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Tsaganomyidae (Rodentia, Mammalia) from the Oligocene of Mongolia (Valley of Lakes)

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(With 16 figures and 6 tables)

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Abstract

In this paper we present new data on tsaganomyid species from the Oligocene of Mongolia. This group of rodents, endemic to Mongolia, China, and Kazakhstan, is not well known. In the context of the well-dated sediments from the Taatsiin Gol and Taatsiin Tsagaan Nuur, Valley of Lakes, we were able to establish their occurrence precisely. We present and discuss additional morphological data of five species. Around 32 Ma all these five species are present in the Taatsiin Gol and Taatsiin Tsagaan Nuur areas. Until 28 Ma, *Tsaganomys altaicus*, *Cyclomylus lohensis*, *Cyclomylus intermedius*, ?*Cyclomylus biforatus* and *Coelodontomys asiaticus* are all part of the rodent fauna in this area. From then on, the diversity of the group decreased steadily, and during the following 3 million years only *Tsaganomys altaicus* and *Coelodontomys asiaticus* were present, and at ~24 Ma, just before the end of the Oligocene, the family disappeared completely. Trends in size seem to reflect changes in climate and food availability. Reviewing all data available, we conclude that tsaganomyid species had a fossorial and digging lifestyle, but most activities took place outside its burrow.

Key-words: Tsaganomyidae, Paleogene, Neogene, taxonomy, biostratigraphy, Valley of Lakes, Mongolia

Kurzfassung

In dieser Arbeit präsentieren wir neue Daten über Arten der Tsaganomyidae aus dem Oligozän der Mongolei. Diese kaum bekannte Nagergruppe ist in der Mongolei, China und Kazachstan

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endemisch. Die gut datierten Sedimente aus der Taatsiin Gol und Taatsiin Tsagaan Nuur Region (Tal der Gobiseen), ermöglichten eine genaue Bestimmung ihrer regionalen und zeitlichen Verbreitung. Wir präsentieren und diskutieren die morphologischen Daten von fünf Arten: *Tsaganomys altaicus*, *Cyclomylus lohensis*, *Cyclomylus intermedius,* ?*Cyclomylus biforatus* und *Coelodontomys asiaticus*. Alle fünf Arten waren vor etwa 32 Ma bis 28 Ma in der Taatsiin Gol und Taatsiin Tsaagaan Nuur Region verbreitet und Teil der Nagetierfaunen. In den folgenden drei Millionen Jahren existierten nur *Tsaganomys altaicus* und *Coelodontomys asiaticus*, und um ~ 24 Ma, kurz vor dem Ende des Oligozäns starb die Familie aus. Größentrends reflektieren Veränderungen von Klima und Nahrungsangebot. Aus den verfügbaren Daten schließen wir, dass die Tsaganomyidae grabende Tiere waren, die teils unterirdisch lebten, meist aber außerhalb ihrer Baue aktiv waren.

Schlüsselwörter: Tsaganomyidae, Paläogen, Neogen, Taxonomie, Biostratigrafie, Tal der Gobiseen, Mongolei

Introduction

The Tsaganomyidae are rodents with hystricognath jaws and protrogomorph skulls, hypsodont cheek teeth and very large incisors. They are known only from Oligocene sediments of Mongolia, China and Kazakhstan. On the surface of the outcrops in the hills of the Valley of Lakes, especially in the Tatal Gol area, quite often tsaganomyid incisors can be found (Fig. 1), often a good indication of a fossiliferous layer nearby.

Matthew & Granger (1923) were the first to describe tsaganomyid genera and species from the Hsanda Gol Formation of the Valley of Lakes in Mongolia. Many other publications by different authors followed (Vinogradov & Gambaryan 1952; Kowalski 1974; Mellett 1966, 1968; Shevyreva 1971, 1972; Bryant & McKenna 1995; Wang 2001).

In 1995, Bryant & McKenna published a thorough paper on Tsaganomyidae. Material collected from the Hsanda Gol Formation (Mongolia) in the early 1990's gave them a good opportunity to clarify the phylogenetic position of this family. Since a good taxonomic consensus was lacking from earlier publications, they updated the taxonomy of this group by providing detailed descriptions of skull and dentition, including measurements. Bryant & McKenna synonymized all tsaganomyid species with *Tsaganomys altaicus*, the variation in morphology interpreted as being the expression of ontogenetic phases. Two morphotypes were distinguished, characterized by differences in size, and interpreted to represent sexual dimorphism. The total range in size, large for each dental element, was interpreted to be a result of differences in individual body size and reflecting age classes. The molars were described as single rooted, the small additional roots were considered to be only present in the deciduous premolars and premolars.

In 2001, Wang provided an overview of all publications concerning the Tsaganomyidae. The material described and measured by Wang (2001) is from many different localities and different geographical areas, collected in earlier years by various research groups and stored away in several collections. Wang redefined the Tsaganomyidae, synonymized species, and provided diagnosis and descriptions of the remaining species

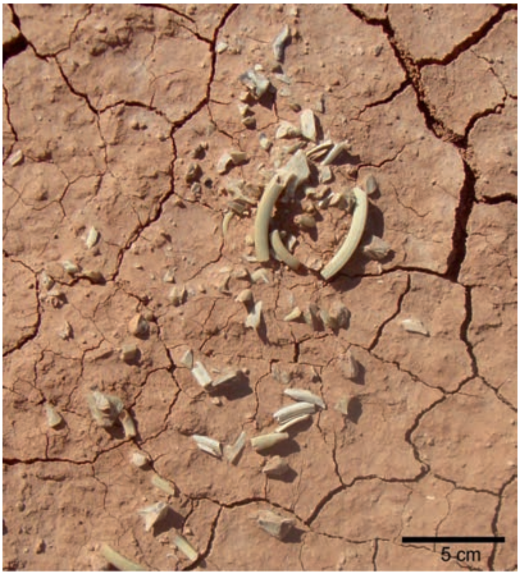

Fig. 1. Teeth and bones from a tsaganomyid on and in the surface (Tatal Gol; Hsanda Gol Formation, Mongolia)

and of some new ones. WANG did not interpret the differences in morphology as differences in individual age or sex, and considered the morphological differences in skull and dentition to be characteristic for new species. In contrast to BRYANT & MCKENNA, she divided the Tsaganomyidae into five species: *Tsaganomys altaicus*, *Cyclomylus lohensis*, *Cyclomylus intermedius*, *Cyclomylus biforatus* and *Coelodontomys asiaticus*. The latter three were newly erected.

Here, we present data on fossil Tsaganomyidae from Taatsiin Gol and Taatsiin Tsagaan Nuur areas in the Valley of Lakes (Mongolia), in order to supplement the existing data base on tsaganomyid species.

Geological setting and chronologic framework

The Valley of Lakes is one of the Pre-Altai depressions in Mongolia. It is situated between the Gobi Altai Mountains in the south and the Khangai Mountains in the north, and extends across ~500 km in a west-east direction in Central Mongolia. Above a Proterozoic and Paleozoic basement the basin is filled with continental sediments ranging from the Cretaceous to the Quaternary. Part of the Valley of Lakes is the Taatsiin Gol and Taatsiin Tsagaan Nuur area (Uvurkhangai Aimag), long known for the fossil richness of Cenozoic sediments and its basaltic volcanism (BERKEY & MORRIS 1927, DEVJATKIN 1981, DEVJATKIN & BADAMGARAV 1993). There, the Oligocene-Miocene sediment sequences of the Hsanda Gol and Loh Formations are exposed (Fig. 2).

In a large part of the study area several basalt flows alternate with the sedimentary deposits. The combination of fossil localities and the age determination of the basalt provides a chronologic calibration of the successive fossil assemblages (HÖCK *et al.* 1999;

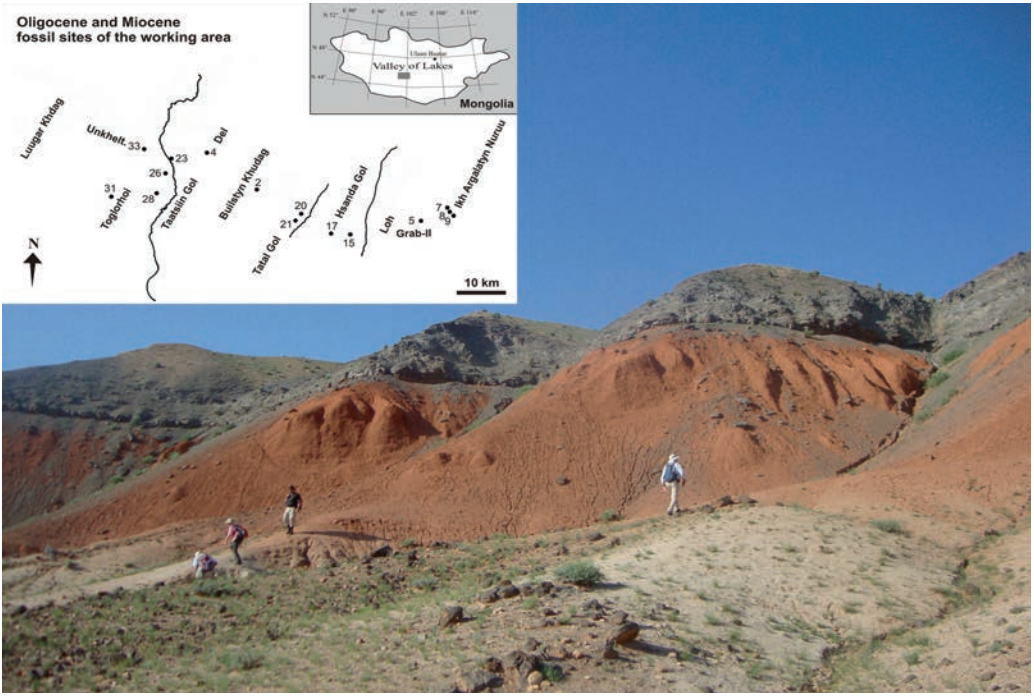

Fig. 2. The Hsanda Gol Formation in the Taatsiin Gol left side section (TGL-B). Insert: vertebrate localities and sections in the Valley of Lakes, Uvurkhangai, Mongolia. Vertebrate localilities and sections in the valley of Lakes, Uvurkhangai, Mongolia. 2: Builstyn Khudag, BUK-A; 4: Del, DEL-B; 5: unnamed locality, GRAB-II; 7: Ikh Argalatyn Nuruu, IKH-A; 8: Ikh Argalatyn Nuruu, IKH-B; 9: Ikh Argalatyn Nuruu, IKH-C; 15: Hsanda Gol, SHG-A; 17: Hsanda Gol, SHG-C; 20: Tatal Gol, TAT-C; 21: Tatal Gol, TAT-D, -E; 23: Taatsiin Gol left, TGL-A; 26: Taatsiin Gol right, TGR-B; 27: Taatsiin Gol right, TGR-AB; 28: Taatsiin Gol right, TGR-C; 33: Unkheltseg, UNCH-A

Daxner-Höck & Badamgarav 2006; Daxner-Höck *et al.* 2013) with a characterization of eight informal biozones based on the rodent faunas (A, B, C, C1, D, D1/1, D1/2 and E; from Early Oligocene to Late Miocene). In Daxner-Höck *et al.* (2010) the four lowermost biozones (A, B, C, C1; early and late Oligocene) were updated using both small and large mammals.

In figure 3 the basalt occurrences are given against the geologic time scale and Mongolian biozones. The occurrences were dated by the ^{40}Ar / ^{39}Ar method. The Early Oligocene basalt I group is dated around 31.5 Ma (range: 30.4–32.2 Ma; errors varying from 0.3 to 0.8 Ma). The second one is the Late Oligocene basalt II, and displays age differences of at least 1 Ma between local occurrences west and east of Taatsiin Gol. The eastern basalt II flows are around 28 Ma in age (range: 27–29 Ma), the western flows around 26.5 Ma (range: 25–27 Ma). Finally, basalt III is of Middle Miocene age (range: 12.2–13.2 Ma; errors vary from 0.2 to 0.7 Ma; Höck *et al.* 1999: fig. 8; Daxner-Höck *et al.* 2010: p. 351).

