme showing the time-stratigraphic position of Raljin, Ugljevik, Paragovo and Banovići together with mammal sites in Anatolia and Germany with *Deperetomys* species. A list of sites with *D. hagni* is in Prieto (2012), all are MN7/8 and in Germany and

Switzerland. The broken lines indicate the possible age range of the sites. The sites of Banovići and Harami have magnetostratigraphic age control (de Leeuw et al. 2011; Krijgsman et al. 1996)

		Early Oligocene	Late Oligocene		
		Raljin	Ugilevik	Paragovo	Banovići
Diatomyidae	<i>Inopinatia balkanica</i>	X			
Muridae	<i>Heterocricetodon</i> n. sp.	X			
	<i>Pseudocricetodon montalbanensis</i>	X			
	<i>Pseudocricetodon</i> n. sp.	X			
	<i>Paracricetodon stajanovici</i>	X			
	<i>Mogilia</i> cf. <i>lautus</i>	X			
	cf. <i>Deperetomys</i> sp. indet.	X			
	<i>Deperetomys calefactus</i> n. sp.		X		
	<i>Eucricetodon</i> (<i>Atavocricetodon</i>) sp.		X		
	<i>Deperetomys saltensis</i> n. sp.			X	
	<i>Deperetomys magnus</i>			X	X
	<i>Eumyarion</i> cf. <i>microps</i>			X	X
	<i>Eumyarion</i> cf. <i>carbonicus</i>			X	
	<i>Eumyarion margueritae</i>				X
	<i>Mirabella</i> aff. <i>anatolica</i>				X
	Spalacinae n. gen. n. sp.			X	
	<i>Vetusspalax progressus</i>				X
Dipodidae	<i>Heosminthus primiveris</i>	X			
	<i>Plesiosminthus</i> cf. <i>schaubi</i>				X
Gliridae	<i>Bransatoglis fugax</i>		X		X
	<i>Bransatoglis bosniensis</i>				X
	<i>Microdyromys</i> cf. <i>monspeliensis</i>			X	X
	Gliridae gen. et sp. indet.			X	
Sciuridae	<i>Palaeosciurus</i> aff. <i>feignouxii</i>				X
	<i>Dehmisciurus obstusidens</i>				X
Ctenodactylidae	Ctenodactylidae gen. B sp.1 (Ünay et al. 2003)		X		
	cf. <i>Sayimys</i> sp. indet.		X		
Eomyidae	<i>Eomys</i> sp. indet.		X		

Fig. 3 Distribution of rodent species in the Oligocene sites of Raljin, Ugljevik, Paragovo and Banovići

externa, PI = portio interna, IPI = internal part of the PI, OPI = external part of the PI. The terminology used for parts of the cheek teeth is according to Fig. 4. The abbreviations used for the localities are UGL (Ugljevik), Ra (Raljin) and PAR (Paragovo). The material will be housed in the Natural History Museum in Belgrade under the inventory numbers: 04 for Ugljevik test samples, 05 for Ugljevik main coal, 015 for Paragovo, 028 for Raljin. A representative set of casts is kept in the comparative collection of the Department of Earth Sciences, Utrecht University.

The recognition of Paleogene Muridae genera and subfamilies

The Paleogene record of the Muridae from Asia has been greatly extended during the last decades (Ünay-Bayraktar 1989; Wang and Dawson 1994; Tong 1997; Emry et al.

1998; Dawson and Tong 1998; Marivaux et al. 1999; Daxner-Höck 2000; de Bruijn et al. 2003; Lopatin 2004; Wang 2007; Maridet and Ni 2013; Gomes Rodrigues et al. 2012; López-Guerrero et al. 2017a, b, and others). A number of the genera established by these authors have remained monospecific so far, while the majority has been allocated to the Eucricetodontinae Mein and Freudenthal, 1971. A major problem is that the type material of many type species of the Paleogene cricetid genera is quite limited and that the micro-structure of the enamel of the lower incisor and the molars has often not yet been studied (Maridet and Ni 2013). This may lead to confusing subfamily allocation. However, Kalthoff (2000, 2006) and Martin (1997) demonstrated that the Paracricetodontinae (*Paracricetodon* and *Trakymys*) share a unique four-layered schmelzmuster of the lower incisor; this characterises the subfamily better than the morphology of the cheek teeth does. Since we consider size not an essential characteristic for defining genera, we illustrate the dentitions of the

Fig. 4 Terminology of parts of *Deperetomys* molars used in the descriptions

type species of selected, formally named extinct genera not to scale (Figs. 5 and 6). All of these are in the Cricetopinae sensu Maridet and Ni (2013). In spite of their overall morphological similarity, these dentitions show sufficient differences to maintain the genera concerned. At the same time, these figures show an unexpected similarity in the dental morphology of *Bagacricetodon* and *Deperetomys* and of *Metamys* and *Enginia*. In such cases, it may be expected that the discovery of new species of these genera will make their separation next to impossible. We are therefore convinced that the limit of the conventional practice to define fossil genera on a few dental characteristics has been reached.

