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Dipodidae (Rodentia, Mammalia) from the Oligocene and Early Miocene of Mongolia

By Gudrun Daxner-Höck[1*], Demchig Badamgarav[2] & Olivier Maridet[3]

(With 27 figures and 21 tables)

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Abstract

Cenozoic sediments and fossils of the Taatsiin Gol and Taatsiin Tsagaan Nuur area in Mongolia yield important information about stratigraphy and mammal evolution in Asia. This issue focuses on the taxonomy, evolution and stratigraphic distribution of the rodent family Dipodidae. Nine genera and 20 species of Dipodidae are identified from 70 fossil beds of the Hsanda Gol and Loh Fms.These include the descriptions of *Onjosminthus baindi* nov. gen. nov. spec., *Heosminthus borrae* nov. spec., *Heosminthus chimidae* nov. spec. and *Plesiosminthus olzi* nov. spec. Dipodidae are the most abundant and species-rich rodent family of the Oligocene in Mongolia. After reaching highest diversity in the Late Oligocene (biozone C1), a remarkable decrease of species toward the Oligocene-Miocene transition initiated the turnover of Dipodidae-associations during the Early Miocene.

Key words: Dipodidae, Paleogene, Neogene, taxonomy, biostratigraphy, Valley of Lakes.

Kurzfassung

Känozoische Sedimente aus der Region um den Taatsiin Fluß und Weißen Taatsiin See in der Mongolei liefern bedeutende Informationen zur Stratigraphie und Entwicklung der Säugetiere in Asien. Die vorliegende Studie setzt sich das Studium der Taxonomie, Evolution und der zeitlichen Verbreitung der Nagerfamilie Dipodidae zum Ziel. Es wurden 9 Gattungen und 20 Arten beschrieben, davon neu: *Onjosminthus baindi* nov. gen. nov. spec., *Heosminthus borrae* nov. spec., *Heosminthus chimidae* nov. spec. und *Plesiosminthus olzi* nov. spec. Dipodidae waren im Oligozän

[1] Rupertusstr. 16, 5201 Seekirchen, Austria; E-mail: gudrun.hoeck@nhm-wien.ac.at, gudrun.hoeck@sbg.at

[2] Paleontological Center, Mongolian Academy of Sciences, Enkhtaivan Avenue 63, Ulaanbaatar 13343, P.O.B-260, Mongolia; E-mail: dbadamgarav@yahoo.com

[3] Natural History Museum Vienna, Department of Geology & Palaeontology, Burgring 7, 1010 Vienna, Austria; olivier.maridet@nhm-wien.ac.at

[*] Corresponding author

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der Mongolei die häufigste und artenreichste Nagetierfamilie. Sie erreichte ihre größte Vielfalt im Ober-Oligozän (Biozone C1). Ein markanter Rückgang oligozäner Arten um die Oligozän-Miozän Wende leitete den Wechsel der Dipodidae-Vergesellschaftungen im Unter-Miozän ein.

Schlüsselwörter: Dipodidae, Paläogen, Neogen, Taxonomie, Biostratigraphie, Tal der Gobiseen.

Introduction

Dipodidae are well represented in almost all small mammal assemblages from the study area and turned out to be excellent biostratigraphic markers. Their stratigraphic occurences can be linked with lithostratigraphic and radiometric data, as showed by continuous improvement of the integrated stratigraphy of the Valley of Lakes, established by previous Mongolian-Austrian Geoscientific Projects since 1995 (Daxner-Höck *et al.* 1997; Höck *et al.* 1999; Daxner-Höck & Badamgarav 2007; Daxner-Höck *et al.* 2010 and Daxner-Höck *et al.* 2013).

Prior to this research, Cenozoic Dipodidae were poorly known from the Valley of Lakes. Earlier findings were mainly limited to remains collected from the surface (Kowalski 1974; Russell & Zhai 1987; Zazhigin & Lopatin 2000). The method of wet-screening of fossil-bearing sediments, introduced by our team in the Valley of Lakes, enabled the recovery of a wide spectrum of tiny to large-sized mammal teeth. Since then numerous systematic-taxonomic investigations on different fossil groups have been conducted,

Table 1. List of investigated fossil sites and sections.

	locality	section		locality	section
1.	Abzag Ovo	ABO-A	19.	Tatal Gol	TAT-037-055
2.	Builstyn Khudag	BUK-A	20.	Tatal Gol	TAT-C
3.	Ulan Tolgoi	UTO-A	21.	Tatal Gol	TAT-D, -E
4.	Del	DEL-B	22.	Tatal Gol	TAT-SE
5.	unnamed locality	GRAB-II	23.	Taatsiin Gol left	TGL-A
6.	Khongil	HL-A	24.	Taatsiin Gol left	TGL-B
7.	Ikh Argalatyn Nuruu	IKH-A	25.	Taatsiin Gol right	TGR-A
8.	Ikh Argalatyn Nuruu	IKH-B	26.	Taatsiin Gol right	TGR-B
9.	Ikh Argalatyn Nuruu	IKH-C	27.	Taatsiin Gol right	TGR-AB
10.	unnamed locality	K-II	28.	Taatsiin Gol right	TGR-C
11.	Loh	LOH-A	29.	Taatsiin Gol right	TGR-ZO
12.	Loh	LOH-B, -C	30.	Taatsiin Gol right	TGR-1564
13.	Luugar Khudag (a,b)	LOG-A, -B	31.	Toglorhoi	TGW-A
14.	Huch Teeg	RHN-A	32.	Toglorhoi	TGW-D
15.	Hsanda Gol	SHG-A	33.	Unkheltseg	UNCH-A
16.	Hsanda Gol	SHG-AB	34.	Hotuliin Teeg	HTE, HTS, HTSE
17.	Hsanda Gol	SHG-C	35.	Luuny Yas	LUS
18.	Unzing Khurem	TAR-A	36.	Olon Ovoony Churem	ODO-A, -B

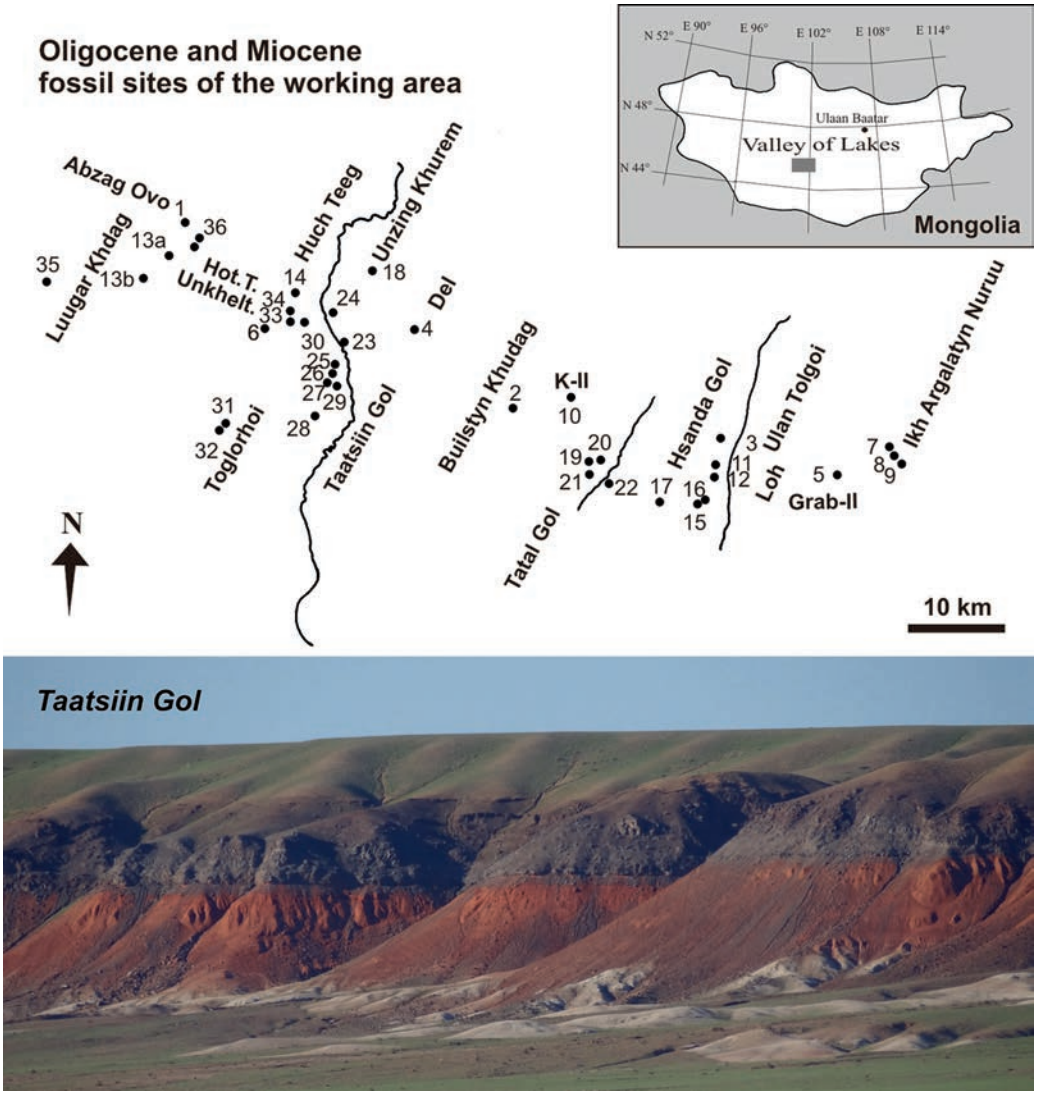


Fig. 1. The investigated fossil sites and sections listed in Tab. 1. The gray rectangle marks the working area in the Taatsiin Gol and Taatsiin Tsagaan Nuur region, Valley of Lakes. The photograph (below) shows basalt I (age 31.5 Ma) and red clay of the Hsanda Gol Fm., and light-coloured sediments of the Tsagan Ovo Fm. along the valley of Taatsiin Gol.

i.e., on Gatropoda (STWORZEWICZ 2007; NEUBAUER *et al.* 2013), Amphibia and Squamata (BÖHME 2007), Didymoconidae, Creodonta and Carnivora (NAGEL & MORLO 2003; MORLO & NAGEL 2002; MORLO & NAGEL 2007), Marsupialia, Erinaceomorpha and Soricomorpha (ZIEGLER, DAHLMANN & STORCH 2007), Lagomorpha (ERBAJEVA & DAXNER-HÖCK 2001; ERBAJEVA 2003; ERBAJEVA 2007), Rodentia (DAXNER-HÖCK 2000; DAXNER-HÖCK 2001; DAXNER-HÖCK & WU 2003; SCHMIDT-KITTLER, VIANEY-LIAUD &

Marivaux 2007; Koenigswald & Kalthoff 2007), Ruminantia (Vislobokova & Daxner-Höck 2002), Rhinocerotidae (Heissig 2007) and Proboscidea (Göhlich 2007).

During eight field-campaigns from 1995 to 2012, several thousands of teeth, numerous jaws and a few skull-fragments of Dipodidae were collected. The investigated area ranges from Luuny Yas in the west to Ikh Argalatyn Nuruu in the east (Fig. 1, Tab.1). Numerous data on Oligocene and Early Miocene Dipodidae derive from the adjacent countries Kazakhstan and China. The famous localities of the Zaisan Depression and the Aral region (Kazakhstan), the Danghe area, Qujing in Yunnan, the Junggar Basin, fossil sites of Nei Mongol and many other places (China) provide comprehensive information on the development of Dipodidae in Asia (Bendukidze *et al.* 2009; Bohlin 1946; Emry *et al.* 1998; Huang 1992; Kimura 2010; Li & Qiu 1980; Lopatin 1999; Lopatin & Zazhigin 2000; Shevyreva 1970; Wang 1985; Wang 2003; Wang & Qiu 2000, 2004; Wang *et al.* 2003; Ye *et al.* 2003; Zazhigin & Lopatin 2000). The current investigation includes the examination of unpublished and partly published fossil assemblages. The material described in this paper extends that knowledge to Mongolia, and forms an important addition to the knowledge on the history of the family.

Geological setting

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 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 Nur area (Uvurkhangai Aimag), long known for the fossil richness of Cenozoic sediments and its basaltic volcanism (Berkey & Morris 1927; Devjatkin 1981; Devjatkin & Badamgarav 1993). The Oligocene-Miocene sediment sequences of the Hasanda Gol and Loh Fms are exposed along steep cliffs of mostly dry river beds (Fig. 1, Tab. 1). In this region there are several basalt layers of different age and regional extension interlayered between fossiliferous sediments of the Hsanda Gol and Loh Fms. During comprehensive geological-paleontological investigations, an integrated stratigraphy of this area was elaborated (1995–1997) and subsequently refined. The focus at that time was on: geological mapping, sedimentological and paleontological studies, and stratigraphy. The stratigraphic framework is based on: definition and description of formations (Tsagan Ovo-, Hsanda Gol-, Loh- and Tuyn Gol Fms), establishment of informal biozones (A, B, C, C1, D, D1/1, D1/2 and E), and radiometric ages of basalts I - III (Daxner-Höck *et al.* 1997; Höck *et al.* 1999; Daxner-Höck & Badamgarav 2007; Daxner-Höck *et al.* 2010).

The basalt occurrences were dated by the ^{40}Ar / ^{39}Ar method (whole rock samples; Höck *et al.* 1999). This yielded two groups of Oligocene basalt ages. The older one is the Early Oligocene basalt I group of around 31.5 Ma (range: 30.4–32.2 Ma; errors varying from 0.3 to 0.8 Ma). The second is the Late Oligocene basalt II group, which displays age differences of at least 1 Ma between local occurrences west and east of Taatsiin Gol. The eastern

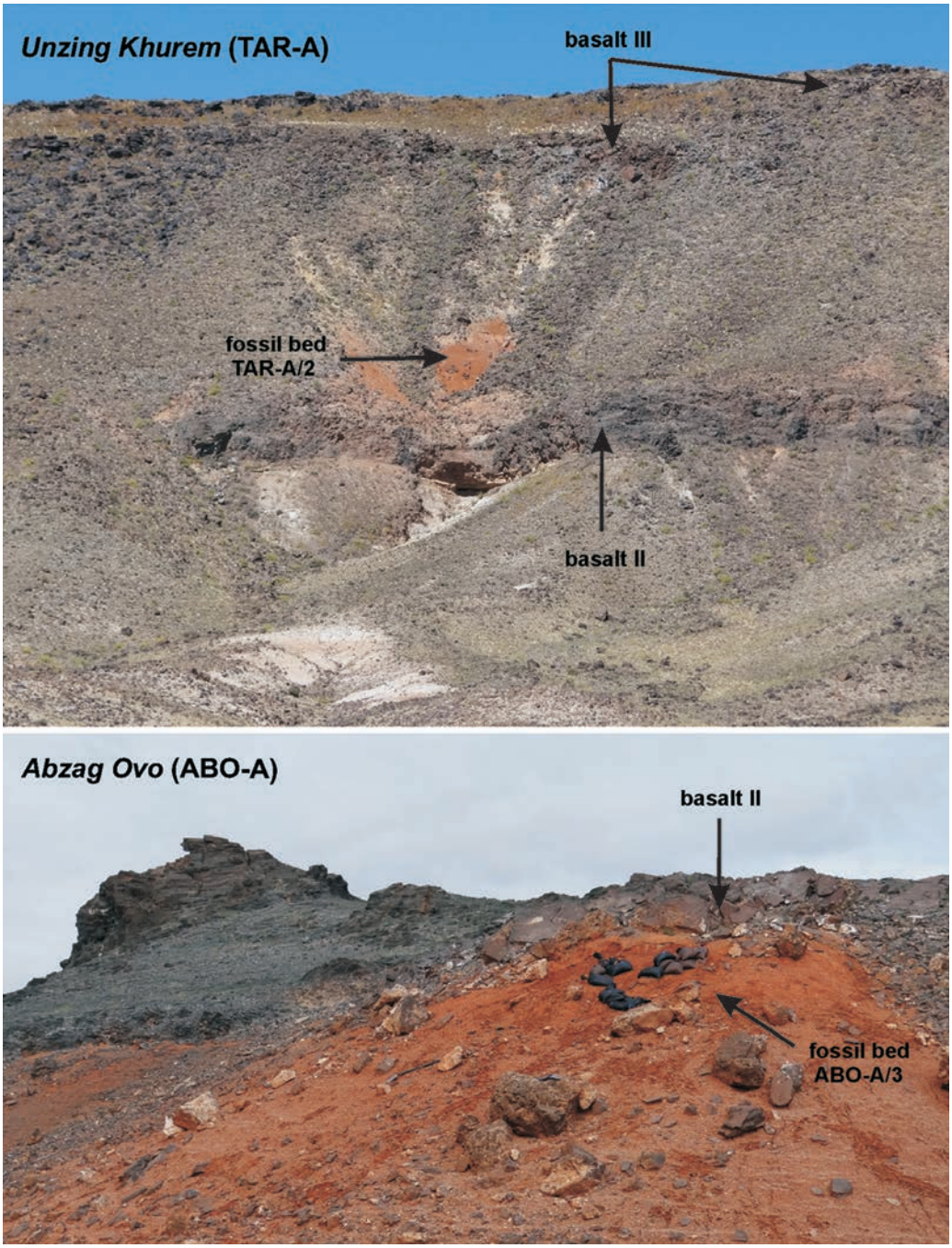


Fig. 2. Sections Unzing Khurem and Abzag Ovo. In the section Unzing Khurem (TAR-A) fossils of biozone C are included in the red-orange silt (TAR-A/2) above basalt II (27.4 ± 0.4 Ma). The section is toped by basalt III (around 13 Ma). In the section Abzag Ovo (ABO-A) the red silt (ABO-A/3) below basalt II (27.0 ± 0.9 Ma) contains fossils of biozone C.

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 around 13 Ma (errors vary from 0.2 to 0.7 Ma). (Höck *et al.* 1999: fig. 8; Daxner-Höck *et al.* 2010: 351).

The paleontological and stratigraphic focus of this study is on the sediments of the Hsanda Gol and Loh Fms, and on the Dipodidae of the Oligocene and Early Miocene. These two formations are of particular interest because of their fossil content and contact with basalts I and II (Höck *et al.* 1999). The Hsanda Gol Fm. consists of brick-red clays and silts divided by basalt I or its time equivalent tuff. The lower Hsanda Gol beds (below basalt I; older than 31.5 Ma) contain fossils of biozone A, and the upper Hsanda Gol beds (immediately above basalt I; younger than 31.5Ma) contain fossils of biozone B. The upper part of the Hsanda Gol sediments extends to the Late Oligocene as indicated by fossils of biozones C to C1. Sediments of the Loh Fm. (sands, silts, gravels of more light colours: rose, yellow, white, green, brown) were deposited in the Late Oligocene and Miocene above sediments of the Hsanda Gol Fm. The lower part of the Loh Fm. locally contains fossils of biozone C immediately below or above basalt II flows. In the section Abzag Ovo (ABO-A/3; Figs 1 and 2/1), fossils of biozone C were recovered from a red silt of the Loh Fm. immediately below basalt II (27.0 $\pm$ 0.9 Ma). In the section Unzing Khurem (TAR-A/2; Figs 1and 2/2) a red-orange silt on top of basalt II (27.4 $\pm$ 0.4 Ma) contains fossils of biozone C also.

More prominent outcrops of basalt II are present in the northwest of the study area, in Olon Ovoony Khurem (ODO-A, B), Luugar Khudag (LOG-B) and Luuny Yas (Yus) and from the northern part of the Tatal Gol area (Höck *et al.* 1999; Daxner-Höck *et al.* 2010). Fossils of biozone C1 and D could not be dated radiometrically, but the litho-stratigraphic position and biostratigraphic data (above fossil-layers of biozone C), as well as stratigraphic correlations with mammal faunas from Kazakhstan, China and Europe, indicate a Late Oligocene and Early Miocene age, respectively. Basalt III and faunas of biozone D1/1, D1/2 and E are beyond the scope of this study.

Material and methods

The fossils were collected by screen washing of about eighty tons of sediment from more than seventy fossil layers along fourty sections (Fig. 1, Tab. 1). In the fieldcamp the teeth and bones were picked out from the dry residue using head-lenses and field microscopes. The subsequent process of cleaning, identification and arrangement of fossils was performed inVienna. SEM-images were taken at the University Vienna. To facilitate comparisons, all right-side teeth are figured as mirror images (reversed) and their figure numbers are underlined (*e.g.*, Fig. 4/$\underline{3}$ = M3 from the right side). All illustrated, measured and described fossils are housed in the Vienna collection (coll. NHMW 2001/0032–00038; 2001/00064–00068; 2012/0067; 2013/0114–0263); only a minor part of fossils from the collection of the Mongolian Paleontological Center are considered in the present issue. These are marked in the material lists (coll. MPC). For each measureable tooth the length and width are provided under the form: 'length'×'width'. All the measurements are given in millimetres. For classification above genus level we follow Mc Kenna & Bell (1997).

Dental terminology

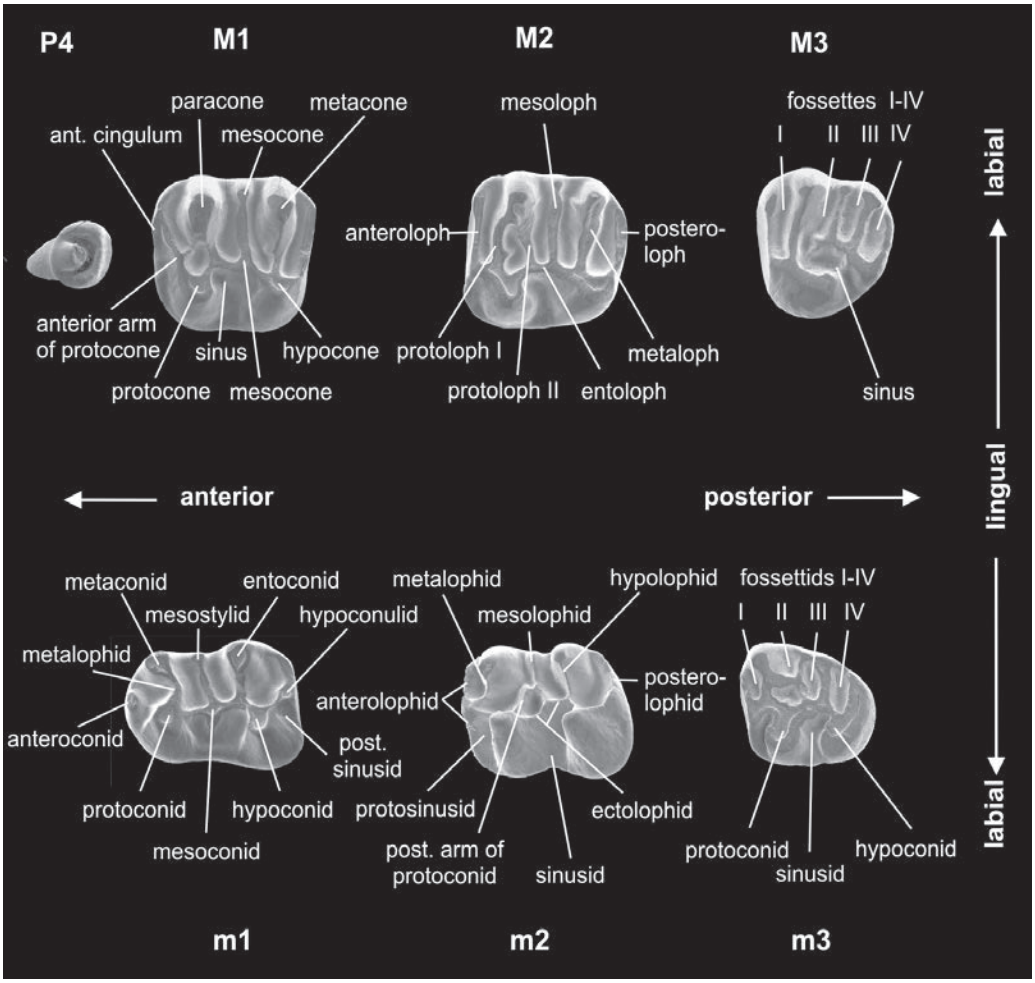


Fig. 3. Dental terminology of Dipodidae modified after WANG (1985).

Abbreviations

coll. NHMW – collection of the Natural History Museum, Department of Geology & Palaeontology, Vienna.

coll. MPC – collection of the Mongolian Paleontological Center, Academy of Sciences, Ulaanbaatar.

PIN – Paleontological Institute of the Russian Academy of Sciences, Moscow.

LOD – last occurrence datum

FOD – first occurrence datum

Systematic Palaeontology

Class Mammalia Linneaus, 1758

Order Rodentia Bowdich, 1821

Family Dipodidae Fischer, 1817

Genus *Allosminthus* Wang, 1985

1985 *Allosminthus* gen. nov. – Wang: 356–361, figs 18–25.
1997 *Banyuesminthus* gen. nov. – Tong: 135–138, 236–237, figs 63–64, pl. XI/15–23.
2001 *Tatalsminthus* n. gen. – Daxner-Höck: 360–363, pl. 1, figs 1–10, text-fig.1, tabs 2–3.
2009 *Allosminthus*. – Wang: 21–24, figs 1–3.

Type species: *Allosminthus ernos* Wang, 1985

Dental characters: Upper incisors with smooth anterior surface; small, low-crowned molars; obtuse main cusps; weak crests; M1–2 almost square and subequal in size; upper molars three-rooted, two labial roots, one lingual root; mesoloph short or of medium length; metaloph complete; M1: anterior arm of protocone joins the paracone, forming protoloph I; protoloph II varies from absent to present; metaloph of M2 meets anterior arm of hypocone; lower molars two-rooted; ectolophid straight; mesolophid short or absent; hypolophid of m1–2 complete; metalophid I and metalophid II of m2–3 variable; trigonid of m1 short and narrow, anteroconid very small or absent; mesoconid of m1 pronounced; hypoconulid of m1–2 and posterior sulcus frequently present.

Referred species / type localities:

- *A. disconjugatus* (Tong, 1997) from Tuqiaogou (China); late Middle Eocene.
- *A. ernos* Wang, 1985 from Caijiachong (China); Early Oligocene.
- *A. khandae* (Daxner-Höck, 2001) from Tatal Gol (Mongolia); Early Oligocene (biozone A).
- *A. majusculus* Wang, 1985 from Caijiachong (China); Early Oligocene.
- *A. minutus* (Daxner-Höck, 2001) from Hsanda Gol (Mongolia); Early Oligocene (biozone B).
- *A. uniconjugatus* (Tong, 1997) from Shanghe (China); late Middle Eocene-Late Eocene.

Allosminthus khandae (Daxner-Höck, 2001)

(Fig. 4/ 1–6, Tab. 2)

1999 *Heosminthus* sp. 2. – Höck *et al.*: 115–116, fig. 20/2.
2001 *Tatalsminthus khandae* n. sp. – Daxner-Höck: 360–363, pl. 1, figs 1–10, text-fig. 1, tabs 2–3.
2009 Allosminthus khandae. – Wang: 84.

Type locality: Tatal Gol (TAT-D/1), Early Oligocene (biozone A).

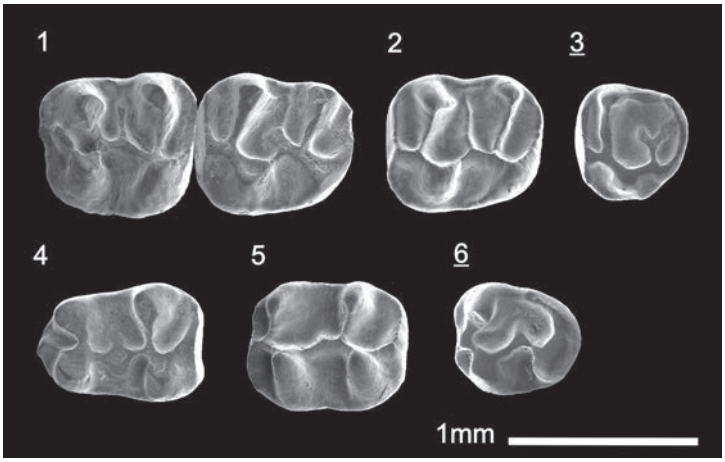


Fig. 4. *Allosminthus khandae* (DAXNER-HÖCK, 2001) from the Valley of Lakes in Mongolia. Early Oligocene (biozone A). All specimens in the NHMW collection. **1**: left M1–2 (NHMW 2001/0032/0005/1) from an unnamed locality, GRAB-II. **2**: left M2 (NHMW 2001/0032/0002/2) from Taatsiin Gol (TGR-A/13). **3**: right M3 (NHMW 2001/0032/0001/21) from Tatal Gol (TAT-D/1). **4**: left m1(NHMW 2001/0032/0002/3) from Taatsiin Gol (TGR-A/13). **5**: left m2 (NHMW 2001/0032/0002/4) from Taatsiin Gol (TGR-A/13). **6**: right m3 (NHMW 2001/0032/0001/9), AO (DAXNER-HÖCK 2001; pl.1, fig. 9) from Tatal Gol (TAT-D/1).