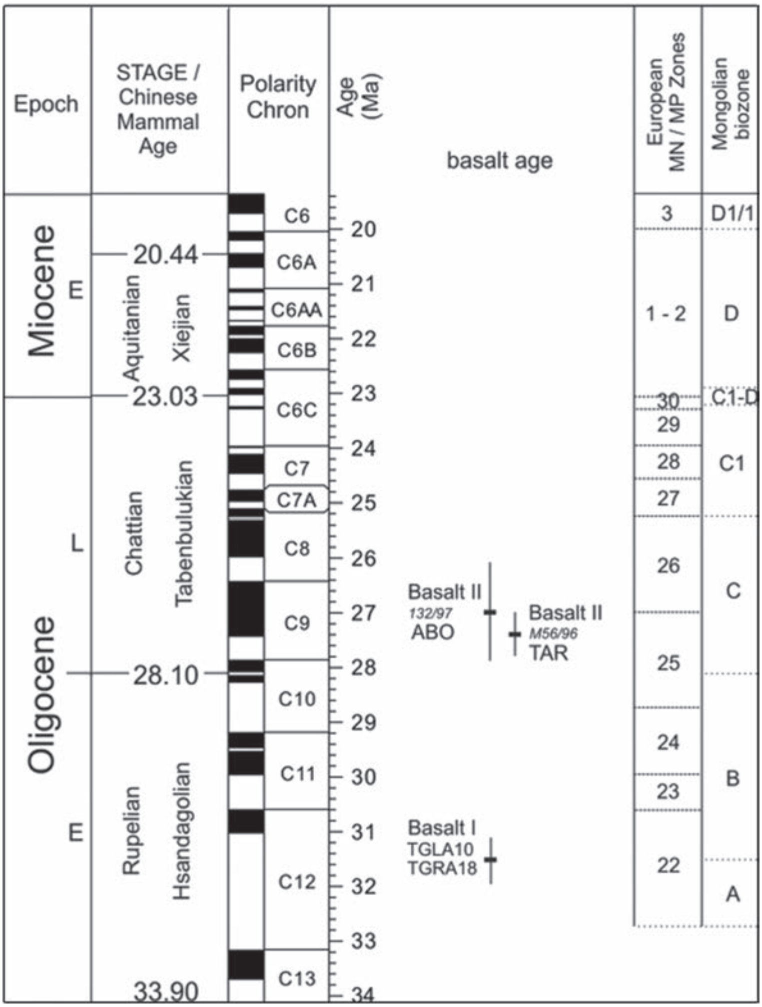

Fig. 3. Geologic time scale, the basalt occurrences and the Mongolian biozones (adapted from DAXNER-HÖCK *et al.* 2010)

Material and methods

The Tsaganomyidae used in this paper were all collected during fieldwork under the auspices of the Mongolian-Austrian Geoscientific Project. Systematic fieldwork in the Taatsiin Gol and Taatsiin Tsagaan Nuur areas in the Valley of Lakes (Mongolia) took place during several field surveys between 1995 and 2012, and produced a huge amount of fossils of Oligocene and Miocene age. The main bulk of the fossils was collected by screen washing of the sediments, thus the fossils can be assigned to a specific sediment layer of a specific stratigraphic section. Only a small part was collected from the surface, and these fossils were only included when it was very clear from which level

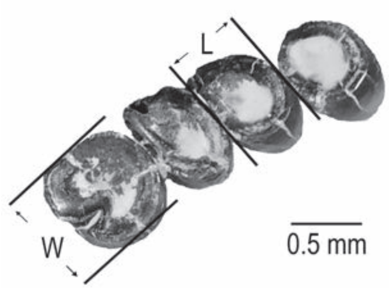

Fig. 4. All cheek teeth were measured in the same way: the maximal length (L) of the premolar and molar and, perpendicular to that, the maximum width (W). The measurements are with a precision of 0.01 mm

in the section they originated. The ranges and distribution outside of our research area of the Tsaganomyidae species are from WANG (2001) and QIU *et al.* (2013), ages of the Kazakhstan occurrences are from ERBAJEVA (1999) and the Chinese ages are from QIU *et al.* (2013).

The fossils are either from surface finds (collection number ending with 'o') or from wet-screening of fossil-bearing sediments. During field-campaigns, numerous cheek teeth, jaws and skulls, of Tsaganomyidae were collected (most jaws and skulls are only partly preserved). They are stored in the collections of the Laboratory of the Paleontological Centre, Mongolian Academy of Sciences, Ulaanbaatar (Mongolia), and in the collections of the Natural History Museum, Geological-Paleontological Department, in Vienna (Austria). The descriptions and measurements are restricted to the fossils from the Vienna collection.

The large number of tsaganomyid fossils available to us provides additional information on the morphology of all species; we will present a general description for each species combined with new observations. Emphasis will be on the cheek teeth since complete jaws and skulls are absent; the *Tsaganomys altaicus* skull in figure 5 is the most complete one. All other specimens are fragments, often damaged or distorted before or after burial. Thus complete descriptions of jaws and skulls are not possible here and only specific characteristics are, when present, added.

Only cheek teeth with an identifiable tooth row position were used in the descriptions and measurements. Two classes of wear are given: F (Fresh) or W (Worn). Fresh implies that the original occlusal pattern is still (partly) visible on all or some cheek teeth in the tooth row, whereas it is absent in the worn category. All cheek teeth were measured in a similar way: the maximal length of the molar and, perpendicular to that, the maximum width (Fig. 4). These measurements are as in WANG (2001: p. 3, fig. 1) except for the less worn lower cheek teeth which were measured longitudinally to the row of cheek teeth. The measurements are with a precision of 0.01 mm. Length of tooth rows are not given because the preservation of many jaws and skulls is highly variable, and in many objects gaps between the cheek teeth prevent a precise measurement. We used a Nikon stereoscopic microscope type 104 and a Nikon Digital sight DS-U2 (SMZ800) with a DS-Fi1 camera (0.7 × DXM lens) connected to a computer with NIS-Elements 3.2 (Build 677), and BR software for measuring.

Abbreviations

NHMW = Naturhistorisches Museum Wien (Natural History Museum, Vienna, Austria)
MPC = Mongolian Paleontologica Center Collection

Upper cheek teeth are indicated by an uppercase letter, lower cheek teeth are indicated by a lowercase letter; DP and dp are deciduous premolars, P and p are premolars, M and m are molars. F indicates fresh, unworn cheek teeth and W indicates worn cheek teeth.

Systematic palaeontology

Class Mammalia LINNEAUS, 1758

Order Rodentia BOWDICH, 1821

Family Tsaganomyidae MATTHEW & GRANGER, 1923

Genus *Tsaganomys* MATTHEW & GRANGER, 1923

Type species: *Tsaganomys altaicus* MATTHEW & GRANGER, 1923

Type locality: Hsanda Gol Formation, red strata, Loh, Tsagan Nor Basin (Mongolia)

Included species: type species only

Remark: WANG (2001) emended the diagnosis and discussed detailed occurrences and synonymies.

Tsaganomys altaicus MATTHEW & GRANGER, 1923
(Figs 5, 6 & 7)

1923 *Tsaganomys altaicus,* new genus and species – MATTHEW & GRANGER: 2; figs 1–3.
2001 *Tsaganomys altaicus* – WANG: 5–18; figs 2–13. [and all synonyms therein]
2010 *Tsaganomys altaicus* – DAXNER-HÖCK *et al.*: 356; fig. 4 (7).
2010 *Tsaganomys altaicus* – DAXNER-HÖCK *et al.*: 361; fig. 5 (10).

Occurrence in Mongolia (Valley of Lakes, Uvurkhangai, this study): Table1.

Other occurrences of *Tsaganomys altaicus*: Late early Oligocene and Late Oligocene of Nei Mongol (China) and Mongolia, Late Oligocene of Kazakhstan.

Measurements: All measurements are summarized in table 2. The plots of Length/ Width are given in figures 8 and 9, and in figures 10 and 11 the scatter plots of the ratio Length / Width and Length (except deciduous teeth).

Remarks: Deciduous premolars (dp3, dp4, dP3 or dP4) are not known from *Tsaganomys altaicus*, nor are p3 and P3. We interpret the p4 and P4 as being true premolars and not retained deciduous premolars.

The cheek teeth are strongly hypsodont. The lower cheek teeth are concave antero-lingually and extend bucally of the lower incisor, the upper cheek teeth are concave

Table 1. Occurrences of *Tsaganomys altaicus*, *Cyclomylus lohensis*, *Cyclomylus intermedius*, ?*Cyclomylus biforatus* and *Coelodontomys asiaticus* in Mongolia (Valley of Lakes, Uvurkhangai). Collection numbers are for specimens used for measurements.

Species	biozone	Profile	NHMW collection number
Tsaganomys altaicus	A	TAT-C/1	2013/0525/0001 a, b; 2013/0525/0002 a, b, c
	A	TAT-D/1 Hü 1	2013/0537/0001 to 2013/0537/0004
Tsaganomys altaicus	B	DEL-B/7	2013/0483/0001
	B	IKH-A/2-4	2013/0492/0001
	B	SHG-A/13+14	2013/0503/0001 to 2013/0503/0003
	B	SHG-A/14	2013/0503/0004
	B	SHG-A/18-20	2013/0509/0001 to 2013/0509/0005
	B	SHG-above sst	MPC
	B	TAT-C/6	2013/0527/0001
	B	TAT-WP 22/23	MPC
	B	TGL-A/11c	2013/0547/0001; 2013/0547/0002
	B	TGR-AB	2009z0136/001
	B	TGR-AB/21	2013/0548/0001; 2013/0548/0002
	B	TGR-AB/22	2013/0549/0001; 2013/0549/0002
	B	UNCH-A/3	2013/0564/0001
Tsaganomys altaicus	C	TGR-C/2	2009z0146/001; 2013/0552/001 to 2013/0552/0003
	C	TGR-C/Bad	2013/0554/0001
	C	TGR-C/Bad6	2013/0554/0002
	C	TGW 2+3 O/2	MPC
	C	TGW-A/2	2013/0563/0001 to 2013/0563/0005
	C	TGW-O/2	MPC
Tsaganomys altaicus	C1	TGW-A/1-4	2013/0560/0001; 2013/0560/0002 a, b
	C1	TGW-A/5 , TAT-051/2, TAT-044 , HTSE	
Cyclomylus lohensis	A	GRAB-II/1	2013/0487/0001; 2013/0487/0002
	A	IKH-A/1	2013/0490/0001 a, b
	A	TAT-basis O	MPC
	A	TAT-basis O 2013	MPC
	A	TAT-D oberfl	2013/0528/0001 to 2013/0528/0003
	A	TAT-D/1 Hü 1	2013/0533/0001 to 2013/0533/0007

Table 1 (continued).

Species	biozone	Profile	NHMW collection number
	A	TAT-D/1 oberfl	2013/0541/0001 to 2013/0541/0003
	A	TAT-D/basis	2013/0543/0001 to 2013/0543/0004
	A	TAT-D1	2013/0542/0001 a, b; 2013/0542/0002 a, b, c; 2009z0134/001
Cyclomylus lohensis	B	DEL-B/7	2013/0486/0001
	B	IKH-A/2-4	2013/0493/0001; 2013/0493/0002
	B	IKH-mix	2013/0499/0001; 2013/0499/0002
	B	SHG-A/13	2013/0500/0001
	B	SHG-A/13+14	2013/0500/0002
	B	SHG-A/14	2013/0500/0003
	B	SHG-A/18-20	2013/0506/0001 to 2013/0506/0007
	B	SHG-above sst	MPC
	B	TAT-C/6	2013/0526/0001; 2013/0526/0002
	B	TGL-A/11c	2013/0546/0001
	B	TGR-AB/22	2013/0550/0001; 2013/0550/0002
Cyclomylus intermedius	A	DEL-B/2	2013/0482/0001
	A	SHG-C/2	2013/0514/0001
	A	TAT-basis O	MPC
	A	TAT-basis O 2013	MPC
	A	TAT-C/1	2013/0523/0001
	A	TAT-D oberfl	2013/0529/0002; 2013/0529/0004 a, b, c, d; 2013/0529/0003 a, b; 2013/0529/0001
	A	TAT-D/1 Hü 1	2013/0532/0001 a, b; 2013/0532/0002 a-k
	A	TAT-D/1 oberfl	2013/0539/0002; 2013/0539/0001
	A	TAT-D/basis	2013/0544/0001 a, b, c
Cyclomylus intermedius	B	DEL-B/7	2013/0485/0001
	B	IKH-A/1	2013/0489/0001 to 2013/0489/0003
	B	IKH-A/2-4	2013/0491/0001
	B	IKH-A/V2	2013/0495/0001 a, b
	B	IKH-B/a	2013/0496/0001
	B	IKH-C	2013/0498/0001
	B	SHG-A/14	2013/0501/0001
	B	SHG-A/18-20	2013/0507/0001 to 2013/0507/0005
	B	SHG-above sst	MPC

Table 1 (continued)

Species	**biozone**	**Profile**	**NHMW collection number**
	B	TGL-A/11c; IKH-A/1; TGR-AB/22	
Cyclomylus intermedius	C	TGR-O	2013/0557/0001
	C	TGW-A/2	2013/0561/0001
?Cyclomylus biforatus	A	TAT-C/1	2013/0522/0001
	A	TAT-D oberfl	2013/0530/0001 a, b
	A	TAT-D/1 Hü 1	2013/0534/0001 to 2013/0534/0004
	A	TAT-D/1 oberfl	2013/0540/0001
?Cyclomylus biforatus	C	TGR-O	2013/0556/0001
Coelodontomys asiaticus	A	TAT-basis O 2013	MPC
	A	TAT-C/1	2013/0524/0001
	A	TAT-D oberfl	2013/0531/0001 to 2013/0531/0003
	A	TAT-D/1 oberfl	2013/0538/0001; 2013/0538/0002
	A	TAT-D/1 Hü 1	2013/0536/0001 to 013/0536/0010
Coelodontomys asiaticus	B	IKH-A/V2	2013/0494/0001
	B	SHG-A/13+14	2013/0504/0001
	B	SHG-A/18-20	2013/0505/0001 a, b
	B	SHG-below sst	MPC
	B	TGR-B/1	2013/0551/0001
	B	UNCH-A/3	2013/0565/0001
Coelodontomys asiaticus	C	TGR-C/2	2013/0553/0001 to 2013/0553/0004
	C	TGR-C/Bad6	2013/0555/0001
	C	TGW-A/2	2013/0562/0001

posteriorly. The upper cheek teeth are slightly more curved than the lower ones. All cheek teeth show wear, lophs and cusps on the occlusal surface are absent, indicating that the enamel on the occlusal surface is very thin, and worn away in early wear. The cheek teeth are cylindrical, the occlusal surface is oval-shaped. In occlusal view, of cheek teeth that are still positioned in the jaw, the enamel surrounding the dentine core seems to be continuous, except that it is very thin on the anterior side of the lower cheek teeth and on the posterior side of the upper cheek teeth. However, in isolated cheek teeth an enamel free zone can be seen on the antero-lingual side in lower cheek teeth and on the postero-labial side in the upper cheek teeth. The difference between enamel and dentine is slight as the dentine has almost the same luster as the enamel, but a thin line separating the two materials can be seen.

