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Cricetidae (Rodentia, Mammalia) from the Valley of Lakes (Central Mongolia): focus on the Miocene record

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(With 11 figures and 3 tables)

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Abstract

The present publication reports new discoveries of Miocene cricetid rodents from the Taatsiin Gol area (Valley of Lakes) in Mongolia. The fossil cricetids recovered in this area are only composed of dental and fragmentary jaws remains, sometimes poorly preserved. Miocene cricetid rodents have been found from Early Miocene (local biozone D) to the Late Miocene (local biozone E). Altogether, nine Miocene taxa belonging to six genera have been identified in the collection of the Austrian-Mongolian project: *Gobicricetodon* sp., *Cricetodon* cf. *volkeri,* cf. *Primus* sp., *Democricetodon sui*, *Democricetodon* aff. *lindsayi, Democricetodon tongi*, *Megacricetodon* aff. *sinensis, Megacricetodon* sp. and *Nannocricetus* aff. *primitivus*. The systematic study reveals that the cricetid taxa that compose the assemblages D1/1 and D1/2 are similar to the Middle Miocene fauna of Northern China, suggesting that both local biozones are likely early Middle Miocene in age rather than Early Miocene as previously proposed. Likewise the comparison of the local assemblage E with the cricetids of the Late Miocene of the Bahe Formation, in China, confirms that the local biozone E is Late Miocene in age, but probably younger than previously proposed. The earliest Miocene assemblage is only composed of two small-sized taxa, *Democricetodon sui* and cf. *Primus* sp., which indicates a drastic renewal of cricetid communities through the Oligocene-Miocene boundary when compared to the latest Oligocene cricetids' assemblage of the Valley of Lakes.

Key-words: Cricetidae, Rodentia, Miocene, Oligo-Miocene transition, Mongolia

Introduction

Since 1995, three successive joint Austrian-Mongolian projects have been carried out in the Taatsiin Gol area in Mongolia (Fig. 1a), including eight field missions. During

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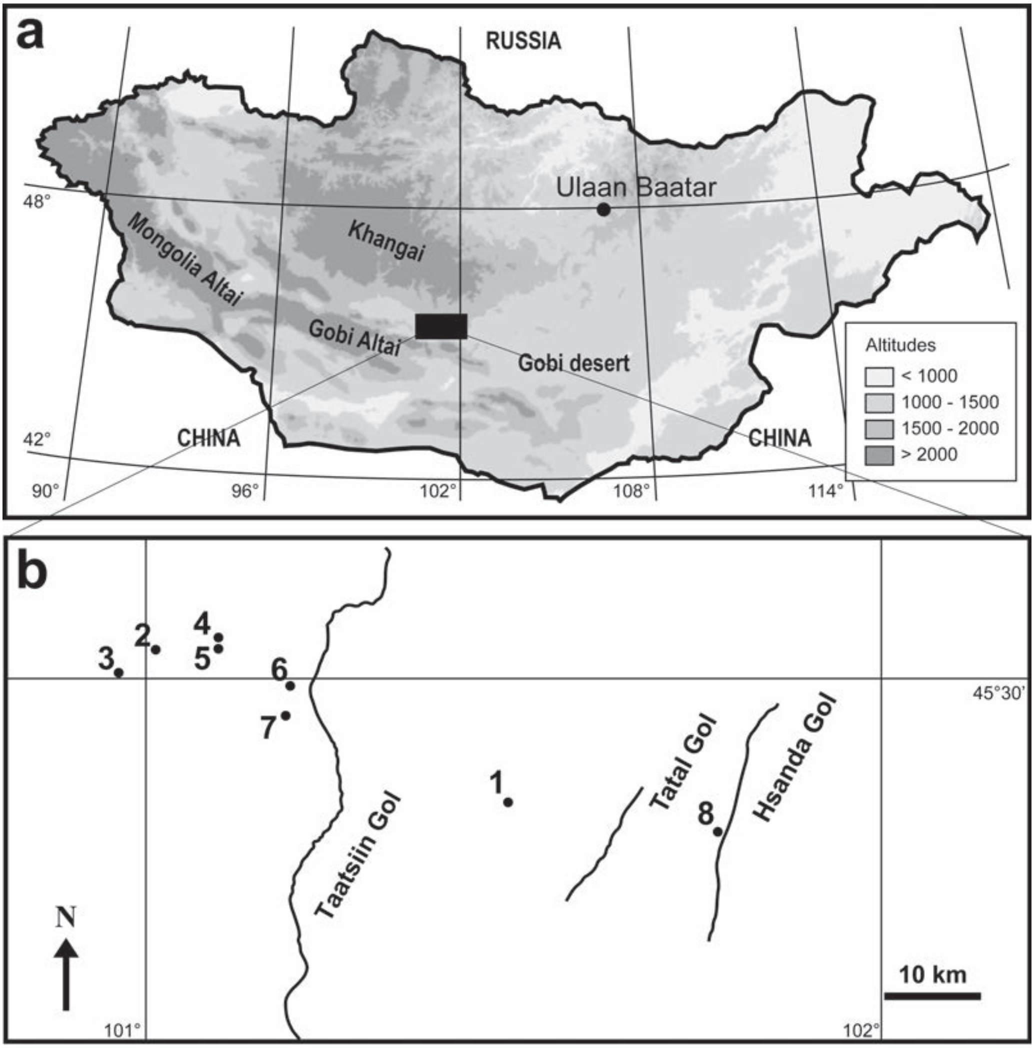

Fig. 1. Working area: **a**. Location of the working area in Mongolia between the Gobi Altai and the Khangai Mountains. **b**. Location of each section and Miocene locality which yielded cricetid fossil remains: 1. Builstyn Khudag; 2., 3. Luugar Khudag; 4., 5. Uolon Ovoony Khurem; 6. Huch Teeg; 7. Unkheltseg; 8. Ulaan Tolgoi (modified after Daxner-Höck & Badamgarav 2007). See also Daxner-Höck & Badamgarav (2007) for the geographic coordinates of each locality.

these missions, an extensive sampling has been undertaken, comprising not only surface sampling but also screen-washing of almost a hundred tons of sediment from more than 40 localities and sections spanning from the Early Oligocene to the Late Miocene. This continental sequence allowed a precise stratigraphic adjustment based on the evolution of mammals and age determination of basalts as elaborated by Daxner-Höck *et al.* (1997) and Höck *et al.* (1999). Between 2001 and 2012 several additional field investigations were conducted and more fossil specimens were collected, especially thousands specimens of Oligocene and Miocene mammals. A part of the mammalian fossil record has already been studied in detail such as Ruminantia (VISLOBOKOVA & DAXNER-HÖCK 2002), Rhinocerotidae (HEISSIG 2007), Proboscidea (GÖHLICH 2007), Marsupialia, Erinaceomorpha and Soricomorpha (ZIEGLER *et al.* 2007), and part of Rodentia (*e.g.*, DAXNER-HÖCK 2000; DAXNER-HÖCK 2001; DAXNER-HÖCK & WU 2003; SCHMIDT-KITTLER *et al.* 2007). Moreover, preliminary results are available for Didymoconidae, Creodonta and Carnivora (*e.g.*, MORLO & NAGEL 2006; MORLO & NAGEL 2007; NAGEL & MORLO 2003) and Lagomorpha (*e.g.*, ERBAJEVA 2007).

The two most abundant groups of rodents found in these localities are the Dipodidae (see DAXNER-HÖCK *et al.* 2014, more than 3,000 specimens) and the Cricetidae with more than 1,000 specimens recovered (mostly from the Oligocene), including only 88 specimens from the Miocene. In the present publication we carry on the study of rodents by presenting the Miocene cricetid rodents yielded from the Early Miocene to the Late Miocene layers. We also provide an updated list of all Oligocene and Miocene cricetids found in the Valley of Lakes, but the study of these Oligocene cricetids will be published later in successive individual papers.

Material and methods

For the present investigation only the dental and jaw remains are considered. They are stored in the collections of the Geological-Paleontological Department, Museum of Natural History in Vienna, Austria (NHMW) and the Paleontological Center of the Mongolian Academy of Sciences in Ulaanbaatar, Mongolia. They are catalogued under the numbers: NHMW 2013/0429/0001 to 2013/0442/0041.

Observations and measurements were done with a binocular microscope Leica WILD M8 allowing precision to 0.01 mm. The classification of Miocene cricetids is taken after MEIN & FREUDENTHAL (1971) and QIU (1996). The terminology used to describe the teeth is taken from MARIDET & NI (2013). For each measureable tooth the length and width are provided under the form: ‘length’×‘width’, and all the measurements are given in millimetres.

Abbreviations

Localities: BUK = Builstyn Khudag; LOG = Luugar Khudag; ODO = Uolon Ovoony Khurem; RHN = Huch Teeg; UNCH = Unkheltseg; UTO = Ulaan Tolgoi. The position of each locality within the Valley of Lakes is indicated on the figure 1b. See DAXNER-HÖCK & BADAMGARAV (2007) for the geographic coordinates of each locality.

Institution: NHMW = Naturhistorisches Museum Wien.

Teeth: M, m = Molar. Upper-case letters indicate upper teeth, whereas lower case letters indicate lower teeth.