Occurrence of *Allosminthus khandae* in Mongolia (Valley of Lakes, Uvurkhangai): Early Oligocene (biozone A).

Type material from Tatal Gol (TAT-D/1). DAXNER-HÖCK (2001: tab. 2)

Holotype: Right fragmentary mandible with m1–3 (NHMW 2001/0032/0001/8). Measurements: m1 = 0.96 × 0.78 mm, m2 = 0.94 × 0.80 mm, m3 = 0.80 × 0.73 mm.

Paratypes: left mandible with m1–3, M1–3l, M1–2l, 1 M1, 3 m2, 2 m3, 5 m1, 4 m2, 2 m3 (NHMW 2001/0032/0001/1–23).

Table 2. Measurements of *Allosminthus khandae*.

	length (mm)			width (mm)	
	range	mean	N = 35	range	mean
M1	0.98 – 1.07	1.02	4	0.86 – 0.91	0.88
M2	0.91 – 1.10	0.97	10	0.84 – 1.05	0.89
M3	0.68 – 0.73	0.70	3	0.68 – 0.73	0.70
m1	0.96 – 1.03	1.00	8	0.70 – 0.78	0.75
m2	0.89 – 1.03	0.98	7	0.73 – 0.82	0.78
m3	0.75 –0.80	0.78	3	0.65 – 0.86	0.73

Additional material studied: Daxner-Höck (2001: tab. 2)

- Taatsiin Gol (TRG-A/13): 5 teeth (NHMW 2001/0032/0002/1–5).
- Khongil (HL-A/1): 1 tooth (NHMW 2001/0032/0003/1).
- Hsanda Gol (SHG-C/1): 2 teeth (NHMW 2001/0032/0004/1–2).
- unnamed locality (GRAB-II): 1 maxilla (NHMW 2001/0032/0005/1).

Description: Daxner-Höck (2001: 360–363).

Remarks: According to Wang (2009) *Tatalsminthus* Daxner-Höck, 2001 is a junior synonym of *Allosminthus* Wang, 1985 and *Tatalsminthus khandae* a synonym of *Allosminthus khandae*. This last species is close to the type species *Allosminthus ernos* in size, but differs by: M1 with complete protoloph II, and metaloph joining the hypocone, by M1–2 with a mesocone and paracone-spur, by m2–3 with complete metalophid I and absent metalophid II (Wang 2009: 84). For comparison with further *Allosminthus*- species from China see Wang (2009: 83).

Allosminthus minutus (Daxner-Höck, 2001)

(Fig. 5/1–6; Tab. 3)

1999 *Heosminthus* sp. 3. – Höck *et al.*: 116.
2001 *Heosminthus minutus* n. sp. – Daxner-Höck: 363–365, pl. 2, figs 1–11, tabs 4–5.
2007 *Heosminthus minutus*. – Daxner-Höck & Badamgarav: 17, Tab. 2.
2010 *Heosminthus minutus*. – Daxner-Höck *et al.*: 358, tab. 4.

Type locality: Hsanda Gol (SGH-A/20), Early Oligocene, biozone B (Daxner-Höck 2001: 363).

Occurrences of *Allosminthus minutus* in Mongolia (Valley of Lakes Uvurkhangai): Early to Late Oligocene (biozone B to biozone C). Daxner-Höck (2001: 364, tab. 4).

Type material from Hsanda Gol (SHG-A/20): Daxner-Höck (2001: Tab. 4):

Holotype: Right mandible with m1–3 (NHMW 2010z0033/0001/1). Measurements: m1 = 0.85 × 0.60 mm, m2 = 0.90 × 0.68 mm, m3 = 0.68 × 0.60 mm (Early Oligocene (biozone B)).

Paratypes: M1–2l, m3r, m2l (NHMW 2010z0033/0001/2–4); SHG-A/15–20 (NHMW 2010z0033/0002/1–2); SHG-A/9 (NHMW 2010z0033/0003/1–9) (Early Oligocene (biozone B)).

Additional material studied:

Early Oligocene (biozone B):

- Hsanda Gol: SHG-AB/17+18 (NHMW 2001z0033/0004/1–8); SHG-AB/17–20 (NHMW 2001z0033/0005/1–16).
- Ikh Argalatyn Nuru: IKH-A/3–4 (NHMW 2001z0033/0006/1–3); IKH-A/1 (NHMW 2001z0033/0007/1–2).
- Taatsiin Gol: TGR-B/1 (NHMW 2001z0033/0008/1–3); TGR-AB/21. (*).
- Tatal Gol: TAT-C/6+7 (NHMW 2001z0033/0011/1–4).
- Tatal Gol: TAT-039: 1 m2l (coll. MPC).

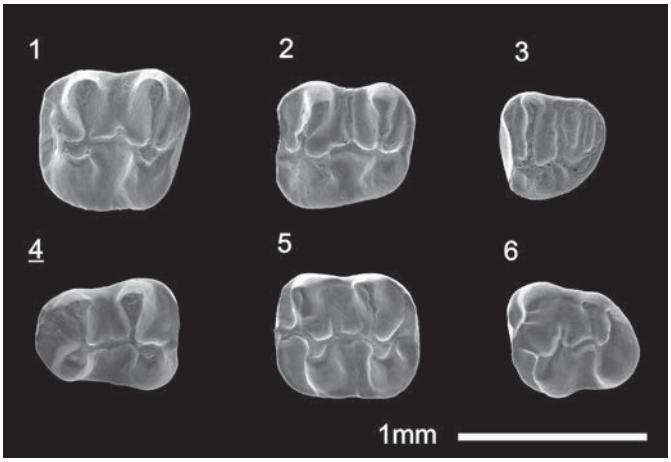


Fig. 5. *Allosminthus minutus* (DAXNER-HÖCK, 2001) from the Valley of Lakes in Mongolia. Early Oligocene (biozone B). All specimens in the NHMW collection. **1**: left M1(NHMW 2001/0033/0005/9) from Hsanda Gol (SHG-AB/17–20). **2**: left M2 (NHMW 2001/0033/0003/2) from Hsanda Gol (SHG-A/9). **3**: left M3 (NHMW 2001/0033/0008/3) from Taatsiin Gol (TGR-B/1). **4**: right m1 (NHMW 2001/0033/0003/5) from Hsanda Gol (SHG-A/9). **5**: left m2 (NHMW 2001/0033/0006/3) from Ikh Argalatyn Nuruu (IKH-A/3–4). **6**: left m3 (NHMW 2001/0033/0011/4) from Tatal Gol (TAT-C/6+7).

Late Oligocene (biozone C):

- Toglorhoi: TGW-A/1: 1 M2r (NHMW 2013/0114/0001).TGW-A/2a: 1 M1r (NHMW 2013/0115/0001).
- Tatal Gol: TAT-055: 1 M1r, 1M2r, 1 m1r, 1 m3r (NHMW 2013/0116/0001–0004); TAT-042: Left lower jaw with m1–2 (Coll. MPC).

Description: DAXNER-HÖCK (2001: 363–365; pl. 2, figs 1–11).

Remarks: *Allosminthus minutus* is the smallest Dipodidae species known from the Oligocene of Mongolia. It is smaller than *Allosminthus khandae* and the type species

Table 3. Measurements of *Allosminthus minutus*.

	length (mm)			width (mm)	
	range	mean	N = 58	range	mean
P4		0.50	1		
M1	0.78 – 0.95	0.86	20/18	0.68 – 0.85	0.78
M2	0.73 – 0.90	0.82	15/14	0.68 – 0.85	0.76
M3	0.55 – 0.65	0.61	4	0.55 – 0.65	0.61
m1	0.68 – 0.95	0.82	10	0.56 – 0.68	0.62
m2	0.78 – 0.90	0.85	9	0.59 – 0.71	0.65
m3	0.68 –0.88	0.77	15	0.55 – 0.70	0.63

Allosminthus ernos. Originally it was described as *Heosminthus minutus* DAXNER-HÖCK, 2001, but its primitive dental structures are indicative of *Allosminthus* rather than of *Heosminthus*: *i.e.*, the strong anterior protocone arm of M1 is connected with the paracone or with the anterior cingulum. The mesoloph of M1–2 is short or of medium length. The anteroconid of m1 is weak or absent. The mesolophid of m1–3 is absent, the metalophid II and the hypolophid are dominating lophids.

Genus *Heosminthus* WANG, 1985

1985 *Heosminthus* gen. nov. – WANG: 352–356.

Type species: *Heosminthus primiveris* WANG, 1985

Dental characters: Upper incisors with smooth anterior surface; upper molars of small to medium size, and with three roots, two labial and one lingual; M1–2 more or less square in outline; labial cusps opposite to lingual cusps; M1 with protoloph II; M2 with protoloph I or double protoloph; mesoloph of medium length or long; metaloph of M1–2 joins hypocone or its anterior arm; anteroconid of m1pronounced; ectolophid straight or slightly oblique; mesolophid of m1–2 long or of medium length; posterior arm of protoconid of m2 (= metalophid II) absent or short; mesolophid longer than posterior arm of protoconid.

Referred species / type locality:

- *H. borrae* nov. spec. from Unkheltseg (Mongolia); Early Oligocene (biozone B).
- *H. chimidae* nov. spec. from Taatsiin Gol (Mongolia); Early Oligocene (biozone B).
- *H. primiveris* WANG, 1985 from Caijiachong (China); Early Oligocene.

Remarks: *Heosminthus primiveris* is the oldest and most primitive species of *Heosminthus*. In the course of the Early Oligocene (biozones A to B) in Mongolia, new species of different size ranges developed, *i.e.*, *Heosminthus borrae* nov. spec. (smallest), *Heosminthus chimidae* n. sp. (small) and a third unnamed group of medium size, *Heosminthus* sp. Strikingly, the conservative dental pattern of *Heosminthus* remained almost unchanged during more than ten million years and was favourable in various environments and living conditions. *Heosminthu*s was an ubiquist, the most abundant and longest-living Dipodidae genus, as evidenced by the high number of individuals, its presence in all rodent faunas, and its long survival.

***Heosminthus borrae* nov. spec.**

(Figs 6/1–18, Tab.4)

Derivatio nominis: In honor to T. BORR, Mongolian member of the field-team.

Type locality: Unkheltseg, Uvurkhangai, Mongolia; fossil layer UNCH-A/3B, silty clay of the Hsanda Gol Fm., Early Oligocene, biozone B.

Holotype (Fig. 6/1): Fragmentary right maxilla with P4–M2 (Inv. Nr. NHMW 2013/0117/0001). Measurements: P4 = 0.42 × 0.40 mm, M1 = 0.94 × 0.96 mm, M2 = 0.89 × 0.94 mm.

Paratypes (Figs 2–18): All specimens from the Type locality: 8 M1l, 1 M2l, 4 M3l, P4–M1r, 9 M1r, 4 M2r, 6 M3r, m1–3r, 4 m1l, 5 m1r, 3 m2l, 1 m2r, 3 m3l, 3 m3r (NHMW 2013/0117/0002–0054).

Additional material studied:

Early Oligocene (biozone B):

- Tatal Gol: TAT-C/6: m1r (NHMW 2013/0118/0001).
- Taatsiin Gol: TGR-B/1: M2l, 2 m1r (NHMW 2013/0119/0001–0003); TGR-AB/21: M1l, M2l, M3l, M3r, 2 m1r, m2r (NHMW 2013/0120/0001–0007); TGR-AB/22: 2 M1, M2l, M3l, 5 M3r, 2 m1r, m2l (NHMW 2013/0121/0001–0012).
- Unkheltseg (UNCH-A/3B): 12 molars (Coll. MPC)

Late Oligocene (biozone C):

- Tatal Gol: TAT-055: 2 M1l, M1r, 3 M2r, m1–3r, m3l (NHMW 2013/0122/0001–0008).
- Taatsiin Gol: TGR-C/7: 2 M2r (NHMW 2013/0123/0001–0002).

Late Oligocene (biozone C1):

- Tatal Gol: TAT-E/27: M2r, m1r, m1–2r (NHMW 2013/0124/0001–0003);

Oligocene-Miocene transition (C1–D):

- TAT-E/32: M1l (NHMW 2013/0125/0001).

Early Miocene (biozone D):

- Hotuliin Teeg: HTE- 005: M1l, M3r, m1l, m1r (NHMW 2013/0126/0001–0004); HTE-015–018: 6 molars (coll. MPC).
- Huch Teeg: RHN-A/12: M1r, M2l, M3r, m1–3r (NHMW 2013/0127/0001–0004).

Diagnosis: Very small-sized species; general dental pattern and root numbers in accordance with the genus, but cones/conids increasingly high and lophodont; valleys deep and narrow specifically of stratigraphic young occurrences; anterior arm of protocone long (80 % of M1); protoloph II of M2 weak or absent; mesoloph(id) long; entoloph continuous; sinus of M-2 deep and in anterior direction; lophids of lower molars almost as high as conids; anteroconid (m1) connected with lingual cingulum (50 %); shallow sinusid (m1–2); frequently ectostylid at the base of sinusid (m1–2); pronounced lingual anterolophid (m2–3); posterior arm of protoconid short or absent (m2–3); mesolophid long.

Differential diagnosis: *Heosminthus borrae* differs from the type species in having a more advanced dental pattern (molars higher and moderately lophodont). It

differs from *Heosminthus chimidae* in having smaller and relatively high and moderately lophodont molars. It differs from *Heosminthus* sp. in being noticeably smaller. It differs from *Bohlinosminthus parvulus* in having three roots of upper molars, a double protoloph of M2, and having both, a mesolophid and a short posterior arm of protoconid in m2.

Description of the holotype (Fig. 6/1): P4–M2r (Inv. Nr. NHMW 2013/0117/0001):

P4 consists of a single cone which is surrounded by a cingulum; one root.

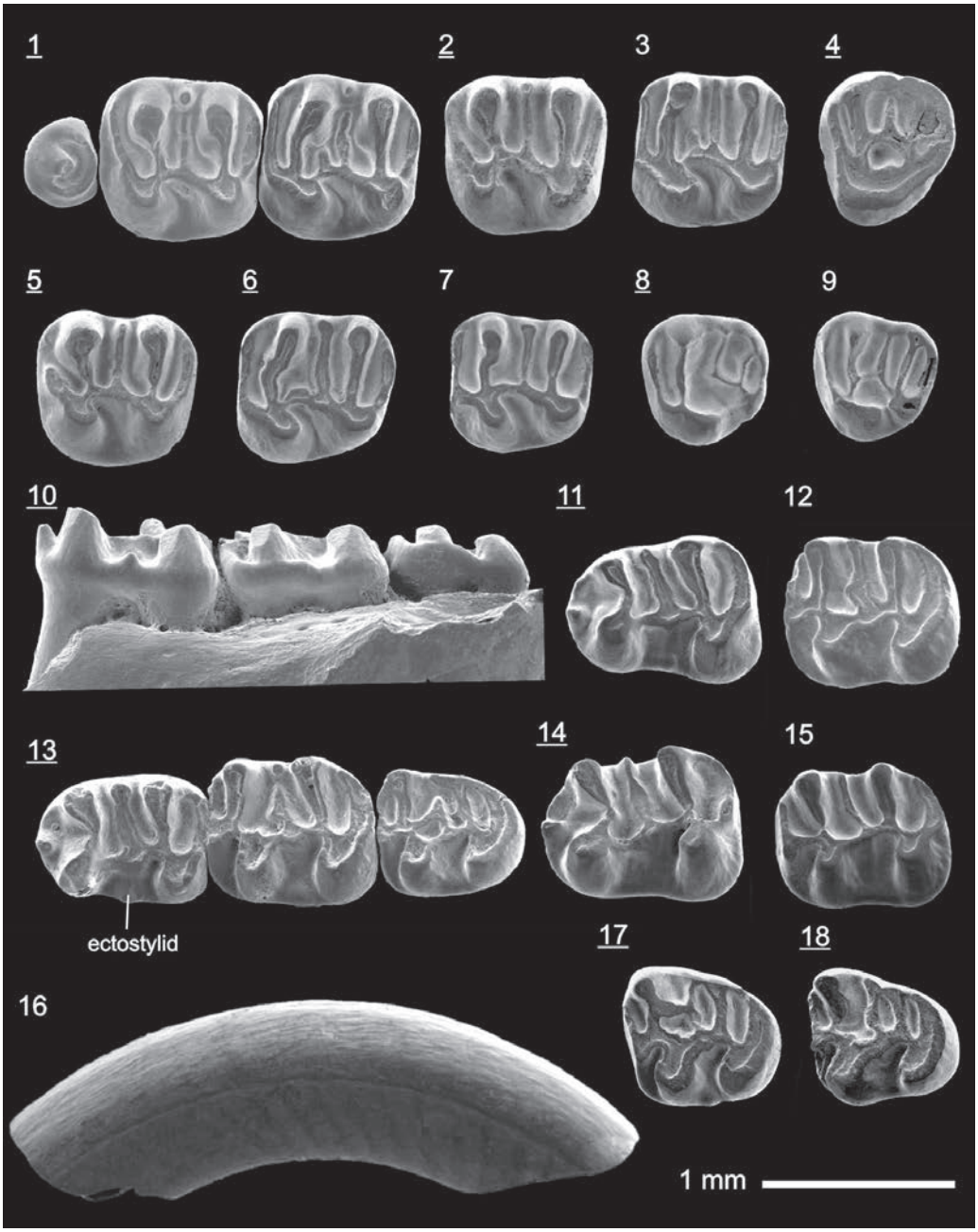
M1 almost square in outline with rounded corners; four main robust cones; five lophs; four narrow labial fossettes; sinus directed forward; long anterior arm of protocone extends to antero-labial edge of the tooth; protoloph II connected with posterior arm of protocone; metaloph connected with hypocone; long, low mesoloph, constricted before reaching mesostyle at the labial boarder; posteroloph long and pronounced, contacts the basal part of metacone.

M2 similar to M1; labial anteroloph long, lingual anteroloph absent; protoloph I strong, connects the anterior arm of protocone; protoloph II short; metaloph connected with hypocone; mesoloph long, ends in a mesostyle; posteroloph long; labial fossettes narrow, sinus directed forward.

Description paratypes and additional material (Figs 6/2–18):

P4–M2 similar to holotype. Anterior arm of protocone of M1 variable: short with paracone-contact (morphotype 1), or long, reaching the labial tooth wall (morphotype 2), and many variations in between; morphotype 1 sometimes (20 % of specimens) occurs in

Fig. 6. *Heosminthus borrae* nov. spec. from the Valley of Lakes in Mongolia. Early Oligocene (biozone B) to Early Miocene (biozone D). All specimens in the NHMW collection. **1**: Right P4–M2; holotype (NHMW2013/0117/0001) from Unkheltsg (UNCH-A/3B; biozone B). **2**: right M1 (NHMW 2013/0127/0001) from Huch Teeg (RHN-A/12; biozone D). **3**: left M2 (NHMW 2013/0127/0002) from Huch Teeg (RHN-A/12; biozone D). **4**: right M3 (NHMW 2013/0127/0003) from Huch Teeg (RHN-A/12; biozone D). **5**: right M1 (NHMW 2013/0117/0002) from Unkheltsg (UNCH-A/3B; biozone B). **6**: left M1 (NHMW 2013/0117/0003) from Unkheltsg (UNCH-A/3B; biozone B). **7**: left M2 (NHMW 2013/0117/0004) from Unkheltsg (UNCH-A/3B; biozone B). **8**: right M3 (NHMW 2013/0117/0005) from Unkheltsg (UNCH-A/3B; biozone B). **9**: left M3 (NHMW 2013/0117/0006) from Unkheltsg (UNCH-A/3B; biozone B). **10**: right m1–2 (NHMW 2013/0117/0007) from Unkheltsg (UNCH-A/3B; biozone B). **11**: right m1 (NHMW 2013/0117/0008) from Unkheltsg (UNCH-A/3B; biozone B). **12**: left m2 (NHMW 2013/0117/0009) from Unkheltsg (UNCH-A/3B; biozone B). **13**: right m1–3 (NHMW 2013/0127/0004) from Huch Teeg (RHN-A/12; biozone D). eclsd = etostylid. **14**: right m1 (NHMW 2013/0117/0010) from Unkheltsg (UNCH-A/3B; biozone B). **15**: left m2 (NHMW 2013/0117/0011) from Unkheltsg (UNCH-A/3B; biozone B). **16**: right Inc. sup. (NHMW 2013/0127/0005) from Huch Teeg (RHN-A/12; biozone D). **17**: right m3 (NHMW 2013/0117/0012) from Unkheltsg (UNCH-A/3B; biozone B). **18**: right m3 (NHMW 2013/0117/0013) from Unkheltsg (UNCH-A/3B; biozone B). ▶



the Early Oligocene, morphotype 2 dominates in the Late Oligocene and Early Miocene; protoloph II of M2 can be short or absent; mesoloph can be constricted before reaching the mesostyle or the labial border; mesostyle can be absent; entoloph continuous, never interrupted.

M3 of variable pattern; smallest of upper molars, but similar to M2; sinus can be closed (lingual connection of protocone and hypocone); or sinus and fossette II are continuous (interrupted entoloph).

m1 rectangular in outline; narrow in its anterior part; four main cuspids, four distinct high lophids, narrow fossettids; anteroconid present; anteroconid continuous with a lingual cingulid (~ 50%); metalophid high and V-shaped; longitudinal or oblique ectolophid connected with protoconid or its basal part; mesolophid long, slightly directed forward, sometimes ending in small mesostylid, or constricted before reaching the mesostylid; hypolophid connected with anterior arm of hypoconid; posterolophid strong, with or without hypoconulid; mesoconid present in most specimens; frequently ectostylid at the basis of the flat sinusid.

m2 similar to m1 except for its anterior part; lingual anterolophid strong, short, as high as lingual lophids; labial anterolophid low, extends to the basal part of protoconid; posterior arm of protoconid absent or very short; mesolophid long.

m3 narrow in its posterior part; smallest lower molar; dental pattern similar to m2.

Root numbers: M1–3 have three roots (two labial, one lingual), m1–3 have three roots.

Upper incisors with flat anterior surface (no longitudinal groove!).

Remarks: *Heosminthus borrae* and *Heosminthus primiveris* are two very small *Heosminthus* species. The older one, *Heosminthus primiveris*, displays the most primitive dental characters, *i.e.*, low-crowned, bunodont molars (Wang 1985). *Heosminthus borrae* developed advanced dental structures (molars higher and moderately lophodont) and is thought to be the immediate descendant of the former. Stratigraphically, *Heosminthus*

Table 4. Measurements of *Heosminthus borrae*.

	length (mm)			width (mm)	
	range	mean	N = 123	range	mean
P4	0.40 – 0.42		2		
M1	0.87 – 1.06	0.97	30/29	0.80 – 0.99	0.92
M2	0.82 – 1.01	0.92	19	0.80 – 0.99	0.89
M3	0.64 – 0.78	0.71	21	0.66 – 0.85	0.74
m1	0.94 – 1.11	1.04	31	0.71 – 0.94	0.79
m2	0.87 – 1.06	0.98	14/13	0.87 – 0.94	0.85
m3	0.73 –0.82	0.80	10	0.66 – 0.75	0.69

borrae ranges from the Early Oligocene (biozone B) to the Early Miocene (biozone D). It is the only *Heosminthus* species that survived the Oligocene-Miocene transition. *Heosminthus borrae*, *Bohlinosminthus parvulus* and *Plesiosminthus promyarion* are the smallest Asian Dipodidae species of the Late Oligocene and Early Miocene.

***Heosminthus chimidae* nov. spec.**

(Figs 7/1–18, Tab. 5)

Derivatio nominis: In honor to U. CHIMID, Mongolian member of the field-team.

Type locality: Taatsiin Gol, Uvurkhangai, Mongolia; fossil layer TGR-B/1, silty clay of the Hsanda Gol Fm., Early Oligocene, biozone B.

Holotype (Fig. 7/1): Left fragmentary maxilla with P4–M2 (NHMW 2013/0128/0001). Measurements: P4 = 0.52 × 0.52 mm, M1 = 1.22 × 1.13 mm, M2 = 1.18 × 1.13 mm.

Paratypes (Figs 7/2–18): 160 fragmentary jaws, isolated molars and premolars from the type locality TGR-B/1(NHMW 2013/0128/0002–0161).

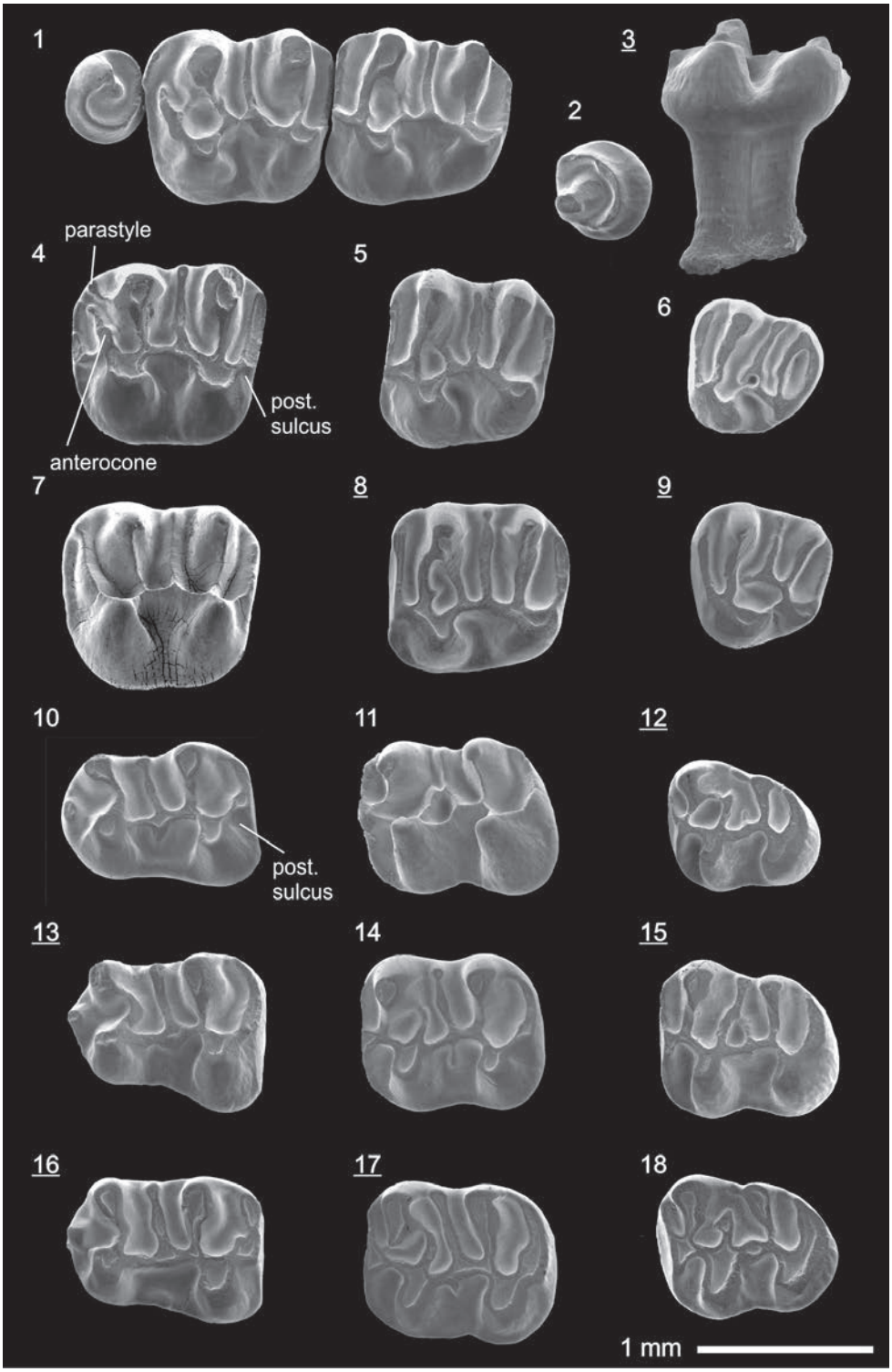
Additional material studied:

Early Oligocene (biozone A):

- Tatal Gol: TAT- D/1: > 250 jaws and isolated teeth (NHMW 2013/0129/0000); TAT-C/1–3: > 160 teeth (NHMW 2013/0130/0000).
- Tatal Gol: TGR-A/13+14: > 100 teeth (NHMW 2013/0131/0000); TGL-A/1+2: > 100 teeth (NHMW 2013/0132/0000).
- Unnamed locality: GRAB-II: 7 teeth (NHMW 2013/0133/0001–0007).
- Khongil: HL-A/1: 5 teeth (NHMW 2013/0134/0001–0005).
- Hsanda Gol: SHG-C/1–2: > 50 teeth (NHMW 2013/0135/0000).