Ünay-Bayraktar (1989) and Freudenthal et al. (1992) suggested subfamily groups including European Oligocene genera only. The conflicting results of these studies were critically tested by Kalthoff (2006) against the results of her data on the microstructure of the enamel of the lower incisor of the genera concerned. This study is an essential contribution to the recognition of clades. Unfortunately, the study of Kalthoff is largely limited to Oligocene European genera, so possible phylogenetic relationships among the primordial Muridae

from central Asia and the European Paleogene remained undetected.

Efforts to group Eurasian Paleogene Muridae genera by a cladistic analysis of characteristics of the dental pattern have been published by Gomes Rodrigues et al. (2010) and Maridet and Ni (2009). Although the results of these analyses are difficult to compare because the set of genera included in these studies is different, it is clear that there is no consensus.

Systematic palaeontology

Order Rodentia Bowdich, 1821

Family Muridae, Illiger, 1811

Subfamily Cricetodontinae Schaub, 1925

(including Gobicricetodontinae Qiu, 1996 = Plesiodipinae Qiu and Li, 2016)

Genera included: *Cricetodon* Lartet, 1851, *Deperetomys* Mein and Freudenthal, 1971, *Hispanomys* Mein and Freudenthal, 1971, *Byzantinia* de Bruijn, 1976 and *Gobicricetodon* Qiu, 1996.

Deperetomys hagni (Fahlbusch) 1964, Kleineisenbach, middle Miocene (MN7/8)

Enginia gertcheki de Bruijn & von Koenigswald, 1994, Keskőy, early Miocene (~MN3)

Meteamys alpani de Bruijn et al., 1991, Inkonak, late Oligocene (~MP28/29).

Bagacricetodon tongi Gomes Rodrigues et al., 2012, Ulaanatal III, late Oligocene

Paracricetops virgatoincisus Maridet & Ni, 2013, Caijiachong, Yunnan, early Oligocene.

Fig. 5 Upper molars of the type species of five selected Eurasian genera of cricetids (not to scale). All figures are from the literature

Deperetomys hagni (Fahlbusch, 1964), Kleineisenbach, early Miocene (MN7/8)

Enginia gertchei de Bruijn & von Koenigswald, 1994, Keseköy, early Miocene (~MN3);

Meteamys alpani de Bruijn et al. 1991, Ikonak, late Oligocene (~MP28/29)

Bagacricetodon tongi Gomes Rodrigues et al. 2012, Ulantatal III, late Oligocene

Paracricetops virgatoincisus Maridet & Ni, 2013, Caijiachong, Yunnan, early Oligocene

Fig. 6 Lower molars of the type species of five selected Eurasian genera of cricetids (not to scale). All figures are from the literature

Fig. 7 Upper molars of several *Deperetomys* species. Figures of *D. hagni*, *D. anatolicus* and *D. intermedius* are from the literature

Deperetomys hagni (Fahlbusch, 1964), Kleinenbach, middle Miocene (MN7/8);

Deperetomys intermedius (de Bruijn et al., 1987), Harami 1, early Miocene (~MN2)

Deperetomys anatolicus de Bruijn et al., 1993, Kılçak 0, early Miocene (~MN1)

Deperetomys magnus de Bruijn et al., 2013, Banovići, Oligo-Miocene (~MP30/MN1)

Deperetomys saltensis n. sp. Paragovo, late Oligocene (~MP29/30)

Deperetomys calefactus n. sp. Ugljevik, late Oligocene (~MP26-28).

Fig. 8 Lower molars of several *Deperetomys* species. Figures of *D. hagni*, *D. anatolicus* and *D. intermedius* are from the literature

Fig. 9 *Deperetomys calefactus* n. sp. from Ugljevik: **a** M1 sin UGL-270, **b** M2 dext UGL-321, **c** M3 dext UGL-375, **d–f** M1–M2–M3 sin UGL-408, **g** M1 sin UGL-266, **h** M2 sin UGL-294, **i** M3 sin UGL-360, **j** m1 sin UGL-110, **k** m2 sin UGL-163, **l** m3 sin UGL-241, **m–o** m1–m2–m3 sin

UGL-407, **p** m1 dext UGL-141, **q** m2 dext UGL-198, **r** m3 dext UGL-241, **s** upper incisor UGL-408, **t** lower incisor UGL-407 (same collection number = same individual)

Remarks

Although we consider Cricetidae obsolete as a family, we continue the informal use of cricetid in for instance “cricetid dental pattern” or early cricetids.