Geologic and chronologic framework

All the below described specimens have been collected in the area of the “Valley of Lakes” in Central Mongolia. This area is part of the Pre-Altai depressions which are

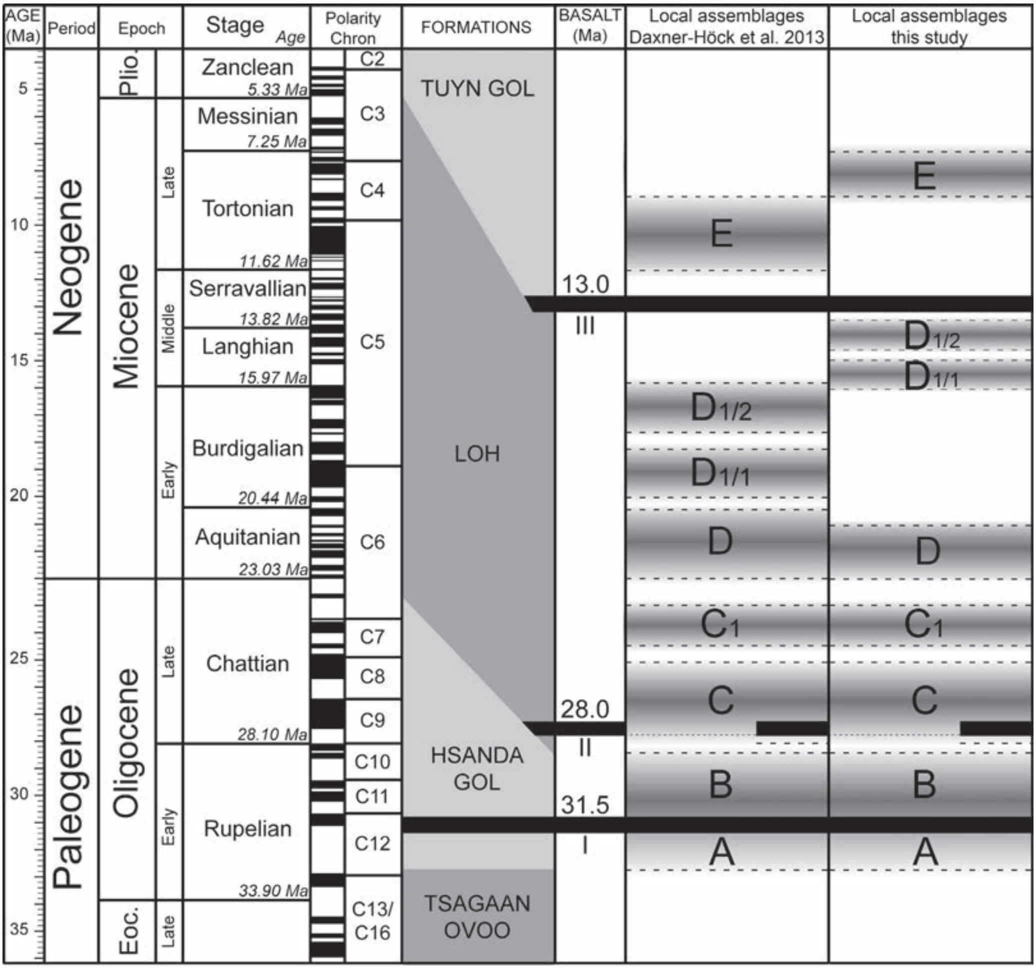

Fig. 2. Sedimentary formations and correlation chart of the Mongolian rodent assemblages with the Geological Time Scale, modified after Höck & Badamgarav (2007) and Gradstein *et al.* (2012). Local Oligocene-Miocene chronology is based on informal local biozones and basalt datings.

situated in Western and South-Central Mongolia between the Mongolian Altai and the Gobi Altai Mountains in the south and the Khangai Mountains in the north (Fig. 1a). Here, above the Proterozoic and Paleozoic basement, are deposited continental sediments ranging continuously from the Cretaceous to the Quaternary. A succession of four Cenozoic formations is recognised in this region ranging in age from the Late Eocene to the Late Miocene: Tsagaan Ovoo, Hsanda Gol, Loh and Tuyn Gol formations (see Daxner-Höck & Badamgarav 2007 for a detailed presentation of the geologic and chronologic framework). In this area, the Cenozoic sedimentary sequence interlays with several basalts deposits. Three coherent basaltic layers (Basalt I, II, III) of variable thickness were distinguished and dated by the 40Ar/39Ar-method (DAXNER-HÖCK *et al.* 1997; HÖCK *et al.* 1999). Basalt I erupted around 31.5 Ma [range 30.4–32.1] (Early Oligocene), Basalt II is about 28.0 Ma [range 27.0–28.0] (Late Oligocene), and Basalt III about 13 Ma [range 12.2–13.2] (Middle Miocene). Basalt II is only found in the very north of the mapped area near the Unzing Khurem area and the Olon Ovoony Khurem area; its thickness also strongly varies: 5–7 m in the Unzing Khurem area whereas it can exceed 25 m in the Olon Ovoony Khurem area (DAXNER-HÖCK & BADAMGARAV 2007).

The successive rodent assemblages from different localities have been grouped into eight informal local biozones (DAXNER-HÖCK & BADAMGARAV 2007): A, B, C, C1, D, D1/1, D1/2, and E (Fig. 2). Each informal biozone was defined by its lithostratigraphic position and the characteristic rodents from all respective fossil horizons (see DAXNER-HÖCK & BADAMGARAV 2007 and DAXNER-HÖCK *et al.* 2013). The present study focuses on the cricetid material from the faunal assemblages D (Early Miocene), D1/1 and D1/2 (possibly Middle Miocene, see 'Conclusions' chapter) and E (Late Miocene).

Systematic palaeontology

Class Mammalia LINNEAUS, 1758

Order Rodentia BOWDICH, 1821

Family Cricetidae FISCHER VON WALDHEIM, 1817

Subfamilly Cricetodontinae STEHLIN & SCHAUB, 1951

Genus *Gobicricetodon* QIU, 1996

***Gobicricetodon* sp.**

(Fig. 3a–b)

Locality/Stratigraphy: Ulaan Tolgoi (biozone D1/2), late Early Miocene. All specimens come from the same layer, UTO-A/5.

Material: right M1 (NHMW 2013/0429/0001: -×1.95 mm); left m3 (NHMW 2013/0429/0002: 2.26×1.69 mm).

Remarks: Both the broken M1 and the complete m3 are characterized by a high crown and an almost flat occlusal surface, which morphology fits the diagnosis of *Gobicricetodon* (QIU 1996). When compared to the species of Middle Miocene of Tunggur (Inner Mongolia, China) they are slightly smaller than *G. flynni* QIU, 1996 and *G. robustus* QIU, 1996 and larger than *G*. sp. (QIU 1996). The species *G. filippovi* SEN & ERBAJEVA, 2001 from the Middle Miocene of the Aya Cave (Lake Baikal area, Russia) is only slightly larger than the Mongolian specimens based on M1s. It is not possible to further identify these specimens at a specific level.

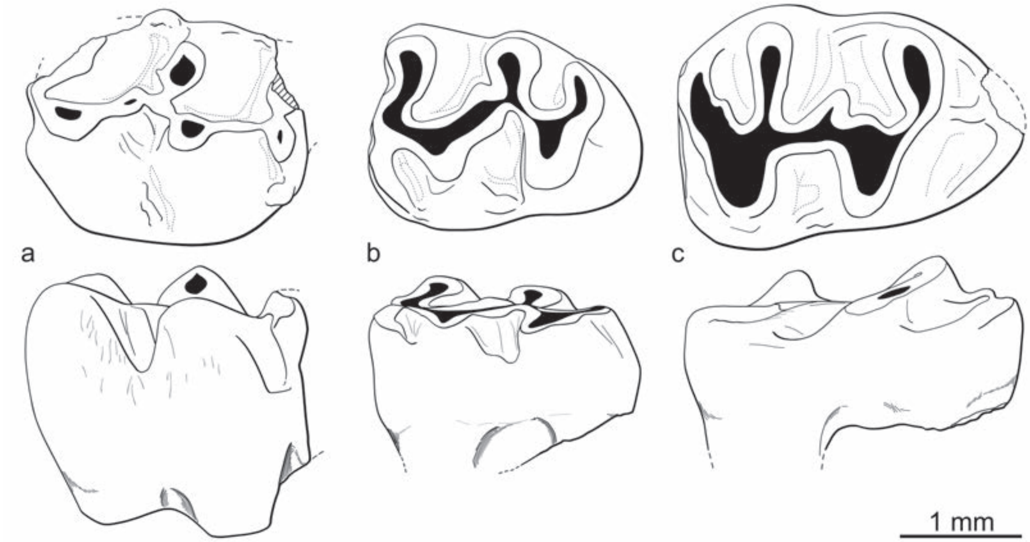

Fig. 3. *Gobicricetodon* sp. (**a-b**) and *Cricetodon* cf. *volkeri* (**c**) from Ulaan Tolgoi (layer UTO-A/5), late Early Miocene. *Gobicricetodon* sp.: **a**. right M1 (NHMW 2013/0429/0001); **b**. left m3 (NHMW 2013/0429/0002). *Cricetodon* cf. *volkeri*: **c**. right m1 (NHMW 2013/0430/0002). For each tooth both the occlusal view (top) and the lateral view (bottom) are illustrated.