Early Oligocene (biozone B):

- Taatsiin Gol: TGR-AB/21: > 200 jaws and isolated teeth (NHMW 2013/0136/0000) and numerous specimens (coll. MPC); TGR-AB/22: > 230 jaws and isolated teeth (NHMW 2013/0137/0000); TGR-ZO/1+2: > 40 isolated teeth (NHMW 2013/0138/0000); TGR-1564: 11 isolated teeth (NHMW 2013/0139/0000); TGR-B/1: numerous specimens (coll. MPC); TGL-A/11: 25 isolated teeth (NHMW 2013/0140/0000).
- Unkheltseg: UNCH-A/3B: > 140 jaws and isolated teeth (NHMW 2013/0141/0000).
- Del: DEL-B/7: > 120 jaws and isolated teeth (NHMW 2013/0142/0000).
- Tatal Gol: TAT-C/6+7: > 110 isolated teeth (NHMW 2013/0143/0000); TAT-E/3: 17 teeth (NHMW 2013/0144/0000); TAT-037, 039: 20 teeth (coll. MPC).
- Hsanda Gol: SHG-A/9: 18 teeth (NHMW 2013/0145/0001–0018); SHG-A/15: 13 teeth (NHMW 2013/0146/0001–0013); SHG-A/20: 58 teeth (NHMW 2013/0147/0000); SHG-A/15+20: 15 teeth (NHMW 2013/0148/0001–0015); SHG-AB/17+20: > 80 fragm. jaws and isolated teeth (NHMW 2013/0149/0000).



- Ikh Argalatyn Nuru: IKH-A/1–4: > 70 isolated teeth (NHMW 2013/0150/0000); IKH-B/2: 15 teeth (NHMW 2013/0151/0001–0015).

Late Oligocene (biozone C):

- Taatsiin Gol: TGR-C/1–2: 21 teeth (NHMW 2013/0152/0001–0021).
- Unzing Khurem: TAR-A/2: 6 teeth (NHMW 2013/0153/0001–0006).
- Abzag Ovo: ABO-A/3: 3 teeth (NHMW 2013/0154/0001–0003); ABO-083: 1 tooth (NHMW 2013/0155/0001).
- Tatal Gol: TAT-055: 20 teeth (NHMW 2013/0156/0001–0020). TAT-040: 2 teeth (coll. MPC); TAT-042: 1 lower jaw (coll. MPC).

Late Oligocene (biozone C1):

- Tatal Gol: TAT-043: 5 teeth (NHMW 2013/0157/0001–0005); TAT-E/22: 3 teeth (NHMW 2013/0158/0001–0003); TAT-051/2: 10 teeth (NHMW 2013/0160/0001–0010); 10 teeth (coll. MPC), TAT-1/2: 2 teeth (coll. MPC); TAT-054: 17 upper and lower jaws, 2 teeth (coll. MPC).

Oligocene-Miocene transition: (biozone C1–D):

- TAT-E/32: 1 tooth (NHMW 2013/0159/0001);

Diagnosis: Small-sized species; general dental pattern and root numbers in accordance with the genus; four main robust cusps; lophs short, thin and lower than cusps; valleys wide; anterior arm of protocone (M1) of varying length; anterior cingulum (M1) of variable shape, can be absent; M1 with protoloph II; M2 mostly with protolophs I+II; mesoloph(id) of M1–3(m1–3) long or of medium length; anteroconid of m1 present; m2: connection of posterior arm of protoconid and mesolophid or metaconid; posterolophid strong; hypoconulid and labial posterior sulcus present or absent.

Differential diagnosis: *Heosminthus chimidae* differs from the type species in being larger and having an increasingly more advanced dental pattern. It differs from *Heosminthus borrae* in being larger, having a more primitive dental pattern (robust cones, lower crests, wide fossettes), having both the protolophs I and II in M2, and having a strong posterior arm of the protoconid in m2. It differs from *Heosminthus* sp. in being smaller. It also differs from all species of *Plesiosminthus* by the smooth anterior

◀ Fig. 7. *Heosminthus chimidae* nov. spec. from the type locality Taatsiin Gol (TGR-B/1),Valley of Lakes in Mongolia. Early Oligocene (biozone B). The figured specimens are the holotype and paratypes from the NHMW collection. **1**: Left P4–M2; holotype (NHMW 2013/0128/0001). **2**: P4 (NHMW 2013/0128/0002). **3**: right M2 (NHMW 2013/0128/0003). **4**: left M1 (NHMW 2013/0128/0004). **5**: left M2 (NHMW 2013/0128/0005). **6**: left M3 (NHMW 2013/0128/0006). **7**: left M1 (NHMW 2013/0128/0007). **8**: right M2 (NHMW 2013/0128/0008). **9**: right M3 (NHMW 2013/0128/0009). **10**: left m1 (NHMW 2013/0128/0010). **11**: left m2 (NHMW 2013/0128/0011). **12**: right m3 (NHMW 2013/0128/0012). **13**: right m1 (NHMW 2013/0128/0013). **14**: left m2 (NHMW 2013/0128/0014). **15**: right m3 (NHMW 2013/0128/0015). **16**: right m1 (NHMW 2013/0128/0016). **17**: right m2 (NHMW 2013/0128/0017). **18**: left m3 (NHMW 2013/0128/0018).

surface of upper incisors, the strong anteroconid of m1, the more or less longitudinal ectolophid in m1, and the continuous entoloph in M1–2 (no interruption).

Description of the holotype (Fig. 7/1): Left fragmentary maxilla with P4–M2 (NHMW 2013/0128/0001).

P4: one cusp surrounded by posterior cingulum; one root.

M1: four main rounded cusps in opposing position; protoloph and metaloph short and low; anterior arm of protocone of medium length; short cingulum at the antero-labial edge of M1; very weak protoloph I contacts anterior arm of protocone; protoloph II connected with entoloph; mesoloph long, reaches labial border; short metaloph connected with hypocone; long, low posteroloph; sinus symmetrical; three roots.

M2: similar to M1; labial anteroloph long; lingual anteroloph absent; strong protoloph I connected with anterior arm of protocone; weak protoloph II connected with entoloph; metaloph connected with hypocone; mesoloph long; three roots.

Description of paratypes and additional material studied (Figs 7/2–18): M1 square in outline; anterior part of M1 with variable pattern: anterior arm of protocone can be long, of medium length or short; if short it can contact the paracone or the anterior cingulum, if long it can reach the antero-labial edge or the small parastyle; in rare cases it connects with a weak protoloph I; anterior cingulum can be labial or double, or can display an anterocone (= protoconule); protoloph I weak or absent; protoloph II strong, connected with entoloph; mesoloph long, can end in a mesostyle; metaloph connected with hypocone; posteroloph long, thin, can be constricted posterior to hypocone; sinus symmetrical or curved in anterior direction.

M2 square to rectangular in outline, with a more narrow posterior part; labial anteroloph long, strong; lingual anteroloph absent or weak; protoloph I strong, connected with anterior arm of protocone; protoloph II weak or absent, if present connected with entoloph; metaloph transverse, connected with hypocone or its anterior arm; mesoloph long, can end in small mesostyle; posteroloph long, thin, can be constricted close to hypocone; entoloph continuous; sinus curved in anterior direction.

Table 5. Measurements of *Heosminthus chimidae*.

	length (mm)			width (mm)	
	range	mean	N = 2456	range	mean
P4	0.42 – 0.68	0.58	235		
M1	0.96 – 1.25	1.14	433/437	0.87 – 1.22	1.05
M2	0.94 – 1.22	1.08	381	0.89 – 1.22	1.05
M3	0.68 – 1.01	0.80	213/209	0.64– 1.04	0.86
m1	0.96 – 1.36	1.20	444/448	0.73 – 1.13	0.89
m2	0.99 – 1.34	1.19	457/453	0.71 – 1.20	0.93
m3	0.78 –1.29	1.03	285/282	0.68 – 1.01	0.84

M3 of variable pattern; smallest of upper molars, but similar to M2; cones can be fused with lophs; sinus can be closed, when protocone and hypocone are connected lingually; or sinus and fossette II are continuous, when entoloph is interrupted; M3 does not display species-characters.

m1 rectangular in outline with narrow anterior part; four main cuspids, four distinct lophids; anteroconid pronounced, in most cases isolated, rarely connected with low anterior cingulid; metalophid U-or V-shaped; hypolophid short, connected with anterior arm of hypoconid; mesolophid long, slightly directed forward, ending with or without mesostylid; mesoconid strong; posterolophid long, frequently continuous to top of entoconid; hypoconulid and sulcus posterior to hypoconid can be present or absent; entolophid longitudinal or slightly oblique; ectolophid in very rare cases constricted or interrupted close to protoconid; sinusid wide; ectostylid present or absent.

m2 rectangular in outline; four main cuspids, lingual ones drop-shaped, labial ones more voluminous; lingual and labial anterolophid more or less equal; metalophid I and anterior arm of protoconid connected with anteroconid; posterior arm of protoconid connected with metaconid or to mesolophid; mesolophid long; hypolophid connected with anterior arm of hypoconid; shape of posterolophid, hypoconulid and posterior sulcus similar to m1; mesoconid stronger than mesostylid; ectolophid in longitudinal direction.

m3 similar to m2, but narrow in its posterior part; double anterolophid, metalophid I, hypolophid and posterolophid present; length and connections of posterior arm of protoconid and mesolophid extremely variable.

Upper molars have three roots, lower molars have two roots. Upper and lower incisors have ungrooved anterior surface.

Remarks: *Heosminthus chimidae* ranges in Mongolia from the Early Oligocene to the Late Oligocene. Only one isolated tooth was recovered from the Oligocene-Miocene transition (TAT-E/32). *Heosminthus chimidae* dominates over all other Dipodidae for almost ten million years. There is, however, a wide variability of dental morphology and size. Specifically at the beginning of the Early Oligocene, different morphotypes co-occur within one fauna: they range from small, primitive specimens of the *Heosminthus primiveris*-type to specimens as large as *Heosminthus* sp., and many intermediate morphotypes are present. Finally, three independent species established in the course of the late Early Oligocene: *Heosminthus borrae*, *Heosminthus chimidae* and *Heosminthus* sp.

***Heosminthus* sp.**

(Figs 8/1–8, Tab. 6)

Occurrences of *H.* sp. in Mongolia (Valley of Lakes, Uvurkhangai): Oligocene.

Material studied:

Early Oligocene (biozone A):

- Tatal Gol: TAT-D/1: 2 M1l (NHMW 2013/0161/0001–0002).
- Taatsiin Gol: TGR-A/13: 1 lower jaw with m1–2 (NHMW 2013/0162/0001).

Early Oligocene (biozone B):

- Taatsiin Gol: TGR-B/1: 2 M1l (NHMW 2013/0163/0001–0002).
- Unkheltseg: UNCH-A/3B: 1 M1l, 2 m2r, 1 m2l (NHMW 2013/0164/0001–0004).
- Tatal Gol: TAT-E/3: 1 M1r (NHMW 2013/0165/0001); TAT-C/6, 7: 1 M1l, 1 M1r, 1 m1l (NHMW 2013/0166/0001–0003).
- Hsanda Gol: SHG-A/20: 1 M1l, 1 M3l, 1 m2r, 3 P (NHMW 2013/0167/0001–0003); SHG-AB/17+20: 1 M1l, 2 M2l, 1 m1l, 1 m2–3l, 1 m3l, 2 P4 (NHMW 2013/0168/0001–0007).
- Ikh Argalatyn Nuru: IKH-A/1, 3+4: 1 P4, 1 M1l, 1 m1l, 1 m2r (NHMW 2013/0169/0001–0004).
- Del: DEL-B/7: 1 M1r (NHMW 2013/0170/0001).

Late Oligocene (biozone C):

- Toglorhoi: TGW-A/2a, 2b: 1 m3l, 2 m1l (NHMW 2013/0171/0001–0003).
- Tatal Gol: TAT-055: 1 M1–2r, 1 M2l, 1 M2r, 1 m2l (NHMW 2013/0172/0001–0004).

Late Oligocene (biozone C1):

- Tatal Gol: TAT-043: 1 maxilla with M1–3l, 1 M1r, 3 m1l, 1m2l, 1 m3l (NHMW 2013/0173/0001–0007).

Remarks: *Heosminthus* sp. is larger than *Heosminthus chimidae*, *Heosminthus borrae* and the type species *Heosminthus primiveris*, but dental characters are within the variability of *Heosminthus borrae*. Since there are no significant morphological differences, we refrain from describing a new species. Some molars (specifically from the Late Oligocene; TAT-043, TAT-55; Fig. 8/1, 3–4, 8) resemble *Heosminthus* sp. as well as *Plesiosminthus asiaticus*. However, grooved upper incisors are not documented from the respective fossil sites, therefore determination has to be *Heosminthus* sp.

Genus *Plesiosminthus* Viret, 1926

Type species: *Plesiosminthus schaubi* Viret, 1926

Table 6. Measurements of *Heosminthus* sp.

	length (mm)			width (mm)	
	range	mean	N = 39	range	mean
P4	0.66 – 0.71	0.68	3		
M1	1.27 – 1.39	1.31	12	1.18 – 1.34	1.23
M2	1.22 – 1.29	1.26	4	1.11 – 1.32	1.24
M3		0.94	1		0.99
m1	1.39 – 1.46	1.43	7/6	0.99 – 1.13	1.05
m2	1.36 – 1.48	1.41	9	1.01 – 1.18	1.11
m3	1.22 –1.29	1.25	3	1.01 – 1.04	1.02

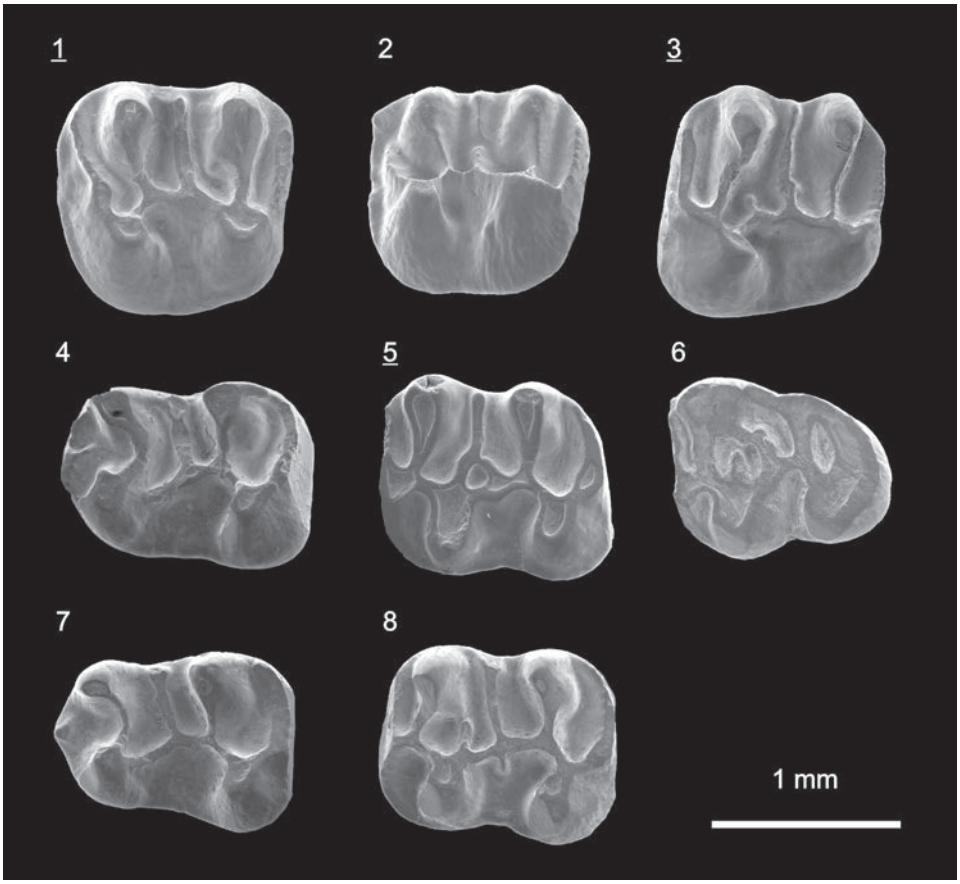


Fig. 8. *Heosminthus* sp. from the Valley of Lakes in Mongolia. Early Oligocene (biozone B) to Late Oligocene (biozone C1). All specimens from the NHMW collection. **1**: right M1 (NHMW 2013/0173/0001) from Tatal Gol (TAT-043), Late Oligocene (biozone C1). **2**: left M1 (NHMW 2013/0169/0001) from Ikh Argalatyn Nuruu (IKH-A/1), Early Oligocene (biozone B). **3**: right M2 (NHMW 2013/0172/0001) from Tatal Gol (TAT-055), Late Oligocene (biozone C). **4**: left m1 (NHMW 2013/0173/0002) from Tatal Gol (TAT-043), Late Oligocene (biozone C1). **5**: right m2 (NHMW 2013/0169/0002) from Ikh Argalatyn Nuruu (IKH-A/3+4), Early Oligocene (biozone B). **6**: left m3 (NHMW 2013/0173/0003) from Tatal Gol (TAT-043), Late Oligocene (biozone C1). **7**: left m1 (NHMW 2013/0171/0001) from Toglorhoi (TGW-A/2a), Late Oligocene (biozone C). **8**: left m2 (NHMW 2013/0172/0002) from Tatal Gol (TAT-055), Late Oligocene (biozone C).

Dental characters: Upper incisors with a longitudinal groove along the anterior surface [in accordance with the diagnose of Schaub (1930: 618)]; small bunodont molars; M1–2 almost square, mesoloph long; M1 with protoloph II; M2 with protoloph I + II, metaloph connected with anterior arm of hypocone, entoloph-protocone connection and hypocone-posteroloph connection frequently constricted or interrupted; mesolophid of m1–2 long; ectolophid of m1 oblique, frequently curved, connected with basal part of protoconid; M1–3 with three roots, m1–3 with two roots.

Referred species/type localities from Eurasia are:

- *P. asiaticus* Daxner-Höck & Wu, 2003 from Tiheersihabahe, Loc.98035 (China); Late Oligocene.
- *P. barsboldi* Daxner-Höck & Wu, 2003from Unkheltseg (Mongolia); Early Miocene (biozone D).
- *P. conjunctus* Ziegler, 1994 from Herrlingen 8 (Germany); Late Oligocene (MP 28).
- *P. moralesi* Alvarez-Sierra *et al.*, 1996 from Sayaton I (Spain); Late Oligocene (MP 29).
- *P. myarion* Schaub, 1930 from Chavroches (France); Early Miocene (MN 1).
- *P. olzi* nov. spec. from Hotuliin Teeg (Mongolia); Early Miocene (biozone D).
- *P. promyarion* Schaub, 1930 from Rickenbach (Switzerland); Late Oligocene (MP 29).
- *P. schaubi* Viret, 1926 from Saint- Gérand-le-Puy (France); Late Oligocene.
- *"P." tereskentensis* Lopatin, 1999 from Altynshokysu, bone bed I (Kazakhstan); Late Oligocene (= Early Miocene according to Lopatin 1999).
- *"P." vegrandis* Kimura, 2010 from Gashunyinadege (China); Early Miocene.
- *P. winistoerferi* Engesser, 1987 from Brochene Fluh (Switzerland); Late Oligocene (MP 30).

Remarks: We agree with Wang (1985: 363) that "*Plesiosminthus" huangshuiensis*, "*Plesiosminthus" xiningensis* and "*Plesiosminthus" lajeensis* (Li & Qiu 1980) have to be excluded from the genus *Plesiosminthus* because of significant morphological differences (*e.g.*, four roots of upper molars, smooth anterior surface of upper incisors). So far no upper incisors are known for "*Plesiosminthus" tereskentensis* Lopatin, 1999 and "*Plesiosminthus" vegrandis* Kimura, 2010, therefore their genus-attribution is still uncertain.

The first occurrences of *Plesiosminthus* are from the Late Oligocene of China, Mongolia and Europe. Its immediate ancestors are unknown, but *Plesiosminthus* probably descended from *Heosminthus* (Wang 1985; Daxner-Höck & Wu 2003) because it shares size and main dental features with *Heosminthus*: small to medium-sized bunodont molars, ± square M1–2 with 3 roots, opposing position of labial and lingual cones (ids) and the number and direction of loph(id)s. Other than *Heosminthus*, *Plesiosminthus* developed a grooved upper incisor. As outlined above, *Heosminthus* was the most abundant rodent of the Early Oligocene in Mongolia, and from that time-interval exclusively upper incisors with smooth anterior surface are known. The first rare findings (1–2 fragments) of incisors with a shallow longitudinal groove were made in faunas of the Late Oligocene (TAR-A/2; biozone C; LOH-C/1 and RHN-A/7; biozone C1; Daxner-Höck & Wu 2003). In younger faunas, the number of grooved upper incisors increased along with the number of *Plesiosminthus*-molars. Simultaneously, *Heosminthus* and *Bohlinosminthus* decreased drastically and finally became extinct, while *Plesiosminthus*, *Litodonomys* and *Heterosminthus* developed rapidly.

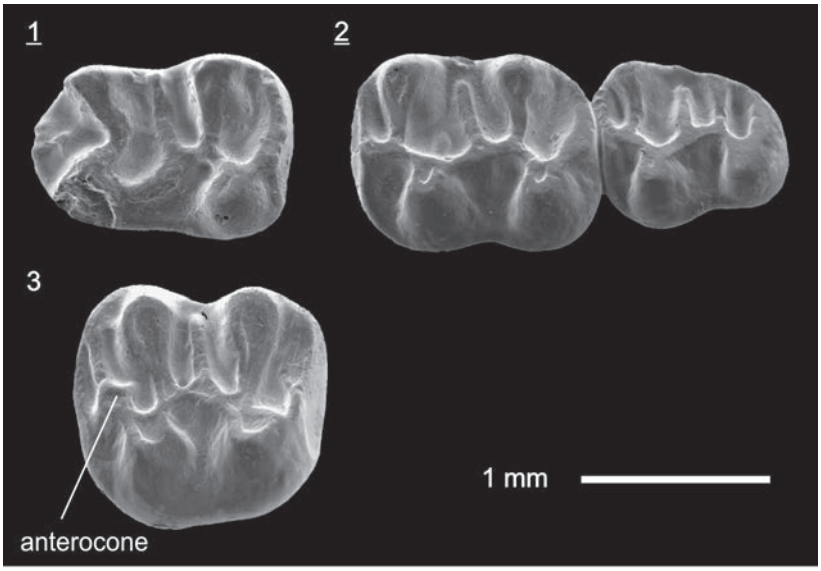


Fig. 9. *Plesiosminthus asiaticus* DAXNER-HÖCK & WU, 2003 from Huch Teeg (RHN-A/7), Valley of Lakes in Mongolia, Late Oligocene (biozone C1). All specimens from the NHMW collection. **1**: right m1 (NHMW 2001/0064/0001/7), AO (DAXNER-HÖCK & WU 2003: fig. 7/7). **2**: right m2–3 (NHMW 2001/0064/0001/9), AO (DAXNER-HÖCK & WU 2003: fig. 7/9). **3**: left M1 (NHMW 2001/0064/0001/2), AO (DAXNER-HÖCK & WU 2003: fig. 7/2).

Plesiosminthus asiaticus DAXNER-HÖCK & WU, 2003

(Figs 9/1–3, Tab. 7)

1999 *Plesiosminthus* sp. 1. – HÖCK *et al.*: 118.
2003 *Plesiosminthus* cf. *asiaticus*. – DAXNER-HÖCK & WU: 137–140, fig. 7/1–9.
2007 *Plesiosminthus* cf. *asiaticus*. – DAXNER-HÖCK & BADAMGARAV: 17, Tab. 3.
2010 *Plesiosminthus* cf. *P. asiaticus*. – DAXNER-HÖCK *et al.*: 358, fig. 6/10–12.

Type locality: Tieersihabahe, loc. 98035, T1; North Junggar Basin (China); Late Oligocene.

Table 7. Measurements of *Plesiosminthus asiaticus*.

	length (mm)			width (mm)	
	range	mean	N = 9	range	mean
P4		0.65	1		0.65
M1	1.30 – 1.35		2		1.30
M2	1.15 – 1.30		2	1.20 – 1.25	
m1		1.25	1		0.90
m2	1.20 – 1.30		2		1.10
m3		1.05	1		0.90

Occurrences of *Plesiosminthus asiaticus* in Mongolia (Valley of Lakes, Uvurkhangai): Late Oligocene (biozone C1).

Material studied:

Huch Teeg: RHN-A/7: The correct name of the locality is Huch Teeg (="Tavan Ovoony Deng" in Daxner-Höck &Wu 2003); Inc. sup., 1 jaw with m 2–3, 7 molars (NHMW 2001/0064/0001/1–9).

Description: Daxner-Höck & Wu (2003: 137–140; fig. 7/1–9).

Remarks: *Plesiosminthus asiaticus* is documented in Mongolia by a few molars and grooved upper incisors, which are in good agreement with *Plesiosminthus asiaticus* from the Junggar Basin (China). *Plesiosminthus asiaticus* from the Late Oligocene and *Plesiosminthus barsboldi* from the Early Miocene are largest of the Mongolian species.

Plesiosminthus promyarion Schaub, 1930

(Figs 10/1–7, Tab. 8)

1999 *Plesiosminthus* sp. 2. – Höck *et al.*: 118.
2003 *Plesiosminthus promyarion*. – Höck & Wu: 140–142, figs. 8/1–9.
2007 *Plesiosminthus promyarion*. – Daxner-Höck & Badamgarav: 17, Tab. 3.
2010 *Plesiosminthus promyarion*. – Daxner-Höck *et al.*: 358, fig. 6/7–9.

Type locality: Rickenbach (Switzerland), Late Oligocene (MP 29).

Occurrences of *Plesiosminthus promyarion* in Mongolia (Valley of Lakes, Uvurkhangai): Late Oligocene to Oligocene-Miocene transition (C1 to C1–D).

Material studied:

Late Oligocene (biozone C1):

- Huch Teeg: RHN-A/9: 12 fragmentary I sup., 15 fragmentary I inf., 1M1r, 2 m1l, 1 m1r, 2 m2l (NHMW 2001/0065/0001–0009) Daxner-Höck &Wu (2003: 140); RHN-019: 2 Inc. sup., 1 M1l, 1 m1r (NHMW 2013/0174/0001–0004).