The growing information on the fossil rodents from Eurasia leads to the recognition of genera that contain many species and have long stratigraphical ranges. The resulting diversity of the dental characteristics observed in such clades not only makes emendation of their diagnosis a must, but also makes these less diagnostic. The differences between the dentitions of *Cricetodon*, *Deperetomys*, *Hispanomys*, *Byzantinia* and *Gobicricetodon* are subtle. The lower incisors of the species included in these genera share a type 10 schmelzmuster. We are unable to decide whether or not these genera are as closely related as the similarity of their dental characters suggests. Are they all members of the Cricetodontinae? Since we cannot distinguish between similarity acquired through convergent evolution or similarity resulting from sharing the same ancestor, we tentatively classify these genera in that subfamily. The subfamily name Cricetodontinae is used here in the restricted sense, that is to say including genera that are considered to be closely related to *Cricetodon*. The genera *Bagacricetodon*, *Paracricetops*, *Meteamys* and *Enginia* are tentatively excluded from the Cricetodontinae because the schmelzmuster of the lower incisor of the first two is not known while the morphology of the cheek teeth of *Meteamys* and *Enginia* differs significantly from those of *Cricetodon* proper.

Recently, Maridet and Ni (2013) discussed phylogeny and systematics of some early cricetids. They included *Cricetops*, *Paracricetops*, *Deperetomy*, *Meteamys*, *Mirabella*, *Enginia* (and some others) in the Cricetopinae Matthew and Granger, 1923. However, the study of von Koenigswald and Kalthoff (2007) on enamel microstructure shows that it is unlikely that *Cricetops* fits in this group of genera; hence, we cannot include genera other than *Cricetops* in this subfamily.

The status and content of the genus *Deperetomys* Mein and Freudenthal, 1971

Deperetomys hagni (Fahlbusch, 1964) from the late Miocene of Giggenhausen (Germany), the type species of the genus *Deperetomys* Mein and Freudenthal, 1971, was originally described as a subspecies of *Cricetodon sansaniensis* Lartet, 1851, the type of *Cricetodon* van de Weerd et al. 2018. The main dental characteristics that induced Fahlbusch (1964) to distinguish his *Cricetodon sansaniensis hagni* from *Cricetodon sansaniensis sansaniensis* were the sinuous ectolophs of the upper molars and the long mesolophs (ids) of the upper and lower cheek teeth. Engesser (1972) recognises Fahlbusch's subspecies in the assemblage from Anwil (Switzerland) and follows the suggestion of Mein and Freudenthal to

consider the characteristics noted by Fahlbusch of enough taxonomic importance to upgrade *C. hagni* to the species level. Meanwhile, Mein and Freudenthal (1971) in their classification of the Cricetidae from the European Tertiary consider the sinuous ectolophs and long mesolophs (ids) of *C. hagni* even more important and defined the subgenus *Deperetomys* on the basis of that species. *Deperetomys* remained a monospecific subgenus until Kordos (1986) established the subspecies *Cricetodon (Deperetomys) hagni hungaricus* which was transferred to *Cricetodon Cricetodon* by de Bruijn et al. in 1993, who upgraded *Deperetomys* to the genus level and transferred *Mirabella intermedius* de Bruijn et al. 1987 (Harami1, Turkey) to *Deperetomys*. This action extended the geographical and stratigraphical ranges of *Deperetomys*, which remained until then restricted to the late middle Miocene of central Europe (Fig. 3). In the meantime, it has become clear that the *Deperetomys* characteristics such as sinuous ectolophs, long mesolophs (ids), relatively large M3 with an open forward directed sinus and an m3 of about the same length as the m2 occur in a number of species of other murid genera from the early Miocene of the Middle East. That is to say that some of the dental characteristics of *Deperetomys*, that were considered to be derived, appear to be primitive (de Bruijn et al. 1993; de Bruijn et al. 2003).

Genus *Deperetomys* Mein and Freudenthal, 1971

Species included

Deperetomys hagni (Fahlbusch, 1964) (typelocality Giggenhausen, Germany; MN7-8).

Deperetomys rhodanicus (Depéret, 1887) (La Grive ancient collection, France details of the type locality not known, MN 7-8?)

Deperetomys anatolicus de Bruijn et al. 1993 (typelocality Kilcak 0", Turkey, MN1,)

Deperetomys intermedius (de Bruijn et al. 1987) (type locality Harami 1, Turkey, MN 2,)

Deperetomys magnus de Bruijn et al. 2013 (typelocality Banovići, Bosnia and Herzegovina; MP 30)

Deperetomys calefactus n. sp. (typelocality Ugljevik, Bosnia and Herzegovina; late Oligocene)

Deperetomys saltensis n. sp. (typelocality Paragovo, Serbia; late Oligocene)

Original diagnosis of *Deperetomys* in Mein and Freudenthal, 1971: Large Cricetodontini with incomplete ectolophs. The posterior ectolophs are not straight, but curved; in fact this does not concern true ectolophs like in the other subgenera, but a very long mesoloph which connects to the metacone via the posterior ectoloph. In other Cricetodontini, the mesoloph is either absent,

◀ **Fig. 10** cf. *Deperetomys* sp. indet. from Raljin: **a** M1 dext. from Raljin RA-7, *Deperetomys magnus* from Paragovo; **b** M1 dext, PAR-101, **c** M1 sin PAR-105, **d** m3 dext PAR-115, **e** m1 sin PAR-111, **f** m2 dext PAR-112, **g** m3 dext PAR-117. *Deperetomys saltensis* n. sp. from Paragovo: **h** M1 sin PAR-121, **i** M2 sin PAR-131, **j** M3 sin PAR-141, **k** m1 sin PAR-161, **l** m2 dext PAR-165, **m** m3 sin PAR-168

short or reaches the straight longitudinal ectoloph. (Translated from French).