Genus *Cricetodon* LARTET, 1851

***Cricetodon* cf. *volkeri* WU *et al.* 2009**
(Fig. 3c)

Locality/Stratigraphy: Ulaan Tolgoi (biozone D1/2), late Early Miocene. All specimens come from the same layer, UTO-A/5.

Material: right broken M2 (NHMW 2013/0430/0001: not measurable); right m1 (NHMW 2013/0430/0002: 2.86×2.00 mm); left broken m2 (NHMW 2013/0430/0003: -×1.80 mm).

Remarks: Although the size of the teeth is somewhat similar to *Gobicricetodon* sp. specimens, only slightly larger, they differ in having a much lower tooth crown and more massive cusps, which fit better the diagnosis of *Cricetodon*. The teeth are larger than those of *C. wangei* QIU, 2010 (late Early Miocene of Jiangzu, China), and only slightly larger than *Cricetodon* n. sp. described by BI (2005) (he described this population as a new species, "*C. orientalis*" from the early Middle Miocene of Xinjiang, China, although this species is not officially published and can't be considered as valid so far). The Mongolian specimens mainly differ from *Cricetodon* n. sp. in having a less elongated M1. On the other hand, the size of Mongolian specimens could fit the size of *C. volkeri* WU *et al.*, 2009. So far only lower molars from Central Mongolia can be used for comparison (the M2, NHMW 2013/0430/0001, it too damaged to be measured or described) whereas the diagnosis of *C. volkeri* (Middle Miocene of Xinjiang, China) is mainly based on upper molars (only one lower molar has been described by WU *et al.* 2009). However, in addition to the size, it noteworthy that the lower teeth have in common an antero-posterior extended ectolophid, transversely oriented main lophids with the hypolophulid connected anteriorly to the hypoconid, and a short oblique mesolophid. We consequently tentatively ascribe the Mongolian specimens to *C. volkeri* keeping in mind that this identification will only be certain when more upper and lower molars will be found in association in the same localities.

Subfamilly Cricetinae FISCHER VON WALDHEIM, 1817

Genus *Primus* DE BRUIJN *et al.*, 1981

cf. *Primus* sp.
(Fig. 4f)

Locality/Stratigraphy: Huch Teeg (biozone D), Early Miocene, layer RHN-A/12.

Material: left M1 (NHMW 2013/0431/0001: 1.49×1.00 mm).

Remarks: This M1 is smaller than all the other cricetids found in the Early Miocene of the Valley of Lakes (even noticeably shorter than *Democricetodon sui*, see below). It has a short and rounded anterior lobe with a cone-shaped anterocone. The protocone is connected to the anterocone by a short anterolophule which joins the lingual extremity of the anterocone. The mesoloph is quite posteriorly located and seems in the prolongation of an anterior arm of the hypocone. The metalophule connects very anteriorly in front of the hypocone, at the base of the mesoloph. The intersection between the mesoloph, the metalophule and the entoloph forms an X pattern. The M1 has no lingual anteroloph as opposed to the *Democricetodon sui* in which the lingual anteroloph is long and connects to the protocone lingually. Furthermore the M1 also differs from *D. sui* in having more inflated and rounded cusps whereas they are rather sharp in *D. sui*.

The small size, the metalophule oriented anteriorly, the weakly-developed mesoloph and the rather narrow and undivided anterocone fit well the diagnosis of the genus *Primus*. However, the M1 from Mongolia differs from the two known species of *Primus*, *P. microps* DE BRUIJN *et al.*, 1981 (Early/Middle Miocene of Pakistan) and *P. pusillus* QIU, 2010 (Early Miocene of Jiangsu province, China), in having more inflated cusps and a more anteriorly connected metalophule. The M1 is also larger than *P. microps* and *P. pusillus*. It is not possible so far to secure this identification at generic level based on a single tooth. We tentatively refer this tooth to the genus *Primus*, but not excluding the possibility that it could also be a new species of *Democricetodon* from the Early Miocene of the Valley of Lakes.

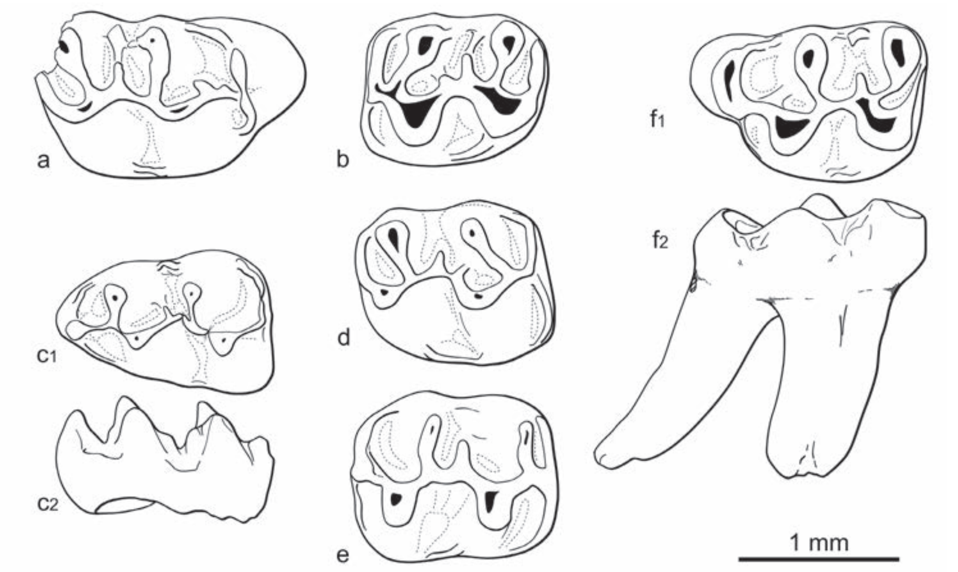

Fig. 4. *Democricetodon sui* (**a-e**) from Unkheltseg (layer UNCH-A/3) and cf. *Primus* sp. (**f**) from Huch Teeg (layer RHN-A/12), Early Miocene. *Democricetodon sui*: **a**. right M1 (NHMW 2013/0432/0001); **b**. left M2 (NHMW 2013/0432/0002); **c**. left m1 (NHMW 2013/0432/0004: **c1**. occlusal view, **c2**. labial view); **d**. right M2 (NHMW 2013/0432/0003); **e**. right m2 (NHMW 2013/0432/0005). cf. *Primus* sp.: f. left M1 (NHMW 2013/0431/0001: **f1**. occlusal view, **f2**. lingual view).

Genus *Democricetodon* FAHLBUSCH, 1969

***Democricetodon sui* MARIDET et al., 2011**
(Fig. 4a–e)

1999 *Democricetodon* sp. – HÖCK *et al.*, fig. 21/4, p. 119.
2013 *Democricetodon* sp. 1 – DAXNER-HÖCK *et al.*, tab. 20.4, p. 488.

Locality/Stratigraphy: Unkheltseg (biozone D), Early Miocene. All specimens come from the same layer, UNCH-A/3.

Material: right M1 (NHMW 2013/0432/0001: 1.67×1.05 mm); left M2 (NHMW 2013/0432/0002: 1.19×0.95 mm); right M2 (NHMW 2013/0432/0003: 1.20×1.03 mm); left m1 (NHMW 2013/0432/0004: 1.36×0.90 mm); right m2 (NHMW 2013/0432/0005: 1.28×1.07 mm)

Remarks: Five teeth have been found from the layer UNCH-A/3. All molars present a morphology characterized by a very low crown and sharp cusp(id)s (Fig. 4c), with also oblique protolophule and metalophule in M2 (Fig. 4b,d), and a weakly-developed (vestigial) mesoconid at the extremity of the hypolophulid in m1 (Fig. 4c). The morphology and size of the present specimens enter in the variability of *D. sui* described by MARIDET *et al.* (2011a). The anteroconid of the m1 about as high as the other cuspids in lateral