Table 8. Measurements of *Plesiosminthus promyarion*.

	length (mm)			width (mm)	
	range	mean	N = 18	range	mean
M1	1.06 – 1.13	1.10	5	0.99 – 1.11	1.02
M2	1.08 – 1.15		3	1.01 – 1.15	
m1	1.13 – 1.27	1.20	7	0.75 – 0.96	0.89
m2	1.11 – 1.18	1.15	4	0.87 – 0.99	0.90
m3		0.99	1		0.89

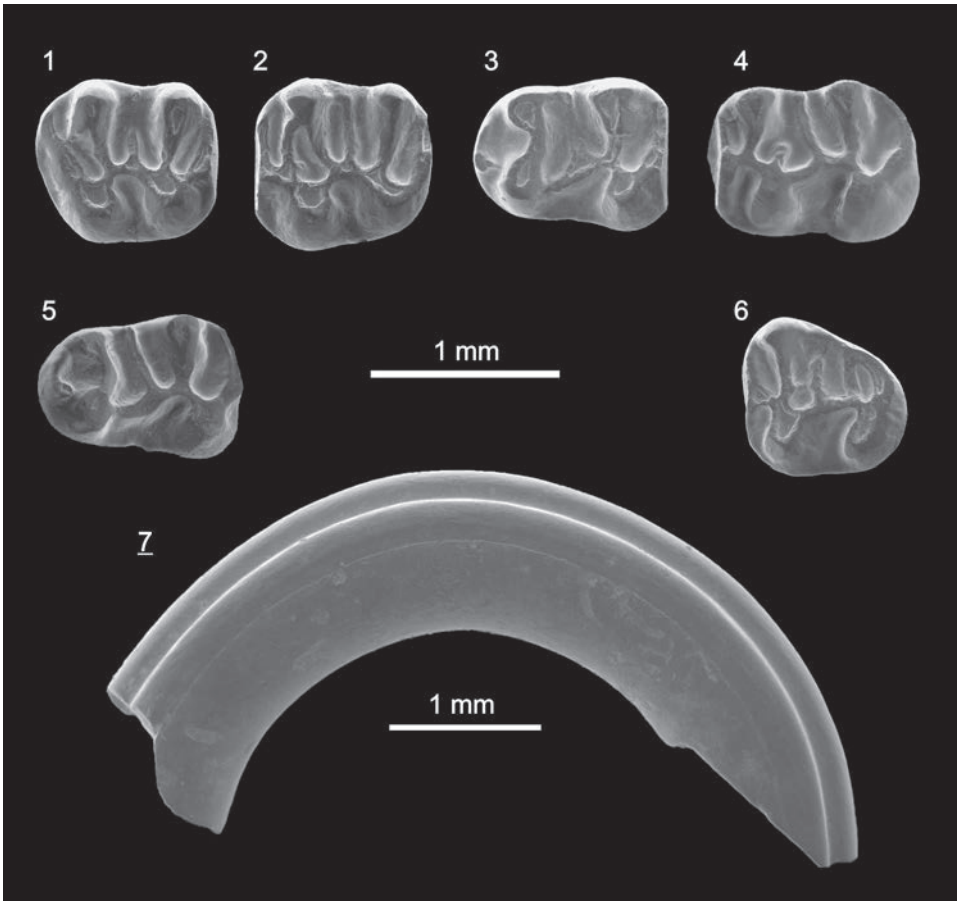


Fig. 10. *Plesiosminthus promyarion* SCHAUB, 1930 from Huch Teeg (RHN-A/9; Late Oligocene, biozone C1) and Hotuliin Teeg (HTS-056/2; Oligocene-Miocene transition, biozone C1–D), Valley of Lakes in Mongolia. All specimens from the NHMW collection. **1**: left M1 (NHMW 2013/0175/0001) from Hotuliin Teeg (HTS-056/2). **2**: left M2 (NHMW 2013/0175/0002) from Hotuliin Teeg (HTS-056/2). **3**: left m1 (NHMW 2013/0175/0003) from Hotuliin Teeg (HTS-056/2). **4**: left m2 (NHMW 2001/0065/0001/8) from Huch Teeg (RHN-A/9), AO (DAXNER-HÖCK & WU 2003: fig. 8/8). **5**: right m1 (NHMW 2001/0065/0001/7) from Huch Teeg (RHN-A/9), AO (DAXNER-HÖCK & WU 2003: fig. 8/7). **6**: left m3 (NHMW 2013/0175/0004) from Hotuliin Teeg (HTS-056/2). **7**: right Inc. sup. (NHMW 2013/0175/0005) from Hotuliin Teeg (HTS-056/2).

Oligocene-Miocene transition (biozone C1–D):

- Hotuliin Teeg: HTS-056/1+2: Inc. sup., 1 M1r, 1 M1l, 1 M2l, 1 m1l, 1 m2l, 1 m3l (NHMW 2013/0175/0001–0007); 1 M1l, 1 M2 r, 2 m1l, 2 Inc. sup (coll. MPC).

Description: Upper incisors with a deep longitudinal groove; small brachyodont molars.

M1: anterior arm of protocone long or almost so, and contacting the weak labial cingulum or parastyle; protoloph II connects with posterior arm of protocone; mesoloph long or of medium length; mesostyle and mesocone weak or absent; metaloph connects with hypocone or its anterior arm; posteroloph constricted posterior to hypocone; posterior lingual sulcus present or absent; entoloph continuous; sinus slightly turned forward.

M2: resembles M1; labial anteroloph pronounced, lingual anteroloph weak or absent; protoloph strong, connected with anterior arm of protocone; protoloph II absent or connected with entoloph; mesoloph long; metaloph connected with anterior arm of hypocone; sinus slightly directed forward.

m1: anteroconid weak, mostly continuous with small anterolophid or with protoconid; metalophid U-shaped; mesolophid long, right-angled with oblique ectolophid; ectolophid curved and connected with postero-labial base of protoconid (6 specimens), or almost longitudinal and connected with posterior part of protoconid; hypolophid connected with anterior arm of hypoconid; posterolophid long; hypoconulid weak; sinusid directed backward.

m2: rectangular in outline; four main cuspids, lingual ones drop-shaped, labial ones more voluminous; lingual and labial anterolophid more or less equal; metalophid I connected with anterior arm of protoconid; posterior arm of protoconid short, with free end; mesolophid long, right-angled with oblique ectolophid; hypolophid connected with anterior arm of hypoconid; posterolophid long; hypoconulid weak; sinusid directed backward.

m3: anterolophid double; entoconid absent; metalophid connected with protoconid; mesolophid almost long, in its middle part connected with metalophid by a weak longitudinal crest; hypolophid short; posterolophid long.

M1–with three roots, m1–3 with two roots.

Remarks: So far, *Plesiosminthus promyarion* is the smallest *Plesiosminthus* species of Mongolia. It resembles "*Plesiosminthus" tereskentensis* and *Heosminthus chimidae* in dental characters and size. It can be distinguished from *Heosminthus chimidae* by: grooved upper incisors, the ectolophid of m1 (oblique, frequently curved and connected with the posterior basal part of protoconid), and the short posterior arm of protoconid of m2. The upper incisors of "*Plesiosminthus" tereskentensis* are not known, therefore genus-attribution is still uncertain.

Three fossil horizons – dated as latest Oligocene (C1) and Oligocene-Miocene transition (C1–D) – yielded *Plesiosminthus promyarion* in Mongolia. This species is known from all over Europe (Germany, Switzerland, France, Spain; Daxner-Höck & Wu 2003: 142). There, its stratigraphic range is restricted to the Late Oligocene (MP28–29) (Engesser 1987; Engesser & Mödden 1997; Hugueney 1997; Freudenthal 1997; Kristkoiz 1992; Hugueney & Vianey-Liaud 1980).

Plesiosminthus olzi nov. spec.

(Figs 11/1–11, Tab. 9)

Derivatio nominis: In honor to L. OLZIBAATAAR, member of the Mongolian field-team.

Type locality: Hotuliin Teeg, Uvurkhangai, Mongolia; fossil layers HTE-008 and HTS-005, silty clay of the Loh Fm., Early Miocene (biozone D).

Holotype (11/1): Left M1 (NHMW 2013/0176/0001) from HTE-008. Measurements: M1 = 1.22 × 1.18 mm.

Paratypes (11/2–11): HTE-008: 2 Inc. sup., 2 M1r, 1 M2l, 1 M2r, 1 M3r, 1 m1l, 1 m2–3l, 2 m3l (NHMW 2013/0176/0002–0012); HTE-005: Inc. sup., 1 M2r, 1 M2l, 1 m1l, 1 m2l (NHMW 2013/0177/0001–0004).

Additional material studied:

Early Miocene (biozone D):

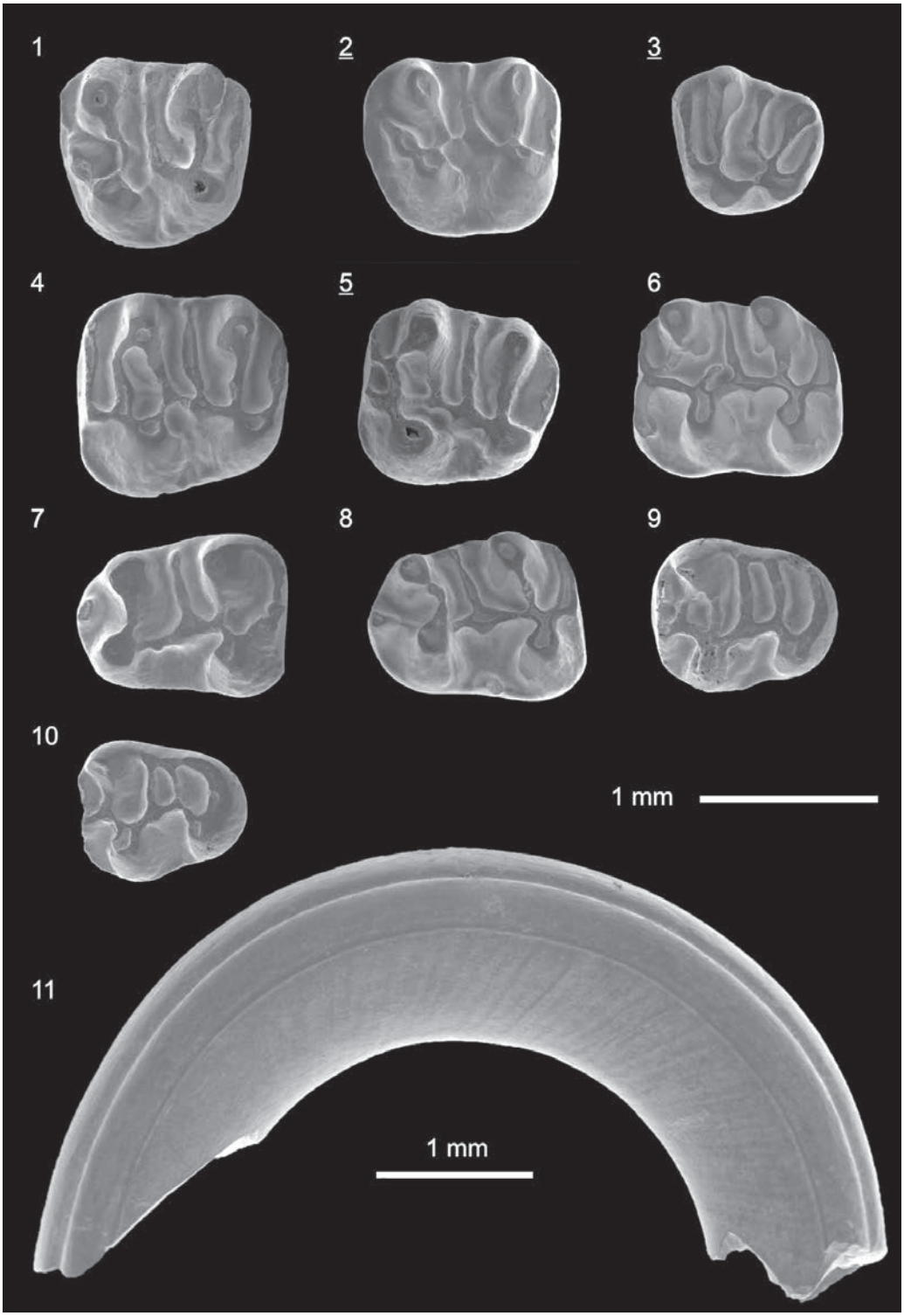
- Hotuliin Teeg: HTE-014–018: 5 Inc. sup., 1 P4, 1 M1r, 1 M2r, 2 m1l, 1 m2–3l, 1 m2l, 1 m3l (coll. MPC).

Diagnosis: Small-sized species; upper incisor with longitudinal groove; rugose enamel structure of molars; occlusal outline of M1–2 almost square; four main robust cusps; loph(id)s robust and almost as high as cusp(id)s; valleys narrow; entoloph of M1–2 constricted or interrupted anterior to mesoloph-connection; anterior part of sinus of M1–2 narrowed or cut off by a low crest, that extends from the posterior slope of protocone toward mesocone; M1 with long anterior arm of protocone, with pronounced anterocone (= protoconule) and with protoloph II; M2 with protolophs I+II, protoloph II less strong than protoloph I; mesoloph(id) of M1–3 (m1–3) long; mesocone(id) present; anteroconid of m1present; posterior arm of protoconid of m2 connected with mesolophid; posterolophid of m1–2 strong, hypoconulid and labial posterior sulcus frequently present.

Differential diagnosis: *Plesiosminthus olzi* has smaller molars than *Plesiosminthus asiaticus*, *Plesiosminthus barsboldi*, *Plesiosminthus winistoerferi* and

Table 9. Measurements of *Plesiosminthus olzi*.

	length (mm)			width (mm)	
	range	mean	N = 21	range	mean
M1	1.15 – 1.22		3	1.06 – 1.18	1.08
M2	1.15 – 1.29	1.21	5	1.08 - 1.27	1.17
M3		0.94	1		0.92
m1	1.13 – 1.39	1.26	4	0.82 – 1.06	0.95
m2	1.06 – 1.34	1.20	4	0.85 – 1.13	0.98
m3	0.87 – 1.13	1.02	4	0.82 – 0.96	0.89



Plesiosminthus schaubi, but larger teeth than *Plesiosminthus promyarion*, "*Plesiosminthus*" *vegrandis* and "*Plesiosminthus*" *tereskentensis*. Tooth sizes are comparable with *Plesiosminthus conjunctus*, *Plesiosminthus moralesi* and *Plesiosminthus myarion*, however, molar-structures of *Plesiosminthus olzi* are more complicated (wrinkled enamel surface, high and voluminous cusps and crests, narrow valleys). Concerning dental pattern *Plesiosminthus olzi* is transitional between *Plesiosminthus promyarion* and *Plesiosminthus barsboldi*. It is more progressive than *Plesiosminthus promyarion* by sharing some advanced dental characters with *Plesiosminthus barsboldi*: high cusps and crests, narrow valleys, entoloph of M1–2 frequently constricted or interrupted before reaching protocone, ectolophid of m1–3 mostly longitudinal. However, it differs from *Plesiosminthus barsboldi* by slightly smaller and less lophodont molars, by the wrinkled enamel, the pronounced protoconule of M1, by rather short M3/m3 and a shorter posterior arm of protoconid of m2–3.

Description of the holotype (Fig. 11/1): Left M1 (NHMW 2013/0176/0001). Wrinkled enamel surface; occlusal outline almost square, anterior wider than posterior; four robust cusps in opposing position; tooth crown relatively high; long anterior arm of protocone with pronounced anterocone (= protoconule) and small crest directed toward base of paracone; pronounced oblique protoloph II connected with posterior arm of protocone; long mesoloph ending in a small mesostyle; transverse metaloph connected with anterior part of hypocone; posteroloph constricted posterior to hypocone; entoloph interrupted anterior to mesocone-mesoloph connection; narrow sinus constricted between posterior slope of protocone and small mesocone; narrow fossettes; three roots.

Description of paratypes and additional material studied: Upper incisor with pronounced longitudinal groove (Fig. 11/11).

M1 (Fig. 11/2) resemble the holotype except for: less complicated pattern of anterior part; constricted, but not interrupted entoloph and sinus.

M2 (Fig. 11/4–5): square in occlusal outline, widest in its anterior part; lingual and labial anteroloph; protoloph I and protoloph II; protoloph I can be connected with labial anteroloph; protoloph II connected with entoloph; long mesoloph; mesostyle smaller than mesocone; transverse metaloph connected with hypocone or its anterior arm; posteroloph constricted posterior to hypocone; entoloph can be constricted or interrupted before

◀ Fig. 11. *Plesiosminthus olzi* nov. spec. from the type locality Hotuliin Teeg (HTE-005 and HTE-008), Valley of Lakes in Mongolia, Early Miocene (biozone D). All specimens are the holotype and paratypes from the NHMW collection. **1**: left M1, holotype (NHMW 2013/0176/0001) from HTE-008. **2**: right M1 (NHMW 2013/0176/0002) from HTE-008. **3**: right M3 (NHMW 2013/0176/0003) from HTE-008. **4**: left M2 (NHMW 2013/0176/0004) from HTE-008. **5**: right M2 (NHMW 2013/0176/0005) from HTE-008. **6**: left m2 (NHMW 2013/0177/0001) from HTE-005. **7**: left m1 (NHMW 2013/0176/0006) from HTE-008. **8**: left m1 (NHMW 2013/0177/0002) from HTE-005. **9**: left m3 (NHMW 2013/0176/0007) from HTE-008. **10**: left m3 (NHMW 2013/0176/0008) from HTE-008. **11**: left Inc. sup. (NHMW 2013/0176/0009) from HTE-008.

reaching protocone; very weak connection of entoloph and anteroloph (Fig. 11/5); narrow sinus (similar to holotype); three roots.

M3 (Fig. 11/3): smallest tooth; five lophs (labial anteroloph, protoloph II, mesoloph, metaloph, posteroloph); mesoloph connected with metaloph; labial cones lophodont; entoloph interrupted; sinus closed; three roots.

m1 (Fig. 11/7–8): anterolophid isolated or connected with protoconid; ectolophid straight and longitudinal (Fig. 118) or slightly oblique (Fig. 11/7); mesolophid long; metalophid curved; hypolophid connected with anterior arm of hypoconid; strong posterolophid; sinusid wide; ectostylid can be present; two roots.

m2 (11/6): labial and lingual anterolophid; metalophid I connected with anterolophid; short posterior arm of protoconid (almost) connected with mesolophid; long mesolophid; hypolophid connected with anterior arm of hypoconid; lingual arm of posterolophid strong, labial arm weak; sinusid symmetrical; two roots.

m3 (11/9–10): relatively long; five to six lophids; posterior arm of protoconid present or absent; long mesolophid, hypolophid and posterolophid; two roots.

Remarks: *Plesiosminthus olzi* is documented by grooved upper incisors and some isolated molars from Early Miocene fossil layers of Hotuliin Teeg. The stratigraphic position of the respective fossil horizons is the lowermost Early Miocene, *i.e.*, above sites of *Plesiosminthus asiaticus* (RHN-A/7; Late Oligocene, biozone C1) and *Plesiosminthus promyarion* (RHN-A/9; biozone C1 and HTS-056/1+2; Oligocene-Miocene transition), but below the type locality of *Plesiosminthus barsboldi* (UNCH-A/3; Early Miocene, biozone D).

Plesiosminthus barsboldi Daxner-Höck & Wu, 2003

(Figs 12/1–3, Tab. 10)

1999 *Plesiosminthus* sp. 3. – Höck *et al.*: 118.
2003 *Plesiosminthus barsboldi*. – Höck & Wu: 142–146, figs 9/1–7, 10/1–12.

Table 10. Measurements of *Plesiosminthus barsboldi* (including data from Daxner-Höck & Wu 2003: 149, Tab. 2).

	length (mm)			width (mm)	
	range	mean	N = 23	range	mean
P4		0.47	1		0.61
M1	1.15 – 1.25	1.20	3	1.25 – 1.30	1.27
M2	1.15 – 1.25	1.20	5	1.20 – 1.30	1.23
M3		1.00	1		1.00
m1	1.25 – 1.40	1.33	4	0.95 – 1.00	0.99
m2	1.30 – 1.40	1.36	5	1.00 – 1.10	1.05
m3	1.05 – 1.25	1.14	4	0.95 – 1.00	0.99

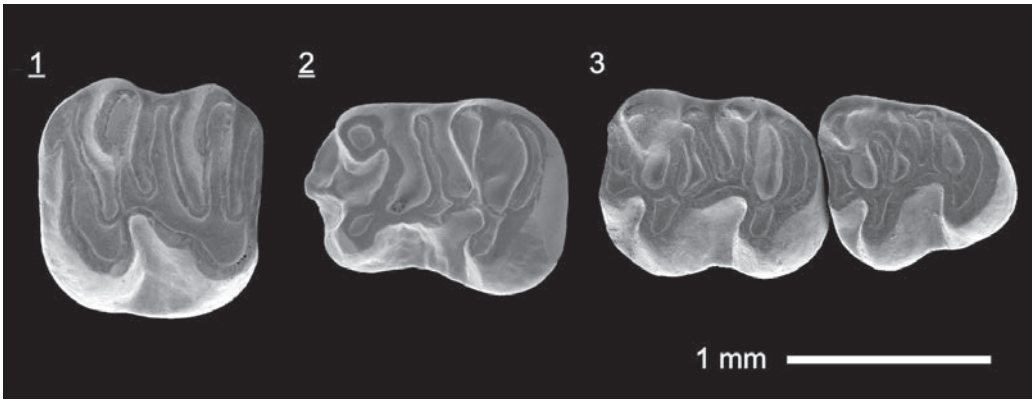


Fig. 12. *Plesiosminthus barsboldi* Daxner-Höck & Wu, 2003 from Unkheltseg (UNCH-A/3), Valley of Lakes, Mongolia. Early Miocene (biozone D). All specimens from the NHMW collection. **1**: right M1, paratype (NHMW 2001/0066/0002/7); AO (DAXNER-HÖCK & WU 2003: fig. 10/2). **2**: right m1, paratype (NHMW 2001/0066/0002/13); AO (DAXNER-HÖCK & WU 2003: fig. 10/10). **3**: left m2–3, paratype (NHMW 2001/0066/0002/19)

Type locality: Unkheltseg, UNCH-A/3 (Mongolia); Early Miocene (biozone D).

Holotype: Right maxilla with P4–M1 (NHMW 2001/0066/0002/1). Measurements: P = 0.47 × 0.61 mm, M1 = 1.25 × 1.20 mm.

Occurrences of *Plesiosminthus barsboldi* in Mongolia (Valley of Lakes, Uvurkhangai): Early Miocene (biozone D).

Type material from Unkheltseg: UNCH-A/3: DAXNER-HÖCK & WU (2003: 142)

Additional material studied:

- Huch Teeg: RHN-A/12: DAXNER-HÖCK & WU (2003: 146).
- Luugar Khudag: LOG-A/1: DAXNER-HÖCK & WU (2003: 146).
- Hotuliin Teeg: HTE-012: 1 M1l, 1 M1r, 1 M2l, m2l (NHMW 2013/0178/0001–0004; = *Plesiosminthus* cf. *barsboldi*).

Description (DAXNER-HÖCK & WU 2003: 142–146): *Plesiosminthus barsboldi* is one of the largest *Plesiosminthus* species; lophodont molar pattern; upper incisors with a pronounced longitudinal groove; upper molars square, sometimes wider than long; cusps situated close to the four corners; narrow and deep valleys between high cusps and lophs; no anterior cingulum of M1; double protoloph of M2; weak connection of protoloph II and protocone; entoloph frequently interrupted; metaloph-connection anterior to hypocone; rectangular lower molars; high alternating cusps, transversely compressed; narrow valleys; ectolophid short, longitudinal, with median connection to protoconid; mesoconid strong; hypolophid-connection anterior to hypoconid; M3/m3 large; upper molars with three roots; lower molars with two roots.

Remarks: *Plesiosminthus barsboldi* is the most advanced *Plesiosminthus* species of Mongolia. It resembles *Plesiosminthus winistoerferi* from the Late Oligocene (MP30) of Switzerland, but differs in: wider m1–2, smaller m3, shorter posterior arm of protoconid of m2, and has no additional conules or ridges in the valleys (Daxner-Höck & Wu 2003: 145–146). In Mongolia the stratigraphic range is the Early Miocene (D). Outside of Mongolia it is known from the Early Miocene of Gashunyinadege in Nei Mongol, China (Kimura 2010).

Plesiosminthus sp.

2003 *Plesiosminthus* sp. A. – Daxner-Höck & Wu: 146, 148.
2003 *Plesiosminthus* sp. B. – Daxner-Höck & Wu: 148.

Occurrences of *Plesiosminthus* sp. in Mongolia (Valley of Lakes, Uvurkhangai): Late Oligocene to Early Miocene.

Material studied (Daxner-Höck & Wu 2003):

Late Oligocene (biozone C):

- Unzimg Khurem (= Tarimalyn Churem): TAR-A/2: *P*. sp. A (Daxner-Höck & Wu 2003: 146, 148).

Late Oligocene (biozone C1):

- Loh: LOH-C/1: *P*. sp. B (Daxner-Höck & Wu 2003: 148).

Early Miocene (biozone D):

- Hotuliin Teeg: HTE-012: 2 m2l, 1 m2r (coll. MPC).
- Luuny Yas: LUS-078: 1 m2l (coll. MPC).

Genus *Onjosminthus* nov. gen.

Type species: *Onjosminthus baindi* nov. spec.

Derivatio nominis: In honor to U. Onjo, member of the Mongolian field-team.

Diagnosis: Upper incisor with smooth anterior surface; molars of medium to large size, with robust cusps and narrow deep valleys; M1 with three roots; M2 with three or four roots; M3 with three rounded roots; lower molars with two roots; upper molars almost square, labial and lingual cusps in opposite position; M1 with protoloph II; M2 with protoloph I + II; M1 with long anterior arm of protocone; long mesoloph of M1–2 frequently connected with paracone-spur ; sinus of M1–3 directed forward; m1–3 rectangular; long mesolophid frequently connected with top of metaconid; posterolophid of m1–2 continuous to top of entoconid; posterior arm of protoconid of m2 absent or weak; m1–2 with hypoconulid and posterior sinusid.

Differential diagnosis: *Onjosminthus* differs by significantly larger size from all small-sized Oligocene to Miocene Dipodidae genera: *Allosminthus*, *Bohlinosminthus*,

Lithodonomys, *Heterosminthus*, *Plesiosminthus* and also from the small-sized species of *Heosminthus* and *Shamosminthus*. Moreover, it differs from *Bohlinosminthus*, *Litodonomys* and *Heterosminthus* by the root numbers of M1 and M3 (three roots), and from *Plesiosminthus* it differs by its larger size and ungrooved upper incisors.

Onjosminthus differs from the medium to large-sized genera and species by the following features: It differs from *Sinosminthus* by the absence of protoloph I in M1, the connection of mesoloph and paracone-spur of M1–2, the metaloph of M1 joining the hypocone, m2 without pronounced posterior arm of protoconid, and the absence of an anterior spur of hypoconulid. It differs from *Parasminthus* (*P. tangingoli*, *P. asiaecentralis* according to the original definition) in having three roots in M1 and M3, in having a more or less square outline of M1–2, also by having a paracone spur and a metaloph joining the hypocone in M1–2, also having a mesolophid of m2 continuous with the top of metaconid. It differs from *Shamosminthus* (*S. tongi*) in having three roots of M1 and M3, M1–2 with square outline and the metaloph of M1 joining the hypocone. It differs from *Gobisminthus* by its lower tooth crown and bunodont cones, also in having transversal protoloph and metaloph and a metaloph joining the hypocone in M1–2.

***Onjosminthus baindi* nov. spec.**

(Figs 13/1–8, 14/1–8, tab. 11)

1974 *Plesiosminthus tangingoli*. – KOWALSKI: 167–168, pl. 1, fig. 1.
1997 Zapodidae indet. – DAXNER-HÖCK *et al.*: 172.
1999 *Parasminthus* sp. 1. – HÖCK *et al.*: 115.
2007 *Parasminthus* sp. 1. – DAXNER-HÖCK & BADAMGARAV: 14, 17, Tab. 3.
2010 *Parasminthus* sp. 1. – DAXNER-HÖCK *et al.*: 358, tab. 4.

Derivatio nominis: In honor of T. BAIND, member of the Mongolian field-team.

Type locality: Tatal Gol, Uvurkhangai, Valley of Lakes, Mongolia. Section: TAT-D, fossil layer TAT-D/1; red clay of the Hsanda Gol Fm. below tuff I (31.5 Ma); Early Oligocene (biozone A).

Holotype (Fig. 13/1): Fragmentary maxilla with left P4–M2 (NHMW 2013/0179/0001). Measurements: P4 = 0.59 × 0.59 mm, M1 = 1.53 × 1.39 mm, M2 = 1.29 × 1.36 mm.