Emended diagnosis in de Bruijn et al. 1993: Cricetodontinae of medium to large size. Cusps of cheek teeth slender, not inflated. Ectolophs sinuous and burgee-shaped. M1 and M2 with four roots. M3 with three or four roots. Mesolophs of the upper cheek teeth usually long and connected to the metacone via the anterior spur of the metacone. Anterocone of the M1 often with a cingulum that closes the valley between the two cusps. Lingual sinus of the M3 large and open. m3 longer than m2 or about as long as the m2. The m1 is rounded anteriorly and with a blade-shaped anteroconid. The m1 is without metalophulid 2. Mesolophids and posterolophids of the m1 and m2 parallel.

Emended diagnosis (this paper): Muridae of medium to large size. The burgee-shaped ectolophs of the upper cheek teeth well developed or incomplete. The M1 of the Oligocene representatives are three-rooted, those of the Miocene species four-rooted. Mesolophs long and connected to the anterior ectoloph and/or the posterior ectoloph in most species. The open sinus of the slightly reduced M3 is deep, forward directed. The m3 and m2 are about equally long. The m1 is rounded anteriorly. Anteroconid blade-shaped with a small cusp. The posterior arm of the protoconid of the lower cheek teeth is usually long and may connect with the metaconid. The m1 and/or m2 of the Oligocene representatives may have a short mesolophid and/or posterior arm of the hypoconid, in the Miocene species these elements are fused.

Remark: Maridet and Ni (2013) included *Deperetomys* together with *Paracricetops*, *Cricetops*, *Meteamys*, *Selenomys*, *Melissiodon*, *Mirrabella*, *Enginia*, *Muhsinia* and *Aralocricetodon* into their Cricetopinae suggesting close phylogenetic relationships among these genera. Within this group there are some genera, such as *Enginia*, *Meteamys* and *Paracricetops* that show similarities with *Deperetomys* (see Figs. 5 and 6), but others, such as *Selenomys*, *Melissiodon* and *Auralocricetodon* have completely different dental patterns. So *Deperetomys* does not seem to cluster within the Cricetopinae (sensu Maridet and Ni 2013).

Differential diagnosis: *Deperetomys* differs from *Cricetodon* in having sinuous ectolophs in the upper molars, a blade-shaped anteroconid bearing a very small cusp and relatively large M3 and m3. *Deperetomys* differs from *Byzantinia* and *Hispanomys* by its blade-shaped anteroconid of the m1. The occlusal surface of the long m3 and M3 is wide posteriorly in *Deperetomys*, but in *Byzantinia* species with a long m3, and M3, these teeth are

narrow posteriorly. The sinus of the M3 of *Deperetomys* is deep, lingually open and directed forward, but shallow, transverse and often lingually closed in *Byzantinia* and *Hispanomys*. *Deperetomys* and *Gobicricetodon* share the shape of the anteroconid of the m1, the well-developed anterosinusid in the m2 and m3 and the relatively large M3 and m3. *Gobicricetodon* may well be closely related to *Deperetomys*, but since the upper molars of its type species (*G. flynni*) are devoid of an ectoloph we prefer to maintain both names.

Deperetomys calefactus n. sp.

(Fig. 9)

Derivatio nominis: Calefacere in Latin means “to heat”, referring to the discovery of this species in the coal used for heating the Natural History Museum in Belgrade.

Type locality: Main coal seam Ugljevik (Bogutovo Selo) mine (Bosnia and Herzegovina). (44° 40' 19"–18° 59' 10").

Type level: Late Oligocene.

Holotype: m1–m3 sin and fragments of the lower incisor of the same individual. UGL-407, Fig. 9m, n, o and t.

Diagnosis: M1 three-rooted with a narrow oblique anterocone, incomplete anterior arm of the protocone, long mesoloph and a short, narrow metalophule that inserts on the posterior part of the hypocone. M2 has a short usually free-ending anterior arm of the protocone, a long mesoloph and a more or less transverse metalophule that inserts on the anterior part of the hypocone. m1 with small anteroconid, long posterior arm of the protoconid which reaches the metaconid, long forward directed mesolophid and usually a short free posterior arm of the hypoconid.

Differential diagnosis: *Deperetomys calefactus* is smaller than *D. magnus*. It differs in morphology from *D. saltensis* n. sp. in its less cusped anteroconid, the stronger posterior arm of the protoconid, better developed mesolophid of the m1 and the presence of a posterior arm of the hypoconid in the m1 and m2. The M1 and M2 of *D. calefactus* differ from those of *D. saltensis* n. sp. in having a free-ending anterior arm of the protocone, a much stronger posterior spur of the paracone, stronger mesolophs and transverse metalophids.