Table 2. Measurements in mm of *Tsaganomys altaicus.*

Tsaganomys altaicus

		Length				Width			
Biozone	**element**	**N**	**Mean ± SE**	**range**	**SD**	**N**	**Mean ± SE**	**range**	**SD**
A	p4	4	3.52 ± 0.25	2.87 – 4.08	0.50	4	5.35 ± 0.22	4.75 – 5.78	0.62
B	p4	20	4.02 ± 0.16	2.81 – 6.32	0.73	19	5.92 ± 0.13	4.40 – 6.99	0.58
C	p4	7	3.14 ± 0.17	2.44 – 3.70	0.47	7	5.41 ± 0.27	4.33 – 6.41	0.70
C1	p4	2	3.19 ± 0.30	2.89 – 3.48	0.42	2	5.43 ± 0.70	4.73 – 6.12	0.98
A	m1	5	4.14 ± 0.30	3.46 – 5.14	0.66	5	5.99 ± 0.41	5.16 – 7.34	0.92
B	m1	20	4.21 ± 0.12	3.37 – 5.78	0.55	15	6.40 ± 0.18	5.03 – 7.49	0.70
C	m1	8	3.69 ± 0.18	2.86 – 4.40	0.51	8	5.96 ± 0.17	5.41 – 6.61	0.48
C1	m1	2	3.40 ± 0.42	2.98 – 3.82	0.60	2	5.68 ± 0.59	5.09 – 6.27	0.83
A	m2	5	3.65 ± 0.21	3.14 – 4.28	0.47	5	5.53 ± 0.33	4.46 – 6.31	0.73
B	m2	16	3.98 ± 0.17	3.06 – 6.03	0.68	15	5.69 ± 0.21	4.28 – 7.71	0.81
C	m2	5	3.22 ± 0.17	2.88 – 3.83	0.39	5	5.27 ± 0.17	4.96 – 5.92	0.38
C1	m2	2	3.25 ± 0.52	2.73 – 3.77	0.73	2	3.22 ± 0.17	4.55 – 5.72	0.83
A	m3	2	3.16 ± 0.53	2.63 – 3.69	0.75	2	4.23 ± 0.56	3.68 – 4.79	0.78
B	m3	12	3.49 ± 0.21	2.58 – 5.16	0.72	12	4.71 ± 0.29	3.33 – 7.28	1.02
C	m3	8	3.00 ± 0.23	2.36 – 4.27	0.64	8	5.98 ± 0.31	3.89 – 6.07	0.86
C1	m3	2	2.65 ±0.58	2.07 – 3.22	0.81	2	4.30 ± 0.68	3.62 – 4.97	0.95
B	P4	5	3.70 ± 0.40	2.56 – 4.93	0.90	5	5.30 ± 0.41	4.72 – 6.92	0.92
C	P4	4	2.28 ± 0.12	2.03 – 2.18	0.23	3	3.30 ± 0.09	3.15 – 3.46	0.16
B	M1	9	3.85 ± 0.19	3.27 – 4.50	0.56	8	6.08 ± 0.39	4.71 – 7.85	1.11
C	M1	4	3.01 ± 0.05	2.85 – 3.09	0.11	4	4.90 ± 0.06	4.73 – 5.03	0.13
B	M2	8	3.97 ± 0.19	3.10 – 4.55	0.53	8	6.09 ± 0.40	4.92 – 7.72	1.13
C	M2	5	3.03 ± 0.08	2.70 - 3.16	0.19	75	4.67 ± 0.12	4.28 – 5.02	0.27
B	M3	10	3.76 ± 0.24	2.68 – 4.96	0.77	9	5.51 ± 0.32	4.17– 7.48	0.95
C	M3	5	2.67 ± 0.10	2.36 – 2.93	0.23	5	4.14 ± 0.09	3.89 – 4.33	0.21

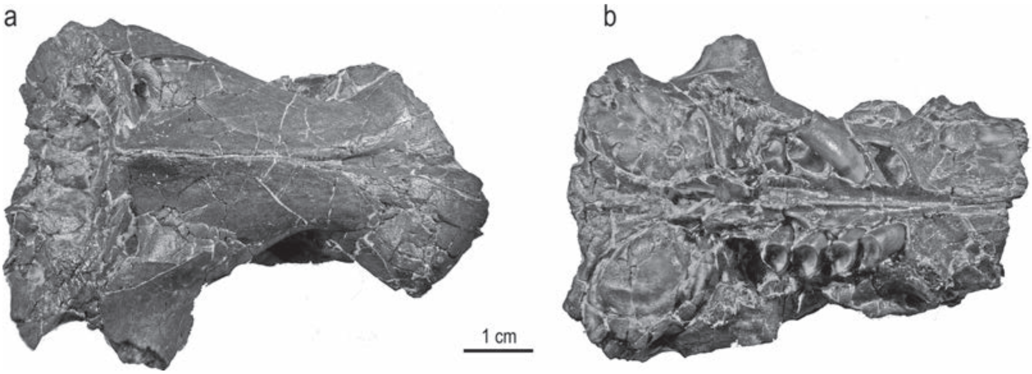

Fig. 5. A partial skull of *Tsaganomys altaicus* MATTHEW & GRANGER, 1923; TGR-AB, NHMW 2013/0548/0001; a: upper view; b: palate

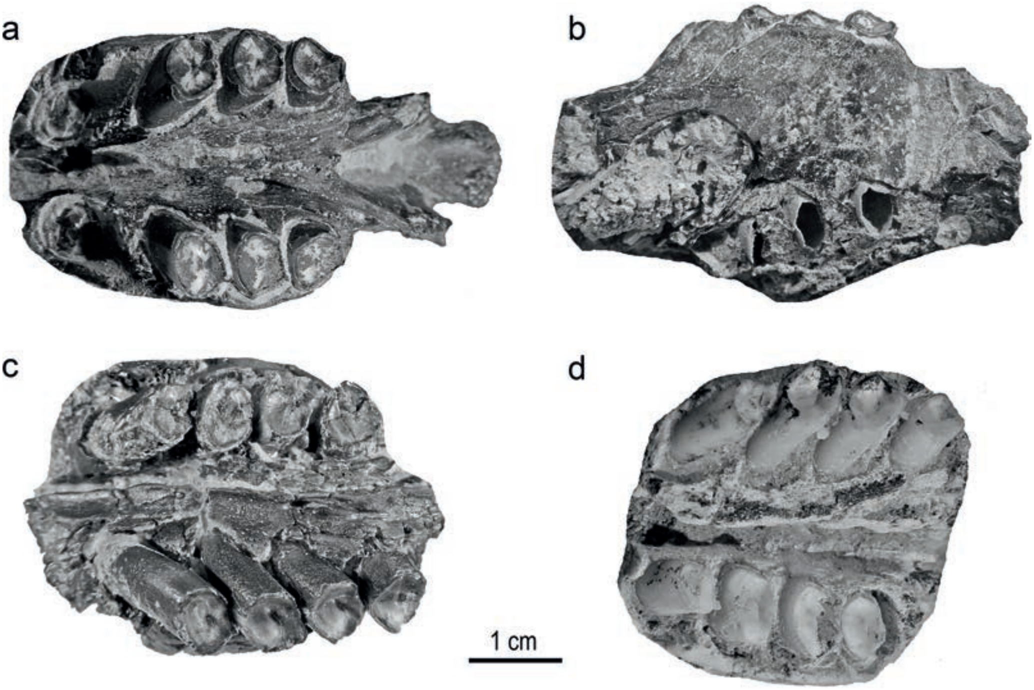

Fig. 6. *Tsaganomys altaicus* MATTHEW & GRANGER, 1923; Skull fragment, SHG-above sst, MPC, a: palatial view, b: root endings. Skull fragment, TGR-AB/21 NHMW 2013/0548/0001, c: palatial view. Skull fragment, TGW-2+3/o, NHMW 2013/0558/0001, d: palatial view.

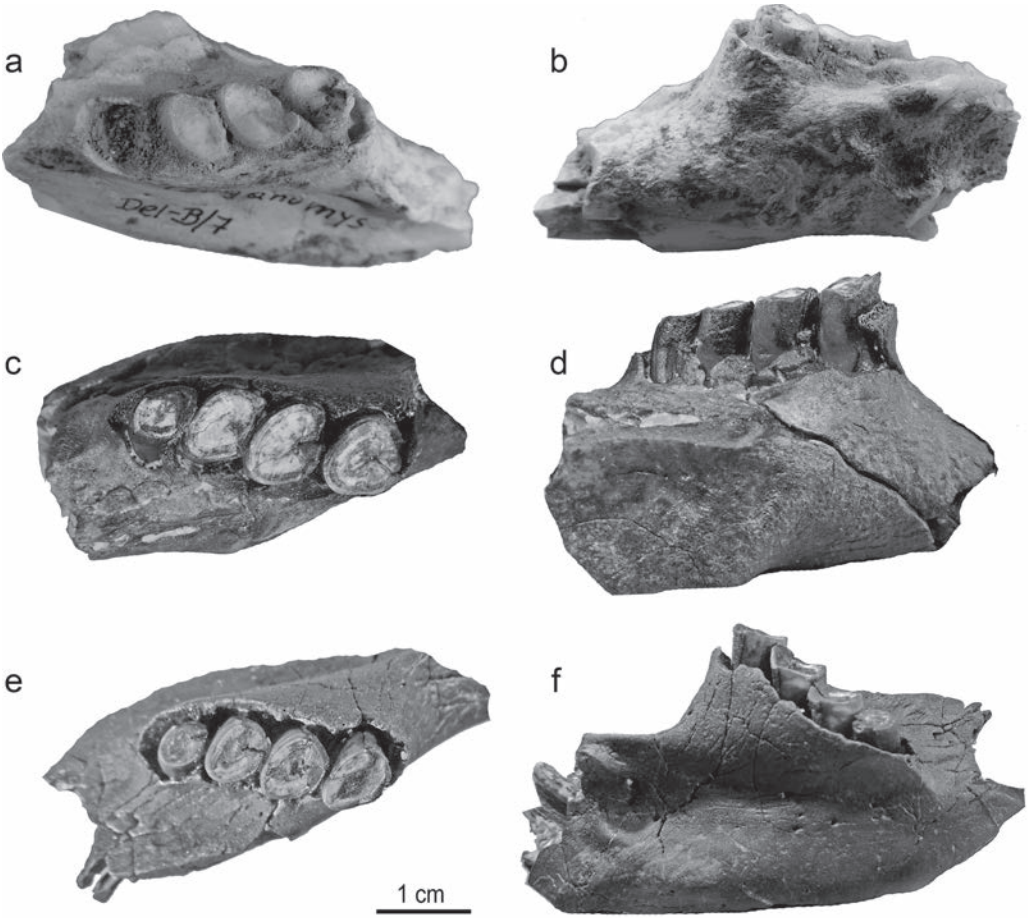

Fig. 7. *Tsaganomys altaicus* MATTHEW & GRANGER, 1923; Jaw fragment, sin, DEL-B/7, NHMW 2013/0483/0001, a: occlusal view, b: labial view. Jaw fragment, dex, SHG-A/14 NHMW 2013/0503/0004, c: occlusal view, d: labial view. Jaw fragment, dex, TAT-D/1/Hü NHMW 2013/0537/0003, e: occlusal view, f: labial view.

The molars are positioned in a step-like manner, in the lower cheek teeth the anterior side is the highest, in the upper cheek teeth the posterior side. These curved high enamel bands appear as sharper ridges on the occlusal surface and are perpendicular to the row of cheek teeth. The cheek teeth have one root, with a wide, oval-shaped open end with a very short circular enamel-free zone. The cheek teeth in *Tsaganomys altaicus* have almost the same thickness from bottom to top,

The size distribution of all *Tsaganomys altaicus* cheek teeth displays a wide range (Figs 8, 9). Since only a few cheek teeth are not worn, a difference in the size of the occlusal surface between fresh and worn cheek teeth cannot be established (Figs 10, 11). Irrespective of wear the occlusal surface of all cheek teeth is always less long than wide,