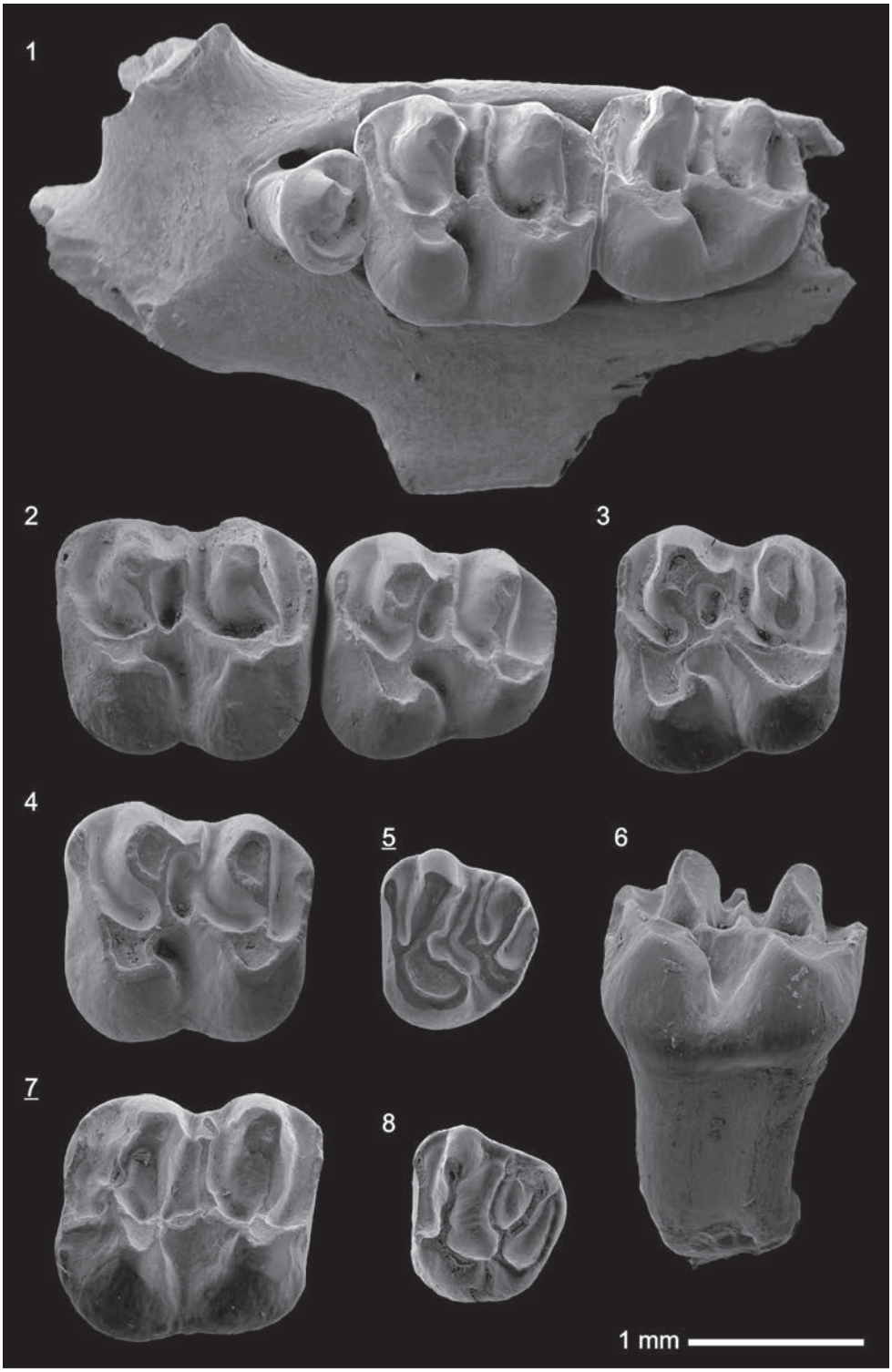
Paratypes (Figs 13/5, 8; 14/2–8): All specimens from the type locality.

TAT-D/1: M1l, 3 M1r, M2–3r, m1l, m2l, 2 m1r, 3 m2r, m1r (NHMW 2013/0179/0002–0013).

Additional material studied:

Early Oligocene (biozone A):

- Taatsiin Gol: TGR-A/13: 4 P4, P4–M3l, M1l, P4–M3r, m1l, m1–2l, 2 m3l, m3r, m2r (NHMW 2013/0180/0001–0028); TGR-A/14: P4, P4–M2l, 2 M1l, M1–2l, P4–M1r, M1r, m1l, m1–2l, 2 m3l, m1r, m2r, m1–2r ; TGL-A/2: 1 M1l, 1 M2l, 1 m1l, 1 m2r (NHMW 2013/0181/0001–0004).
- Unnamed locality: GRAB-II: m2r, m3r (NHMW 2013/0182/0001–0002).
- Hsanda Gol: SHG-C/1: P4, M1l, m1–2l (NHMW 2013/0183/0001–0003).



Early Oligocene (biozone B):

- Taatsiin Gol: TGR-AB/21: P4, M1r, M2r (NHMW 2013/0184/0001–0003); TGR-AB/22: M1l (NHMW 2013/0185/0001); TGR-B/1: M2r, 2m1–frag., m2l (NHMW 2013/0186/0001–0004).
- Unkheltseg: UNCH-A/3B: M2r (NHMW 2013/0187/0001).
- Tatal Gol: TAT-037: m1r, m2r (coll. MPC).
- Hsanda Gol: SHG-A/20: M3l (NHMW 2013/0188/0001); SHG-AB/17–20: M3l (NHMW 2013/0189/0001).
- Ikh Argalatyn Nuru: IKH-A/1: M1r (NHMW 2013/0190/0001).

Stratigraphic range: Early Oligocene, biozones A to B, red clay of the Hsanda Gol Fm. below and above basalt I or respective tuff layer (of 31.5 Ma.).

Diagnosis and differential diagnosis: The same as for the genus.

Description of the holotype (Fig. 13/1): Fragmentary left maxilla with P4–M2 (NHMW 2013/0179/0001).

P4: consists of a single cone which is surrounded by a cingulum; one root.

M1: almost square in outline; four main robust cones: five lophs; four narrow labial fossettes; sinus directed forward; long anterior arm of protocone extends to antero-labial edge, turns backward and contacts the basal part of paracone; paracone and metacone with convex anterior side and plane posterior side; protoloph II connected with posterior arm of protocone; metaloph II connected with hypocone; long mesoloph extends to the labial border; posteroloph long; three roots (a wide lingual and two rounded labial roots).

M2: slightly smaller than M1; narrow in its posterior part; labial anteroloph extends to the antero-labial edge, lingual anteroloph short and weak; double protoloph, protoloph I and II connected with anterior and posterior arm of protocone, respectively; metaloph connected with hypocone; mesoloph low in its labial part; posteroloph long; entoloph continuous; sinus directed forward; three roots (a wide lingual and two rounded labial roots).

Description of paratypes and additional material (Figs 13/2–8; 14/1–8):

P4–M2 similar to holotype except for one out of nineteen M1with protoloph I (Fig. 13/7); long mesoloph interrupted or constricted in its middle part in five out of sixteen specimens; frequently paracone spur connected with mesoloph; entoloph continuous;

◀ Fig. 13. *Onjosminthus baindi* nov. gen. nov. spec. from the Valley of Lakes, Mongolia. Early Oligocene (biozones A to B). Upper molars. All specimens from the NHMW collection. **1**: left maxilla with P4–M3, holotype (NHMW 2013/0179/0001) from Tatal Gol (TAT-D/1; biozone A). **2**: left M1–2 (NHMW 2013/0180/0001) from Taatsiin Gol (TGR-A/14; biozone A). **3**: left M2 (NHMW 2013/0181/0001) from Taatsiin Gol (TGL-A/2; biozone A). **4**: left M1 (NHMW 2013/0180/0002) from Taatsiin Gol (TGR-A/14; biozone A). **5**: right M3, paratype (NHMW 2013/0179/0002) from Tatal Gol (TAT-D/1; biozone A). **6**: left M1, lingual view (NHMW 2013/0183/0001) from Hsanda Gol (SHG-C/1; biozone A). **7**: right M1 (NHMW 2013/0184/0001) from Taatsiin Gol (TGR-AB/21; biozone B). **8**: left M3 paratype (NHMW 2013/0179/0003) from Tatal Gol (TAT-D/1; biozone A).

four M2 with protoloph I+II, two M2 only with protoloph II; mesoloph sometimes constricted; connection of paracone spur and mesoloph in four out of six M2; M2 of biozone A with three roots (a wide lingual and two rounded labial ones), specimens of biozone B with three or four roots (lingual root can be divided).

M3 smallest upper molar; paracone, protocone and hypocone well developed; metacone reduced or absent; anteroloph, protoloph I and mesoloph present; metaloph and posteroloph absent or interrupted; entoloph can be constricted or interrupted; thus sinus and fossette II frequently continuous; M3 with three rounded roots.

m1 rectangular in outline; longest molar; opposing metaconid and protoconid connected by v-shaped metalophid II; anteroconid small cusp, or weak crest, or absent; position of entoconid anterior to hypoconid; short hypolophid connected with ectolophid close to strong mesoconid; short ectolophid anteriorly connected with basal part of protoconid or without connection; mesolophid strong, long and frequently fused with posterior metaconid spur; posterolophid long and continuous to top of entoconid, closing fossettid IV; hypoconulid accentuated cusp; posterior sinusid between labial posterolophid and hypoconid; sinusid directed forward.

m2 similar to m1 except for: strong labial and lingual anterolophids; position of metaconid anterior to protoconid; metalophid I strong, posterior arm of protoconid absent or weak; ectolophid longerthan of m1; mesolophid long, frequently reaches lingual edge of the tooth and continues to top of metaconid, or can be interrupted in its middle part.

m3 smaller than m2, but similar in dental feature; differences: narrow posterior part; less pronounced mesolophid-metaconid and posterolophid-entoconid connections; hypoconulid, posterior sinusid, posterior arm of protoconid or mesolophid absent.

Remarks: So far, *Onjosminthus* is a monospecific genus. Among the medium to large-sized Dipodidae of the Early Oligocene, *Onjosminthus* and *Sinosminthus* are of similar size and tooth pattern. They share some general dental structures with *Heosminthus*: the more or less square outline of M1–2, three roots of M1 and M3 and the un-grooved upper incisors. *Parasminthus*, known to range from the Late Oligocene to the Early Miocene, is of similar size, but has more derived dental characters as outlined below (Wang & Qiu 2000).

Table 11. Measurements of *Onjosminthus baindi*.

	length (mm)			width (mm)	
	range	mean	N = 68	range	mean
P4	0.59 – 0.82	0.65	10	0.59 – 0.82	0.65
M1	1.41 – 1.72	1.56	19/18	1.39 – 1.55	1.48
M2	1.29 – 1.55	1.43	8	1.36 – 1.48	1.43
M3	0.92 – 1.01	0.97	5	0.99 – 1.18	1.10
m1	1.48 – 1.76	1.64	10	1.08 – 1.29	1.20
m2	1.55 – 1.76	1.66	11	1.13 – 1.32	1.23
m3	1.27 –1.51	1.39	5	0.99 – 1.18	1.08

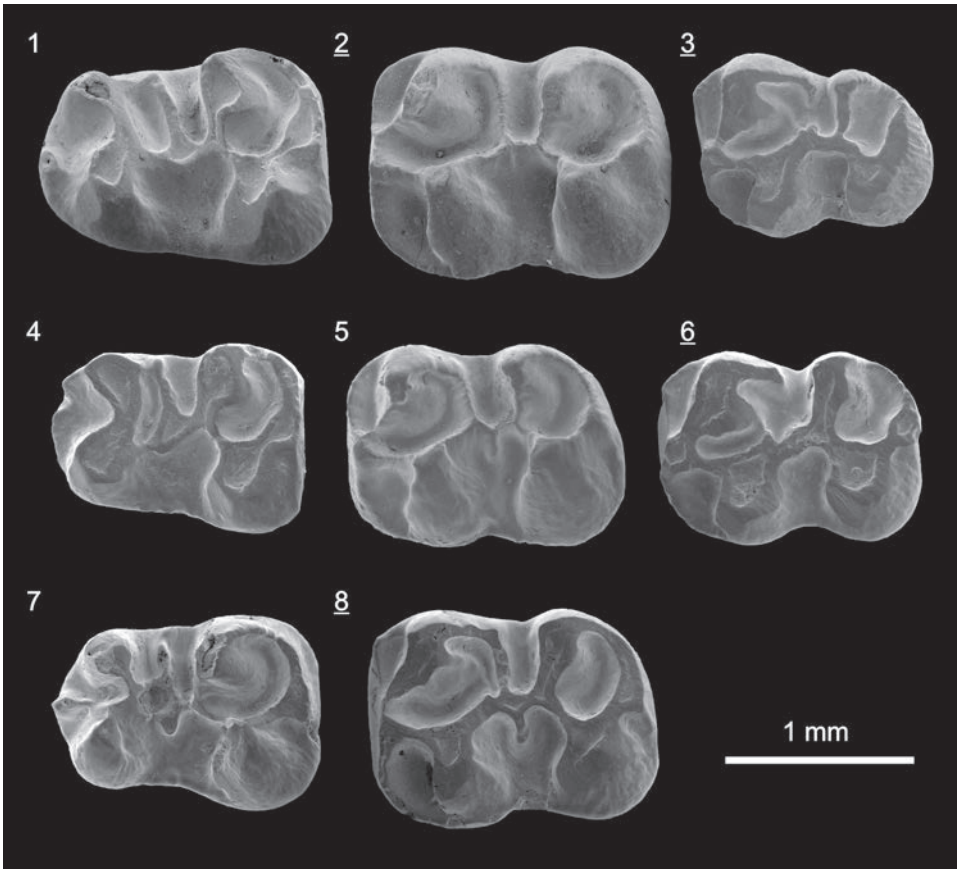


Fig. 14. *Onjosminthus baindi* nov. gen. nov. spec. from the Valley of Lakes, Mongolia. Early Oligocene (biozone A). Lower molars. All specimens from the NHMW collection. **1**: left m1 (NHMW 2013/0180/0003) from Taatsiin Gol (TGR-A/13; biozone A). **2**: right m2 (NHMW 2013/0179/0004) from Taatsiin Gol (TGL-A/2; biozone A). **3**: right m3, paratype (NHMW 2013/0179/0005) from Tatal Gol (TAT-D/1; biozone A). **4**: left m1, paratype (NHMW 2013/0179/0006) from Tatal Gol (TAT-D/1; biozone A). **5**: left m2, paratype (NHMW 2013/0179/0007) from Tatal Gol (TAT-D/1; biozone A). **6**: right m2, paratype (NHMW 2013/0179/0008) from Tatal Gol (TAT-D/1; biozone A). **7**: left m1, paratype (NHMW 2013/0179/0009) from Tatal Gol (TAT-D/1; biozone A). **8**: right m2, paratype (NHMW 2013/0179/0010) from Tatal Gol (TAT-D/1; biozone A).

Genus *Parasminthus* BOHLIN, 1946

Type species: *Parasminthus asiaecentralis* BOHLIN, 1946

Dental characters based on the type material of *Parasminthus asiaecentralis* and *Parasminthus tangingoli* from Tabenbuluk and from other Late Oligocene deposits of Gansu in China (BOHLIN 1946; WANG & QIU 2000; WANG 2003): No longitudinal groove of upper incisors; medium to large tooth sizes; M1–2 rectangular in outline;

double protoloph of M2; metaloph of M1joining the posterior arm of hypocone or the posteroloph; posterior concavity (= posterior sinus) between hypocone and posteroloph of M1–2. M1–2 with four roots, M3 with three roots, lower teeth with two roots. *Parasminthus tangingoli* and *Parasminthus asiaecentralis* have a similar molar pattern, but differ in size: M1–2 / m1–2 < 1.6 mm = *Parasminthus tangingoli*), M1–2 / m1–2 > 1.6 mm = *Parasminthus asiaecentralis* (Wang & Qiu 2000).

Considering the material from Ulantatal in Nei Mongol in China (Huang 1992: 279), *Parasminthus asiaecentralis* and *Parasminthus tangingoli* have variable dental characters: 3–4 roots of M1–2; M2 with single or double protoloph; metaloph of M1 connected with posteroloph, posterior arm of hypocone or middle part of hypocone.

Referred species / type locality:

- *P. asiaecentralis* Bohlin, 1946 from Tabebbuluk, Gansu (China); Late Oligocene.
- *P. debruijni* Lopatin, 1999 from Altynschokysu, bone bed I (Kazakstan); Late Oligocene (= Early Miocene according to Lopatin 1999).
- *P. tangingoli* Bohlin, 1946 from Tabenbuluk Gansu (China); Late Oligocene.

Remarks: We agree with Lopatin (1999) that *Parasminthus parvulus* Bohlin, 1946 has to be excluded from the genus *Parasminthus* Bohlin, 1946 and belongs to *Bohlinosminthus* Lopatin, 1999 because of the significant smaller size and morphological differences such as: the absence of a connection between metaloph and posteroloph or posterior arm of hypocone of M1–2, the absence of protoloph II of M2.

Parasminthus cf. *asiaecentralis* Bohlin, 1946

(Figs 15/1–3)

1999 *Parasminthus* cf. *asiae-centralis*. – Höck *et al.*: 116, 118.
2007 *Parasminthus* cf. *asiae-centralis*. – Daxner-Höck & Badamgarav: 17–18, Tab. 3.
2010 *Parasminthus* cf. *asiae-centralis*. – Daxner-Höck *et al.*: 358, tab. 4

Type locality: Tabenbuluk, Gansu (China), Late Oligocene.

Occurrence of *Parasminthus* cf. *asiaecentralis* in Mongolia (Valley of Lakes, Uvurkhangai): Late Oligocene (biozones C to C1).

Material studied:

- Unzing Khurem: TAR-A/2 (biozone C): 1 M2r (NHMW 2013/0263/0001)
- Del: DEL-B/12 (biozone C1): 1 M2l, 1 m2l (NHMW 2013/0191/0001–0002).

Measurements: M2l = 1.65 × 1.39 mm, m2l = 1.69 × 1.22 mm.

Description (Figs 15/1–3):

M2 (Figs 15/1–2): rectangular in outline; lingual anteroloph absent or weak, labial one strong; protoloph double; protoloph I connected with anterior arm of protocone;

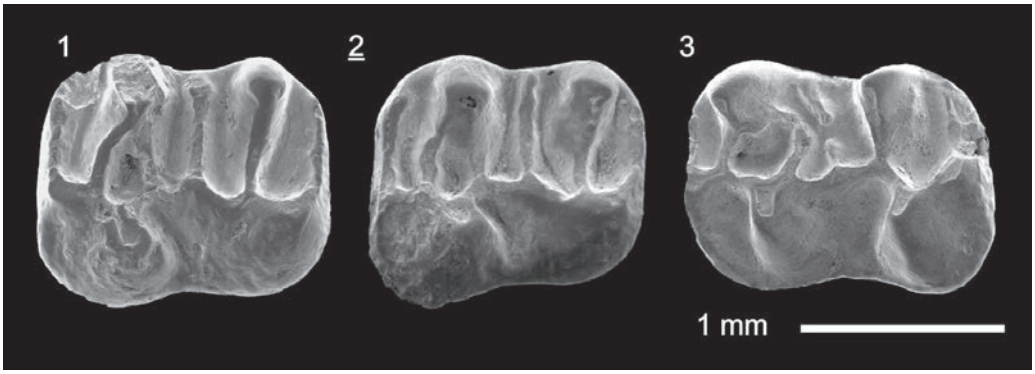


Fig. 15. *Parasminthus* cf. *asiae-centralis* BOHLIN, 1946 from the Valley of Lakes, Mongolia. Late Oligocene (biozones C to C1). All specimens from the NHMW collection. **1**: left M2 (NHMW 2013/0191/0001) from Del (DEL-B/12; biozone C1). **2**: right M2 (NHMW 2013/0263/0001) from Unzing Khurem (TAR-A/2; biozone C). **3**: left m2 (NHMW 2013/0191/0002) from Del (DEL-B/12; biozone C1).

protoloph II connected with entoloph; mesoloph long; metaloph connected with anterior arm of hypocone; posteroloph thin, long; sinus directed forward; four rounded roots.

m2 (Fig. 15/2): rectangular in outline; lingual and labial anterolophid present; metalophid I connected with anterior arm of protoconid; posterior arm of protoconid strong, curved forward and connected with metaconid; mesolophid thin, constricted in its middle part; hypolophid short, connected with anterior arm of hypoconid; posterolophid strong, with hypoconulid; ectolophid oblique; sinusid directed backward; two roots.

Remarks: The two teeth from Del B/12 are within the size range of *Parasminthus asiaecentralis*, which is the largest among all *Parasminthus* species. The tooth morphology resembles *Parasminthus asiaecentralis* from the type area, except that the M2 from Mongolia has no posterior sinus between hypocone and posteroloph.

Table 12. Measurements of *Parasminthus* cf. *tangingoli*.

	length (mm)			width (mm)	
	range	mean	N = 22	range	mean
M1	1.27 – 1.34		2	1.06 – 1.13	
M2	1.18 – 1.51	1.36	7	1.04 – 1.41	1.23
M3		0.78	1		0.75
m1	1.34 – 1.53	1.42	7	0.99 – 1.18	1.06
m2	1.34 – 1.55	1.48	7	0.99 – 1.18	1.11
m3		1.46	1		1.13

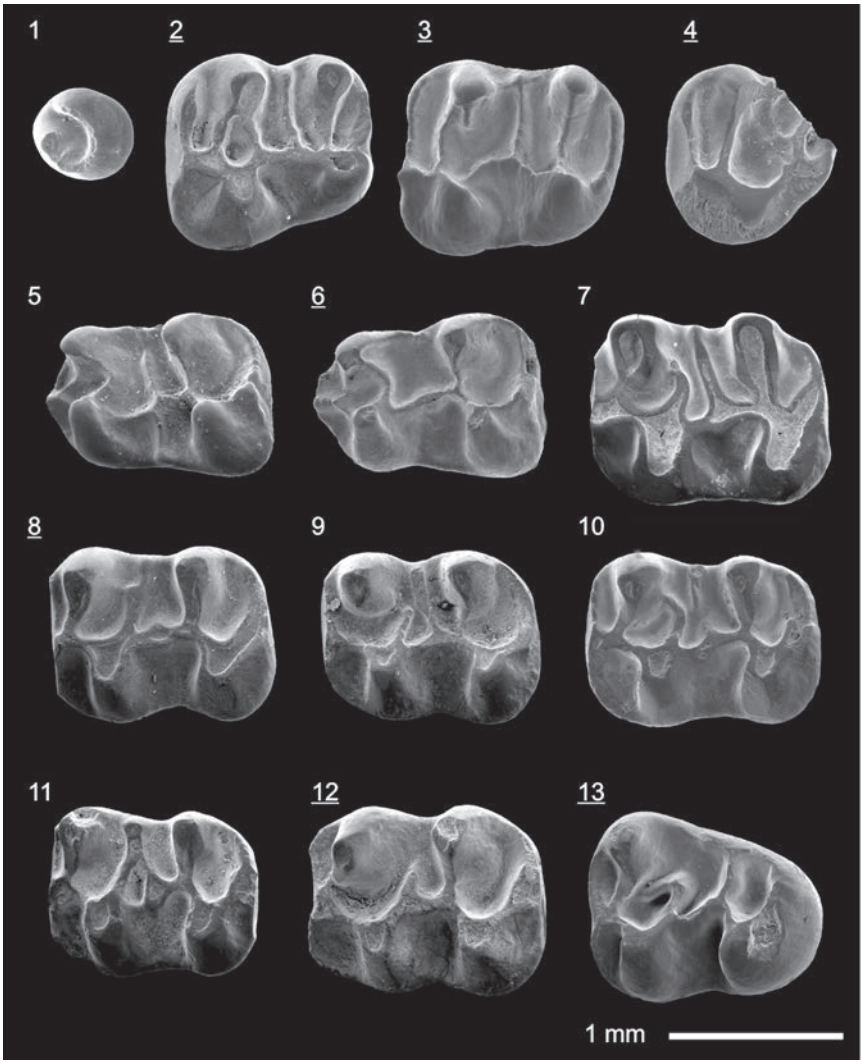


Fig. 16. *Parasminthus* cf. *tangingoli* Bohlin, 1946 from the Valley of Lakes, Mongolia. Late Oligocene (biozones C to C1). All specimens from the NHMW collection. **1**: P4 (NHMW 2013/0192/0001) from Taatsiin Gol (TGR-C/1; biozone C). **2**: right M2 (NHMW 2013/0196/0001) from Del (DEL-B/12; biozone C1). **3**: right M2 (NHMW 2013/0192/0002) from Taatsiin Gol (TGR-C/1; biozone C). **4**: right M3 (NHMW 2013/0196/0002) from Del (DEL-B/12; biozone C1). **5**: left m1 (NHMW 2013/0194/0001) from Toglorhoi (TGW-A/2b; biozone C). **6**: right m1 (NHMW 2013/0192/0003) from Taatsiin Gol (TGR-C/1; biozone C). **7**: left m2: (NHMW 2013/0195/0001) from Unzing Khurem (TAR-A/2; biozone C). **8**: right m2 (NHMW 2013/0192/0004) from Taatsiin Gol (TGR-C/1; biozone C). **9**: left m2 (NHMW 2013/0194/0002) from Toglorhoi (TGW-A/2b; biozone C). **10**: left m2 (NHMW 2013/0192/0005) from Taatsiin Gol (TGR-C/1; biozone C). **11**: left m2 (NHMW 2013/0196/0003) from Del (DEL-B/12; biozone C1). **12**: right m2 (NHMW 2013/0195/0002) from Unzing Khurem (TAR-A/2; biozone C). **13**: right m3 (NHMW 2013/0192/0006) from Taatsiin Gol (TGR-C/5–6; biozone C).

Parasminthus cf. *tangingoli* BOHLIN, 1946
(Figs 16/1–13, Tab. 12)

2007 *Parasminthus* cf. *tangingoli*. – DAXNER-HÖCK & BADAMGARAV: 17, tab. 3.
2010 *Parasminthus* cf. *tangingoli*. – DAXNER-HÖCK *et al.*: 358, tab. 4.

Type locality: Tabenbuluk, Gansu (China), Late Oligocene.

Occurrences of *Parasminthus* cf. *tangingoli* in Mongolia (Valley of Lakes, Uvurkhangai): Late Oligocene (biozones C to C1).

Material studied:

Late Oligocene (biozone C):

- Taatsiin Gol: TGR-C/1, 6: 1 M2r, 3 m1r, 2 m1l, 2 m2l, 1 m2r, 1 m3r (NHMW 2013/0192/0001).
- Toglorhoi: TGW-A/2a: 1 M1r, 1 M2l (NHMW 2013/0193/0001); TGW-A/2b: 1 m1l, 1 m1r, 1 m2l (NHMW 2013/0194/0001).
- Unzing Khurem: TAR-A/2: 1 M2r, 1 m2l, 1 m2r (NHMW 2013/0195/0001).

Late Oligocene (biozone C1):

- Del: DEL-B/12: 1 M2l, 1 M2r, 1 m1l, 1 m2l (NHMW 2013/0196/0001).
- Tatal Gol: TAT-043: 1 M2l (NHMW 2013/0197/0001).

Description (Figs 16/1–13): Medium-sized buno-lophodont molars; M1–2 rectangular.

M1–2: long anterior arm of protocone, small anterior cingulum; long mesoloph; M1 with protoloph II; M2 with single or double protoloph; M1 with metaloph joining the posterior arm of hypocone or posteroloph; M2 with joinng the hypocone or its anterior arm.

M3: smallest upper molar, with rounded outline; four transverse lophs (labial anteroloph, protoloph, metaloph and posteroloph) and closed sinus.

m1: anteroconid isolated or connected with protoconid and metaconid by weak, low crests; metalophid U-shaped; hypolophid short, connected with entolophid halfway between mesoconid and hypoconid; posterolophid strong, long, with hypoconulid; ectolophid oblique, attached to the posterior wall of protoconid; ectomesolophid and ectostylid (one m1; Fig. 16/5).

m2: rectangular in outline; labial and lingual anterolophid; short metalophid I and hypolophid; mesolophid mostly long, can be weak or absent; posterior arm of protoconid strong, connected with metaconid or reaching the lingual edge of the tooth (one m2); ectolophid short, contacts the posterior part of protoconid.

m3: large; with five lophids (anterolophid, metalophid, posterior arm of protoconid, hypolophid and posterolophid); posterior arm of protoconid turned forward.