Table 1 Measurements of *Deperetomys calefactus* n. sp. from Ugljevik

<i>D. califactus</i>	Length (mm)			Width (mm)		
	Range	Mean	N	Mean	Range	N
Ugljevik						
M1	2.78–3.08	2.92	20	2.06	1.88–2.20	21
M2	1.73–2.20	2.03	54	2.12	1.87–2.21	54
M3	1.53–2.11	1.75	46	1.85	1.70–2.00	44
m1	2.17–2.60	2.37	54	1.63	1.46–1.79	55
m2	2.08–2.40	2.31	58	1.74	1.59–1.95	57
m3	2.10–2.40	2.34	42	1.75	1.59–1.88	42

Table 2 Measurements of *Deperetomys saltensis* n. sp. from Paragovo

<i>D. saltensis</i>	Length (mm)			Width (mm)		
	Range	Mean	N	Mean	Range	N
Paragovo						
M1	2.79–2.89	2.84	2	1.94	1.79–20.4	4
M2	1.98–2.25	2.15	9	2.00	1.90–2.21	9
M3	1.64–2.01	1.92	12	1.91	1.70–2.01	10
m1	2.26–2.48	2.37	2	1.64	1.55–1.73	2
m2	2.33–2.35	2.34	2	1.92	1.91–1.92	2
m3	2.30–2.33	2.32	3	1.81	1.74–1.91	4

The morphology of the m1 of *D. calefactus* differs from those of *D. magnus* in its less cusped anteroconid, stronger posterior arm of the protoconid and the stronger mesolophid. The free-ending anterior arm of the protocone in the M1 and M2 of *D. calefactus* is absent in these teeth of *D. magnus*. Moreover, the posterior spur of the paracone and the mesolophids of the M1 and M2 are much stronger while the metalophids are transverse in the *D. calefactus* but posteriorly directed in *D. saltensis* and *D. magnus*.

Material: UGL (= 04 test samples): 1 M1 UGL-61; 7 M2 UGL-37, -38, -64 - 69; 4 M3 UGL-37, -38, -71, -73; 6 m1 UGL-31–36, -41, -43; 6 m2, UGL-31–36, -45–49; 9 m3 UGL-31, -32, -34, -51–57.

UGL (= 05 main coal): 23 M1 UGL-261–281, -408, -410; 56 M2 UGL-291–313, -321–349, 408–411; 46 M3 UGL-351–368, 371–395, 408, -409, -411; 51 m1 UGL-101–125, -131–150, -401, -402, -404–407; 58 m2 UGL-151–177, -181–203, -401–407; 46 m3 UGL-351–368, -371–395, -408, -409, -411. Most incisors are broken, fragments have not been counted.

Measurements: See Table 1

Description

M1: The oblique anterocone is indistinctly bifid, has a labial position and is devoid of a lingual branch. The curved anterolophule bears a small cusp or a short lingually directed spur, but does not reach the lingual part of the anterocone in unworn specimens. The anterior arm of the protocone is either absent, short or complete and connected to the labial part of the anterocone. The labial branch of the anterocone tapers out at the base of the paracone. In a few specimens, there is a more lingually situated second connection between the labial cusp of the anterocone and the paracone which seems to be the homologue of the distal part of the anterior arm of the protocone. The parallel protolophule and metalophule insert just behind the protocone on the longitudinal ridge respectively just behind the hypocone on the posteroloph. The posterior spur of the paracone and the anterior spur of the metacone form a sinuous ectoloph. The long mesoloph is connected to

this ectoloph. The thin, weak posteroloph encloses a narrow, shallow postero-labial sinus. The M1 has three roots.

M2: The anteroloph has a very weak lingual branch and a long cingulum-like labial branch that reaches the base of the paracone. All fresh M2 have a short forward directed anterior arm of the protocone that ends free in the antero-labial sinus. The narrow lingual part of the protolophule inserts on the longitudinal ridge behind the protocone. The configuration of the metalophule shows much more variation: in some this ridge inserts in front of the hypocone, in others on the hypocone or on the posteroloph. The sinuous ectoloph that is formed by a strong posterior spur of the paracone and a much weaker anterior spur of the metacone is not situated on the edge of the occlusal surface, but somewhat lingually thereof. Many specimens have a low cingulum along the labial outline that forms a second ectoloph. The mesoloph is long and connected to the ectoloph in all M2. The weak posteroloph reaches the metacone in most M2 enclosing a narrow, shallow posterosinus. The M2 has three roots.