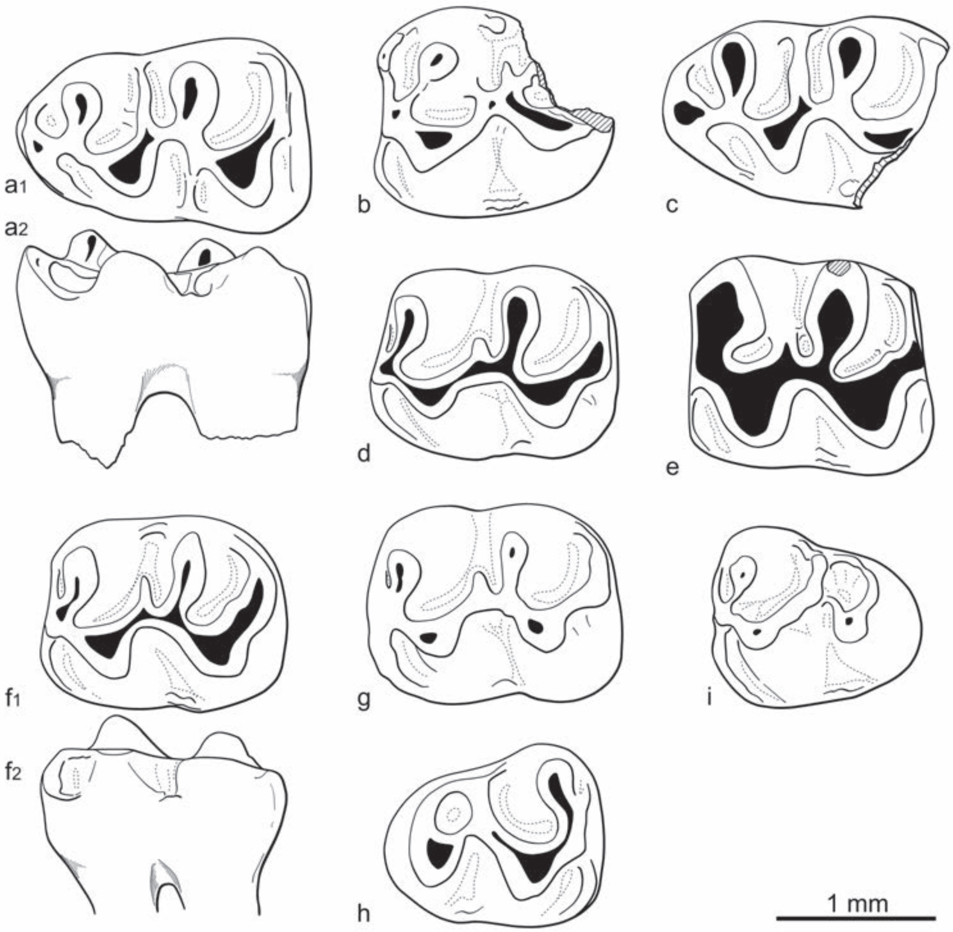

Fig. 5. *Democricetodon* aff. *lindsayi* from Uolon Ovoony Khurem (layer UTO-A/5) and Ulaan Tolgoi (layer ODO-A/2), late Early Miocene: **a**. left m1, ODO-A/2 (NHMW 2013/0434/0001: **a1**. occlusal view, **a2**. labial view); **b**. left M2, UTO-A/5 (NHMW 2013/0433/0001); **c**. left m1, UTO-A/5 (NHMW 2013/0433/0002); **d**. left m2, UTO-A/5 (NHMW 2013/0433/0003); **e**. left m2, UTO-A/5 (NHMW 2013/0433/0005); **f**. left m2, UTO-A/5 (NHMW 2013/0433/0004: **f1**. occlusal view, **f2**. labial view); **g**. left m2, ODO-A/2 (NHMW 2013/0434/0002); **h**. left m3, ODO-A/2 (NHMW 2013/0434/0003); **i**. left m3, UTO-A/5 (NHMW 2013/0433/0006).

view (Fig. 4c) which excludes it from the genus *Karydomys* THEOCHAROPOULOS, 2000 (see MARIDET *et al.* 2011b).

***Democricetodon* aff. *lindsayi* QIU, 1996**
(Fig. 5a–h)

1999 *Democricetodon* cf. – HÖCK *et al.*, fig. 21/7, p. 119.
2013 *Democricetodon* sp. 2 – DAXNER-HÖCK *et al.*, tab. 20.4, p. 488.
2013 *Democricetodon* cf. *lindsayi* – DAXNER-HÖCK *et al.*, tab. 20.4, p. 488.

Localities/Stratigraphy: Uolon Ovoony Khurem (biozone D1/1) and Ulaan Tolgoi (biozone D1/2), late Early Miocene.

Material: left M2 with postero-labial corner broken, UTO-A/5 (NHMW 2013/0433/0001: 1.51×1.34 mm); left m1 with posterior border broken, UTO-A/5 (NHMW 2013/0433/0002: -×1.20 mm); left m1, ODO-A/2 (NHMW 2013/0434/0001: 1.84×1.24 mm); left m2, UTO-A/5 (NHMW 2013/0433/0003: 1.56×1.23 mm); left m2, UTO-A/5 (NHMW 2013/0433/0004: 1.55×1.26 mm); left m2, UTO-A/5 (NHMW 2013/0433/0005: 1.53×1.40 mm); left m2, ODO-A/2 (NHMW 2013/0434/0002: 1.60×1.28 mm); left m3, UTO-A/5 (NHMW 2013/0433/0006: 1.32×1.16 mm); left m3, ODO-A/2 (NHMW 2013/0434/0003: 1.40×1.16 mm).

Remarks: The morphology of the first lower molars is very similar to *D. lindsayi* with a long mesolophid, a single rounded anteroconid, and possible presence of a well-developed ectomesolophid (Fig. 5a, c). However the m2 from Mongolia has a shorter mesolophid, the m3 has no mesolophid and the M2 has a second posterior protolophule whereas these characters are rather rare or absent in the type population of *D. lindsayi* from the Middle Miocene of Tunggur (Inner Mongolia, Qiu 1996). The present specimens are only slightly larger than those from Tunggur suggesting that they could belong to the same lineage; however more material, especially upper teeth, will be necessary to confirm this hypothesis.

Like in *D. sui*, the anteroconid of the m1 is about as high as the other cuspids in lateral view (Fig. 5a) which excludes it from the genus *Karydomys* (see Maridet *et al.* 2011b).

***Democricetodon tongi* Qiu, 1996**
(Fig. 6a–c)

2013 *Democricetodon* cf. *tongi* – Daxner-Höck *et al.*, tab. 20.4, p. 488.

Localities/Stratigraphy: Uolon Ovoony Khurem (biozone D1/1) and Ulaan Tolgoi (biozone D1/2), late Early Miocene.

Material: left M1, UTO-A/5 (NHMW 2013/0435/0001: 1.50×1.09 mm); right M2, strongly worn, UTO-A/5 (NHMW 2013/0435/0002: 1.17×1.29 mm); right m2, strongly worn, UTO-A/5 (NHMW 2013/0435/0003: 1.21×1.03 mm); left m3, ODO-A/2 (NHMW 2013/0436/0001: 1.19×1.12 mm).

Remarks: These molars are significantly smaller than that of *D.* aff. *lindsayi*. The morphology and size enter in the variability of *D. tongi* from Tunggur as described by Qiu (1996). We tentatively ascribe these teeth to the same species.

Genus *Megacricetodon* Fahlbusch, 1969

***Megacricetodon* aff. *sinensis* Qiu, 1996**
(Fig. 7a–n)

1999 *Megacricetodon* cf. *sinensis* – Höck *et al.*, fig. 21/6, p. 119.
2013 *Megacricetodon* sp. 1 – Daxner-Höck *et al.*, tab. 20.4, p. 488.
2013 *Megacricetodon* sp. 2 – Daxner-Höck *et al.*, tab. 20.4, p. 488.

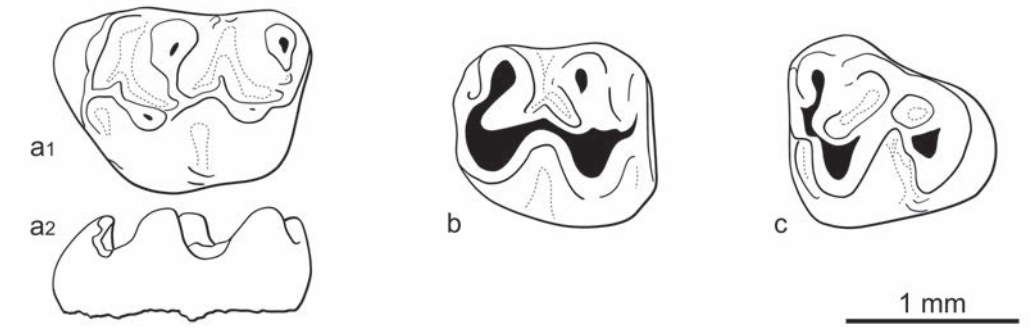

Fig. 6. *Democricetodon tongi* from Uolon Ovoony Khurem (layer UTO-a/5) and Ulaan Tolgoi (layer ODO-A/2), late Early Miocene: **a**. left M1, UTO-A/5 (NHMW 2013/0435/0001: **a1**. occlusal view, **a2**. lingual view); **b**. right M2, strongly worn, UTO-A/5 (NHMW 2013/0435/0002); **c**. left m3, ODO-A/2 (NHMW 2013/0436/0001).

Localities/Stratigraphy: Uolon Ovoony Khurem, Luugar Khudag (biozone D1/1) and Ulaan Tolgoi (biozone D1/2), late Early Miocene.