M1–2 with four roots, M3 with three roots, m1–3 with two roots.

Remarks: The Mongolian fossils are within the size range of *Parasminthus tangingoli*, but differ from the type material by the variable outline of M2 and m2 and the direction of the metaloph of M1–2.

Parasminthus debruijni Lopatin, 1999

(Figs 17/1–7, Tab. 13)

2007 *Parasminthus* cf. *debruijni*. – Daxner-Höck & Badamgarav: 17, tab. 3.
2010 *Parasminthus* cf. *debruijni*. – Daxner-Höck *et al.*: 358, tab. 4.

Type locality: Altynshokysu, bonebed II (Kazakhstan), Late Oligocene (= Early Miocene according to Lopatin 1999).

Occurrences of *Parasminthus debruijni* in Mongolia (Valley of Lakes, Uvurkhangai): Late Oligocene (biozones C to C1).

Material studied:

Late Oligocene (biozone C):

- Taatsiin Gol (TGR-C/1): 1 M1r, 1 M 2r, 2 m3l (NHMW 2013/0199/0001–0004).

Late Oligocene (biozone C1):

- Del (DEL-B/12): 1 M1r, 1 M2r, 1 M3r, 1 m2l (NHMW 2013/0200/0001).
- Huch Teeg (RHN-A/9): 1M1l (NHMW 2013/0201/0001).
- Tatal Gol: TAT-E/27: Max. P4–M3l (NHMW 2013/0198/0001; = *Parasminthus* cf. *debruijni*: Fig. 17/4).

Description (Fig. 17/1–7): Small to medium-sized buno-lophodont molars.

M1–2: rectangular outline; M1 with long anterior arm of protocone and single protoloph, M2 with double protoloph; M1–2 with long mesoloph; metaloph of M1 joins the hypocone or posteroloph; metaloph of M2 joins the hypocone.

M3: smallest upper molar, with rounded outline, four transverse lophs (labial anteroloph, protoloph, metaloph and posteroloph).

m1: oblique ectolophid; long mesolophid; long posterolophid; ectostylid.

Table 13. Measurements of *Parasminthus debruijni*.

	length (mm)			width (mm)	
	range	mean	N = 10	range	mean
P4		0.82	1		
M1	1.18 – 1.27	1.25	3	0.96 – 1.04	
M2	1.13 – 1.18		2	1.04 – 1.11	
M3		0.94	1		0.96
m2		1.22	1		0.94
m3	1.20 –1.25		2	1.01 – 1.13	

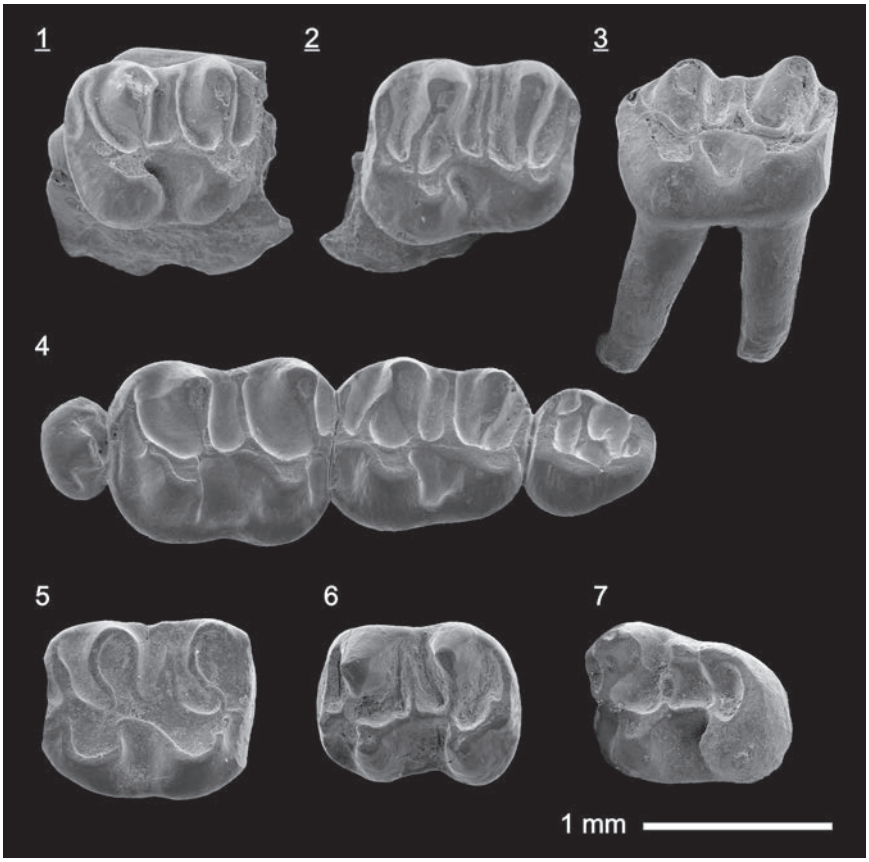


Fig. 17. *Parasminthus debruijni* LOPATIN, 1999 from the Valley of Lakes, Mongolia. Late Oligocene (biozones C to C1). All specimens from the NHMW collection. **1**: right M1 (NHMW 2013/0200/0001) from Del (DEL-B/12; biozone C1). **2**: right M2 (NHMW 2013/0200/0002) from Del (DEL-B/12; biozone C1). **3**: right M1 (NHMW 2013/0199/0001) from Taatsiin Gol (TGR-C/1; biozone C). **4**: left P4–M2 (NHMW 2013/0198/0001) from Tatal Gol (TAT-E/27; biozone C1). **5**: left M1 (NHMW 2013/0201/0001) from Huch Teeg (RHN-A/9; biozone C1). **6**: left m2 (NHMW 2013/0200/0003) from Del (DEL-B/12, biozone C1). **7**: left m3 (NHMW 2013/0199/0002) from Taatsiin Gol (TGR-C/1; biozone C).

m2: rectangular with mesolophid

m3: five transverse lophids, mesolophid absent or weak.

M1–2 have four roots, M3 three roots and m1–3 have two roots.

R e m a r k s : The Mongolian teeth resemble *Parasminthus debruijni* from Kazakhstan in molar morphology and size. They are smaller than *Parasminthus tangingoli* and *Parasminthus asiaecentralis*. *Parasminthus debruijni* differs from *Plesiosminthus* and *Heosminthus* by having rectangular M1–2 with four roots, and by the metaloph of M1 frequently joining the posteroloph.

Genus *Bohlinosminthus* Lopatin, 1999

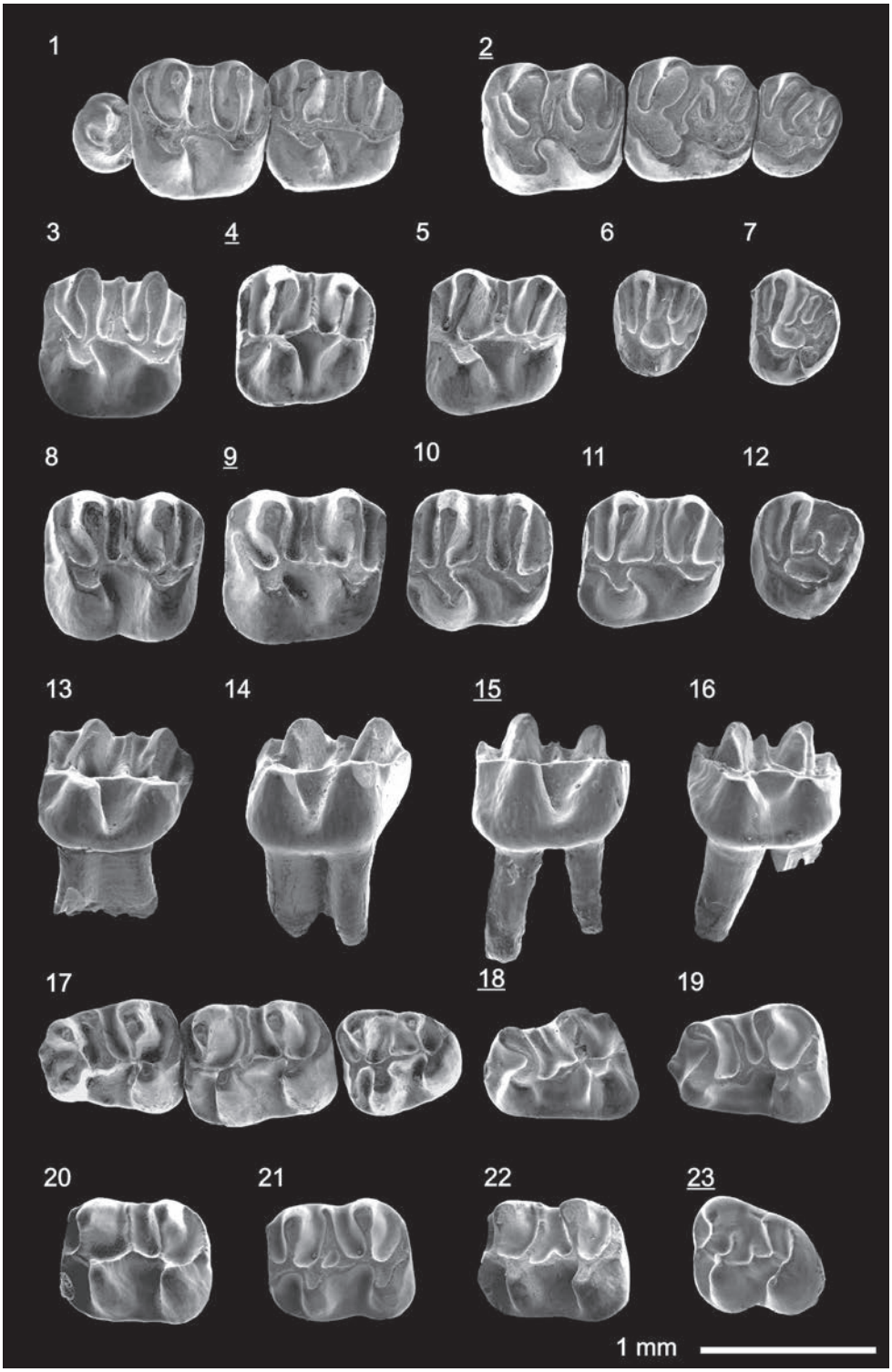
Type species: *Bohlinosminthus cubitalus* Lopatin, 1999

Original diagnosis of *Bohlinosminthus*: "Small primitive Sicistinae with bunodont molars. Upper incisors lack longitudinal groove on anterior surface. M1 and M2 three-or four rooted. M1 with protoloph II, metaloph I, and complete posteroloph. M2 with one protoloph (I) and complete entoloph. Entosinus of M1 and M2 small and straight. Entosinus of M3 closed. On m1, ectolophid and metalophid connected with protoconid at the same point. On m2, mesolophid usually developed to greater extent than posterior arm of protoconid." (Lopatin 1999: 433). *Bohlinosminthus* differs from *Parasminthus* by: "Substantially smaller size, the absence of metaloph II on M1 and protoloph II on M2…" (Lopatin 1999: 433).

Referred species and their type localities:

- *B. cubitalus* Lopatin, 1999 from Altynshokysu, bone bed II (Kazakhstan); Late Oligocene (= Early Miocene according to Lopatin 1999)
- *B. parvulus* (Bohlin, 1946) from Tabenbuluk, Western Gansu (China); Late Oligocene.
- *B. quartus* (Shevyreva, 1970) from Kazakhstan (described as *Parasminthus quartus* by Shevyreva 1970, and transferred to *Bohlinosminthus* by Lopatin 1999).

Fig. 18. *Bohlinosminthus parvulus* (Bohlin, 1946) from the Valley of Lakes, Mongolia. Early to Late Oligocene (biozones A to C1). All specimens from the NHMW collection. **1**: left P4–M2 (NHMW 2013/0211/0001) from Toglorhoi (TGW-A/2b; biozone C). **2**: right M1–3 (NHMW 2013/0211/0002) from Toglorhoi (TGW-A/2b; biozone C). **3**: left M1 (NHMW 2013/0206/0001) from Taatsiin Gol (TGR-C/1; biozone C). **4**: right M2 (NHMW 2013/0203/0001) from Tatal Gol (TAT-C/1, biozone C). **5**: left M2 (NHMW 2013/0205/0001) from Hsanda Gol (SHG-AB/17–20; biozone B). **6**: left M3 (2009/0147/0007) from Taatsiin Gol (TGR-C/2; biozone C). **7**: left M3 (NHMW 2013/0205/0002) from Hsanda Gol (SHG-AB/17–20; biozone B). **8**: left M1 (NHMW 2013/0210/0001) from Toglorhoi (TGW-A/2a; biozone C). **9**: right M1 (NHMW 2013/0219/0001) from Del (DEL-B/12; biozone C1). **10**: left M2 (NHMW 2013/0210/0002) from Toglorhoi (TGW-A/2a; biozone C). **11**: left M2 (NHMW 2013/0210/0003) from Toglorhoi (TGW-A/2a; biozone C). **12**: left M3 (NHMW 2013/0210/0004) from Toglorhoi (TGW-A/2a; biozone C). **13**: left M2, lingual view (NHMW 2013/0205/0003) from Hsanda Gol (SHG-AB/17-20; biozone B). **14**: left M1, lingual view (NHMW 2013/0205/0004) from Hsanda Gol (SHG-AB/17-20; biozone B). **15**: right M2, lingual view (NHMW 2013/0203/0002) from Tatal Gol (TAT-C/1, biozone C). **16**: left M1, lingual view (NHMW 2013/0203/0003) from Tatal Gol (TAT-C/1, biozone C). **17**: left m1–3 (NHMW 2013/0211/0003) from Toglorhoi (TGW-A/2b; biozone C). **18**: right m1 (NHMW 2013/0206/0002) from Taatsiin Gol (TGR-C/1; biozone C). **19**: left m1 (NHMW 2013/0210/0005) from Toglorhoi (TGW-A/2a; biozone C). **20**: left m2 (NHMW 2013/0205/0005) from Hsanda Gol (SHG-AB/17-20; biozone B). **21**: left m2 (NHMW 2013/0210/0006) from Toglorhoi (TGW-A/2a; biozone C). **22**: left m2 (NHMW 2013/0206/0003) from Taatsiin Gol (TGR-C/1; biozone C). **23**: right m3 (NHMW 2013/0211/0004) from Toglorhoi (TGW-A/2b; biozone C).



Bohlinosminthus parvulus (Bohlin, 1946)

(Figs 18/1–23, Tab.14)

1946 *Parasminthus parvulus* – Bohlin: 30–41, figs 2–4.
1992 *Parasminthus parvulus* – Huang: pp. 260–265, 279–281, pl. 4, figs 1–13.
1997 *Parasminthus parvulus* – Daxner-Höck *et al.*: 172.
1999 *Parasminthus parvulus* – Höck *et al.*: 116, fig. 20/11.
2000 *Parasminthus parvulus* – Wang & Qiu: 17–19, pl. 2, 1–4.
2003 *Parasminthus parvulus* – Wang: 91–92, 100, fig. 2.
2003 *Bohlinosminthus parvulus* – Daxner-Höck & Wu: 140.
2006 *Bohlinosminthus parvulus* – Meng *et al.*: 213, fig. 3.
2010 *Bohlinosminthus parvulus* – Daxner-Höck *et al.*: 358, tab. 4, fig. 5/11–16.
2010 *Bohlinosminthus* sp. – Daxner-Höck *et al.*: 358, tab. 4.

Type locality: Tabenbuluk, Gansu (China); Late Oligocene.

Occurrences of *Bohlinosminthus parvulus* in Mongolia (Valley of Lakes, Uvurkhangai): Early Oligocene to Early Miocene.

Material studied:

Early Oligocene (biozone A):

- Khongil (HL-A/1): 1 M1l, 1 m1r (NHMW 2013/0202/0001–0002).
- Tatal Gol (TAT-C/1): 2 M1l, 1 M1r, 1 M2l, 2 M2r, 1 m1l (NHMW 2013/0203/0001–0008).

Early Oligocene (biozone B):

- Tatal Gol: TAT-038: 1 m1r, 1 m1l, 2 m2r (coll. MPC); TAT-039: 1M2r, 2 m1r, 2 m2r, 1 m3r (coll. MPC).
- Ikh Argalatyn Nuruu: IKH-A/3–4: 1M1l, 1M2l, 1m1l, 1 m1r (NHMW 2013/0204/0001–0004).
- Hsanda Gol: SHG-AB/17–20: 4 M1l, 4 M1r, 4 M2l, 2 M2r, 2 M3l, 1 m1l, 1 m1r, 1 m2l, 2 m2r, 5 m3l (NHMW 2013/0205/0001–0026).

Late Oligocene (biozone C):

- Taatsiin Gol: TGR-C/1: 8 M1l, 5 M1r, 1 M2l, 3 M2r, 3 mand. m1–3l, 2 m1l, 2 m1r, 5 m2l, 4 m2r, 1 mand. m2–3r, 1 m3l (NHMW 2013/0206/0000); TGR-C/2: 2 M1l, 8 M1r, 4 M2l, 3 M2r, 1 M3r, 1 M3l, 7 m1l, 6m1r, 6 m2l, 6 m2r, 3 m3l, 1 m3r (2009/0147/0001–0006, and 0000); TGR-C/7: 1 M1l, 2 M1r, 1 M3l, 1 m1r, 2 m2r, 1 m2l (NHMW 2013/0207/0001–0008).
- Abzag Ovoo: ABO-A/3: 1 m1r, 1 m2r, 1 m2l, 1 m3r (NHMW 2012/0214/0001–0004).
- Unzing Khurem: TAR-A/2: 6 M1l, 2 M2l, 3 M3l, 1 max. M1–2r, 3 M1r, 3 M2r, 1 M3r, 7 m1l, 1 mand. m1–2l, 4 m2l, 2 m3l, 2 m1r, 1 mand. m1–2r, 3 m2r, 3 m3r (NHMW 2013/0208/0000).
- Toglorhoi: TGW-A/1: 1m1r, 1 m2r (NHMW 2013/0209/0001–0002); TGW-A/2a: 1 max.P4–M1r, 7 M1r, 10 M2r, 3 M3r, 1 max.P4– M1l, 9, M1l, 10Ml, 3 M3l, 12 m1r, 1 mand. m2–3l, 2 mand. m1–2l, 1 mand. m1–3l, 10 m1l, 12 m2l,

6 m3l (NHMW 2013/0210/0000); TGW-A/2b: 3 P4, 3 max. P4–M1l, 6 M1l, 9 M2l, 6 M3l, 1 max.P4–M2, 12 M1r, 8 M2r, 3 M3r, 1 mand. m1–3l, 10 m1l, 10 m2l, 7 m3l, 1 mand. m1–3r, 6 m1r, 12 m2r, 1 mand. m2–3r, 7 m3r (NHMW 2013/0211/0000).

Late Oligocene (biozone C1):

- Tatal Gol: TAT-051/2: 1 M1r, 1 M1l, 1 max. P4–M1r, 1 M2l, 1mand. m1–2r, 1 mand. m1–2l, 1 mand. m1–3r, 1 mand. m2–3r, 1m1l, 4 m2r (NHMW 2013/0212/0000); TAT-043: 1 max. P4–M1l, 4 M1l, 1 max. M1–3r, 1 max. P4–M1r, 2 M1r, 1 M2r, 1 max. M1–2r, 1 mand. m1–3l, 2 mand. m1–2l, 1 mand. m2–3l, 3 m1l, 1 m2l, 4 mand. m1–3r, 2 m1r, 3 m2r, 1 m3r (NHMW 2013/0213/0000); TAT-E/22: 4 M1l, 4 M2l, 5 M1r, 3 M2r, 1 mand. m1–3l, 1 mand. m2–3l, 2 m1l, 4 m2l, 2 m3l, 1 mand. m1–2r, 1 mand. m1–3r, 7 m1r, 2 m3r, 4 m2r (NHMW 2013/0215/0000); TAT-E/27: 1 max. M1–3l, 2 M1l, 1 P4, 1 M2r, 1 m3r, 1 mand. m1–2l, 1 m1l, 1 mand. m1–3r, 4 m2r, 2 m3r (NHMW 2013/0216/0000).
- Ikh Argalatyn Nuruu: IKH-B/5: 1 M1l, 2 M1r, 1 M2r, 1 M1l, 1 mand. m1–3r, 1 m1l, 1 m2l, 1 m2r (NHMW 2013/0217/0000).
- Toglorhoi: TGW-A/5: 1 max. P4–M1r, 2 M1r, 1 M2r, 3 M1l, 2 mand. m1–3l, 1 mand. m2–3r, 2 m1l, 1 m1r, 3 m2l, 1 m3r (NHMW 2013/0218/0000).
- Del: DEL-B/12: 1 max. M1–2l, 9 M1l, 9 M2l, 1 P4, 1 max. P4–M1r, 1 max. M1–2r, 8 M1r, 8 M2r, 3 M3r, 11 m1l, 7 m2l, 1mand. m2–3l, 4 m3l, 10 m1r, 1 mand. m1–3r, 8 m2r, 2 mand. m2–3r, 4 m3r (NHMW 2013/0219/0000).
- Loh: LOH-C1: 1 max. M1–3l, 7 M1l, 1max. M1–2l,1 M2l, 5 m1r, 2 M2r, 1 P, 1 mand. m1–2l, 1 mand. m1–3l, 5 m1l, 3 m2l, 4 m1r, 1 mand. m1–3r, 4 m2r (NHMW 2013/0220/0000).
- Huch Teeg: RHN-A/7: 3 M1r, 1 M1l, 2 M3l, 4 m1l, 1 m1r, 2 m2l, 1 m2r, 1 m3l (NHMW 2013/0221/0000); RHN-023: 1 m1 (NHMW 2013/0222/0001).
- Hotuliin Teeg: HTSE-009+013: 2 M1r, 2 m1l, 1 mand. m2–3l, 1mand. m2–3r (NHMW 2013/0223/0001–0006);
- HTE-057: 1 mand. m1–3l, 1 m2r (NHMW 2013/0224/0001–0002).

Table 14. Measurements of *Bohlinosminthus parvulus*.

	length (mm)			width (mm)	
	range	mean	N = 820	range	mean
P4	0.35 – 0 66	0.49	18	0.42 – 0.66	0.52
M1	0.82 – 1.13	0.96	175	0.71 – 1.06	0.88
M2	0.75 – 1.06	0.89	109/108	0.75 – 1.01	0.84
M3	0.45 – 0.80	0.60	34	0.59 – 0.78	0.65
m1	0.82 – 1.18	1.00	181/185	0.64 – 0.89	0.74
m2	0.82 – 1.13	0.97	197/199	0.66 – 0.94	0.78
m3	0.71 – 0.94	0.79	100	0.54 – 0.82	0.68

Oligocene-Miocene transition (C1–D):

- Hotuliin Teeg: HTS-056/1+2: 1 M1r, 1 mand. m2–3l, 1 m1r, 1 m3l (NHMW 2013/0225/0001–0004).
- Tatal Gol: TAT-E/32: 1 mand. m1–3l, 3 m1l, 1 m2l, 3m2r (NHMW 2013/0226/0001–0008).

Early Miocene (biozone D):

- Hotuliin Teeg: HTE-003: 1 P4r, 1 m2r, 1 m2l (NHMW 2013/0227/0001–0003); HTE-014–018: 2 m1l, 1 m1r, 1 mand. m2–3r (NHMW 2013/0228/0001–0004).

Description (Figs 18/1–23): Very small-sized buno-lophodont molars; P4 with one cusp, surrounded by a cingulum; M1–2 almost square, with single protoloph and metaloph, and long mesoloph (most specimens); metaloph of M1 joins the hypocone; metaloph of M2 joins the entoloph anterior to the hypocone; M3 smallest upper molar, with varying structures; m1–2 rectangular; m1 with anteroconid, long mesolophid and longitudinal or slightly oblique ectolophid; m2 with long mesolophid or a long posterior arm of protoconid (pseudomesolophid); P4 with one root; M1–2 with rarely three, mostly four roots; M3 with three roots; m1–3 with two roots.

Remarks: The dental characters of the Mongolian specimens agree with the diagnosis of *Bohlinosminthus* Lopatin, 1999. *Parasminthus* Bohlin, 1946 (*Parasminthus tangingoli*, *Parasminthus asiaecentralis* and *Parasminthus debruijni*) differs by significantly larger tooth sizes, the double protoloph of M2, and the metaloph of M1 joining the posterior arm of hypocone or the posteroloph. Hence, we follow Lopatin (1999) to transfer *Parasminthus parvulus* to the genus *Bohlinosminthus*.

Bohlinosminthus parvulus has been recovered from thirtyone fossil layers out of twelve sections of the Tataatsiin Gol and Taatsiin Tsagaan Nuur area (Mongolia). There, the species ranges from the Early Oligocene to the Early Miocene. The main time of distributions is the Late Oligocene (biozones C and C1). Only rare occurrences are present from the Early Oligocene (biozones A and B) and the Early Miocene (biozone D). These more than eighthundred jaws and isolated teeth from Mongolian sites are in agreement with the size ranges and tooth structures of *Bohlinosminthus parvulus* from the type locality Gansu in China (Bohlin 1946; Wang & Qiu 2000; Wang 2003) and parts of *Bohlinosminthus parvulus* from Ulantatal in China (Huang 1992). Parts of *Bohlinosminthus parvulus* from Ulantatal most probably belong to *Parasminthus tangingoli* because of the typical *Parasminthus*-pattern and larger size (Wang & Qiu 2000: 19). The majority of M1 and M2 from Mongolia have four roots (Figs 18/15–16), *i.e.*, the specimens from the Late Oligocene and Early Miocene, and the majority of m2 (Figs 18/20, 22) displays either a long mesolophid or a long posterior arm of protoconid. These two types of m2 frequently co-occur in one assemblage. However, sporadically atypical specimens have been found from the Early Oligocene fossil sites in Mongolia: M1 with three roots (Figs 18/13–14: lingual root wide, tips can be split), and some scattered m2 with mesolophid+posterior arm of protoconid (Fig. 18/21). Although the rich Mongolian fossil

material displays these variable dental characters, only one species, *Bohlinosminthus parvulus*, could be verified with confidence.

So far three species, *Bohlinosminthus parvulus*, *Bohlinosminthus cubitalus* and *Bohlinosminthus quartus*, have been described, which are similar in size and dental pattern. Nevertheless, WANG (2003) and LOPATIN (1999) emphasize the following differences:

Bohlinosminthus parvulus (BOHLIN, 1946) from the type locality Tabenbuluk and Danghe area (Gansu, China): m2 has only a posterior arm of protoconid, no mesolophid (WANG 2003: 41).

Bohlinosminthus cubitalus LOPATIN, 1999 from Altynchokysu (Kazakstan): m2 has a mesolophid connected with mesostylid in most specimens; closed entosinus of M3 (LOPATIN 1999: 435–436).

Bohlinosminthus quartus (SHEVYREVA, 1970) from Kazakhstan has slightly larger teeth than *Bohlinosminthus parvulus* and *Bohlinosminthus cubitalus*, and its m2 has a posterior arm of protoconid (LOPATIN 1999: 435).

However, it remains questionable whether *Bohlinosminthus cubitalus* LOPATIN, 1999 and *Bohlinosminthus quartus* (SHEVYREVA, 1970) are independent species.

Genus *Litodonomys* WANG & QIU, 2000

Type species: *Litodonomys huangheensis* WANG & QIU, 2000

Type locality: GL9601B in Shangxigou, Lanzhou Basin, China; Late Oligocene.

Type material: Eight isolated lower teeth (1 m1, 3 m2, 4 m3) from the type locality

Original diagnosis of *Litodonomys*: "Medium-sized dipodoid**;** cheek teeth proportionally wide and short, with simple occlusal pattern and compressed main cusps; on lower molars posterior arm of protoconid absent, mesolophid short and oblique antero-buccally or absent, ectolophid obliquely extending from protoconid to anterior arm of hypoconid; m1 with distinct metastylid; m2 with only four transverse lingual lophids; m3 reduced with fused hypolophid and posterolophid."(WANG & QIU 2000: 25).

The Mongolian collection comprises partial skulls and complete tooth-rows of the upper and lower dentition of *Litodonomys huangheensis*. Therefore an emended diagnosis is given here.