M3: The lingual branch of the anteroloph is either absent or indicated by a shallow indentation, but the labial branch is long and reaches the base of the paracone. The transverse protolophule inserts on the longitudinal ridge just behind the protocone. The posterior spur of the paracone is strong and connected to the long mesoloph in some M3, but much weaker and separated from that ridge in others. The deep lingual sinus is strongly forward directed. The hypocone and the metacone of the majority of the M3 are completely incorporated into a posteroloph that continues along the edge of the occlusal surface and connects with the labial end of the long mesoloph. The M3 has three roots.

m1: The anteroconid of the m1 is blade-shaped. This weak cusp has a very strong labial branch that connects to the base of the protoconid and a much shorter lingual branch that connects to the metaconid. A strong anterolophulid connects the protoconid to the anteroconid. The strong posterior arm of the protoconid is connected to the metaconid in 32/41 m1. The long forward directed mesolophid is connected to the thin entolophid which connects the metaconid and the entoconid along the border of the occlusal surface. A posterior arm of the hypoconid is present in all fresh m1, but this ridge fuses with the much stronger posterolophid at a rather early wear stage.

Table 3 Measurements of *Deperetomys magnus* from Paragovo

<i>D. magnus</i>	Length			Width		
	Range	Mean	N	Mean	Range	N
Paragovo						
M1	–	3.74	1	2.39	2.28–2.45	3
M1	–	2.78	1	1.75	–	1
m2	–	2.62	1	1.91	–	1
m3	2.55–3.13	2.90	3	2.09	1.84–2.21	3

Fig. 11 Transverse section of the lower incisor of *Depertomys calefactus* from Ugljevik. **a** Exterior of the incisor showing the two ridges, **b** transverse section of the incisor, **c** detail of a showing the two ridges, **d**

detail of c showing the mesial (left) ridge, **e** detail of c showing the lateral ridge

Fig. 12 Transverse sections of the part of the lower incisor of **a** *Depertomys calefactus*, **b** *D. major* and **c** *D. saltensis*. In each case, the mesial ridge is shown in detail

An ectomesolophid of variable length is present in many specimens.

m2: The lingual and labial branches of the anterolophid are about equal in length. The short anterolophulid and the forward directed metalophulid reach the anterolophid closely together. The very strong posterior arm of the protoconid is connected to the posterior spur of the metaconid in almost all m2. The mesolophid is short or absent. The transverse hypolophid inserts on the longitudinal ridge in front of the hypoconid. A short posterior arm of the hypoconid is present in 29/48 m2. An ectomesolophid is absent in the majority of the specimens.

m3: The lingual and labial branches of the anterolophid are about equal in length. The forward directed metalophulid and the short anterolophulid reach the anterolophid further apart than in the m2. The strong posterior arm of the protoconid is connected to the entolophid. The mesolophid is either short or absent. The hypolophid inserts on the longitudinal ridge on the apex of the sinusid. The posterior arm of the hypoconid is absent, but may be indicated by thickening of the posterolophid.

Lower incisor: For the description of the microstructure of the enamel of the lower incisor and molars, see below.

Fig. 13 **a** Longitudinal section through an M1 of *D. calefactus*. **b** Detail of the enamel low at the back side of the M1 showing the transition from lamellar enamel (left) to radial enamel (right)

Deperetomys saltensis nov. sp.
(Fig. 10h–m)

Derivatio nominis: *saltus* in Latin means “forested hill”. This name is appropriate because the locality Paragovo is situated in the forest of the Fruška Gora nature reserve.

Type locality: Paragovo (Serbia), coordinates: 45° 10' 59"–19° 50' 51"

Type level: Late Oligocene.

Holotype: m1 sin PAR-161 (Fig. 10k).

Material: PAR. (015): 4 M1 PAR-121, -122, -125, -126; 9 M2 PAR-131–133, -135–140; 12 M3 PAR-141–149, -151–153; 2 m1 PAR-161, -162; 3 m2 PAR-163, -165, -166; 4 m3 PAR-167–170. Most incisors are broken and fragments have not been counted.

Measurements: see Table 2

Diagnosis: The M1 has three roots. The labial part of the anterocone has a strong burgee-shaped posterior spur. The ridge connecting the lingual part of the anterocone to the protocone is weak and does not bear a cusp. The posterior spur of the paracone and the mesoloph are short in the M1 and M2, but long in the M3. The metalophule of the M1 and M2 is short, posteriorly directed and connected to the posteroloph, but the metalophule of the M3 is forward directed and fused with the posteroloph in a few specimens. The anteroconid of the m1 is a low cusp with a short and weak lingual and labial arm. The posterior arm of the protoconid and the mesolophid form one low ridge. The ectomesolophid of the m1 and m2 is long. The short posterior arm of the protoconid of the m2 ends at the base of the metaconid. The mesolophid and the posterior arm of the hypoconid are absent in the m2.

Differential diagnosis: *Deperetomys saltensis* differs from the about equally large *D. calefactus* in the absence of a free-ending anterior arm of the protocone, the shorter mesolophs and the posteriorly directed metalophule of the M1 and M2. *D. saltensis* differs from the larger *D. magnus* mainly in size (Figs. 7 and 8). *D. saltensis* differs from the Miocene species *D. anatolicus*, *D. intermedius* and *D. hagni* by its narrow anterocone of the M1 that lacks a strong postero-lingual spur, the less lophodont dental pattern of the M1 and M2 and m1 and m2. The characteristic X-pattern of Miocene *Deperetomys* on lower cheek teeth is not developed in *D. saltensis* (see Fig. 8).