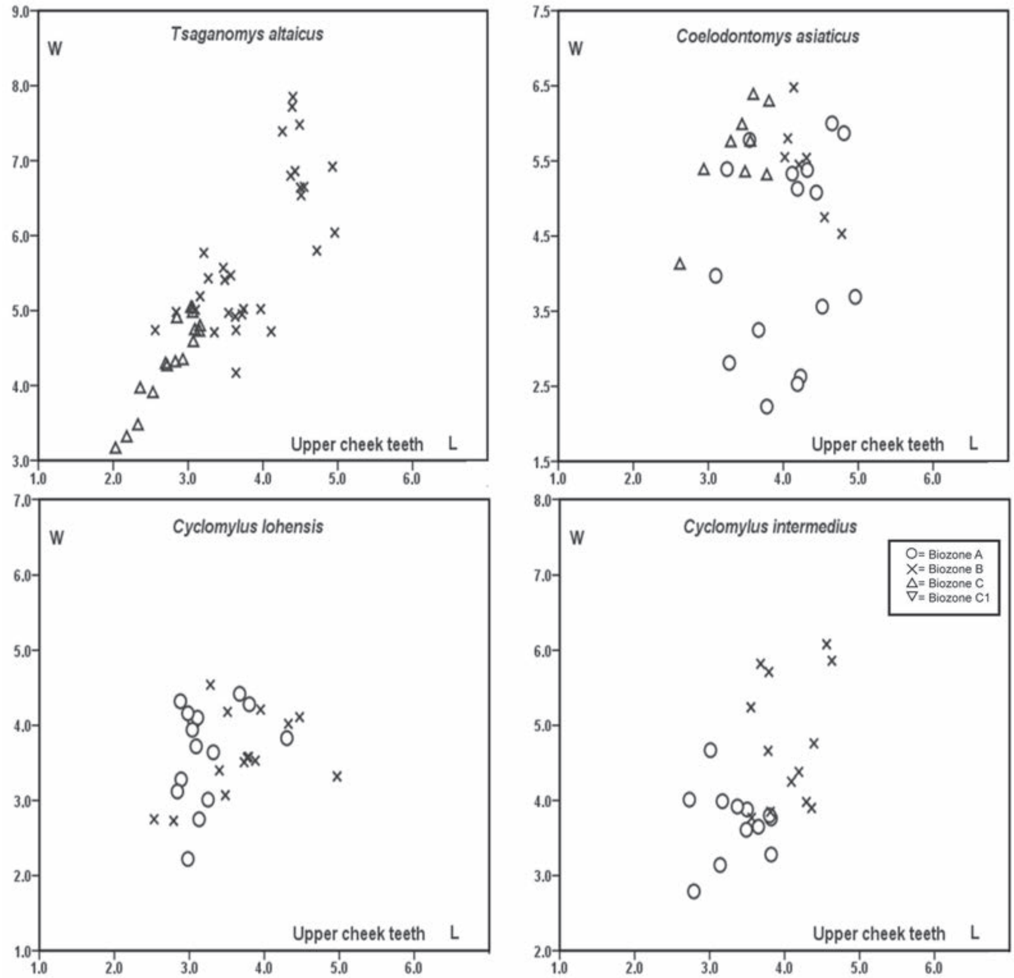

Fig. 8. Scatter plots of length and width of upper cheek teeth of *Tsaganomys altaicus*, *Cyclomylus lohensis*, *Cyclomylus intermedius*, *Coelodontomys asiaticus*, per biozone (deciduous teeth excluded).

the range of the L/W ratio is compared to that from the other species quite small. The cheek teeth with the greatest length are m1 and M2.

In the skull the premaxilla-frontale suture is posterior to the nasale-frontale suture, and the posterior part of the nasals lies at midpoint of the orbit. The infraorbital foramen lies anterior to the suture of the premaxilla-maxilla. The antepremolar crests, inclined strongly inwards, vary in thickness, either strongly or weakly developed. In the lower jaw the anterior part of the massetric fossa is weakly developed.

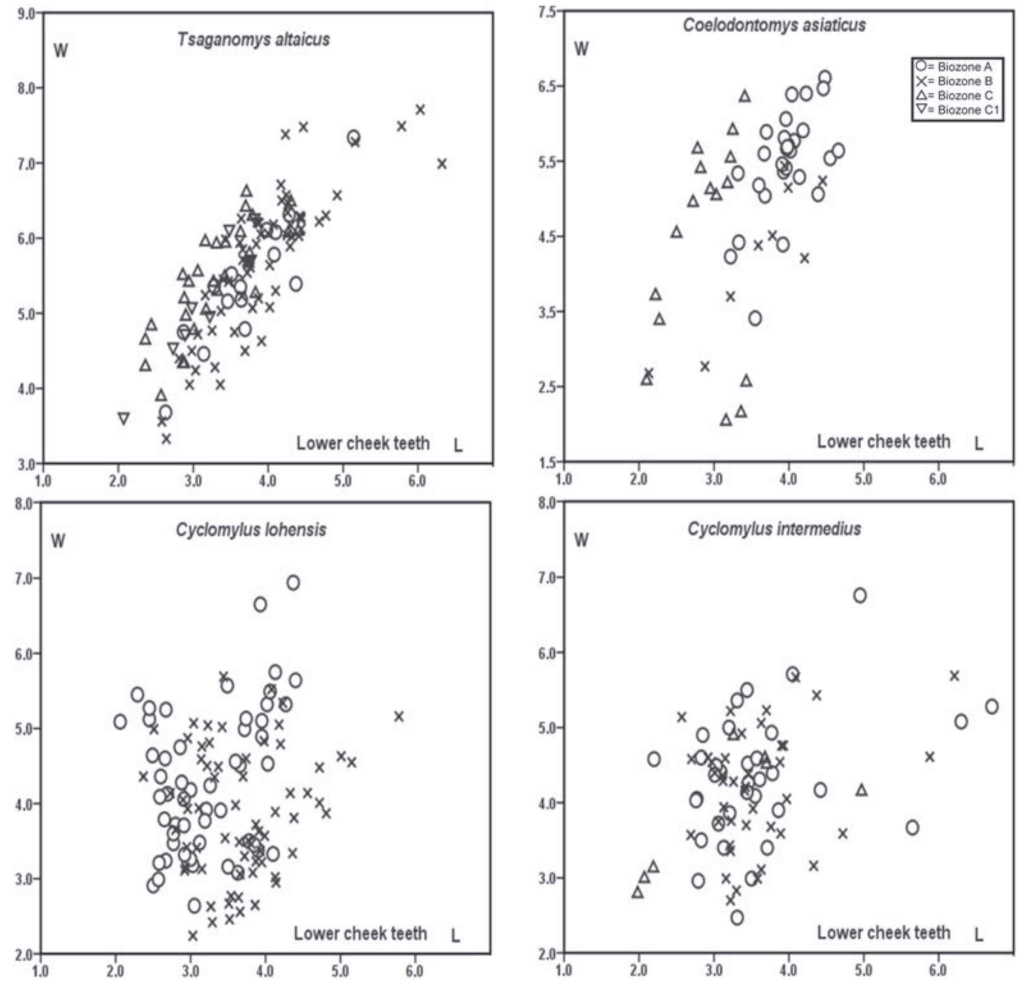

Fig. 9.Scatter plots of Length and Width of lower cheek teeth of *Tsaganomys altaicus*, *Cyclomylus lohensis*, *Cyclomylus intermedius*, *Coelodontomys asiaticus*, per biozone (deciduous teeth excluded).

Genus *Cyclomylus* MATTHEW & GRANGER, 1923

Type species: *Cyclomylus lohensis* MATTHEW & GRANGER, 1923

Type locality: Hsanda Gol Formation, red strata, Loh, Tsagan Nor basin (outer Mongolia)

Included species:

- *Cyclomylus biforatus* WANG, 2001
- *Cyclomylus intermedius* WANG, 2001
- *Cyclomylus lohensis* MATTHEW & GRANGER, 1923

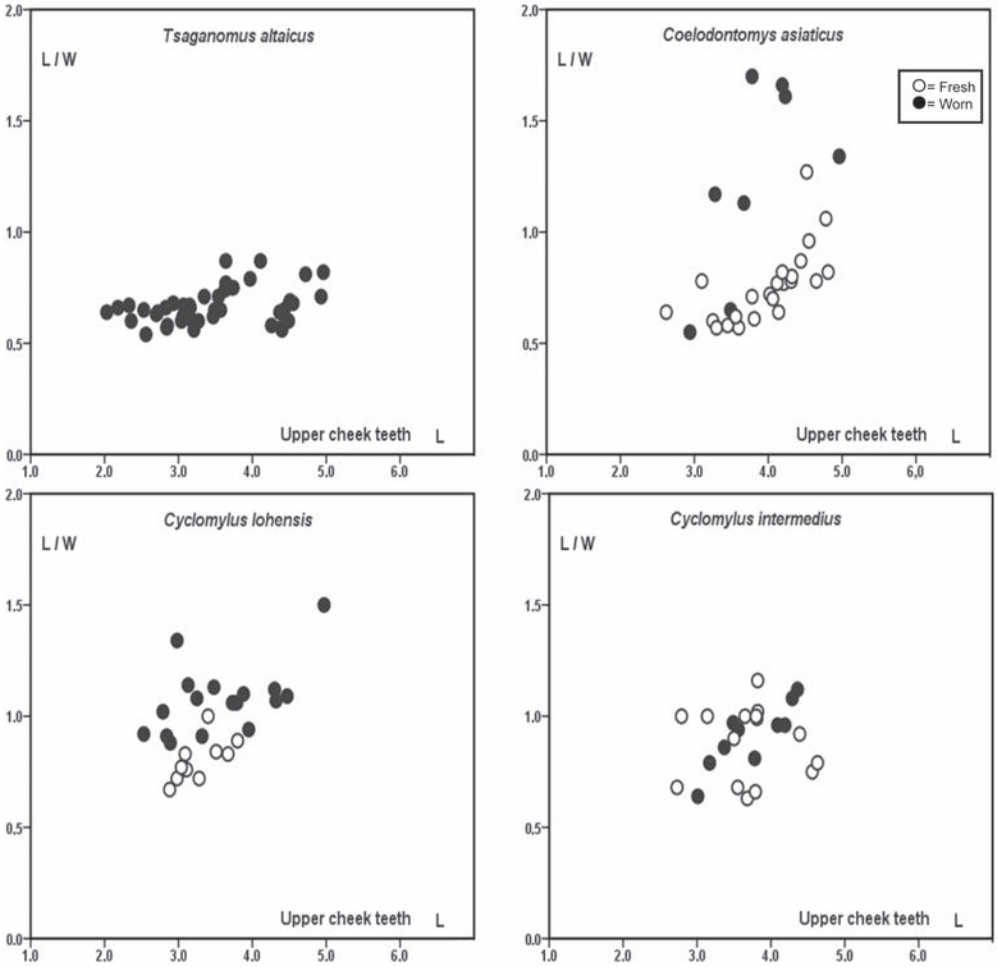

Fig. 10. Scatter plots of the ratio length / width and length of upper cheek teeth of *Tsaganomys altaicus*, *Cyclomylus lohensis*, *Cyclomylus intermedius*, *Coelodontomys asiaticus*, status of worn and fresh indicated. (deciduous teeth excluded)

Remarks: Differentiation between *Cyclomylus lohensis*, *Cyclomylus intermedius* and *Cyclomylus biforatus* is only possible when the roots of the premolars and molars can be seen clearly, because the largest difference between the first two species lies in the ratio crown height – main root length, whereas *Cyclomylus biforatus* has only one root. In specimens where the cheek teeth are completely covered by bone (lower jaw or upper jaw) or consolidated sediment, differentiation between these species is difficult and the specimens are assigned to *Cyclomylus* sp. (and not further considered in this paper).

Cyclomylus lohensis and *Cyclomylus intermedius* both have dp3, DP3, dp4, DP4. Only a few specimens are assigned to ?*C. biforatus*, where absence nor presence could be proven for dp3, DP3, and dp4 and DP4.

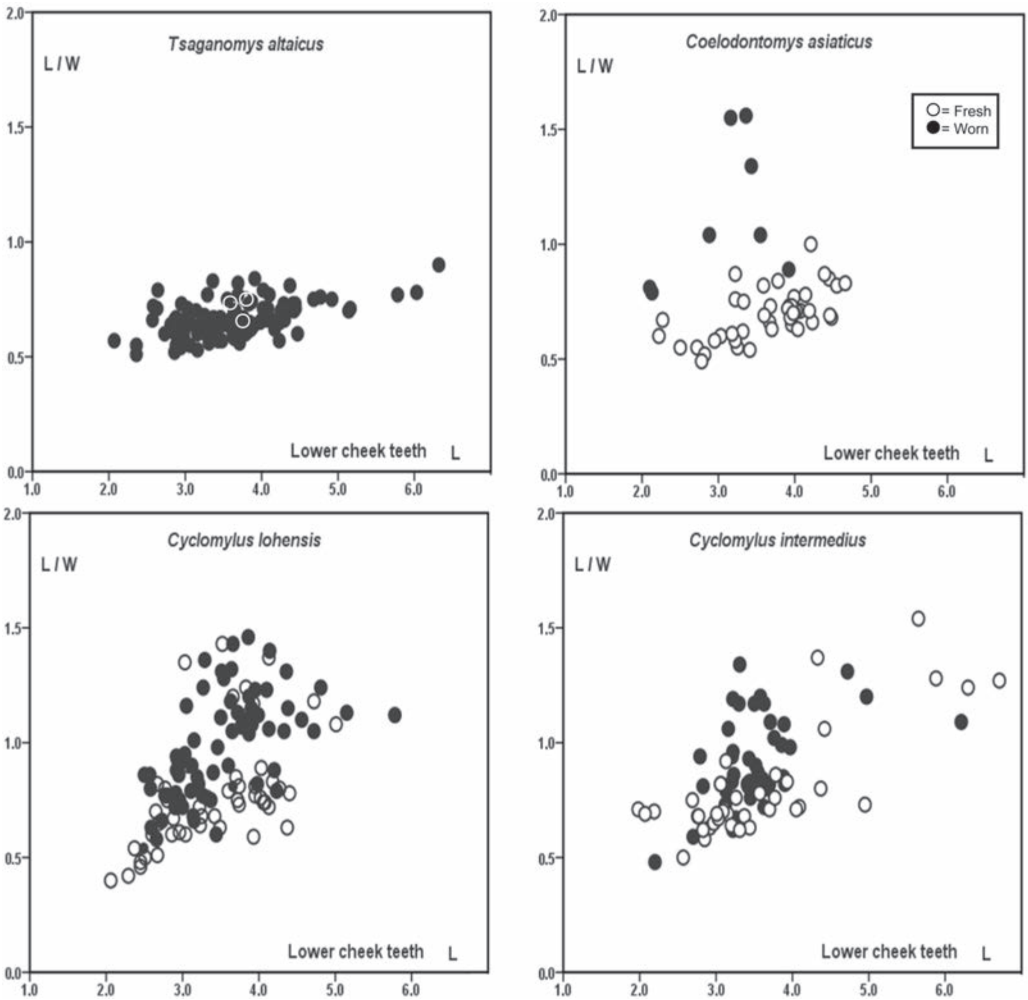

Fig. 11. Scatter plots of the ratio length / width and length of lower cheek teeth of *Tsaganomys altaicus*, *Cyclomylus lohensis*, *Cyclomylus intermedius*, *Coelodontomys asiaticus*, status of worn and fresh indicated. (deciduous teeth excluded)

Cyclomylus lohensis MATTHEW & GRANGER, 1923
(Fig. 12)

1923 *Cyclomylus lohensis* – MATTHEW & GRANGER: 5; fig. 4.
2001 *Cyclomylus lohensis* WANG: 18–25; figs 15–19. [and all synonyms therein]
2010 ?*Cyclomylus* sp. – DAXNER-HÖCK *et al.*: 354; fig. 3 (13).
2011 *Cyclomylus lohensis* – VON KOENIGSWALD: 76; fig. 7 F.