Emended diagnosis: Rostrum of skull short and wide; diastema between I and P4 longer than the maxillar tooth-row; incisiv foramina long and narrow with the posterior edge anterior to P4; maxillar tooth-row posterior to the zygomatic plate; no masseteric tubercle, but a curved crest for insertion of the masseter on the zygma; premaxillary-maxillary sutur immediately anterior to this crest. Lower jaw: robust, mandibular ramus high; diastema concave; masseteric fossa extends to below m1.

Molars: Low-crowned molars with plane occlusal surface; lophodont robust molars, having thick enamel; elevation of crests as high as weak cusps; paracone and protocone of M1–3 transversely aligned; M1–2 almost square, m1–2 rectangular, M3/m3 short and triangular; protoloph I of M1–M2 single; hypocone of M1–2 in postero-lingual position; protocone postero-lingually elongate; entoloph/ectolophid and sinus/sinusid oblique; upper incisors without longitudinal groove; M1–2 four roots; M3 three roots; m1–3 two roots.

Referred species / type localities:

- *L. huangheensis* Wang & Qiu, 2000 from GL9601B in Shangxigou (China); Late Oligocene.
- *L. lajeensis* (Li & Qiu, 1980) from Xiejia, Xining Basin (China); Early Miocene.
- *L. minimus* Kimura, 2010 from Gashunyinadege, Nei Mongol (China); Early Miocene
- *L. xishuiensis* Wang, 2003 from Xishuigou, Gansu (China); Early Miocene.

Litodonomys huangheensis Wang & Qiu, 2000

(Figs 19/1–3, 20/1–5, Tab. 15)

1999 Zapodidae n.g. n.sp. (p. p.) – Höck *et al.*: p. 118.
2000 *Lithodonomys huangheensis* sp. nov. – Wang & Qiu: 11, 25–27, pl. 3, figs 9–12.
2007 *Litodonomys* sp.1 – Daxner-Höck & Badamgarav: 17, tab. 2.
2010 *Litodonomys* sp.1 – Daxner-Höck *et al.*: 358, tab. 4.

Type locality: Shangxigou (Gansu, China); Late Oligocene.

Diagnosis: Same as the genus (Wang & Qiu 2000: 26) and emended diagnose (above). Mesoloph and mesolophid absent or very short.

Occurrences of *Litodonomys huangheensis* in Mongolia (Valley of Lakes, Uvurkhangai): Late Oligocene to Early Miocene.

Material studied:

Late Oligocene (biozone C):

- Taatsiin Gol: TGR-C/1: 1 M1r (NHMW 2013/0229/0001; *Litodonomys* cf. *huangheensis*).

Table 15. Measurements of *Litodonomys huangheensis*.

	Length (mm)			Width (mm)	
	range	mean	N = 45	range	mean
P4	0.31 – 0.45	0.40	5	0.45 – 0.59	0.54
M1	1.29 – 1.44	1.30	8/9	1.22 – 1.34	1.30
M2	1.06 – 1.29	1.22	8	1.13 – 1.36	1.29
M3	0.73 – 0.80	0.76	4	0.89 – 1.04	0.97
m1	1.22 – 1.46	1.36	10	0.87 – 1.13	0.99
m2	1.25 – 1.39	1.35	5/4	1.06 – 1.18	1.11
m3	0.92 – 1.01	0.94	4	0.87 – 1.01	0.92

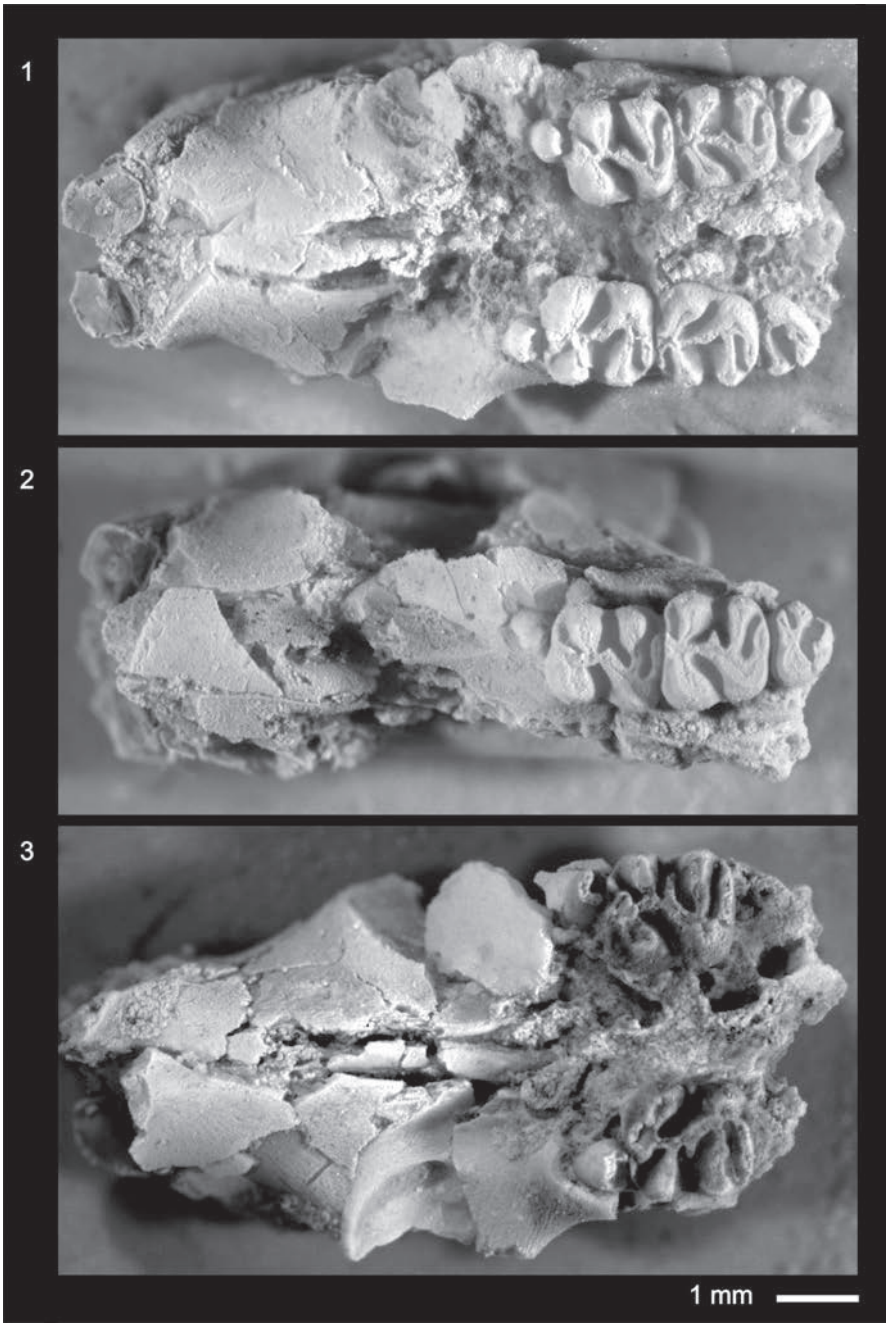


Fig. 19. *Litodonomys huangheensis* WANG & QIU, from Unkheltseg (UNCH-A/3), the Valley of Lakes, Mongolia. Early Miocene (biozone D). All specimens from the NHMW collection. **1**: partial skull with left and right tooth-rows (NHMW 2013/0232/0001). **2**: partial skull with left tooth-row (NHMW 2013/0232/0002). **3**: partial skull with left and right P4–M1 (NHMW 2013/0232/0003).

Late Oligocene (biozone C1):

- Loh: LOH-C/1: mand. m1–2l (NHMW 2013/0230/0001).

Oligocene- Miocene transition (biozone C1–D)

- Tatal Gol: TAT-E/32: m1r (NHMW 2013/0231/0001).

Early Miocene (biozone D):

- Unkheltseg: UNCH-A/3: partial skull with I, P4–M3 l+r (NHMW 2013/0232/0001), partial skull with I, P4–M3 l (NHMW 2013/0232/0002), partial skull with P4–M1 l+r (NHMW 2013/0232/0003), 2M1r (NHMW 2013/0239/0012–0013), 2 M2l (NHMW 2013/0232/0014–0015), 2 mand. m1–3r (NHMW 2013/0232/0004–0005), 1 mand. m1–3l (NHMW 2013/0232/0006), 4 m1r (NHMW 2013/0232/0007–0010), 1 m3r (NHMW 2013/0232/0014).
- Hotuliin Teeg: HTE-005: M1r, M1l fr., (NHMW 2013/0234/0001–0002), M2l, M3l, m2l, (NHMW 2013/0235/0001–0003; *Litodonomys* cf. *huangheensis*); HTE-008: m1r (NHMW 2013/0236/0001); HTE-003: 1 M2r (coll. MPC; *Litodonomys* cf. *huangheensis*).

Description: There are three fragmentary, strongly deformed skulls which preserve parts of the maxilla and the premaxilla bones and the tooth rows.

Skull 1 (NHMW 2013/0232/0001: Fig.19/1): displays left and right tooth rows with I, P4, M1–3.

Skull 2 (NHMW 2013/0232/0002: Fig. 19/2): the rostrum with the fragmentary left and right incisors and the left M1–3.

Skull 3 (NHMW 2013/0232/0003: Fig. 19/3): parts of praemaxilla and maxilla with fragmentary incisors and left and right P4–M1. Rostrum of skulls 1–3 short and wide; diastema (5–6 mm between I and P4) longer than P4–M3; incisiv foramina 2–3 mm long and narrow, extending from 2 mm posterior to the incisors to 1 mm anterior to P4; tooth-rows not extending as far as the zygomatic plate; no masseteric tubercule at the anteromedial margin of the zygma, but a curved crest for insertion of the masseter lateralis superficialis (skull 3: Fig. 19/3); premaxillary-maxillary sutur immediately anterior to this crest.

Mandible (Fig. 20/5): robust with a concave diastema almost as long as the mandibular toothrow; mandibular ramus high; masseteric fossa extending to below m1; mental foramen below the anterior root of m1, approximately halfway between the dorsal and the ventral edge of the ramus.

Upper I: plane to slightly convex, but smooth anterior surface.

P4 (Figs 19/1, 3): relatively small; one main cusp and a single root; cusp tilting backwards; can be associated by a weak postero-labial cusp or circled by a posterior cingulum.

M1 (Figs 19/1–3, Fig. 20/1): almost square, slightly longer than wide; labial cusps transversely elongate; protocone postero-lingually elongate; hypocone in postero-lingual

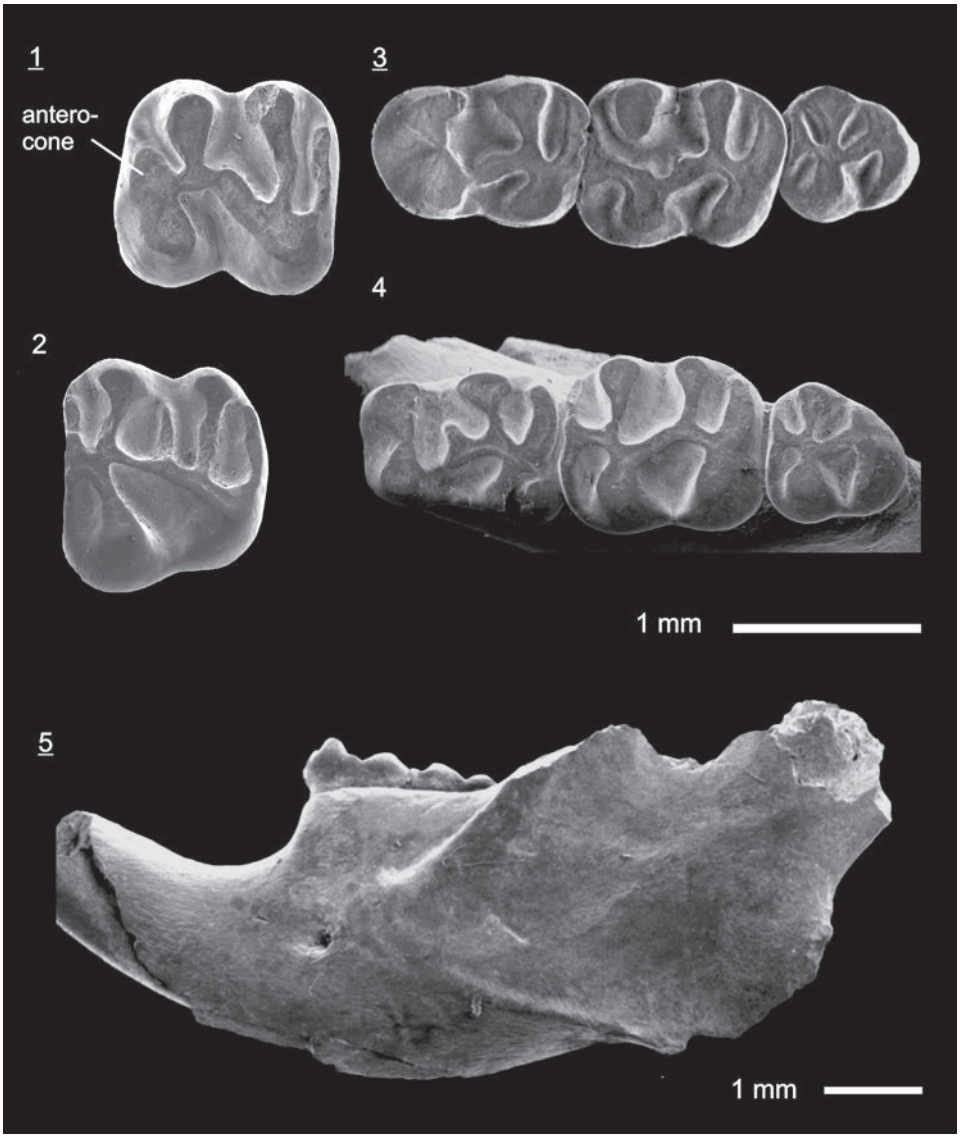


Fig. 20. *Litodonomys huangheensis* WANG & QIU, 2000 from Unkheltseg (UNCH-A/3), Valley of Lakes, Mongolia. Early Miocene (biozone D). All specimens from the NHMW collection. **1**: right M1 (NHMW 2013/0232/0007). **2**: left M2 (NHMW 2013/0232/0008). **3**: right lower jaw with m1–3, occlusal view (NHMW 2013/0232/0005). **4**: left lower jaw with m1–3, occlusal view (NHMW 2013/0232/0006). **5**: right lower jaw, labial view (NHMW 2013/0232/0004).

position; oblique entoloph extending from hypocone to protoloph; protocone continuous with pronounced anterocone; weak parastyle in some specimens; protoloph attaching the entoloph posterior to protocone; protocone-entoloph connection may be constricted; metaloph connected with entoloph anterior to hypocone; mesoloph absent or very short;

weak mesocone in some specimens; sinus oblique and strongly directed forward; central fossette (II+III) wide; posterior fossette (IV) narrow; long transverse posteroloph, its connection with hypocone may be constricted.

M2 (Figs 19/1–2, 20/2): anteriorly wider than posteriorly; labial anteroloph longer than the lingual; protoloph slightly directed forward; transverse metaloph connected with entoloph anterior to hypocone; mesoloph absent, short or of medium length; sinus oblique, directed forward; entoloph oblique.

M3 (Figs 19/1–2): short tooth; protoloph and metaloph surrounding the wide fossette II+III; posteroloph weak or fused with metaloph; entoloph absent or weak.

m1 (Figs 20/3–4): trigonid wide; robust metaconid and protoconid dominating; anteroconid extremely small or absent; sometimes small mesostylid; entoconid anterior to hypoconid; hypolophid connected with anterior arm of the hypoconid or with ectolophid anterior to hypoconid; ectolophid oblique, can be continuous, constricted or interrupted anterior to mesoconid; robust lingual posterolophid can be isolated from the hypoconid; labial posterolophid short or absent; sinusid wide, obliquely directed in posterior direction; central fossettid (II+III) wide.

m2 (Figs 20/3–4): mesolophid absent or extremely short; mesoconid weak or absent; entoconid anterior to hypoconid; hypolophid transverse, connected with anterior arm of hypoconid or the ectolophid; ectolophid oblique and complete; metalophid absent or attached to the anterior arm of protoconid; anterolophid labial and lingual; posterolophid continuous with hypoconid; sinusid and the fossettid II+III wide.

m3 (Figs 20/3–4): smallest of all mandibular molars; labial and lingual anterolophid; metaconid and protoconid in opposing position; metalophid transverse and attaching protoconid; ectolophid short; entoconid and hypolphid absent; weak hypoconid continuous with posterolophid.

Remarks: The dental pattern and tooth sizes of the Mongolian fossils agree well with *Litodonomys huangheensis*. *Litodonomys xishuiensis* has similar molar morphology, but significantly larger size. *Litodonomys lajeensis* and *Litodonomys minimus* differ by pronounced slender lophs/lophids, the distinct mesoloph(id) of M1–2 and m1, and by the presence of an anteroconid of m1.

So far, *Litodonomys huangheensis* was known from the Late Oligocene of China only:

1. GL9601B in Shangxigou (type locality) and GL 9513C in Xiagou, Lanzhou Basin, Gansu, China (Wang & Qiu 2000), Late Oligocene.

2. DH 199904D, Yantandu (Yindirte), Danghe area, Gansu, China (Wang 2003: 96, 102, fig. 4; *Litodonomys* cf. *huangheensis*), Late Oligocene.

In Mongolia, the species is documented from several fossil layers of five localities. There, the main distribution is Early Miocene (biozone D), with rare first occurrences from the Late Oligocene (biozones C and C1).

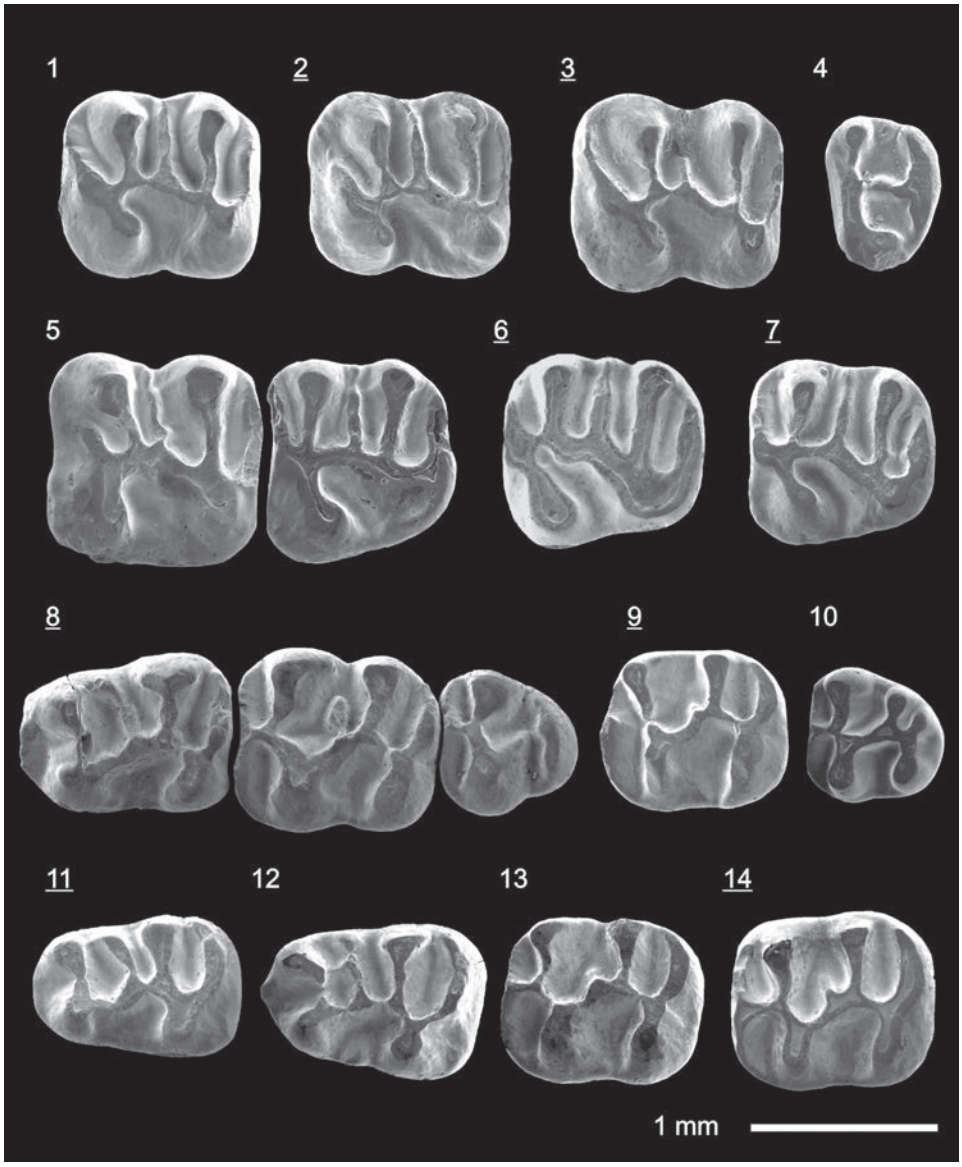


Fig. 21. *Litodonomys lajeensis* LI & QIU, 1980 from Hotuliin Teeg (HTE-005–012), Huch Teeg (RHN-A/12) and Unkheltseg (UNCH-A/3) in the Valley of Lakes, Mongolia. Early Miocene (biozone D). All specimens from the NHMW collection. **1**: left M1 (NHMW 2013/0248/0001) from HTE-012. **2**: right M1 (NHMW 2013/0242/0013) from UNCH-A/3. **3**: right M1 (NHMW 2013/0242/0012) from UNCH-A/3. **4**: left M3 (NHMW 2013/0242/0017) from UNCH-A/3. **5**: left M1–2 (NHMW 2013/0247/0001) from HTE-005. **6**: right M2 (NHMW 2013/0249/0003) from RHN-A/12. **7**: right M2 (NHMW 2013/0242/0015) from UNCH-A/3. **8**: right m1–3 (NHMW 2013/0246/0001) from HTE-007. **9**: right m2 (NHMW 2013/0247/0002) from HTE-005. **10**: left m3 (NHMW 2013/0242/0011) from UNCH-A/3. **11**: right m1 (NHMW 2013/0242/0004) from UNCH-A/3. **12**: left m1 (NHMW 2013/0242/0006) from UNCH-A/3. **13**: left m2 (NHMW 2013/0242/0008) from UNCH-A/3. **14**: right m2 (NHMW 2013/0242/0007) from UNCH-A/3.

Litodonomys lajeensis (Li & Qiu, 1980)

(Figs 21/1–14, Tab. 16)

1980 *Plesiosminthus lajeensis* – Li & Qiu: 204–205, 212; fig. 6.
1999 Zapodidae n.g.n.sp. (p.p.) – Höck *et al.*: 118.
2007 *Litodonomys* sp. 2 – Daxner-Höck & Badamgarav: 17, tab. 2.

Type locality: Xiejia, Xining Basin (China); Early Miocene.

Diagnosis: "Typical lophodont, with five transverse crests; mesocone and mesostyle distinct; mesoloph developed; inner valley more narrow point far forward; anterior cingulum weaker, anterosinus very small; posterosinus long, enclosed by the posterior cingulum and posteroloph" (Li & Qiu, 1980: 204, 212; fig.6).

Remarks: *Plesiosminthus lajeensis* Li & Qiu, 1980 will be transferred to *Litodonomys* because the dental characters and the shape of the type specimen are in agreement with the genus *Lithodonomys* rather than with *Plesiosminthus*. The type material from Xiejia (China) is limited to one M2. Nevertheless, it is a valid species. Five assemblages from Mongolia yielded mandibles and numerous isolated upper and lower molars (the material includes fourteen M2), which resemble the holotype in morphology and size. Because of the poor record of the type material, an emended diagnosis of the species is given.

Emended diagnosis: Mandibular ramus high; diastema concave; mental foramen below the anterior root of m1; low crowned lophodont cheek-teeth with plane occlusal surface; upper and lower molars display weak cones/conids, but pronounced lophs/lophids, which are equal in elevation; protoloph of M1–2 single; mesoloph(id) of M1–2 and m1 of long or medium length; mesolophid of m2 of medium length or short; anteroconid of m1 pronounced or weak; entoloph/ectolophid and sinus/sinusid oblique; M3/m3 short and of simplified pattern; M1–2 four roots; M3 three roots; m1–3 two roots.

Occurrences of *Litodonomys lajeensis* in Mongolia (Valley of Lakes, Uvurkhangai): Late Oligocene to Early Miocene.

Table 16. Measurements of *Litodonomys lajeensis*.

	length (mm)			width (mm)	
	range	mean	N = 82	range	mean
P4		0.47	1		0.61
M1	1.15 – 1.36	1.27	13	1.01 – 1.27	1.20
M2	1.11 – 1.32	1.20	14	1.01 – 1.32	1.19
M3	0.71 – 0.89	0.78	4	0.80 – 1.15	0.98
m1	1.18 – 1.58	1.31	20/21	0.80 – 1.08	0.88
m2	1.06 – 1.41	1.24	20/21	0.85 – 1.22	1.01
m3	0.78 – 0.95	0.86	8/7	0.73 – 0.92	0.82

Material studied:

Late Oligocene (biozone C1):

- Tatal Gol: TAT-E/27: m1–2r frag. (NHMW 2013/0237/0001); TAT-051/2: 1 M2r, 1 M3l (NHMW 2013/0238/0001–0002), TAT-043: 1 M1r (NHMW 2013/0239/0001; *Litodonomys* cf. *lajeensis*).

Oligocene-Miocene transition (biozone C1–D):

- Tatal Gol: TAT-E/32: m1–3r, M1r, 2 M2r (NHMW 2013/0240/0001–0004).
- Hotuliin Teeg: HTS-056/1+2: 1 M2r, 1 M1r, 1 m1r, 1 m1l (NHMW 2013/0241/0001–0004.

Early Miocene (biozone D):

- Unkheltseg: UNCH-A/3: 1 mand. m1r (NHMW 2013/0242/0001), 1 mand. m2r (NHMW 2013/0242/0002), 1 mand. m1r (NHMW 2013/0242/0003), 1 m1r (NHMW 2013/0242/0004), 2 m1l (NHMW 2013/0242/0005–0006), 1 m2r (NHMW 2013/0242/0007), 2 m2l (NHMW 2013/0242/0008–0009), 1 mand. m2–3l (NHMW 2013/0242/0010), 1 m3l (NHMW 2013/0242/0011), 2 M1r (NHMW 2013/0242/0012–0013), 2 M2l (NHMW 2013/0242/0014, 0016), 1 M2rl (NHMW 2013/0242/0015), 1 M3l (NHMW 2013/0242/0017).
- Hotuliin Teeg: HTE-005: 4 m1r, 3 m1l, 2 m2r, 2 m2l, 4 m3r, 2 M1l, 1 M1r, 2 M2r, 1 M3l, 1 m1r, 1 m2–fragm, P4–M1l, 1 m2r, 1 M2l (NHMW 2013/0243/0001–0024); HTE-014–018: 1 m1r, 1 m1l, 1 m2l (coll. MPC); HTE-003: 3 m2l, m2r, m1–2l, 1 m3r, 1 M1l, 1 M2l, P (coll. MPC), m1–2l, 1 M2l (coll. MPC; *Litodonomys* cf. *lajeensis*); HTE-007: mand. m1–3r (NHMW 2013/0246/0001); HTE-012: 2 M1l (NHMW 2013/0248/0001–0002).
- Huch Teeg: RHN-A/12: 1 m2r, 2 m2l, 1 M1r, 2 M2r (NHMW 2013/0249/0001–0006).
- Luugar Khudag: LOG-A/1: 1 m1r, 1 M1l (NHMW 2013/0250/0001–0002).

Description: M1 (Figs 21/3, 5): slightly longer than wide; narrowest behind paracone and protocone; labial cusps transversely elongate; protocone postero-lingually elongate; hypocone in postero-lingual position; oblique entoloph extending from the hypocone to the protoloph; protocone continuous with anteroloph; single protoloph attaching the entoloph posterior to the protocone; metaloph attaching the entoloph at or anterior to the hypocone; mesoloph long or of medium length; sinus oblique and strongly directed forwards; posterior fossette narrow; long posteroloph transverse; its connection to the hypocone may be constricted.

M2 (Figs 21/5–7): resembles M1; widest in the anterior, narrow in the posterior part; labial anteroloph stronger than lingual one; protoloph single; mesoloph mostly long.