Description

M1: The anterocone has a rather labial position due to the absence of a lingual spur on this indistinctly bi-cuspid cusp. The minute anterior arm of the protocone does not reach the base of the paracone. The short protolophule inserts on the longitudinal ridge behind the protocone. The short posterior spur of the paracone and mesoloph end freely. The metacone is situated very close and connected to the posteroloph. The M1 has three roots.

M2: The occlusal surface of the M2 is sub-square and its dental pattern is dominated by the four strong main cusps. The anterolophule connects the protocone to the middle of the anteroloph. The posterior spur of the paracone and the mesoloph are short in all the nine specimens. The protolophule inserts on the longitudinal ridge behind the protocone, and the posteriorly directed metalophule connects to the posteroloph.

M3: The lingual branch of the anteroloph is either weak or absent, but the labial branch is long and reaches the base of the paracone. The lingual sinus is progressively more forward directed from M1 through M3. The protolophule inserts on the longitudinal ridge. The posterior spur of the paracone is better developed in the M3 than in the M1 and M2. The mesoloph is long and connected to the loop formed by the posteroloph and metacone in 9 out of the 11 M3, but absent in the others. The forward directed metalophule is variable in length.

m1: The small anteroconid is much lower than the protoconid and metaconid and has a short lingual and labial branch. The anteroconid is connected to the protoconid by a low anterolophulid and to the metaconid by a weak metalophulid 1. The posterior arm of the protoconid and the mesolophid are poorly developed, though the mesolophid reaches the posterior slope of the metaconid. The long thin ectomesolophid reaches the labial outline of the occlusal surface. The short hypolophid inserts on the longitudinal ridge. The posterior arm of the hypoconid is absent and the strong posterolophid descends from the hypoconid and ascends to the tip of the entoconid.

m2: A strong anterolophulid divides the anterolophid into a long labial branch that reaches the base of the protoconid and a short weak lingual branch. The posterior branch of the protoconid is of medium length and does not form a metalophulid 2. The mesolophid is absent, but the ectomesolophid is long. The hypolophid inserts on the longitudinal ridge and the strong posterolophid reaches the base of the entoconid.

m3: The dental pattern of the m3 is very similar to that of the m2, but the relatively long ectomesolophid seen in the m2 is missing in all the four m3 available.

Deperetomys magnus de Bruijn et al. 2013
(Fig. 10b–g)

Type locality: Banovići (Bosnia and Herzegovina), latest Oligocene.

Locality: Paragovo (Serbia), coordinates: 45° 10' 59"–19° 50' 51"

Material: PAR (015): 4 M1 PAR-101–103, 105; 1 m1 PAR-111; 1 m2 PAR-112; 4 m3 PAR-115–118.

Measurements: see Table 3

These *Deperetomys* molars that are clearly too large for inclusion in *D. saltensis* and identical to *Deperetomys magnus* from Banovići.

cf. *Deperetomys* sp.
(Fig. 10a)

Locality: Raljin 2 (Serbia) coordinates: 43° 00'14"–22° 29' 06"

Level: Early Oligocene

Material and measurements: One specimen, RA 7, M1 dext. (2.80 × 1.95)

Description

M1: The morphology of this tooth, which is within the range of the size variation of *Deperetomys calefactus* and *D. saltensis*, is in many respects far more primitive than the M1 of these species. The indistinctly bifid anterocone has a rather labial position. The straight lingual and labial branches of the anterocone connect respectively to the base of the protocone and the anterior spur of the paracone. Lingual to the anterior arm of the protocone, which connects the protocone and the labial part of the anterocone, there are two incomplete ridges of unknown homology. The lingual part of the proto- lophule 2 bends anteriorly and inserts on the anterior side of the protocone. The paracone has a sinuous posterior spur, which is connected to the labial end of the long, straight mesoloph. The shallow lingual sinus is more or less transverse. The metalophule is parallel to the proto- lophule 2 and inserts on the anterior side of the hypocone. The posteroloph connects the apices of the hypocone and the metacone.

Discussion: Features such as the complete connection between the protocone and the labial part of the anterocone, the parallel protolophule 2 and metalophule that insert on the anterior sides of the protocone and metacone and the shallow transverse lingual sinus are considered to be primitive and make this tooth quite different from the M1 of the late Oligocene *Deperetomys* species described above. At the same time it might well represent the ancestor of the *Deperetomys* species from the Balkans.