Occurrence in Mongolia (Valley of Lakes, Uvurkhangai): Table 1.

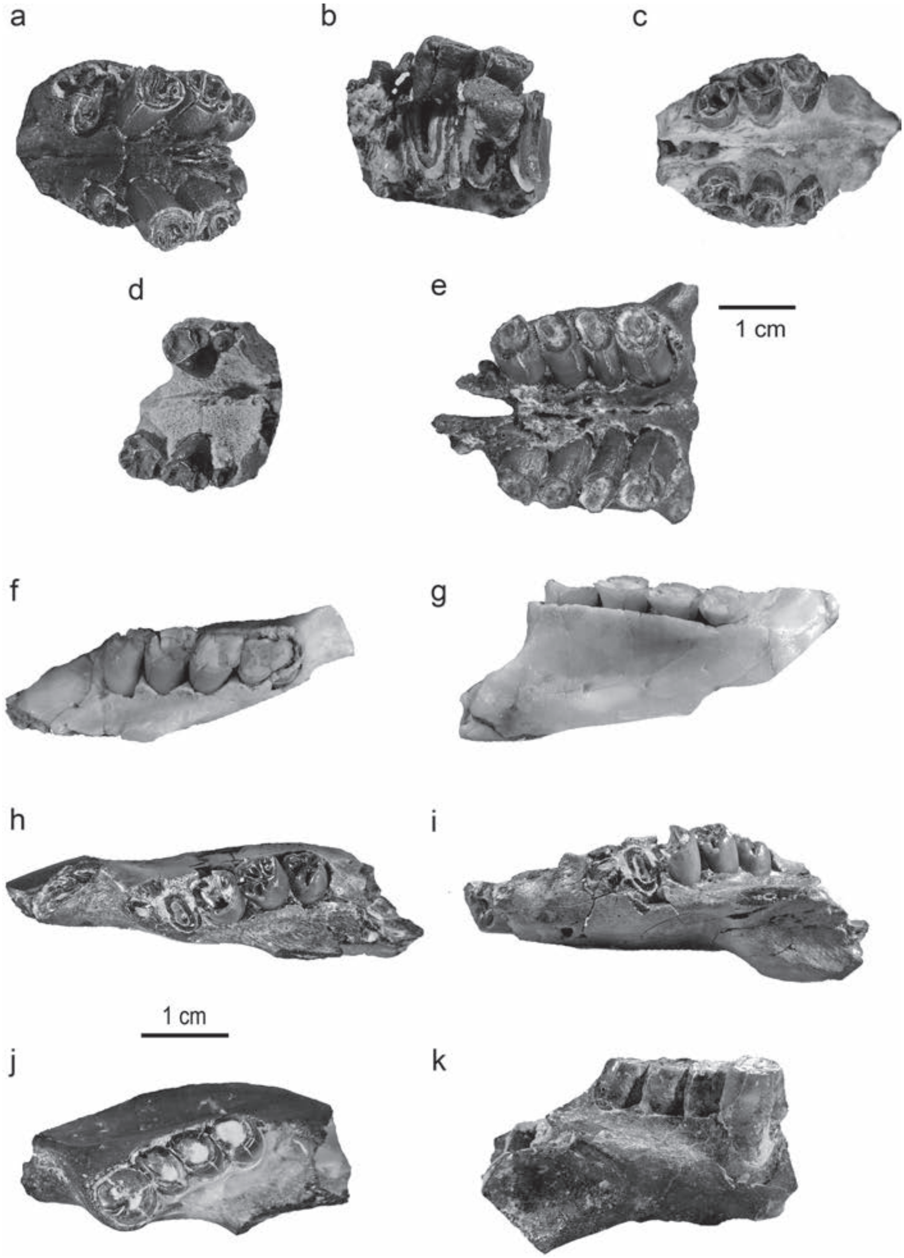

Fig. 12. *Cyclomylus lohensis* Matthew & Granger, 1923. Skull fragment, SHG-A/18–20 NHMW 2013/0506/0007, a: occlusal view, b: view of the open roots. Skull fragment, TAT-D/basis NHMW 2013/0543/0004, c: occlusal view. Skull fragment, TAT-D/basis NHMW 2013/0543/0003(a,b), d: occlusal view. Skull fragment, TAT-D/1 NHMW2009z0134/001, e: occlusal view. Jaw fragment, dex, IKH-mix NHMW 2013/0493/0002, f: occlusal view, g: lingual view. Jaw fragment, sin, TAT-D/1 NHMW 2013/0542/0001(a,b), h: occlusal view, i: labial view. Jaw fragment, sin, SHG-A18–20 NHMW 2013/0508/0003, j: occlusal view, k: lingual view.

Other occurrences of *Cyclomylus lohensis*: Early Oligocene Nei Mongol (China), Mongolia and the Late Oligocene of Kazakhstan

Measurements: All measurements are summarized in table 3. The plots of Length/ Width are given in figures 8 and 9, and in figures 10 and 11 the scatter plots of the ratio Length / Width and Length (except deciduous teeth).

Remarks: The cheek teeth of *Cyclomylus lohensis* are hypsodont with a closed, tapering main root, and one small root on the antero-lingual side in the lower cheek teeth and two small roots on the postero-labial side in the upper molars. The lower cheek teeth are concave anteriorly and are positioned above the lower incisor, the upper cheek teeth are concave posteriorly. The upper cheek teeth are slightly more curved than the lower ones.

Unworn upper cheek teeth are ovate, or rounded. Worn P4 and M3 are rounded, M1 and M2 have a teardrop form. Unworn lower cheek teeth are oval, and m1 and m2 become

Table 3. Measurements in mm of *Cyclomylus lohensis*.

Cyclomylus lohensis

		Length				Width			
Biozone	**element**	**N**	**Mean ± SE**	**range**	**SD**	**N**	**Mean ± SE**	**range**	**SD**
A	d3	1	1.38			1	2.07		
A	d4	2	2.44 ± 0.68	1.76 – 3.12	0.96	1	3.17		
A	p4	10	3.62 ± 0.17	2.77 – 4.27	0.54	10	4.54 ± 0.230	3.26 – 5.75	0.94
B	p4	17	4.18 ± 0.18	2.79 – 5.78	0.76	17	3.90 ± 0.22	2.56 – 5.52	0.93
A	m1	15	2.96 ± 0.17	2.06 – 4.40	0.65	17	4.31 ± 0.20	3.21 – 5.64	0.82
B	m1	19	3.45 ± 0.15	2.37 – 4.38	0.65	18	4.15 ± 0.20	2.67 – 5.69	0.86
A	m2	16	3.20 ± 0.14	2.45 – 4.37	0.58	16	4.47 ± 0.28	3.08 – 6.94	1.13
B	m2	17	3.50 ± 0.10	2.90 – 4.13	0.41	18	3.98 ± 0.18	2.77 – 5.04	0.74
A	m3	12	3.25 ± 0.18	2.50 – 4.03	0.61	12	3.70 ± 0.25	2.64 – 5.32	0.87
B	m3	16	3.33 ± 0.09	2.80 – 4.14	0.37	16	3.26 ± 0.16	2.12 – 4.36	0.66
A	D3	1	0.90			1	0.81		
B	D3	2	1.32 ± 0.42	0.90 – 1.74	0.59	2	2.03 ± 0.63	1.40 – 2.65	0.88
A	D4	1	2.98			1	2.93		
B	D4	3	2.02 ± 0.76	0.79 – 3.71	1.732	2	3.20 ± 0.87	1.64 – 4.66	1.51
A	P4	4	3.76 ± 0.22	3.25 – 4.30	0.43	4	3.89 ± 0.32	3.01 – 4.42	0.64
B	P4	3	3.58 ± 0.20	3.28 – 3.95	0.34	3	4.31 ± 0.12	4.18 – 4.54	0.20
A	M1	5	3.01 ± 0.05	2.88 – 3.13	0.12	5	3.70 ± 0.30	2.75 – 4.32	0.66
B	M1	6	3.60 ± 0.22	2.94 – 4.47	0.55	4	3.58 ± 0.21	3.07 – 4.11	0.42
A	M2	5	3.03 ± 0.08	2.84 – 3.32	0.18	5	3.42 ± 0.35	2.22 – 4.16	0.77
B	M2	4	3.95 ± 0.46	2.79 – 4.97	0.92	4	3.40 ± 0.27	2.73 – 4.02	0.53
A	M3	1	3.09			2	3.56 ± 0.16	3.40 – 3.72	0.23
B	M3	3	3.27 ± 0.40	2.53 – 3.88	0.68	4	3.27 ± 0.18	2.75 – 3.53	0.35

teardrop-shaped during wear. The width of all cheek teeth increases during wear. Worn cheek teeth show concentric rings in the dentine often with a slightly elevated central core (secondary dentine). The total occlusal surface of the lower cheek teeth is less step-like with less prominent curved enamel ridges than in *Tsaganomys altaicus*

The size distribution of all *Cyclomylus lohensis* cheek teeth displays a wide range (Fig. 8). The occlusal surface becomes wider during wear (Fig. 9). Of the lower cheek teeth the p4 has the greatest length, the m1 the smallest. Of the upper cheek teeth the P4 is the largest.

In the skull the premaxila-frontale suture is more or less in one line with the nasale-frontale suture. The antepremolar crests are parallel and vary a lot in thickness, either strongly or weakly developed. In the lower jaw the anterior part of the massetric fossa is variably expressed.

In *Cyclomylus lohensis*, as well as in *C. intermedius,* the main root of the cheek teeth is tapering downwards, is almost closed or closed (depending on individual age), the lower cheek teeth have one extra small root and the upper cheek teeth have two extra small roots. The small roots are always present, in fresh as well as in worn cheek teeth. The difference between the two species is that in *C. lohensis* the cheek teeth have shorter roots and the enamel crown is lower in fresh specimens.

Cyclomylus intermedius WANG, 2001
(Figs 13 & 14a–f)

2001 *Cyclomylus intermedius* – WANG: 25; figs 20–23.

Occurrence in Mongolia (Valley of Lakes, Uvurkhangai): Table 1.

Other occurrences of *Cyclomylus intermedius*: Early Oligocene from Nei Mongol (China) and Mongolia

Measurements: All measurements are summarized in table 4. The plots of Length/ Width are given in figures 8 and 9 (except deciduous teeth), and in figures 10 and 11 the scatter plots of the ratio Length / Width and Length (except deciduous teeth).

Remarks: The morphology of skull and jaws, as well as the size-distribution of fresh and worn specimens, are comparable to *C. lohensis* (Figs. 8 and 9): except for the upper cheek teeth where the P4 and M3 are about the same size and are the largest. The main difference is in the height of the cheek teeth: in *C. intermedius* the roots and the enamel crowns are higher.

The premaxila-frontale suture is more or less in one line with the nasale-frontale suture (Fig. 13b). In one specimen (TAT-basis/o NHMW 2013/0518/0001) a very small bony protrusion is visible on the medial sidewall of the infraorbital foramen. It is in the same position as the horizontal bone in the IOF of *C. biforatus* (type specimen, Wang 2001: p. 35, fig. 25). In a few specimens of *Cyclomylus intermedius* and *Cyclomylus* sp., a small

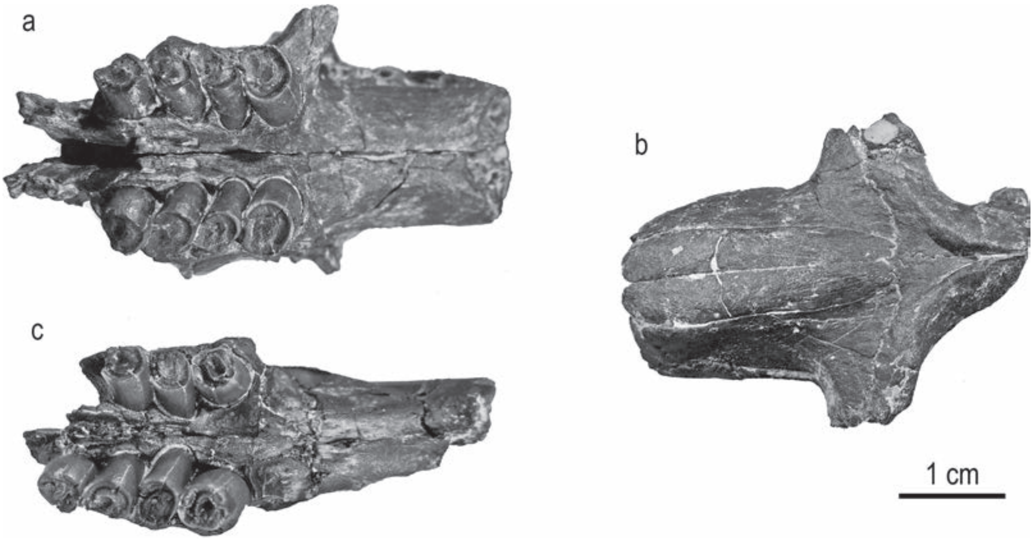

Fig. 13. *Cyclomylus intermedius* WANG, 2001. Skull fragment, SHG-A/18–20 NHMW 2013/0507/0005, a: occlusal view, b: dorsal view. Skull fragment, SHG-A/18–20 NHMW 2013/0507/0002, c: occlusal view.