Material: left fragment of maxillary with M1–M3, ODO-B/1 (NHMW 2013/0439/0001: M1 1.56×1.08 mm, M2 1.10×1.01 mm, M3 0.79×0.87 mm); right M1 with postero-labial corner broken, UTO-A/5 (NHMW 2013/0437/ 0001: 1.65×1.02 mm); left M1 with posterior part broken, ODO-A/2 (NHMW 2013/0438/0001: not measurable); right M1 with posterior part broken, ODO-A/2 (NHMW 2013/0438/0002: not measurable); left M1, ODO-B/1 (NHMW 2013/0439/0002: 1.48×1.07 mm); right M1, ODO-B/1 (NHMW 2013/0439/0003: 1.58×1.04 mm); left M1, LOG-B/1 (NHMW 2013/0440/0001: 1.45×0.95 mm); right M2 with anterior part broken, ODO-A/2 (NHMW 2013/0438/0003: not measurable); left M2, ODO-B/1 (NHMW 2013/0439/0004: 1.07×1.03 mm); left m1, UTO-A/5 (NHMW 2013/0437/0002: 1.37×0.92 mm); right m1 with postero-lingual border broken, UTO-A/5 (NHMW 2013/0437/0003: 1.40×- mm); left m1,

Table 1. Measurements (in mm) of *Megacricetodon* aff. *sinensis* from the localities Uolon Ovoony Khurem, Luugar Khudag (biozone D1/1) and Ulaan Tolgoi (biozone D1/2). N: number of teeth measured; Min: minimum; Max: maximum; σ: standard deviation; CV: variation coefficient of Simpson.

	Length						Width					
	N	Min	Max	Mean	σ	CV	N	Min	Max	Mean	σ	CV
M1	5	1.45	1.65	1.54	0.080	5.19	5	0.95	1.08	1.03	0.052	5.01
M2	2	1.07	1.10	1.09	-	-	2	1.01	1.03	1.02	-	-
M3	1	0.79	0.79	0.79	-	-	1	0.87	0.87	0.87	-	-
m1	5	1.28	1.48	1.37	0.080	5.89	4	0.83	0.92	0.88	0.042	4.82
m2	2	1.03	1.12	1.08	-	-	2	0.90	1.02	0.96	-	-
m3	3	0.93	1.05	0.98	-	-	3	0.79	0.86	0.82	-	-

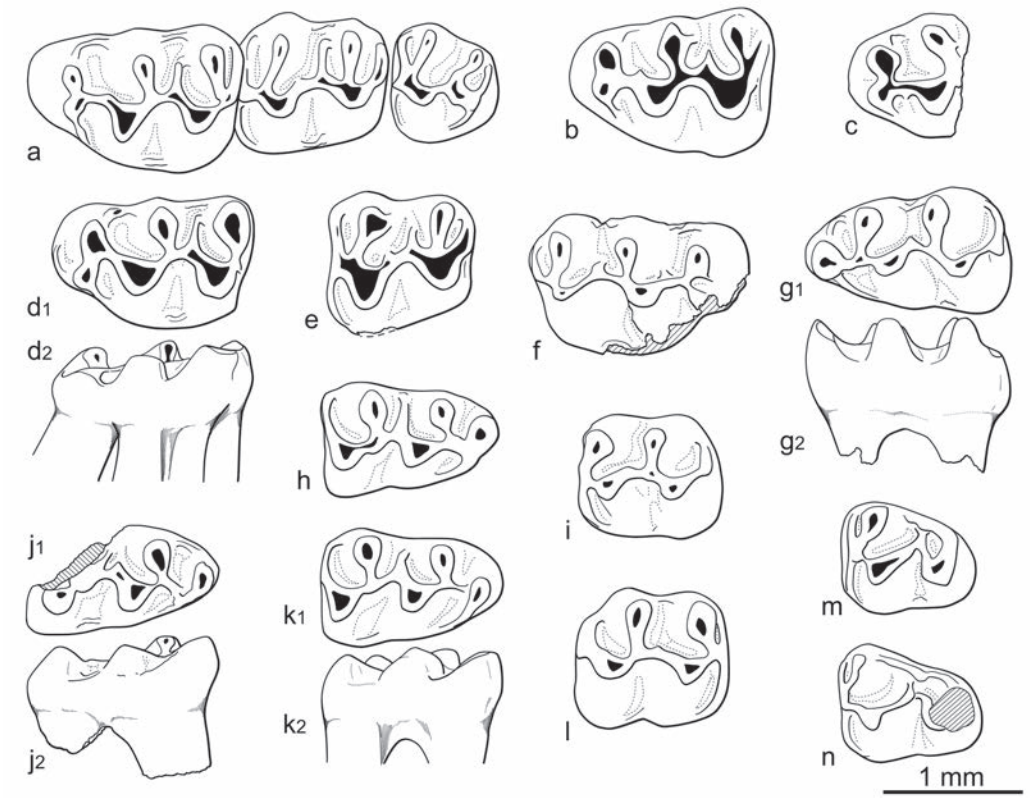

Fig. 7. *Megacricetodon* aff. *sinensis* from Uolon Ovoony Khurem (layers ODO-A/2 and ODO-B/1), Luugar Khudag (layer LOG-B/1) and Ulaan Tolgoi (layer UTO-A/5), late Early Miocene: **a**. left maxillary, fragment with M1–M3, ODO-B/1 (NHMW 2013/0439/0001); **b**. left M1, ODO-B/1 (NHMW 2013/0439/0002); **c**. left M1, anterior fragment, ODO-A/2 (NHMW 2013/0438/0001); **d**. left M1, LOG-B/1 (NHMW 2013/0440/0001: **d1**. occlusal view, **d2**. lingual view); **e**. left M2, ODO-B/1 (NHMW 2013/0439/0004); **f**. right M1, ODO-B/1 (NHMW 2013/0439/0003); **g**. left m1, ODO-A/2 (NHMW 2013/0438/0004: **g1**. occlusal view, **g2**. labial view); **h**. right m1, ODO-B/1 (NHMW 2013/0439/0006); **i**. left m2, ODO-A/2 (NHMW 2013/0438/0005); **j**. right m1, UTO-A/5 (NHMW 2013/0437/0003: **j1**. oclusal view, **j2**. labial view); **k**. right m1, ODO-B/1 (NHMW 2013/0439/0007: **k1**. occlusal view, **k2**. labial view); **l**. right m2, ODO-A/2 (NHMW 2013/0438/0006); **m**. left m3, ODO-A/2 (NHMW 2013/0438/0007); **n**. left m3, ODO-B/1 (NHMW 2013/0439/0009).

ODO-A/2 (NHMW 2013/0438/0004: 1.48×0.91 mm); right m1, ODO-B/1 (NHMW 2013/0439/0006: 1.28×0.83 mm); right m1, ODO-B/1 (NHMW 2013/0439/0007: 1.30×0.86 mm); right m1, poorly preserved, ODO-B/1 (NHMW 2013/0439/0008: not measurable); left m2 poorly preserved, UTO-A/5 (NHMW 2013/0437/0004: not measurable); left m2, ODO-A/2 (NHMW 2013/0438/0005: 1.03×0.90 mm); right m2, ODO-A/2 (NHMW 2013/0438/0006: 1.12×1.02 mm); right m2 with anterior border broken, ODO-B/1 (NHMW 2013/0439/0005: not measurable); left m3, ODO-A/2 (NHMW

2013/0438/0007: 0.97×0.81 mm); right m3, ODO-A/2 (NHMW 2013/0438/0008: 0.93×0.79 mm); left m3, ODO-B/1 (NHMW 2013/0439/0009: 1.05×0.86 mm); undetermined molar fragment, ODO-A/2 (NHMW 2013/0438/0009: not measurable). All measurement of *Megacricetodon* aff. *sinensis* are summarized in the table 1

Remarks: The size of the specimens is similar to *M. beijiangensis* MARIDET *et al.*, 2011 but the morphology differs noticeably in lower molars rarely possessing an ectomesolophid, in M2 not having a double protolophule, in M3 having a metacone developed in cusp and in m1 having the anterolophulid connecting sometimes to the labial end of the anteroconid. The same association of features also differentiates them from *M. dzhungaricus* (KORDIKOVA & DE BRUIJN, 2001), *M. yei* BI *et al.*, 2008, and *M. pusillus* QIU, 1996. In contrast, compared to *M. sinensis*, the specimens are slightly larger but only differ in having a frequent posterior spur of the paracone and a less divided anterocone in M1, a long mesolophid in m1, suggesting that they could be closely related. MARIDET *et al.* (2011b) noticed a continuous evolution from the Early Miocene to the Middle Miocene for the genus *Megacricetodon* in northern and central Asia, including a size decrease and the division of the anterocone more frequent. With regard to these trends *M.* aff. *sinensis* from Mongolia and *M. sinensis* from Tunggur could belong to a same lineage, *M.* aff. *sinensis* representing a less advanced stage.

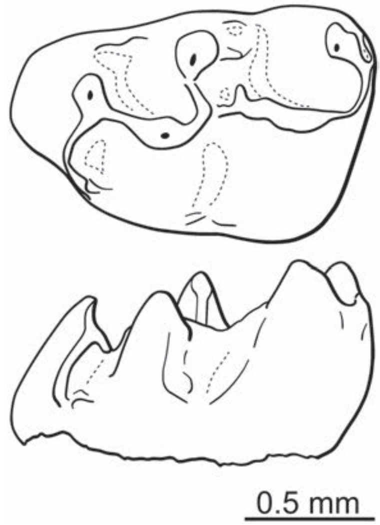

Fig. 8. *Megacricetodon* sp. from Builstyn Khudag (layer BUK-A/12+14), Late Miocene: left M1 (NHMW 2013/0441/0001).

Megacricetodon sp.
(Fig. 8)

1999 *Megacricetodon* sp. – HÖCK *et al.*, fig. 21/13, p. 119.
2013 *Democricetodon* sp. 3 – DAXNER-HÖCK *et al.*, tab. 20.4, p. 488.