The enamel microstructure of the lower incisors and molars

The rather thick lower incisors of *Deperetomys calefactus* (Figs. 9t, 11a,c, 12a), *D. saltensis* (Fig. 12c) and *D. magnus* (Fig. 12b) show two longitudinal ridges and similar microstructure of the enamel (Fig. 12a–c). The thick PI (85%) consisting of not inclined longitudinal HSB is divided into two layers. In the PI close to the EDJ (=IPI), the IPM is at about right angles to the prisms. In the outer part of the PI (=OPI), the IPM is parallel to the prisms. The thin PE consists of tangential enamel. The

prisms of the PI change direction in a narrow zone below the mesial ridge (Figs. 11 and 12). This typical type 10 schmelzmuster has also been observed in *Deperetomys hagni* and *D. anatolicus* (Kalthoff 2000) and thus seems to be a consistent property of *Deperetomys* through time.

The cross section of a molar of *Deperetomys calefactus* (Fig. 13) shows a broad band of lamellar enamel around the base of their crowns which grades into radial enamel toward the occlusal surface (= C-type of von Koenigswald 2004). This schmelzmuster is very common among Muridae since the middle Eocene and is therefore not useful for detecting the phylogenetic affinities of the genus *Deperetomys*.

Unfortunately, the shared type 10 enamel of the incisors as well as the C-type enamel of the molars occur in many genera and several subfamilies of the Muridae (Kalthoff 2000; von Koenigswald 2004). Lower incisors with two longitudinal ridges, longitudinal HSB and a zone below the mesial ridge in which the crystallites bend in the opposite direction occur in the Cricetodontinae, Eumyarioninae, Myospalacinae, Spalacinae as well as in some genera of uncertain subfamily status such as *Enginia*, *Meteomys*, *Aralocricetodon* and surprisingly also in the supposed rhizomyine *Prokanisamys* (Kalthoff 2000). Although the biomechanical function of this peculiar feature is not known, it is clear that it originated independently in a number of different groups of Muridae and does therefore neither support, nor contradict our tentative assignment of *Deperetomys* to the Cricetodontinae.

Conclusions

Allocation of the new species *Deperetomys calefactus* and *D. saltensis* from the late Oligocene of Serbia and Bosnia and Herzegovina to the genus *Deperetomys* is primarily based on overall similarity in dental pattern with the late middle Miocene type species *D. hagni*, the late Oligocene *D. magnus* and the early Miocene *D. anatolicus* and *D. intermedius* (Figs. 7 and 8). Other features that support this assignment are the shared unusually long m3 relative to the m2 and the only slightly reduced M3 with deep, open, forward directed lingual sinus. Although absolute size is not considered to be of great taxonomic importance, it is striking that all species allocated to *Deperetomys* so far are relatively large. In order to test our dental pattern-based generic allocation, the enamel microstructure of the lower incisors and the cheek teeth has been studied: all species show a type 10 structure. The hitherto geologically oldest record of a lower incisor with a type 10 schmelzmuster is from *Aralocricetodon* (erroneously identified as *Eumysodon* in Kalthoff 2006) from the latest Oligocene of Altyn Schokysu, Aral Formation, Kazakhstan. Although biostratigraphical correlation of the Aral Fm. and Ugljevik rodent assemblages is full of uncertainties, it seems to us that the Bosnian site is the older of the two.

Deperetomys calefactus, *D. saltensis*, *D. magnus*, *D. anaticus*, *D. intermedius* and *D. hagni* are considered to represent one clade consisting of at least three lineages. *D. saltensis* and *D. magnus* occur together in the Serbian locality Paragovo. It seems very unlikely that the small *D. anaticus* from Kılçak (an Anatolian site slightly younger than Paragovo, see Fig. 3) with upper cheek teeth with complete sinuous ectoloph is the descendant of the robust *D. saltensis*; thus, these species are considered to represent separate branches. The single first molar found in the lower Oligocene locality of Raljin seems related to *Deperetomys* and possibly represents an ancestor.

On the basis of differences in dental morphology, we can divide the *Deperetomys* clade into a group of species that remains so far restricted to the Balkan and an Anatolian-central European group. In the Balkan group (*Deperetomys calefactus*, *D. saltensis* and *D. magnus*), the evolutionary trend is toward reduction of the anterior arm of the protocone, the ectoloph and the mesoloph in the M1 and M2 as well as toward a progressively more posteriorly directed metalophule. In the lower dentition, the trend is toward reduction of the posterior arm of the protoconid and hypoconid through time.

In the Anatolian-central European species (*D. anaticus*, *D. intermedius* and *D. hagni*), there is a gradual increase in size and in crown height of the cheek teeth through time, while the dental morphology remains surprisingly stable. Figure 3 shows the localities and species of *Deperetomys* with their relative stratigraphic position; *D. hagni* is found in a number of sites in North Alpine foreland basin of Germany and Switzerland (for a list of these sites, see Prieto 2012).

Assuming that our interpretation of the *Deperetomys* record is correct, *Deperetomys* is the first Miocene murid genus based on a Miocene species from Europe that can be traced to its Oligocene ancestors. This implies too that *Deperetomys hagni* immigrated into Europe after “the cricetid vacuum” (the period without cricetids in Western Europe; MN3).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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