Table 4: Measurements in mm of *Cyclomylus intermedius.*

Cyclomylus intermedius

		Length				Width			
Biozone	**element**	**N**	**Mean ± SE**	**range**	**SD**	**N**	**Mean ± SE**	**range**	**SD**
A	d4	1	3.91			1	3.04		
A	p4	8	4.15 ± 0.38	3.44 – 6.71	1.08	8	4.46 ± 0.16	3.90 – 5.28	0.45
B	p4	13	4.32 ± 0.23	3.46 – 6.21	0.84	13	4.48 ± 0.23	3.16 – 5.69	0.84
C	p4	2	3.52 ± 1.45	2.07 – 4.97	2.05	2	3.57 ± 0.58	2.99 – 4.15	0.82
A	m1	11	3.37 ± 0.21	2.20 – 4.95	0.70	10	4.85 ± 0.31	3.40 – 6.76	0.98
B	m1	13	3.10 ± 0.08	2.57 – 3.70	0.29	10	4.28 ± 0.23	2.70 – 5.22	0.80
C	m1	2	2.73 ± 0.54	2.19 – 3.26	0.76	1	4.01 ±0.88	3.13 – 4.89	1.24
A	m2	10	3.53 ± 0.32	2.76 – 6.30	1.01	9	4.30 ± 0.23	2.99 – 5.36	0.69
B	m2	12	3.39 ± 0.08	3.06 – 3.95	0.26	10	3.98 ± 0.19	2.99 – 4.92	0.61
C	m2	1	1.98			1	2.79		
A	m3	8	3.28 ± 0.35	2.75 – 5.65	0.97	7	3.50 ± 0.25	2.47 – 4.49	0.66
B	m3	9	3.31 ± 0.11	2.96 - 3.90	0.33	6	3.70 ± 0.30	2.83 – 4.76	0.74
C	m3	2	3.69 ± 0.01	3.68 – 3.70	0.14	2	4.55 ± 0.04	4.51 – 4.59	0.57
A	P4	4	3.63 ± 0.11	3.37 – 3.82	0.22	3	3.83 ± 0.48	3.76 – 3.92	0.08
B	P4	4	4.46 ± 0.08	4.29 – 4.63	0.16	4	4.96 ± 0.59	3.90 – 6.08	1.18
A	M1	4	2.92 ± 0.10	2.73 – 3.17	0.20	4	3.87 ± 0.39	2.79 – 4.67	0.78
B	M1	4	3.73 ± 0.07	3.55 – 3.90	0.15	3	5.24 ± 0.33	4.66 – 5.82	0.58
A	M2	4	3.19 ± 0.11	2. 98 – 3.50	0.22	2	3.51 ± 0.37	3. 14 – 3.88	0.52
B	M2	4	3.97 ± 0.10	3.79 – 4.19	0.20	4	4.55 ± 0.40	3.85 – 5.71	0.81
A	M3	3	3.65 ± 0.10	3.49 – 3.82	0.17	3	3.51 ± 0.12	3.28 – 3.65	0.20
B	M3	3	4.11 ± 0.27	3.56 – 4.39	0.47	2	4.27 ± 0.50	3.77 – 4.76	0.70

cavity below the IOF is visible, due to damage of the bone covering. This cavity is closed at the posterior side and cannot be interpreted as the lower part of a divided IOF as in the type specimen of *C. biforatus*.

?*Cyclomylus biforatus* Wang, 2001
(Fig. 14g–h)

2001 *Cyclomylus biforatus* – Wang: 31; figs 24–27.

Occurrence in Mongolia (Valley of Lakes, Uvurkhangai): Table 1.

Other occurrences of *Cyclomylus biforatus*: Early Oligocene of Nei Mongol (China)

Measurements: All measurements are summarized in table 5.

Remarks: Only a few specimens are present in our collection, all lower cheek teeth and all worn. The cheek teeth of ?*Cyclomylus biforatus* are hypsodont with a closed, main root, smaller roots in lower cheek teeth. The root is almost as long as in *Tsaganomys altaicus*, but tapers sharply downward. The lower cheek teeth are concave anteriorly and are positioned above the lower incisor, they are ovate, and m1 and m2 become teardrop-shaped during wear. They show concentric rings in the enamel, often with a slightly elevated central core. The curved enamel ridges are perpendicular to the row of cheek teeth.

In *Cyclomylus lohensis* and *C. intermedius* one extra root in the lower cheek teeth and two extra small roots in the upper cheek teeth are always present, as well as in unworn cheek teeth. In ?*C. biforatus* the single closed root is tapering downwards and an extra root is absent.

Except for the lack of small extra roots, the main difference between ?*C. biforatus* on the one hand, and *C. lohensis* and *C. intermedius* on the other is the presence of an

Table 5. Measurements in mm of *Cyclomylus biforatus*.

?Cyclomylus biforatus

		Length				Width			
Biozone	element	N	Mean ± SE	range	SD	N	Mean ± SE	range	SD
A	p4	3	3.88 ± 0.30	3.32 – 4.35	0.52	4	4.64 ± 0.50	3.40 – 5.55	1.00
C	p4	1	4.62						
A	m1	4	3.72 ± 0.25	3.27 – 4.45	0.51	4	6.14 ± 0134	5.85 – 6.40	0.26
C	m1	1	4.19			1	6.31		
A	m2	4	3.65 ± 0.20	3.10 – 4.04	0.39	5	5.19 ± 0.31	4.10 – 5.83	0.70
C	m2	1	4.19			1	6.02		
A	m3	4	3.44 ± 0.22	2.88 – 3.89	0.44	4	5.09 ± 0.49	4.30 – 6.51	0.98

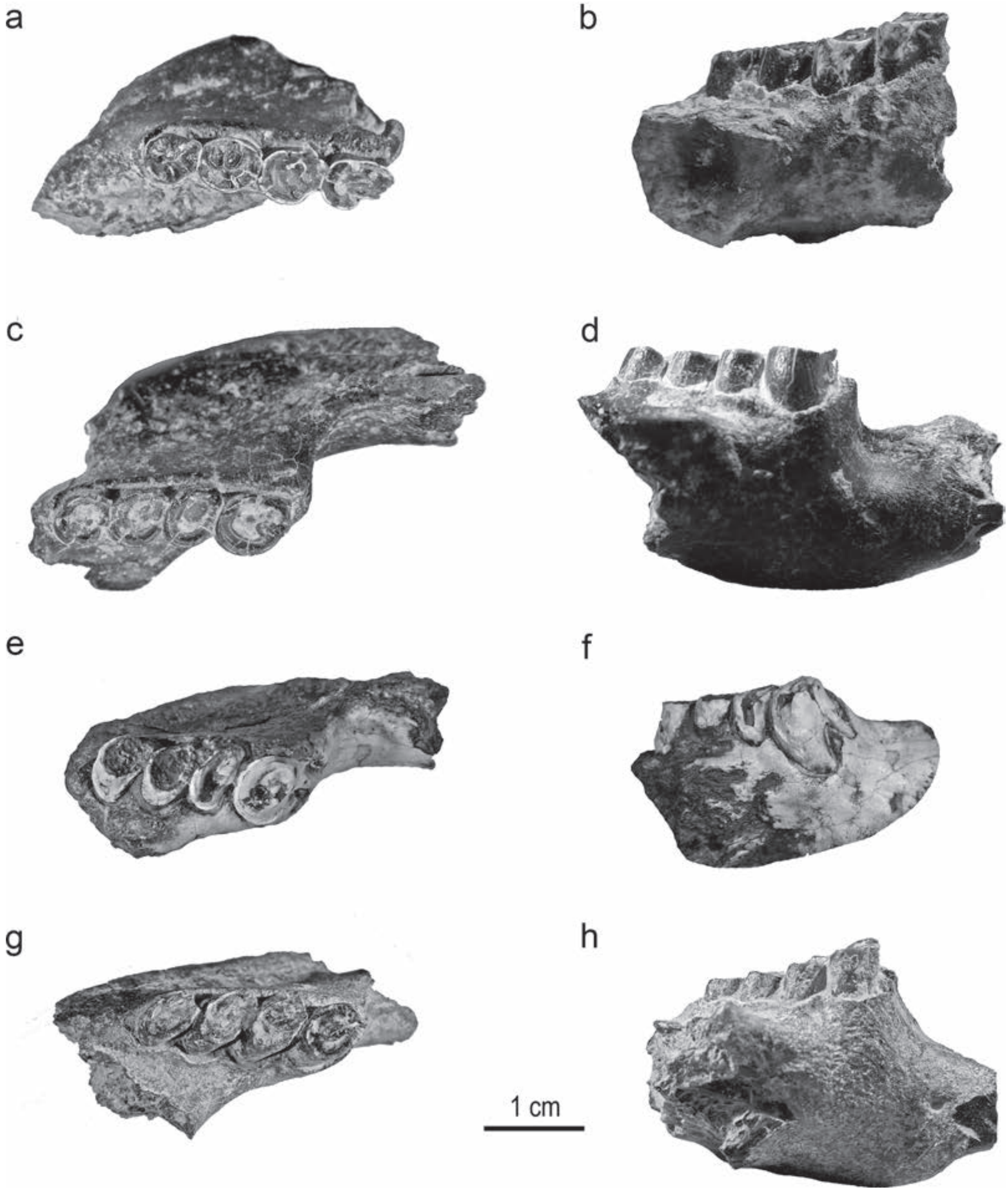

Fig. 14. *Cyclomylus intermedius* WANG, 2001. Jaw fragment, dex, TAT/D/o NHMW 2013/0529/0001, a: occlusal view, b: labial view. Jaw fragment, dex, TAT-D/12/o NHMW 2013/0529/0002, c: occlusal view, d: labial view. Jaw fragment, dex, TAT-D/1/o/ NHMW 2013/0539/0001, e: occlusal surface, f: labial view. *Cyclomylus biforatus* WANG, 2001. Jaw fragment, dex, TAT-D/o NHMW 2013/0530/0001(a, b), g: occlusal view, h: labial view.

extra bone separating the infraorbital foramen into two. Since it is also present in one specimen of *C. intermedius*, but less prominently so, this could be a character which is not species-related but more related to individual differences, perhaps the expression of ontogeny. The absence of the extra roots, could also be interpreted as caused by ongoing wear, present in older individuals.

The absence of fresh specimens and thus the absence of knowledge whether the small roots are present or not in young individuals, restrains us to re-assign ?*Cyclomylus biforatus* to another species.

Genus *Coelodontomys* Wang, 2001

Type species: *Coelodontomys asiaticus* Wang, 2001

Included species: type species only.

***Coelodontomys asiaticus* Wang, 2001**
(Figs 15 & 16)

2001 *Coelodontomys asiaticus* – Wang: 33; figs 28–31.

Occurrence in Mongolia (Valley of Lakes, Uvurkhangai): Table 1.

Other occurrences of *Coelodontomys asiaticus*: Late Early Oligocene of North China, Mongolia, and the Late Oligocene of Kazakhstan.

Measurements: All measurements are summarized in table 6. The plots of Length/ Width are given in figures 8 and 9 (except deciduous teeth), and in figures 10 and 11 the scatter plots of the ratio Length / Width and Length (except deciduous teeth).

Remarks: *Coelodontomys asiaticus* has deciduous premolars (dp4); in one specimen, next to the p4, a remnant of a root is visible (Fig. 16a) and is interpreted as a remnant of a dp4.

The cheek teeth of *Coelodontomys asiaticus* are hypsodont with a wide open main root and no smaller roots in upper and lower cheek teeth. The root opening is oval and uneven: much higher on the concave side than on the convex side. On the antero-lingual side of the lower cheek teeth and on the postero-labial side of the upper cheek teeth a slight thickening of dentine is clearly visible (Figs 15f, 15h). The lower cheek teeth are concave anteriorly and are positioned above the lower incisor, the upper cheek teeth are concave posteriorly. The upper cheek teeth are slightly more curved than the lower ones. The P4 is, unlike in *T. altaicus*, strongly concave. In the enamel often a groove is visible on the concave side of the cheek teeth.

Unworn upper cheek teeth are ovate (P4 and M3) or oval (M1 and M2), when worn they are square to rounded or teardrop-shaped. The lower cheek teeth are ovate and become square or teardrop-shaped during wear. The cheek teeth show concentric rings in the occlusal surface of the dentine, often with a slightly elevated central core. The curved enamel ridges are more or less perpendicular to the row of cheek teeth. The total occlusal surface of the lower cheek teeth is less step-like than in *Tsaganomys altaicus*.

The size distribution of all *Coelodontomys asiaticus* cheek teeth displays a wide range (Figs 8 and 9). The occlusal surface becomes wider during wear, more than in *Cyclomylus* (Figs 10 and 11). Of the lower cheek teeth the m3 is the smallest and m1 the largest. Of the upper cheek teeth the M3 is larger than the other cheek teeth, which are about the same size.