Locality/Stratigraphy: Builstyn Khudag (biozone E), Late Miocene, layer BUK-A/12+14.

Material: left M1 (NHMW 2013/0441/0001: 1.42×0.93 mm).

Remarks: One M1 has been found of which general morphology resembles *Megacricetodon*, especially due to its small size and elongated anterior lobe. However it shows an undivided anterocone and a very long and curved lingual anteroloph, whereas all *Megacricetodon* species known in Central Asia usually have a well-divided anterocone in M1. This single tooth is not sufficient to further identify this taxon at specific level.

Genus *Nannocricetus* SCHAUB, 1934

Nannocricetus aff. *primitivus* ZHANG *et al.*, 2008
(Fig. 9a–m, Fig. 10a–i)

1999 *Allocricetus*? sp. – HÖCK *et al.*, fig. 21/13, p. 119.
2013 ?*Allocricetus* sp. – DAXNER-HÖCK *et al.*, tab. 20.4, p. 488.

Locality/Stratigraphy: Builstyn Khudag (biozone E), Late Miocene. All specimens come from the same layer, BUK-A/12+14.

Material: left M1 (NHMW 2013/0442/0001: 1.84×1.24 mm); left M1 (NHMW 2013/0442/0002: 1.99×1.33 mm); left M1 (NHMW 2013/0442/0003: 1.80×1.23 mm); left M1 (NHMW 2013/0442/0004: 1.79×1.16 mm); left M1 (NHMW 2013/0442/0005: 1.79×1.28 mm); left M1 with posterior border broken (NHMW 2013/0442/0006: not measurable); right M1 (NHMW 2013/0442/0007: 1.91×1.20 mm); left M2 (NHMW 2013/0442/0008: 1.40×1.20 mm); right M2 (NHMW 2013/0442/0009: 1.45×1.24 mm); right M2, strongly worn (NHMW 2013/0442/0010: 1.53×1.34 mm); right M2 (NHMW 2013/0442/0011: 1.47×1.21 mm); right M2 (NHMW 2013/0442/0012: 1.38×1.20 mm); right M2 (NHMW 2013/0442/0013: 1.47×1.19 mm); right M2 (NHMW 2013/0442/0014: 1.35×1.20 mm); right M2 (NHMW 2013/0442/0015: 1.41×1.23 mm); right fragment of maxillar with M2–M3 (NHMW 2013/0442/0016: M2 1.42×1.25 mm, M3 1.07×1.09 mm); right M3 (NHMW 2013/0442/0017: 1.09×1.07 mm); right M3 (NHMW 2013/0442/0018: 1.14×1.03 mm); left m1 (NHMW 2013/0442/0019: 1.70×1.07 mm); left m1 (NHMW 2013/0442/0020: 1.69×0.99 mm); right m1 (NHMW 2013/0442/0021: 1.63×1.05 mm); right m1 (NHMW 2013/0442/0022: 1.73×1.15 mm); right m1 (NHMW 2013/0442/0023: 1.77×1.12 mm); right m1 with anterior border broken (NHMW 2013/0442/0024: -×1.14 mm); right fragment of mandible with m1–m2 (NHMW 2013/0442/0025: m1 1.70×1.08 mm, m2 1.44×1.17 mm); right fragment of

Table 2. Measurements (in mm) of *Nannocricetus* aff. *primitivus* from the locality Builstyn Khudag (biozone E). N: number of teeth measured; Min: minimum; Max: maximum; σ: standard deviation; CV: variation coefficient of Simpson.

	Length						Width					
	N	Min	Max	Mean	σ	CV	N	Min	Max	Mean	σ	CV
M1	6	1.79	1.99	1.85	0.081	4.38	6	1.16	1.33	1.24	0.060	4.81
M2	9	1.35	1.53	1.43	0.055	3.82	9	1.19	1.34	1.23	0.046	3.75
M3	3	1.07	1.14	1.10	–	–	3	1.03	1.09	1.06	–	–
m1	7	1.63	1.77	1.71	0.049	2.87	8	0.99	1.15	1.09	0.055	5.08
m2	12	1.40	1.58	1.48	0.054	3.64	12	1.14	1.26	1.20	0.035	2.89
m3	4	1.19	1.34	1.29	0.069	5.33	4	1.05	1.07	1.06	0.010	0.90

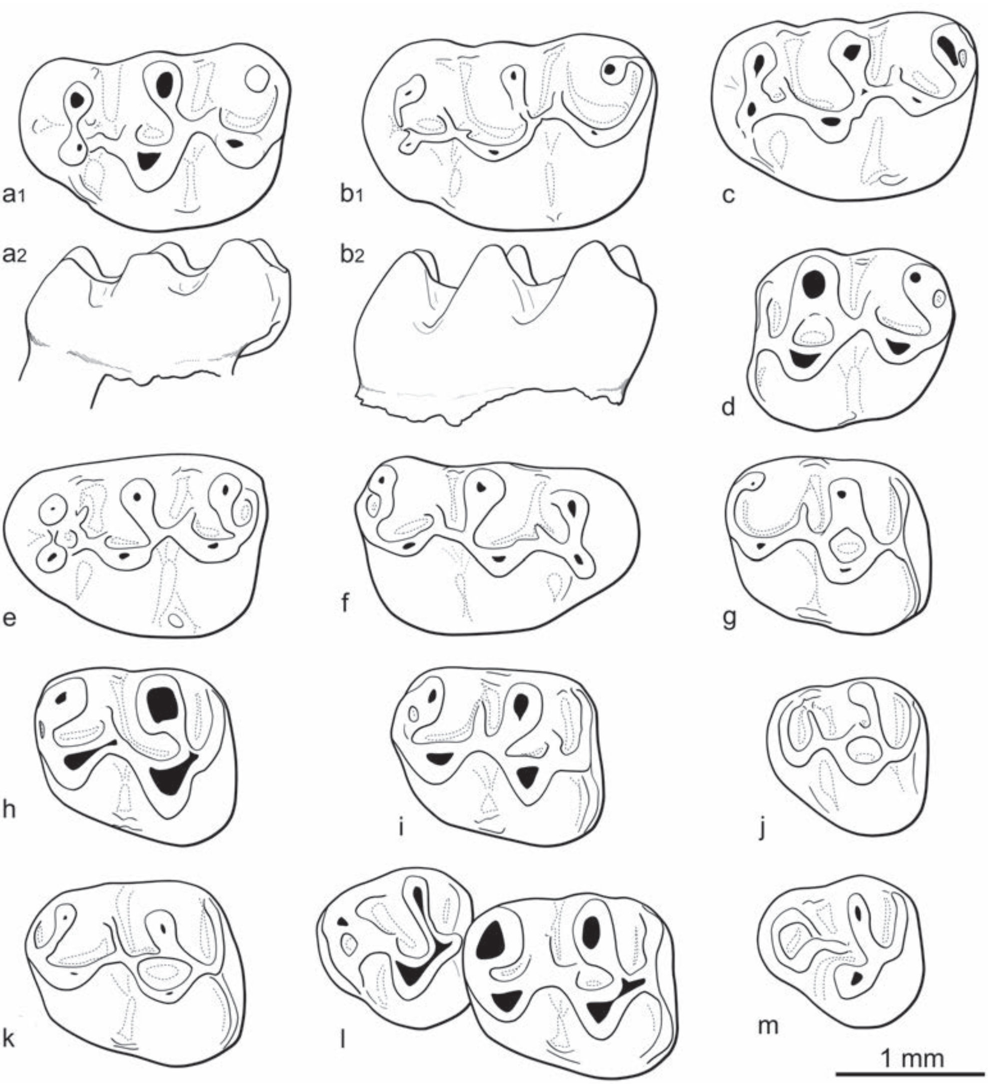

Fig. 9. Upper molars of *Nannocricetus* aff. *primitivus* from Builstyn Khudag (layer BUK-A/12+14), Late Miocene: **a**. left M1 (NHMW 2013/0442/0001: **a1**. occlusal view, **a2**. lingual view); **b**. left M1 (NHMW 2013/0442/0002: **b1**. occlusal view, **b2**. lingual view); **c**. left M1 (NHMW 2013/0442/0005); **d**. left M2 (NHMW 2013/0442/0008); **e**. left M1 (NHMW 2013/0442/0003); **f**. right M1 (NHMW 2013/0442/0007); **g**. right M2 (NHMW 2013/0442/0012); **h**. right M2 (NHMW 2013/0442/0014); **i**. right M2 (NHMW 2013/0442/0013); **j**. right M3 (NHMW 2013/0442/0017); **k**. right M2 (NHMW 2013/0442/0009); **l**. right maxillar, fragment with M2–M3 (NHMW 2013/0442/0016); **m**. right M3 (NHMW 2013/0442/0018).

mandible with m1–m2 (NHMW 2013/0442/0026: m1 1.77×1.14 mm, m2 1.40×1.20 mm); left m2 (NHMW 2013/0442/0027: 1.44×1.15 mm); left m2 (NHMW 2013/0442/0028: 1.52×1.23 mm); left m2 with labial border broken (NHMW 2013/0442/0029: not