The cheek teeth of *Coelodontomys asiaticus* are as in *T. altaicus*, single and open rooted, but the shape of the open root is quite different. The measurements of most dental

Table 6. Measurements in mm of *Coelodontomys asiaticus*.

Coelodontomys asiaticus

		Length				Width			
Biozone	element	N	Mean ± SE	range	SD	N	Mean ± SE	range	SD
A	p4	10	3.96 ± 0.14	3.22 – 4.66	0.43	11	5.31 ± 0.18	4.23 – 6.39	0.60
B	p4	2	3.07 ± 0.78	2.88 - 4.45	1.11	1	4.01 ± 1.24	1.77 - 5.24	1.75
C	p4	4	2.85 ± 0.22	2.27 – 3.22	0.44	4	4.16 ± 0.88	2.04 – 5.66	1.76
A	m1	9	4.16 ± 0.10	3.67 – 4.55	0.30	10	5.92 ± 0.13	5.48 – 6.61	0.42
B	m1	3	3.47 ± 0.47	2.53 - 3.94	0.81	1	5.44		
C	m1	4	3.17 ± 0.15	2.82 – 3.43	0.30	4	4.83 ± 0.81	2.56 – 6.35	1.62
A	m2	6	3.82 ± 0.11	3.32 -4.07	0.27	7	5.36 ± 0.24	4.39 – 6.06	0.62
B	m2	4	3.61 ± 0.40	2.45 – 4.21	0.79	3	4.62 ± 0.28	4.21 – 5.15	0.48
C	m2	4	3.07 ± 0.15	2.72 – 3.36	0.29	4	4.53 ± 0.82	2.15 – 5.91	0.51
A	m3	3	3.61 ± 0.04	3.55 – 3.68	0.07	3	4.51 ± 0.57	3.41 – 5.18	0.98
B	m3	4	3.07 ± 0.32	2.13 – 3.59	0.66	2	4.04 ± 0.34	3.70 – 4.38	0.48
C	m3	4	2.50 ± 0.24	2.10 – 3.18	0.48	4	4.01 ± 0.57	2.58 – 5.20	1.13
A	P4	4	4.17 ± 0.22	3.55 – 4.52	0.44	4	4.49 ± 0.56	3.52 – 5.78	1.13
B	P4	1	4.14			1	6.48		
C	P4	1	2.62			1	4.11		
A	M1	6	3.68 ± 0.46	3.10 – 4.65	0.60	6	4.45 ± 0.53	2.81 – 6.00	0.53
B	M1	2	4.04 ± 0.02	4.02 – 4.06	0.03	2	5.68 ± 0.13	5.55 – 5.80	0.18
C	M1	3	3.63 ± 0.09	3.49 – 3.81	0.16	3	6.00 ± 0.33	5.34 – 6.37	0.57
A	M2	5	4.27 ± 1.64	3.78 – 4.81	0.37	5	4.25 ± 0.75	2.23 – 5.87	1.69
B	M2	2	4.26 ± 0.05	4.21 - 4.31	0.07	2	5.50 ± 0.04	5.45 – 5.54	0.06
C	M2	3	3.23 ± 0.15	2.94 – 3.45	0.26	3	5.69 ± 0.17	5.37 – 5.97	0.30
A	M3	2	4.58 ± 0.39	4.19 – 4.96	0.54	2	3.11 ± 0.58	2.53 – 3.69	0.82
B	M3	2	4.67 ± 0.12	4.55 – 4.78	0.16	2	4.64 ± 0.11	4.53 – 4.75	0.16
C	M3	2	3.67 ± 0.11	3.56 – 3.78	0.16	2	5.53 ± 0.23	5.30 – 5.75	0.32

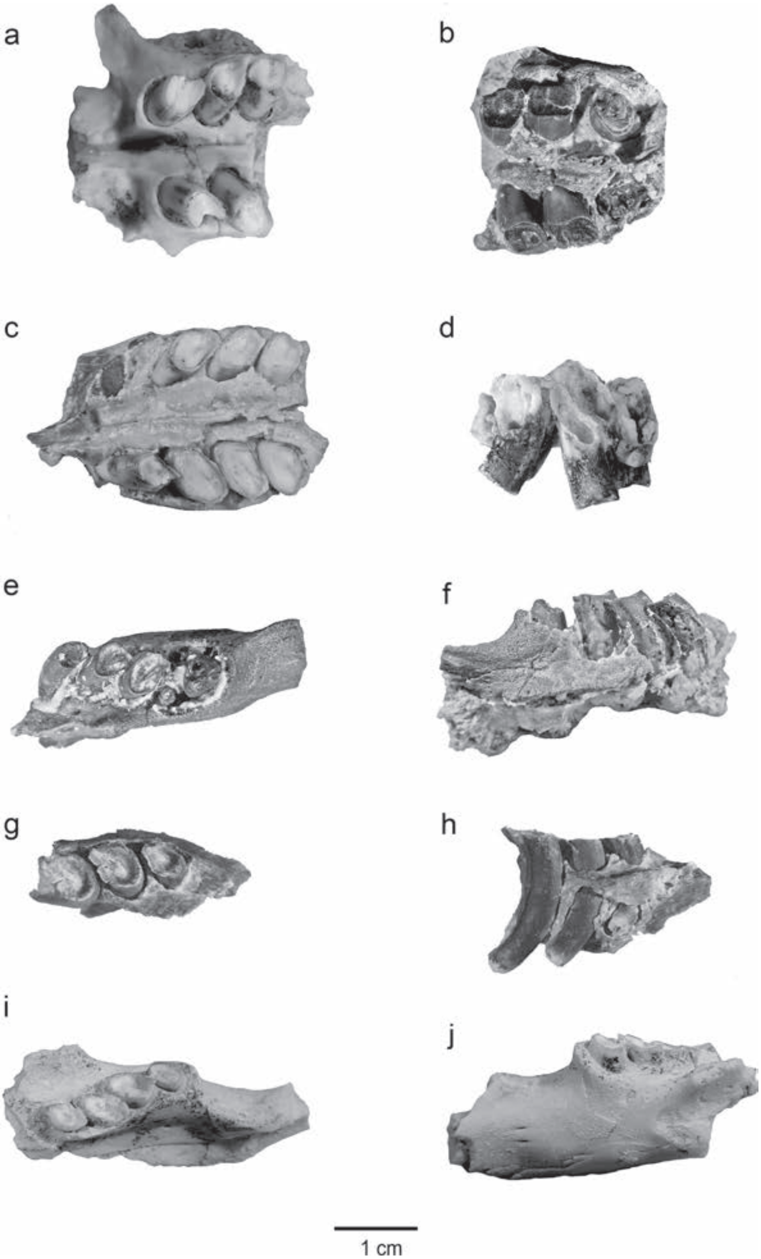

Fig. 15. *Coelodontomys asiaticus* WANG, 2001. Skull fragments, TAT-D/1/o NHMW 2013/0538/0001, a: occlusal view. Skull fragment, TAT-D/1/o NHMW 2013/0538/0002, b: occlusal view. Skull fragment, TGR-C/2 NHMW 2013/0553/0002, c: occlusal view. Skull fragment, TGR-C/Bad6 NHMW 2013/0555/0001, d: posterior view. Jaw fragment, dex, SHG-A/13 NHMW 2013/0504/0001; e: occlusal view, f: lingual view. Jaw fragment, sin, TAT-D/1 NHMW 2013/0536/0003, g: occlusal view, h: labial view. Jaw fragment, sin, TGR-C/2 NHMW 2013/0553/0004(a,b) ; i: occlusal view, j: labial view.

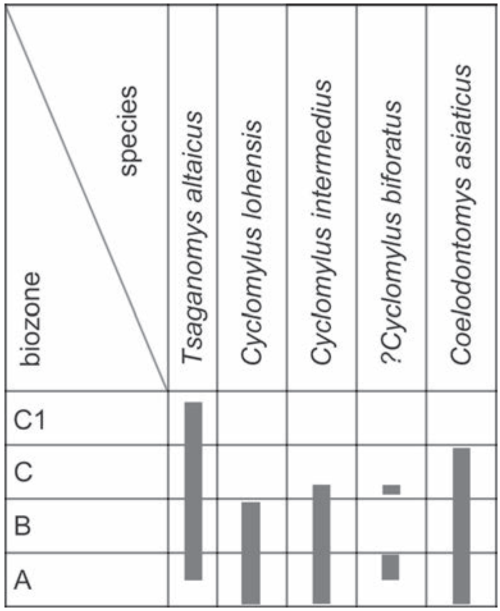

Fig. 16. Distribution chart of the Tsaganomyidae from the Valley of Lakes, Uvurkhangai, Mongolia per biozone.

elements fall in the higher range of *T. altaicus*. These characters could be interpreted as representing older *T. altaicus* individuals, in which the growth of the dentition has almost stopped and the root changed its shape. However, also unworn or almost unworn specimens with the original occlusal pattern are found, thus representing young individuals and not old individuals. *Coelodontomys asiaticus* is clearly a separate species, and comparing the skull characteristics as given in Wang (2001), it is more similar to *Cyclomylus* than to *Tsaganomys*.

Discussion and conclusions

Premolars and molars of the Tsaganomyidae are all hypsodont. Hypsodonty in rodents is seen as a result of extension of the ontogenetic phase during which the enamel is formed on the sidewall of the cheek teeth (SCHMIDT-KITTLER 2002). Recently, VON KOENIGSWALD (2011) classified the diversity in hypsodonty, in which each type represents a specific combination and duration of ontogenetic phases.

The cheek teeth with one or two small roots and one large root, in *Cyclomylus lohensis* and *C. intermedius*, show partial hypsodonty (VON KOENIGSWALD 2011). The small roots are attached strongly in the jaw, whereas the open larger root continues to grow during eruption of the tooth. This creates a strongly curved tooth. During wear, the original occlusal enamel pattern disappears and only dentine remains surrounded by an enamel ring, the further the wear the broader the tooth becomes. The root closes when the eruption is completed. *Tsaganomys altaicus*, as well as *Coelodontomys asiaticus,* have high hypsodont teeth of which the largest part is in the jaw. The large root is open and small roots are absent. The teeth are not completely surrounded by enamel, a narrow dentine tract is present one side of the teeth (on the posterior side of the upper cheek teeth and on the anterior side in the lower cheek teeth). The dentine tract is less than one third on the outline of the tooth and would be classified by VON KOENIGSWALD (2011) as sidewall hypsodonty.

We interpret the differences in cheek teeth morphology between *Tsaganomys, Cyclomylus* and *Coelodontomys* as the evolutionary result of differences in ontogenetic development, and not as expression of ontogenetic phases within one species as BRYANT & MCKENNA (1995) did. The taxonomic position of ?*Cyclomylus biforatus* is not clear: it is possible that these specimens represent old *C. intermedius* individuals.

The Tsaganomyidae are an unusual group of rodents, endemic to Mongolia, China and Kazakhstan, and difficult to assign to a clear phylogenetic position. The combination of a protrogomorphous skull and hytricognathus jaw sets the Tsaganomyidae apart from all other rodents. This led to various phylogenetic positions, such as in the Bathyergidae (among others MATTHEW & GRANGER 1923), in the Cylindrodontinae (among others BURKE 1935; WOOD 1937; PATTERSON & WOOD 1982), as a sister group of the Ctenodactylidae (BRYANT & MCKENNA 1995), as a hystricognathiformes (MARIVAUX 2001), and as sister group of the Hystricognathi (MARIVAUX *et al.* 2004). WANG (2001) places the Tsaganomyidae in Rodentia incertae sedis.

Several authors acknowledge that the morphological characters of the Tsaganomyidae are most similar to other groups of rodents which are predominantly fossorial (BRYANT & MCKENNA 1995; VINOGRADOV & GAMBARYAN 1952; WANG 2001). This implies that the typical morphology of the Tsaganomyidae does not necessarily indicate a phylogenetic connection, but can be seen as a result of convergent evolution. In this context it should be noted that BRYANT & KENNA (1995) suggested that the protrogomorphous skull of the Tsaganomyidae is derived from a hystricomorphous ancestor, which is seen as an autapomorphic character by MARIVAUX (2001). However, DRUZINSKY (2010 a, b) clearly demonstrates on the Aplodontia that the protrogomorphous skull is the most primitive condition in the Rodentia. Following DRUZINSKY we consider it highly unlikely that such a basic morphology can be derived from a more advanced one.

In hystricognathous jaws, the incisors and cheek teeth do not lie in one plane with the angular process, which is clearly positioned more laterally. All rodents displaying such a jaw are included in the Hystricognathi (WOOD 1955; LUCKETT 1985). DRUZINSKY (2010 a) argues that many kinds of sciuromorphy and hystricomorphy exist, which have to be seen as expression of differences in the “arrangement of the masticatory muscles”, representing differences in adaptation to diet. Also HAUTIER *et al.* (2011) found a “significant variation and differentiation among hystricognathous rodents that are characterized by distinct diet or habitat”. Following this reasoning, the hystricognath condition of the *Tsaganomys* lower jaw should not be used as a phylogenetic character, but interpreted as the morphological expression to diet.

Tsaganomys is always considered to have had a fossorial lifestyle (WOOD 1970, 1974; BRYANT & MCKENNA 1995; WANG 2001), and similarities between the skull of

Tsaganomys and the bathyergids skull has led many researchers to interpret Tsaganomyidae as an early Bathyergidae (among others MATTHEW & GRANGER 1923; DAWSON 2003). Typical skull characters for a subterranean and fossorial lifestyle are a broad skull with wide cheekbones, the upper incisor extended near the orbit, a narrow orbital distance, a forward-sloping occipit and a triangular braincase. The lower jaw is enlarged and has a very strong coronoid process.