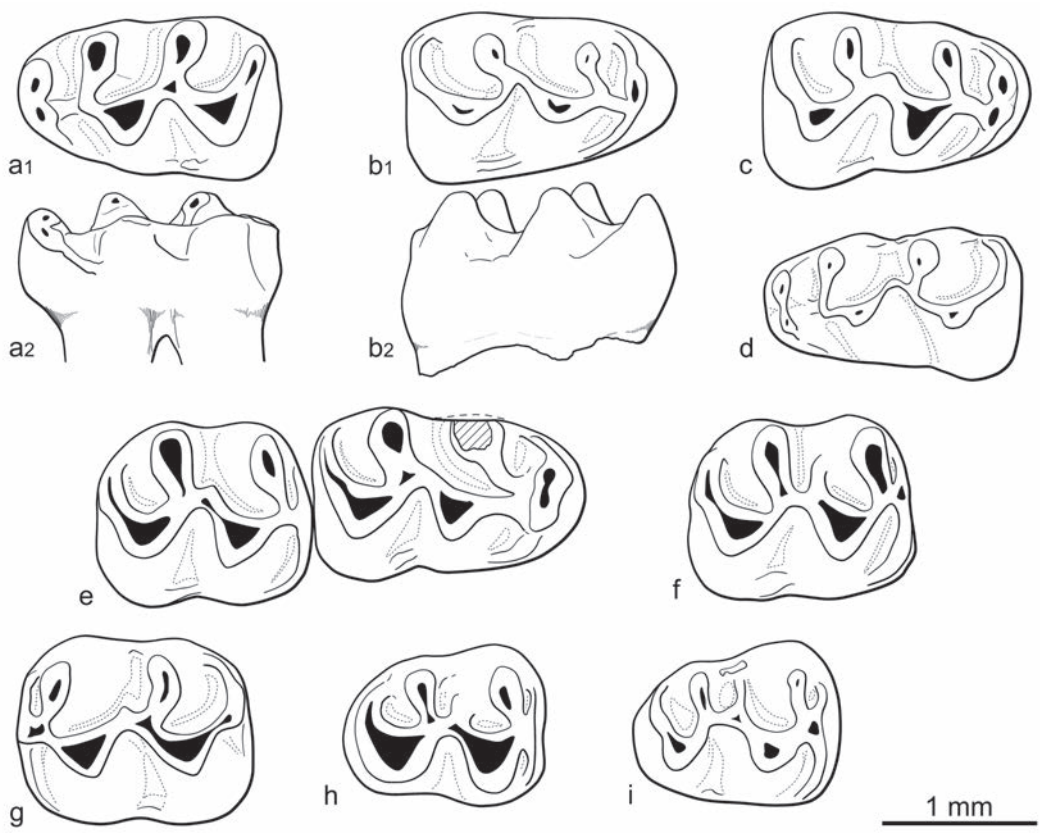

Fig. 10. Lower molars of *Nannocricetus* aff. *primitivus* from Builstyn Khudag (layer BUK-A/12+14), Late Miocene: **a**. left m1 (NHMW 2013/0442/0019: **a1**. occlusal view, **a2**. labial view); **b**. right m1 (NHMW 2013/0442/0023: **b1**. occlusal view, **b2**. labial view); **c**. right m1 (NHMW 2013/0442/0022); **d**. left m1 (NHMW 2013/0442/0020); **e**. right mandible, fragment with m1–m2 (NHMW 2013/0442/0026); **f**. right m2 (NHMW 2013/0442/0035); **g**. left m2 (NHMW 2013/0442/0028); **h**. right m3 (NHMW 2013/0442/0038); **i**. right m3 (NHMW 2013/0442/0041).

measurable); left m2 (NHMW 2013/0442/0030: 1.44×1.14 mm); left m2 (NHMW 2013/0442/0031: 1.49×1.21 mm); left m2 (NHMW 2013/0442/0032: 1.58×1.24 mm); left m2 (NHMW 2013/0442/0033: 1.51×1.20 mm); left m2 (NHMW 2013/0442/0034: 1.47×1.20 mm); right m2 (NHMW 2013/0442/0035: 1.48×1.20 mm); right m2 (NHMW 2013/0442/0036: 1.56×1.26 mm); right m2 (NHMW 2013/0442/0037: 1.44×1.21 mm); right m3 (NHMW 2013/0442/0038: 1.30×1.06 mm); right m3 (NHMW 2013/0442/0039: 1.19×1.05 mm); right m3 (NHMW 2013/0442/0040: 1.33×1.07 mm); right m3 (NHMW 2013/0442/0041: 1.34×1.07 mm); and 17 broken or poorly preserved unstudied specimens (NHMW 2013/0442/0000). All measurements of *Nannocricetus* aff. *primitivus* are summarized in the table 2.

Remarks: The specimens differ from *Sinocricetus* SCHAUB, 1930 and *Neocricetodon* SCHAUB, 1934 (and *Kowalskia* FAHLBUSCH, 1969 which we consider here as a junior synonym of *Neocricetodon*) in having less elongated teeth and less divided anterocon(id)es on first molars. They differ from *Allocricetus* SCHAUB, 1930 in being much smaller with a lower crown and in having almost transverse metalophulid and hypolophulid (whereas they are oblique in *Allocricetus*). Although the above presented specimen are more similar to the genus *Nannocricetus*, they differ from the type species *Nannocricetus mongolicus* SCHAUB, 1934 in being smaller and having less elongated molars, especially much less elongated M3 (based on the comparison with *Nannocricetus mongolicus* from Ertemte 2; WU 1991). ZHANG *et al.* (2008) described a new species of *Nannocricetus: N. primitivus* ZHANG *et al.*, 2008. In their diagnosis ZHANG *et al.* (2008) pointed out that *N. primitivus* differ from *N. mongolicus* in having a weakly divided anteroconid in m1, absent or reduced mesolophid in m1, and a reduced M3, which characters we also see in the Mongolian specimens. However the Mongolian specimens are also slightly larger than those of *N. primitivus* from the early Late Miocene of the Bahe Formation (Shaanxi, China: ZHANG *et al.* 2008). We consequently ascribe them to an affine form of *N. primitivus*, not excluding the possibility that the present population from Builstyn Khudag could represent a slightly more advanced stage of the same lineage.

Conclusions

The fossil cricetids recovered in the Taatsiin Gol area (Valley of Lakes, Mongolia) are only composed of dental and fragmentary jaws remains, sometime poorly preserved as it is also the case for other groups of rodents in the Early Miocene of the Valley of Lakes (*e.g.*, MARIDET *et al.* 2014). In contrast the Oligocene localities generally yielded much better preserved and more abundant material. However nine Miocene taxa belonging to six genera have been identified in the scope of the Austrian-Mongolian project (Table 3): *Gobicricetodon* sp., *Cricetodon* cf. *volkeri,* cf. *Primus* sp., *Democricetodon sui*, *Democricetodon* aff. *lindsayi, Democricetodon tongi*, *Megacricetodon* aff. *sinensis, Megacricetodon* sp. and *Nannocricetus* aff. *primitivus*.

As it is also the case in the Xinjiang province (Northwestern China), the genus *Democricetodon* occurs in the very beginning of the Miocene (MARIDET *et al.* 2011a) and the species *Democricetodon sui* seems characteristic of both the Xiejian Chinese land mammal age in China (MENG *et al.* 2013) and the upper part of local biozone D in central Mongolia. It is noteworthy that *D. sui* is only found in the assemblages II and III of the Suosuoquan Formation in the Junggar Basin (MENG *et al.* 2006). There estimated time spans are from *c*. 23.2 to *c*. 21.1 Ma (MENG *et al.* 2006) which doesn't cover the entire Aquitanian stage. Likewise the faunal assemblage D probably ends before the end of the Aquitanian stage.

Following in the Mongolian record are the mammalian assemblages of the biozone D1/1 and D1/2. One of the horizon from the Olon Ovoony Khurem profile (ODO-B/1) which provided a D1/1 assemblage is in fact sandwiched within the basalt layers II (28 Ma) and

Table 3. Occurrences of the cricetid taxa in each layer from the Early Oligocene to the Late Miocene, and their correlation with the local biochronology. Biozones correspond to the local biochronologic assemblages defined by DAXNER-HÖCK & BADAMGARAV (2007).