To interpret the life-style of Tsaganomyidae, COURANT (2004) used a morphometric method to compare *Tsaganomys altaicus* and the extant *Heterocephalus glaber*, a member of the Bathyergidae. *H. glaber* is a subterranean rodent from eastern Africa, and uses its incisors for burrowing passages (chisel-tooth digging). COURANT interprets the similarities with the skull of *Tsaganomys* as indicative of a similar adaptation to a subterranean lifestyle, a so-called "shape convergence", implying that skull morphology is highly constrained by environmental factors and especially by locomotion. In his view the burrowing technique of *Tsaganomys* was to bite the substrate with the upper and lower incisors (like the chisel-tooth digging of *Heterocephalus glaber*) and by headlift digging. *Tsaganomys* was thus not a claw-digging animal, which was also concluded earlier on basis of the postcranial skeleton by VINOGRADOV & GAMBARYAN (1952).

For *Tsaganomys* COURANT (2004) thus suggested a subterranean and digging lifestyle. This is not contradicted by the size of the eyes of *Tsaganomys*, which must have been quite small, a typical fossorial or subterranean adaptation. However, following MUCHLINSKI (2008), the absence of a large infraorbital foramen (IOF) indicates that they are neither blind nor constantly living in subterranean burrows. MUCHLINSKI, in his study on the tissues running through the IOF, observed that the IOF only contains an infraorbital artery (IOA) and an infraorbital nerve (ION). The nerve is always the largest of these two, indicating that the artery does not play a significant role in the heating of the face. The ION is the nerve for 'mystacial vibrissae', connected to the whiskers, which are "necessary for spatial exploration and tactile object recognition tasks". Nocturnal species and subterranean species have more of these nerves than diurnal species since they highly depend on the sense of touch and thus a large IOF is necessary (MUCHLINSKI 2008). Although the study of COURANT indicates a subterranean lifestyle for *Tsaganomys*, the small IOF implies a more fossorial lifestyle. Considering all available evidence we conclude that *Tsaganomys* can be seen as a rodent that was able to dig with the incisors, but most activities were outside its burrow.

As WANG (2001) argues, the attachment of the masseter indicates a vertical movement of this muscle, and only crushing and transverse chewing must have been possible. Moreover, the condyloid process is wide, short and knob-like. Movement of the jaw was possible in all directions, but propalinal movement was restricted, and in combination with the simple, cylindrical-shaped cheek teeth, this suggests a possible diet of insects and worms (WANG 2001).

Body size of mammals is affected by a number of relevant ecological characteristics, such as diet, climate and vegetation. Teeth can be used for body mass estimates, but differences in wear can influence the outcome of the predicted body mass (DAMUTH & MACFADDEN 1990). Based on the average molar size, our data indicate that for most species discussed here body size was largest in biozone B, although in biozone A in C*yclomylus intermedius* and in *Coelodontomys asiaticus* also relatively large body sizes occurred. In biozone C body size was smallest for all species discussed. The best known, and most used, ecogeographic principle is probably BERGMANN's rule: larger species, within a broadly distributed taxonomic clade, are found in colder environments while smaller sized species are found in warmer regions (BERGMANN 1848). Moreover, smaller sized animals have an evolutionary advantage over larger animals when temperatures increase, since their relative surface area is larger and they are more resistant to higher ambient temperatures (GARDNER *et al.* 2011). As soon as resources become scarce, mammals show a tendency to decrease in size to become less dependent on resources (BOYCE 1978). Therefore, the smaller sizes in biozone C might indicate changed environmental conditions, a rise in temperature or less available food resources.

In biozone A (Fig. 16) all species are present in the Taatsiin Gol and Taatsiin Tsagaan Nuur areas, although *Tsaganomys altaicus* is only found in two localities, and all species but *?Cyclomylus biforatus* are present until the end of biozone B. From that time on, the diversity of the group steadily decreased and in biozone C1 only *Tsaganomys altaicus* is found. All five species were present during the Early Oligocene until ~31.5 Ma. Over the following 3 million years, only three species were present in the assemblages and before the end of the Oligocene at ~24 Ma the family disappeared completely.

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References

BERGMANN, C. (1848): Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. – *Göttinger Studien*, **3**: 595–708.

BERKEY, C.P. & MORRIS, F.K. (1927): Geology of Mongolia. A reconnaissance report based on the investigations of the years 1922–1923. Natural history of Central Asia, II. – 474 pp., New York (American Museum of Natural History).

BOYCE, M.S. (1978): Climatic variability and body size variation in the muskrats (*Ondatra zibethicus*) of North America. – *Oecologia*, **36**: 1–19.

BRYANT, J. & MCKENNA, M. (1995): Cranial anatomy and phylogenetic position of *Tsaganomys altaicus* (Mammalia, Rodentia) from the Hsanda Gol Formation (Oligocene), Mongolia. – American Museum Novitates, **3156**: 1–42.

BURKE, J.J. (1935): *Pseudocylindrodon*, a new rodent genus from the Pipestone Springs Oligocene of Montana. – Annals Carnegie Museum, **25**: 1–4.

COURANT, F. (2004): Comparative anatomy of *Tsaganomys altaicus* (Rodentia, Tsaganomyidae) from the Oligocene of Mongolia: paleobiological implications. – Reveu de Paléobiologie, **9**: 111–125.

DAMUTH, J. & MACFADDEN, B. (1990): Body size in mammalian paleobiology: estimation and biological implications. – In: DAMUTH, J. & MACFADDEN, B. J. (eds): Body size in mammalian paleobiology: estimation and biological implications. – pp. 1–10, Cambridge (Cambridge University Press).

DAWSON, M. (2003): Paleogene rodents of Eurasia. – *Deinsea*, **10**: 97–126.

DAXNER-HÖCK, G. & BADAMGARAV, D. (2006): Geological and stratigraphic setting. – In: DAXNER-HÖCK, G. (ed.): Oligocene-Miocene Vertebrates from the Valley of Lakes (Central Mongolia): Morphology, phylogenetic and stratigraphic implications. − Annalen des Naturhistorischen Museums in Wien, Serie A, **108**: 173–125.

DAXNER-HÖCK, G., BADAMGARAV, D. & ERBAJEVA, M. (2010): Oligocene stratigraphy based on a sediment-basalt association in Central Mongolia (Taatsiin Gol and Taatsiin Tsagaan Nuur Area, Valley of Lakes): review of a Mongolian-Austrian project. – Vertebrata PalAsiatica, **10**: 348–366.

DAXNER-HÖCK, G., BADAMGARAV, D., ERBAJEVA, M. & GÖHLICH, U. (2013): Miocene mammal biostratigraphy of Central Mongolia (Valley of Lakes); New results. – In: WANG, X., FLYNN, L.J. & FORTELIUS, M. (eds): Fossil mammals of Asia.– pp. 477–494, New York, USA (Columbia University Press).

DEVYATKIN, E.V. (1981): The Cenozoic of inner Asia. (Stratigraphy, geochronology andcorrelation). – Nikiforova, **27**: 1–196.

DEVYATKIN, E.V. & BADAMGARAV, D. (1993): Geological essay on Paleogene and Neogene deposits of the Valley of Lakes and Prealtai depressions. – In: BARSBOLD, R. & AKHMETIEV, M.A (eds): International Geological Correlation Programm, project 326 Oligocene-Miocene transitions in the Northern Hemisphere. – pp. 7–27, Excursion guide-book Mongolia: Oligocene- Miocene boundary in Mongolia, Joint publication of the Mongolian Academy of Sciences, Ulaan Baatar and the Russian Academy, Moscow.

DRUZINSKY, R.E. (2010a): Functional anatomy of incisal biting in *Aplodontia rufa* and sciuromorph rodents – part 1: masticatory muscles, skull shape and digging. – Cells, tissues, organs, **191**/6: 510–522.

DRUZINSKY, R.E. (2010b): Functional anatomy of incisal biting in *Aplodontia rufa* and sciuromorph rodents – part 2: sciuromorphy is efficacious for production of force at the incisors. – Cells, tissues, organs, **192**/1: 50–63.

ERBAJEVA, M.A. (1999): Paleogene Hares (Leporidae, Lagomorpha) from the Zaisan Depression (Eastern Kazakhstan). – Paleontological Journal (Translated from Paleontologicheskii Zhurnal), **33**: 557–560.

GARDNER, J.L., PETERS, A., KEARNEY, M.R., JOSEPH, L. & HEINSOHN, R. (2011): Declining body size: a third universal response to warming? – Trends in ecology & evolution, **26**/6: 285–91.

HAUTIER, L., LEBRUN, R., SAKSIRI, S., MICHAUX, J., VIANEY-LIAUD, M. & MARIVAUX, L. (2011): Hystricognathy vs sciurognathy in the rodent jaw: a new morphometric assessment of hystricognathy applied to the living fossil *Laonastes* (Diatomyidae). – PloS one, **6**/4: 1–11.

Höck, V., Badamgarav, D., Schmid, H. & Daxner-Höck, G. (1999): Oligocene-Miocene sediments, fossils and basalts from the Valley of Lakes (Central Mongolia): an integrated study. – Mitteilungen der Österreichischen Geologischen Gesellschaft, **90**: 83–125.

Kowalski, K. (1974): Middle Oligocene rodents from Mongolia. Results of the Polish-Mongolian paleontological expeditions. – Palaeontology Polonica, **30**: 147–178.

Luckett, P.W. (1985): Subordinal and infraorbital affinities of rodents: developmental evidence from the dentition and placentation. – In: Luckett, P.W. & Hartenberger, J. (eds): Evolutionary relationships among rodents a multidisciplinary analysis. – NATO ASI Series, Series A: Life sciences, **92**: 567–588.

Marivaux, L. (2001): The role of Asia in the origin and diversification of hystricognathous rodents. – Zoologica Scripta, **31**: 225–239.

Marivaux, L., Vianey-Liaud, M. & Jaeger, J.-J. (2004): High-level phylogeny of early Tertiary rodents: dental evidence. – Zoological Journal of the Linnean Society, **142**/1: 105–134.

Matthew, W.D. & Granger, W. (1923): Nine new rodents from the Oligocene of Mongolia. – American Museum Novitates, **102**:1–10.

Mellet, J.S. (1966): Fossil mammals from the Oligocene Hsanda Gol Formation, Mongolia. Part I: Insectivora, Rodentia, and Deltatheridia, with notes on the paleobiology of *Cricetops dormitor*. Ph. D. Dissertation. – 282 pp., New York (Colombia University).

Mellet, J.S. (1968): The Oligocene Hsanda Gol Formation, Mongolia: A revised faunal list. – American Museum Novitates, **2318**: 1–16.

Muchlinski, M.N. (2008): The relationship between the infraorbital foramen, infraorbital nerve, and maxillary mechanoreception: implications for interpreting the paleoecology of fossil mammals based on infraorbital foramen size. – The Anatomical Record, **291**: 1221–1226.

Patterson, B. & Wood A.E. (1982): Rodents from the Deseadan Oligocene of Bolivia and the relationships of the Caviomorpha. – Bulletin Museum Comparative Zoology, **149**/7: 371–543.

Qiu, Zx., Qiu, Zh., Deng, T., Li, Ck., Zhang, Zq., Wang, By. & Wang, X. (2013): Chapter 1. Neogene Land mammalstages / ages of China. Toward the goal to establish an Asian land mammal stage / age scheme. – In: Wang, X., Flynn, L.J.& Fortelius, F. (eds): Fossil mammals of Asia. Neogene biostratigraphy and chronology. – pp. 20–90, New York (Columbia University Press).

Schmidt-Kittler, N. (2002): Feeding specializations in rodents. – Senckenbergiana lethaea, **82**: 141–152.

Shevyreva, N.S. (1971): K voprosu o sistematicheskom polozhenii “*Tsaganomys altaicus*” (Mammalia, Rodentia). – Ispytateli Prirody Otdela Geologii, **46**/6: 1–144.

Shevyreva, N.S (1972): Novye gryzuny iz Paleogena Mongolii i Kazakhstana. – Paleontologicheskii Zhurnal, **272**/3: 134–145.

Vinogradov, B. & Gambaryan, P. (1952): Oligotsenovye tsilindrodonty Mongolii i Kazakhstana (Cylindrodontidae, Glires, Mammalia). – Trudy Paleontologicheskogo Instituta Akademii, Nauk SSSR, **41**: 13–42.

von Koenigswald, W. (2011): Diversity of hypsodont teeth in mammalian dentitions, construction and classification. – Palaeontographica, Abteilung A: Palaeozoology – Stratigraphy, **294**/1–4: 63–94.

Wang, B. (2001): On Tsaganomyidae (Rodentia, Mammalia) of Asia. – American Museum Novitates, **3317**: 1–50.

Wood, A.E (1937): The mammalian fauna of the White River Oligocene. Part II. Rodentia. – Transactions American Philosophical Society, **28**: 1–269.

Wood, A.E (1955): A revised classification of the rodents. – Journal of Mammalogy, **36**: 165–187.

Wood, A.E (1970): The early Oligocene rodent *Ardynomys* (Family Cylindrodontidae) from Mongolia and Montana. – American Museum Novitates, **2418**: 1–18.

Wood, A.E (1974): Early Tertiary vertebrate faunas Vieja Group Trans-Pecos Texas: Rodentia. – Texas Memorial Museum Bulletin, **21**: 1–112.