Epoch	local biozone	Layer	*Selenomys mimicus*	*Selenomys* sp.	*Cricetops dormitor*	*Cricetops elephanteus*	cf. *Edirnella* sp.	*Ulaancricetodon badamae*	*Eocricetodon* cf. *meridionalis*	*Eucricetodon caducus*	*Eucricetodon bagus*	*Eucricetodon asiaticus*	*Eucricetodon* sp. 1	*Eucricetodon* sp. 2	cf. *Plesiodipus wangae*	cf. *Aralocricetodon* sp.	*Aralocricetodon* aff. *schokensis*	*Bagacricetodon tongi*	*Democricetodon sui*	*Democricetodon* aff. *lindsayi*	*Democricetodon tongi*	cf. *Primus* sp.	*Megacricetodon* aff. *sinensis*	*Megacricetodon* sp.	*Gobicricetodon* sp.	*Cricetodon* cf. *volkeri*	*Nannocricetus* aff. *primitivus*
Late Miocene	E	BUK-A/12+14																						+			
Middle Miocene	D1/2	UTO-A/5																		+	+		+		+	+	
	D1/1	ODO-B/1																					+				
	D1/1	ODO-A/2																		+	+		+				
	D1/1	LOG-B/1																					+				
Early Miocene	D	RHN-A/12																				+					
	D	UNCH-A/3																	+								
Late Oligocene	C1	TAT-E/27								aff.	+																
	C1	IKH-B/5												+													
	C1	IKH-A/5												+		+											
	C1	DEL-B/12								aff.	+			+				+									
	C	TGW-A/2b									+		+		+	+	+										
	C	TGW-A/2a									+		+		+												
	C	TGW-A/1														+											
	C	TGR-C/2									+		+				+										
	C	TGR-C/1									+		+		+		+										
	C	TAR-A/2									+		+				+										
	C	ABO-A/3											+														
	C	ABO-083									+																
Early Oligocene	B	UNCH-A/3B			+						aff.																
	B	TGR-surface			+																						
	B	TGR-ZO/2						+	+		aff.																
	B	TGR-ZO/1						+			aff.																
	B	TGR-B/1			+			+	+		aff.	aff.															
	B	TGR-AB/22			+	+		+	+		aff.	aff.															
	B	TGR-AB/21			+			+	+		aff.	aff.															
	B	TGL-A/11c										aff.															
	B	TGL-A/11b									aff.																
	B	TGL-A/11						+																			
	B	TAT-E/3							+		aff.	aff.															
	B	TAT-D/2	+	+		+																					
	B	TAT-C/7							+			aff.															
	B	TAT-C/6						+			aff.	aff.															
	B	SHG-AB/17-18							+		aff.	aff.															
	B	SHG-AB/15+20						+			aff.																
	B	SHG-AB/12						+																			
	B	SHG-A/20									aff.	aff.															
	B	SHG-A/15							+																		
	B	SHG-A/9									aff.																
	B	SHG-basis	+		+																						
	B	IKH-A/3+4						+	+		aff.	aff.															
	B	IKH-A/1+2			+																						
	B	IKH-A/2							+		aff.	aff.															
	B	IKH-A/1						+	+		aff.	aff.															
	B	DEL-B/7						+	+		aff.																
	A	TGR-A/14					+	+	+	+		+															
	A	TGR-A/13	+						+	+		+															
	A	TGL-A/2	+		+					+																	
	A	TGL-A/1			+																						
	A	TAT-D/1	+		+			+	+	+		+															
	A	TAT-C/3						+		+		+															
	A	TAT-C/2								+		+															
	A	TAT-C/1								+																	
	A	SHG-C/2						+	+																		
	A	SHG-C/1						+				+															
	A	HL-A/2						+																			

III (13 Ma), but doesn't allow a more precise absolute datation. The Early Miocene age estimation proposed by DAXNER-HÖCK & BADAMGARAV (2007) was in fact tentative and based only on the mammalian fauna composition only. Likewise the D1/2 assemblage was tentatively correlated either with the late Early Miocene or possibly the early Middle Miocene (DAXNER-HÖCK & BADAMGARAV 2007; DAXNER-HÖCK *et al.* 2013). The above systematic study reveals that the cricetid taxa that compose both biozones are different from the cricetid found in the late Early Miocene of Xinjiang (MARIDET *et al.* 2011b) such as *Eumyarion* sp., *Karydomys debruijni* MARIDET *et al.* 2011 and *Megacricetodon beijiangensis* MARIDET *et al.*, 2011. In contrast the species found in both Mongolian biozones are similar to that of the Middle Miocene of Northern China (Inner Mongolia, QIU, 1996; Xinjiang, WU *et al.* 2009), suggesting a younger age than previously assumed, possibly the end of the Early Miocene for D1/1 or early Middle Miocene for both D1/1 and D1/2. The evolutionary stages of dipodids (DAXNER-HÖCK *et al.* 2014) in D1/2 still indicate a slightly younger age than D1/1.

The Builstyn Khudag locality yielded the only Late Miocene assemblage of the Valley of Lakes. The occurrence of *N.* aff. *primitivus*, of which type population was describe from the early Late Miocene of the Bahe Formation (Shaanxi province, China; ZHANG *et al.* 2008), confirms the Late Miocene age of the Mongolian locality. However, as explained above, the population of Builstyn Khudag might constitute a slightly more advanced stage of the same lineage. This observation implies that Builstyn Khudag age would be younger than the Bahe Formation faunas where *N. primitivus* was found (*e.g.*, younger than *c*. 8 Ma; ZHANG *et al.* 2013), and consequently younger than the age proposed by DAXNER-HÖCK *et al.* (2013). A revised age of the Miocene local biozones D, D1/1, D1/2 and E is proposed following these observations (Fig. 2).

The Figure 11 shows the taxonomic composition and richness of cricetids at specific (Fig. 11b) and generic (Fig. 11a, c) levels from the Early Oligocene to the Late Miocene. The latest Oligocene assemblage (biozone C1) is mainly composed of middle-to-large-sized eucricetodontines such as the genera *Eucricetodon* THALER, 1966 and *Aralocricetodon* BENDUKIDZE, 1993 (see DAXNER-HÖCK *et al.* 2013) whereas the earliest Miocene assemblage is only composed of small-sized cricetines (*Democricetodon sui* and cf. *Primus* sp.). Both the specific and generic richness display a similar evolution characterized by a decrease from the Early Oligocene to the earliest Miocene followed by an increase of richness during the late Early Miocene. This increase of diversity is very likely underestimated, due to the fact that the material recovered from the late Early Miocene (localities Ulaan Tolgoi, Uolon Ovoony Khurem and Luugar Khudag) is often poorly preserved (MARIDET *et al.* 2014). Likewise the specimens from Builstyn Khudag are relatively scarce compared to the Oligocene and earliest Miocene localities. However the diversity curves show that the earliest Miocene just after the Oligocene/Miocene transition (biozone D) is a critical period when the diversity of cricetids is at its lowest. The poly-cohort of cricetids at generic level (Fig. 11d) all shows that all of the Oligocene genera disappear at the Oligocene/Miocene transition. These observations emphasize a drastic renewal of cricetid communities through the Oligocene-Miocene boundary

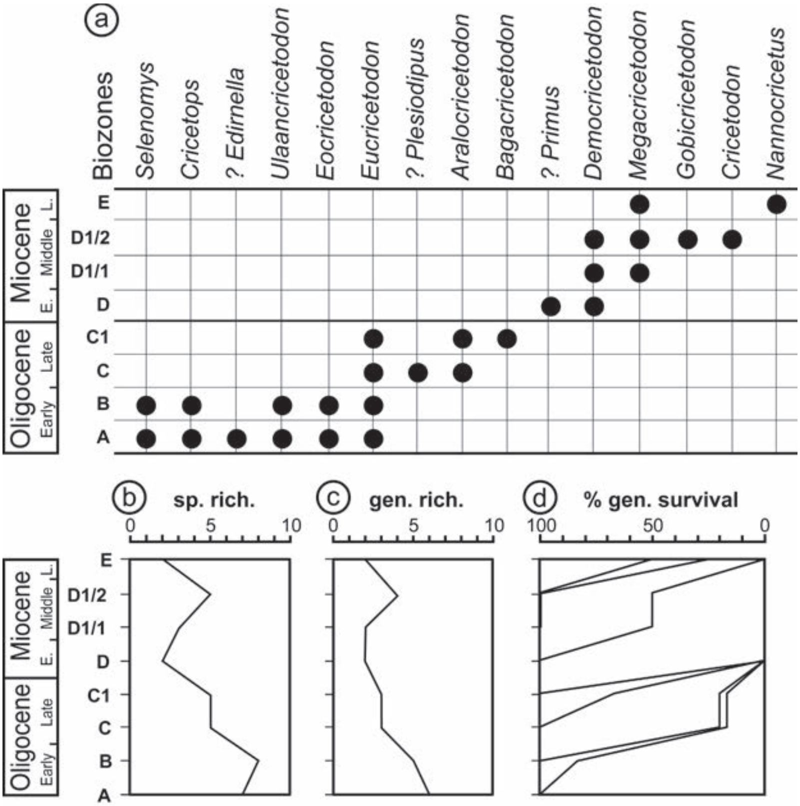

Fig. 11. Evolution of cricetids diversity, in each local biozone, from the Early Oligocene to the Late Miocene in the Taatsiin Gol area, Valley of Lakes: **a**. occurrence of cricetid genera in the local stratigraphy; **b**. cricetid species richness; **c**. cricetid generic richness; **d**. percentage of survival of the local cricetid assemblages thought time.

(Table 3). The second main renewal in the cricetids assemblages occurs between the early Middle and Late Miocene. However, as already explained above, this observation might be partly biased by the fact that the sampling effort is insufficient for these periods of time. Furthermore most of the Middle and the early Late Miocene record being absent from the Taatsiin Gol area it is not possible to further interpret this change. However, the only two taxa of cricetids found in the Late Miocene of Builstyn Khudag indicate that the cricetids' communities have likely undergone a new decrease of their diversity at some point between the Middle and Late Miocene in the Valley of Lakes.

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