M3 (Fig. 21/4): reduced in its longitudinal direction; similar to *L. huangheensis.*

m1(Figs 21/8, 11–12): trigonid narrow; metaconid and protoconid slender; anteroconid pronounced or weak; mesolophid long and straight; sometimes small mesostylid and/or

mesoconid present; entoconid anterior to hypoconid; hypolophid connected with anterior arm of the hypoconid; ectolophid oblique, can be continuous or constricted anterior and/or posterior to mesolophid; transverse posterolophid can be constricted close to hypoconid; sinusid wide, directed backward, oblique; central fossettid divided by pronounced mesolophid; posterior fossettid (IV) relatively wide.

m2 (Figs 21/8–9,13–14): mesolophid short or of medium length, sometimes curved; ectolophid oblique; weak mesoconid; entoconid anterior to hypoconid; hypolophid transverse, connected to ectolophid anterior to hypoconid; metalophid connected to anterior arm of protoconid; anterolophid labial and lingual; posterolophid continuous with the hypoconid; sinusid oblique, wide, directed backward.

m3 (Figs 21/8, 10): strongly reduced structures similar to *Litodonomys huangheensis*; smallest of all mandibular molars; labial and lingual anterolophid; metaconid and protoconid in opposing position; metalophid transverse, connected with protoconid; ectolophid short; entoconid and hypolphid weak or absent; weak hypoconid continuous with the posterolophid.

Remarks: Two *Litodonomys*-species, *Litodonomys huangheensis* and *Litodonomys lajeensis* have been documented from three localities in Mongolia (Unkhelt-seg, Hotuliin Teeg and Tatal Gol). *Litodonomys lajeensis* differs from *Litodonomys huangheensis* by: relatively slender molars, more delicate, transverse lophs/lophids, the longer mesoloph/mesolophid, narrow fossettes and the m1 having an anteroconid and a long mesolophid.

So far the genus *Litodonomys* comprises four species. Two species (*Litodonomys huangheensis* and *Litodonomys xishuiensis*) have rather simple tooth structures, as outlined above. The other two species (*Litodonomys lajeensis* and *Litodonomys minimus*) display the lophodont dental pattern, but overlap in size. It is worth mentioning, that dental pattern and size of *Xenosminthus zayssanensis* Lopatin & Zazhigin, 2000 from Kazakhstan is similar with both, *Litodonomys lajeensis* and *Litodonomys minimus*, however a revision of these species lies outside the scope of this paper.

Litodonomys lajeensis ranges from the Late Oligocene to the Early Miocene of China and Mongolia.

Genus *Shamosminthus* Huang, 1992

Type species: *Shamosminthus tongi* Huang, 1992

Dental characters: Upper and lower incisors without longitudinal groove; small to medium sized, low crowned, bunodont molars; pronounced cusps, weak crests.

M1–2 with pronounced mesocone and hypoconule; weak or interrupted entoloph; only one protoloph, short lingual and long labial posteroloph; small posterior sinus or posterior sulcus; metaloph of M1 frequently connected with posterior arm of hypocone; M1–2 with 3–4 roots.

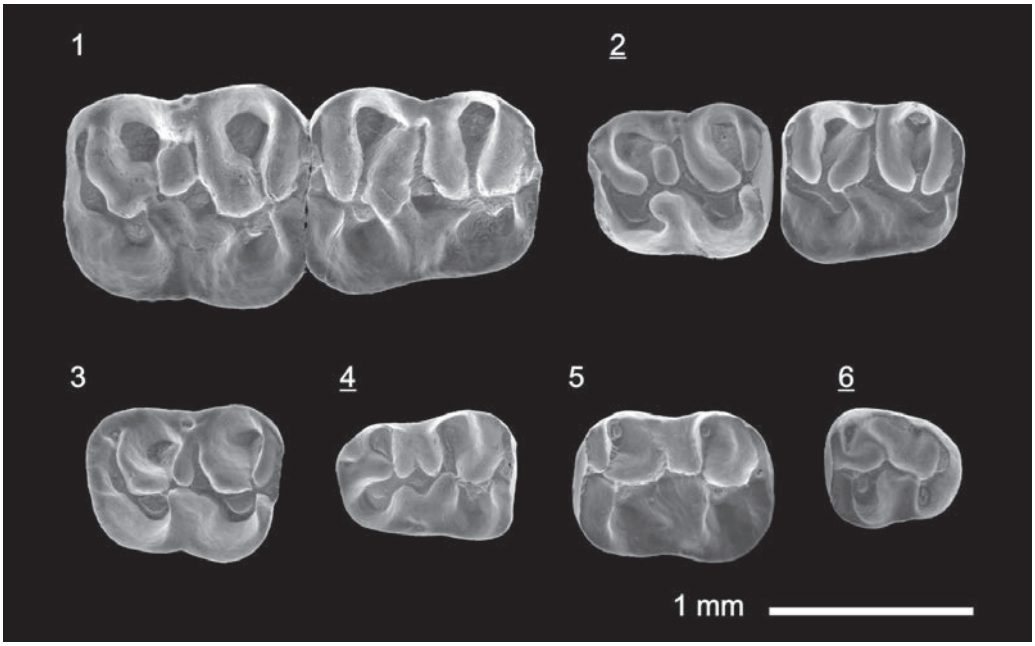


Fig. 22. *Shamosminthus* species from the Valley of Lakes, Mongolia. Early to Late Oligocene (biozones B to C). All specimens from the NHMW collection. **1**: *S. tongi* HUANG, 1992, left M1–2 (NHMW 2013/0251/0001) from Tatal Gol (TAT-055; biozone C). **2**–**6**: *S. sodovis* DAXNER-HÖCK, 2001; **2**: right M1–2 (NHMW 2001/0034/0003/1) from Taatsiin Gol (TGR-B/1; biozone B). **3**: left M1 (NHMW 2001/0034/0003/3) from Taatsiin Gol (TGR-B/1; biozone B). **4**: right m1 (NHMW 2001/0034/0003/13) from Taatsiin Gol (TGR-B/1; biozone B). **5**: left m2 (NHMW 2001/0034/0006/2) from Taatsiin Gol (TGL-A/11; biozone B). **6**: right m3 (NHMW 2001/0034/0003/16) from Taatsiin Gol (TGR-B/1; biozone B).

m1: anteroconid small or absent, mesolophid weak or absent, mesoconid and hypoconulid pronounced; ectolophid weak, longitudinal or slightly oblique, can be interrupted; labial posterior sinusid present; entoconid shifted in anterior direction.

Referred species and their type localities:

- *S. sodovis* DAXNER-HÖCK, 2001 from TGR-AB/22, Taatsiin Gol (Mongolia); Early Oligocene (biozone B).
- *S. tongi* HUANG, 1992 from Ulan Tatal, Nei Mongol (China); Late Oligocene.

Shamosminthus tongi HUANG, 1992
(Fig. 22/1)

1992 *Shamosminthus tongi* sp. nov. – HUANG: 283–284, pl. II, figs 5–6.

Occurrence of *S. tongi* in Mongolia (Valley of Lakes, Uvurkhangai): Tatal Gol: TAT-055: Late Oligocene (biozone C).

Material studied: left maxilla with M1–2 (NHMW 2013/0251/0001). Fig. 22/1. Measurements: M1 = 1.27 × 1.25 mm, M2 = 1.20 × 1.11 mm.

Description (Fig. 22/1): M1–2: of rectangular outline; four roots; single protoloph and metaloph; thickness and elevation of mesoloph decreases toward labial

M1: narrowest in its anterior part; strong anterior arm of protocone reaching the altero-labial edge; small anterocone; protoloph attaches the posterior arm of protocone; metaloph connected with posterior arm of hypocone, which connects the posteroloph right angled; mesoloph of medium length, attaches paracone-spur; entoloph constricted posterior to protocone; small isolated mesostyle; mesocone and hypoconule strong cusps; posterior sinus pronounced.

M2: narrowest in its posterior part; labial anteroloph; protoloph I connected with protocone; metaloph connected with anterior arm of hypocone; mesoloph in accordance with M1; entoloph interrupted before contacting protocone; sinus continuous with fossette II; posteroloph pronounced.

Remarks: So far, *Shamosminthus tongi* was documented only from Ulan Tatal (UTL 3, 4a+b, 8b; China). The Mongolian specimen is in agreement with the type species in size, dental morphology and with the Late Oligocene age.

Shamosminthus sodovis Daxner-Höck, 2001

(Figs 22/2–6, Tab. 17)

1997 *Shamosminthus* sp. 1. – Daxner-Höck *et al.*: 172.
1999 *Parasminthus* cf. *tangingoli*. – Höck *et al.*: 115.
2001 *Shamosminthus sodovis*. – Daxner-Höck: 366–367, pl. 3, figs 1–15, tabs 6–7.
2007 *Shamosminthus sodovis*. – Daxner-Höck & Badamgarav: 17, tab. 3.
2010 *Shamosminthus sodovis*. – Daxner-Höck *et al.*: 358, tab. 4.

Type locality: Taatsiin Gol (TGR-AB/22), Early Oligocene.

Table. 17. Measurements of *Shamosminthus sodovis* (including data from Daxner-Höck 2001: Tab. 7).

	length (mm)			width (mm)	
	range	mean	N = 145	range	mean
M1	0.95 – 1.20	1.09	42	0.80 – 0.98	0.90
M2	0.80 – 1.14	1.01	29/30	0.77 – 0.95	0.87
M3	0.59 – 0.75	0.66	3	0.66 – 0.70	0.68
m1	0.91 – 1.05	1.16	30	0.61 – 0.83	0.73
m2	0.93 – 1.20	1.08	24	0.70 – 0.95	0.90
m3	0.73 – 1.05	0.87	16	0.65 – 0.80	0.71

Holotype: Left maxilla with M1–2 (NHMW2001/0034/0001/1). Measurements: M1 = 1.06 × 0.92 mm, M2 = 1.01 × 0.85 mm.

Dental characters: (DAXNER-HÖCK 2001: 366–367, pl. 3, Figs 1–15): Small *Shamosminthus*-species with low crowned buno-lophdont molars; pronounced cusps; wide valleys and weak crests. Smooth anterior surface of upper incisors.

Maxilla: posterior extension of foramen incisivum as far as M1. Main cusps of upper molars in opposing position; mesocone and hypoconule pronounced.

Mandible: foramen mentale in dorsal position, close to the diastema, anterior to the root of m1; cuspids of lower molars slightly alternating, lingual pair of cuspids anterior to labial one; mesoconid and hypoconulid pronounced.

Occurrences of *Shamosminthus sodovis* in Mongolia (Valley of Lakes, Uvurkhangai): Early Oligocene (biozones A to B).

Material studied:

Early Oligocene (biozone A):

- Taatsiin Gol: TGR-A/13: jaws and molars (NHMW 2001/0034/0015/1–5); TGL-A/2: 3 molars (NHMW 2001/0034/0014/1–3).
- Tatal Gol: TAT-D/1: jaws and molars (NHMW 2001/0034/0012/1–9); TAT-C/1+2: 3 molars (NHMW 2001/0034/0013/1–3).

Early Oligocene (biozone B):

- Taatsiin Gol: TGR-AB/22: type material (NHMW 2001/0034/0001/1–10); TGR-AB/21: 20 molars (NHMW 2001/0034/0002/1–20); TGR-B/1: 20 jaws and molars (NHMW 2001/0034/0003/1–20); TGR-ZO/2: 4 molars (NHMW 2001/0034/0004/1–4); TGR-1564: 3 molars (NHMW 2001/0034/0005/1–3); TGL-A/11: 3 molars (NHMW 2001/0034/0006/1–3); Del: DEL-B/7: jaws and molars (NHMW 2001/0034/0007/1–12).
- Ikh Argalatyn Nuruu: IKH-A/1–4: 4 molars (NHMW 2001/0034/0010/1–4).
- Tatal Gol: TAT-038: 1 M1l, 1 m1l (coll. MPC); TAT-E/3: 1 M1r, 1 m1–2l, 1 m2r (coll. MPC).
- Unkheltseg: UNCH-A/3B: jaws and molars (NHMW 2001/0034/0011/1–40).

Description: M1 (Figs. 22/2–3): trapezoidal in occlusal outline; anterior arm of protocone long, occasionally ends in a small parastyle; anterior cingulum present or absent; protoloph II connected with posterior arm of protocone; metaloph connected with posterior arm of hypocone; mesoloph of medium length or long, can attach paracone-spur; narrow posterior sinus or postero-lingual sulcus between hypocone and posteroloph.

M2 (Fig. 22/2): protoloph I and metaloph connected with protocone and hypocone or their anterior arms, respectively; mesoloph long or of medium length, sometimes connected with paracone-spur; small posterior sinus or sulcus; entoloph weak or interrupted posterior to protocone.

M3: lophodont molar pattern; narrow labial valleys between lophs; entoloph can be interrupted.

m1 (Fig. 22/4): anteroconid small or absent; anterior main cusps in opposingposition, connected by v-shaped metalophid; entoconid shifted forward; mesolophid absent or weak; hypolophid connected with anterior arm of hypoconid, posterolophid most prominent lophid, with strong hypoconulid; posterior sinusid between hypoconid and hypoconulid; sinusid and fossettids wide and shallow; ectolophid short, in longitudinal direction or slightely oblique; ectostylid sometimes present; mesoconid pronounced.

m2 (Fig. 22/5): double anterolophid, anteroconid weak or strong; metalophid I short, connected with anteroconid; hypolophid connected with anterior arm of hypoconid; mesolophid of medium length, sometimes curved in anterior direction and attached with metaconid.

m3 (Fig. 22/6): resembles m2 in its anterior part; entoconid absent; mesolophid and hypolophid present or absent.

M1–2: three or four roots, M3 three roots, m1–3 two roots.

Remarks: *Shamosminthus sodovis* is smaller and has more primitive dental structures than the younger species *Shamosminthus tongi*. *Shamosminthus sodovis* is very well represented in Mongolia in rodent assemblages of the Early Oligocene (Hsanda Gol Fm. below and above basalt I).

Shamosminthus sp.

2001 *Shamosminthus* sp. – Daxner-Höck: 367–368, pl. 3, figs 16–17, tab. 6.

Occurrence in Mongolia (Valley of Lakes, Uvurkhangai): Early Oligocene (biozone B).

Hsanda Gol: SHG-AB/17–20: 1 M1r, 1 m1l (NHMW 2001/0035/0001/1–2).

Measurements: length × width (mm): M1: 1.18 × 0.93; m1: 1.30 × 0.80.

Remarks: Two molars from the upper part of the Hsanda Gol section (SHG-AB/17–20; uppermost Early Oligocene, biozone B) have more complicated dental structures than older ones. They are intermediate between *Shamosminthus sodovis* and *Heterosminthus* in morphology and size and are identified as *Shamosminthus* sp. (Daxner-Höck 2001: 367–368, pl. 3, figs 16–17).

Shamosminthus is thought to be stem group of *Heterosminthus* (Daxner-Höck 2001: 368). The first ocurrences of *Shamosminthus sodovis* in Mongolia (Early Oligocene, biozone A) exhibit small teeth with primitive structures, and three-rooted M1 (wide lingual root, partly with split tips). Later (Early Oligocene, biozone B) *Shamosminthus sodovis* and *Shamosminthus* sp. have slightly larger teeth and four rooted M1–2, finally, *Shamosminthus tongi* of the Late Oligocene (biozone C) has large teeth and four-rooted M1–2. Subsequently, the molar-pattern of *Heterosminthus* developed in the course of the Late Oligocene (biozone C1) and Early Miocene (biozone D).

Genus *Heterosminthus* SCHAUB, 1930

Type species: *Heterosminthus orientalis* SCHAUB, 1930

Type locality: Xiansuihe, Gansu (China); Middle Miocene.

Dental characters: Upper and lower incisors without longitudinal groove; small to medium sized bunodont molars of rectangular shape; M1–2 and m1–2 with four main cusps connected by weak crests; labial and lingual pair of cones(ids) alternate; entoconid shifted forward; ectolopohid of m1–2 of variable shape and length; protocone of M1–2 elongate forming a postero-lingual crest with or without protostyle; M1–2 four roots, M3 three roots, m1–3 two roots.

Referred species and their type localities:

- *H. erbajevae* LOPATIN, 2001 from Aya (Siberia); Middle Miocene.
- *H. firmus* ZAZHIGIN & LOPATIN, 2000 from Ayaguz (Kazakhstan); Early Miocene.
- *H. gansus* ZHENG, 1982 from Tianzhu (China); Late Miocene.
- *H. honestus* ZAZHIGIN & LOPATIN, 2000 from Batpaksunde (Kazakstan); Early Miocene.
- *H. intermedius* WANG, 2003 from Tiejianggou, loc. DH 199903 (China); Early Miocene.
- *H. jucundus* ZAZHIGIN & LOPATIN, 2000 from Zaisan Depression, point T. (Kazakstan); Middle Miocene.
- *H. lanzhouensis* WANG & QIU, 2000 from Shangxigou (China); Late Oligocene.
- *H. mongoliensis* ZAZHIGIN & LOPATIN, 2000 from Ulan Tolgoi (Mongolia); Early Miocene.
- *H. mugodzharicus* ZAZHIGIN & LOPATIN, 2000 from Shet-Irgiz (Kazakstan); Late Miocene.
- *H. nanus* ZAZHIGIN & LOPATIN, 2000 from Batpaksunde (Kazakstan); Early Miocene.
- *H. orientalis* SCHAUB, 1930 from Xiansuihe (China); Middle Miocene.

Heterosminthus firmus ZAZHIGIN & LOPATIN, 2000

(Figs 23/1–11, Tab. 18–19)

1997 *Shamosminthus* sp. 3. – DAXNER-HÖCK *et al.*: 173.
1999 *Heterosminthus* sp. 1. – HÖCK *et al.*: 118, text-fig. 21/2.
1999 *Heterosminthus* cf. *orientalis*. – HÖCK *et al.*: 118.
2000 *Heterosminthus firmus* sp. nov. – ZAZHIGIN & LOPATIN: 325–327, fig. 3.
2001 *Heterosminthus firmus*. – DAXNER-HÖCK: 368–370, pl. 4, figs 1–12, tabs 8–9.
2001 *Heterosminthus* cf. *firmus*. – DAXNER-HÖCK: 370, pl. 5, figs 5–16, tabs 10–11.
2001 *Heterosminthus* cf. *firmus* p.p. – DAXNER-HÖCK: 370–371, pl. 5, figs 1–4, tabs 8, 10.

Type locality: Ayaguz (Kazakstan); Early Miocene.

Occurrences of *Heterosminthus firmus* in Mongolia (Valley of Lakes, Uvurkhangai): Oligocene-Miocene transition (biozone C1–D) to Early Miocene (biozone D).

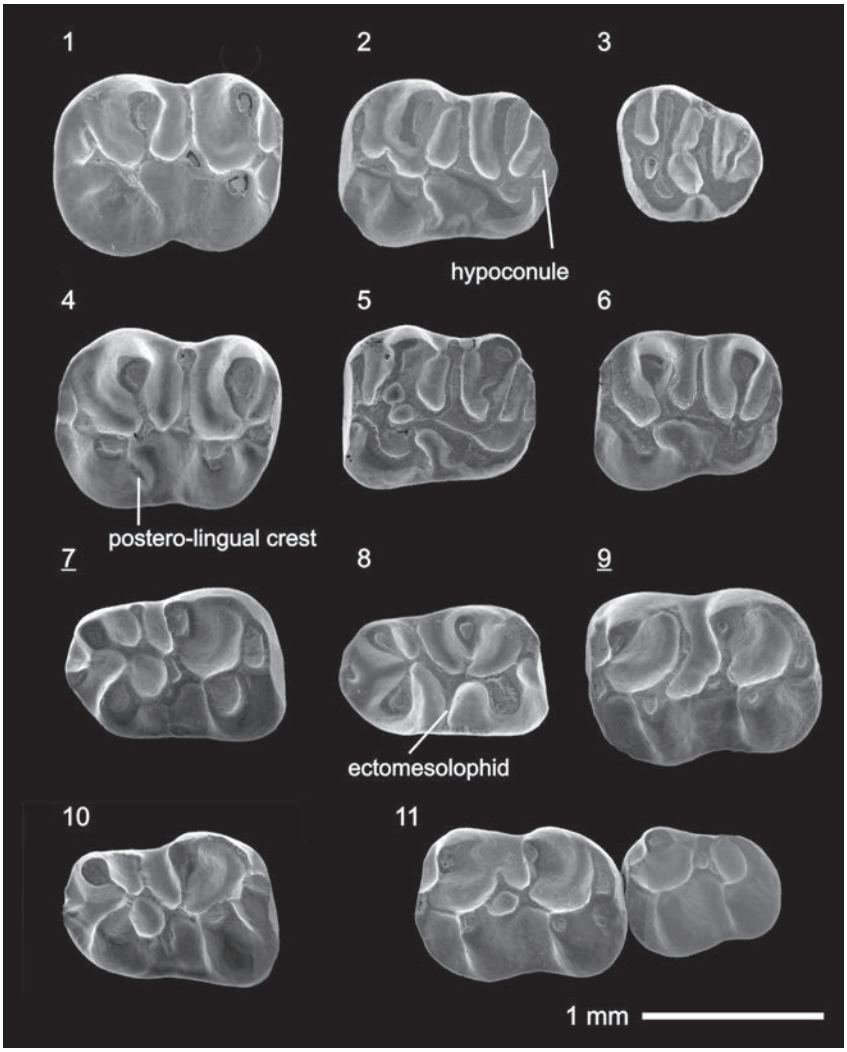


Fig. 23. *Heterosminthus firmus* Zazhigin & Lopatin, 2000 from Unkheltseg (UNCH-A/3) in the Valley of Lakes, Mongolia. Early Miocene (biozone D). All specimens from the NHMW collection. **1**: left M1 (NHMW 2001/0036/0001/1). **2**: left M2 (NHMW 2001/0036/0001/22). **3**: left M3 (NHMW 2001/0036/0001/36). **4**: left M1 (NHMW 2001/0036/0001/2). **5**: left M2 (NHMW 2001/0036/0001/31). **6**: left M2 (NHMW 2001/0036/0001/32). **7**: right m1 (NHMW 2001/0036/0001/55). **8**: left m1 (NHMW 2001/0036/0001/47). **9**: right m2 (NHMW 2001/0036/0001/73). **10**: left m1 (NHMW 2001/0036/0001/53). **11**: left m2–3 (NHMW 2001/0036/0001/84), AO (Daxner-Höck 2001: pl. 4/8).

Material studied:

Oligocene-Miocene transition (biozone C1–D):

- Hotuliin Teeg: HTS-056/1+2: 2 M1l, 1 M2l, 1 m2l, 1 m1r (NHMW 2013/0252/0001–0005):
- Huch Teeg: RHN-019: 1 m1r (NHMW 2013/0253/0001).

Early Miocene (biozone D):

- Hotuliin Teeg: HTE-014–018: 1 m2r, 2 m2l (coll. MPC); HTE-005: 1 M2r, 1 m2l, 1 M1l, 1 M1r, 1 m1r, 1 m1l, 1 m2r, 1 M1l, m1–2r, m2–3r (NHMW 2013/0254/0001–0010); HTE-007+008: 1 m1l, 1 m1r (NHMW 2013/0255/0001–0002).
- Unkheltseg: UNCH-A/3: div. upper and lower jaws (fragm.) and numerous molars (NHMW 2001/0036/0001/1–86; DAXNER-HÖCK 2001: 368, tab. 8), 5 specimens (coll. MPC).
- Huch Teeg: RHN-A/12: 9 molars (NHMW 2001/0037/0001/1–9; DAXNER-HÖCK 2001: 368, tab. 8).
- Luugar Khudag: LOG-A/1: 5 molars (NHMW 2001/0037/0002/2–5; DAXNER-HÖCK 2001: 368, tab. 8).

Occurrences of *Heterosminthus* cf. *firmus* in Mongolia (Valley of Lakes, Uvurkhangai): Late Oligocene (biozone C1).

Material studied:

- Loh: LOH-C/1: 1 m1 (NHMW 2001/0037/0003/1).
- Huch Teeg: RHN-A/7: 1 m1l, 1 m2r, 1 m3l (NHMW 2001/0037/0004/1–3); RHN-A/9: div. Inc. sup., 1 m1r, 1 m2r, 1 m2l (NHMW 2013/0258/0001–0003).
- Tatal Gol: TAT-E/22: 1 m1r (coll. UB); TAT-E/32: 1 m1r (coll. MPC).

Table 18. Measurements of *Heterosminthus firmus*.

	length (mm)			width (mm)	
	range	mean	N = 119	range	mean
M1	1.20 – 1.48	1.33	25	0.91 – 1.20	1.04
M2	1.09 – 1.36	1.23	24	0.80 – 1.02	1.00
M3	0.91 – 0.95	0.93	3	0.77 – 0.84	0.80
m1	1.16 – 1.45	1.30	35	0.77 – 1.01	0.88
m2	1.14 – 1.43	1.27	27	0.82 – 1.11	0.91
m3	0.89 – 1.07	1.00	5	0.73 – 0.84	0.97

Table 19. Measurements of *Heterosminthus* cf. *firmus*.

	length (mm)			width (mm)	
	range	mean	N = 7	range	mean
m1	1.35 – 1.60	1.44	4	0.92 – 1.15	1.05
m2	1.30 – 1.45	1.39	3	1.00 – 1.18	1.07

Description: Daxner-Höck (2001: 368–371; pl. 4–5, tab. 8–10).

M1 (Fig. 23/1, 4): rectangular in outline; rounded corners; widest in its anterior part and narrowest posterior to paracone and protocone; anterior arm of protocone long, sometimes ending in a weak parastyle, or short and connected with anterior cingulum; weak anterocone possible; postero-lingual crest of protocone varying from strong to weak, without protostyle; protoloph II and metaloph directed backward; protoloph II connected with entoloph; metaloph connected with posterior arm of hypocone or to hypoconule; mesoloph long, extending from mesocone to mesostyle; posteroloph with labial and lingual arm; posterior sinus present; entoloph short, continuous or interrupted anterior to its connection with protoloph II. Sinus directed forward.

M2 (Fig. 23/2,5): rectangular molar with narrow posterior part; protocone anterior to paracone; metacone and hypocone almost in opposing position; weak lingual, strong labial anteroloph; anterocone can be present; protocone with postero-lingual crest, but without protostyle; anterior arm of protocone short and with free end, or connected with anteroloph or connected with paracone (protoloph I); protoloph II connected with entoloph; metaloph connected with hypocone or its anterior arm; mesoloph long, rarely of medium length; labial posteroloph dominates; hypoconule weak or strong; posterior sinus weak or absent; entoloph oblique; sinus directed forward.

M3 (Fig. 23/3): smallest tooth; five labial lophs and two lingual cusps; narrow fossettes between lophs; sinus shallow or absent.

m1 (Fig. 23/7,8,10): four main conids alternating; entoconid strongly shifted forward; anteroconid, mesoconid and hypoconulid strong, but lower than main conids; one or two small crests can connect anteroconid with metaconid or/and protoconid; metalophid V-shaped; short hypolophid connected with mesoconid just opposing to ectomesolophid; ectomesolophid can be long, short or absent; ectolophid curved in antero-lingual direction and connected with the posterior part of metalophid; mesolophid extends from mesoconid or from ectolophid (halfway between mesoconid and metalophid) toward lingual boarder; small labial crest can connect posterior part of protoconid and mesoconid; wide sinusid; posterior sinusid present.

m2 (Fig. 23/9, 11): widest lower molar; resembles m1; alternating main cusps, lingual cusps anterior to labial ones; double anterolophid; anterior arm of protoconid and metalophid I connected with anteroconid; posterior arm of protoconid curved forward and connected with metaconid or with mesolophid; mesolophid short or absent; mesoconid weak or absent; short ectolophid; strong lingual posterolophid with hypoconulid; anterior sinusid pronounced; sinusid wide; posterior sinusid weak or absent.

m3 (Fig. 23/11): smallest tooth; resembles m2; entoconid absent.

M1–2 with four roots, M3 with three roots, m1–3 with two roots.

Remarks: *Heterosminthus firmus* is very well represented from the localities Unkheltseg and Hotuliin Teeg (Early Miocene; biozone D) in Mongolia by numerous toothrows and isolated teeth, which show a wide range in size and dental characters. Some

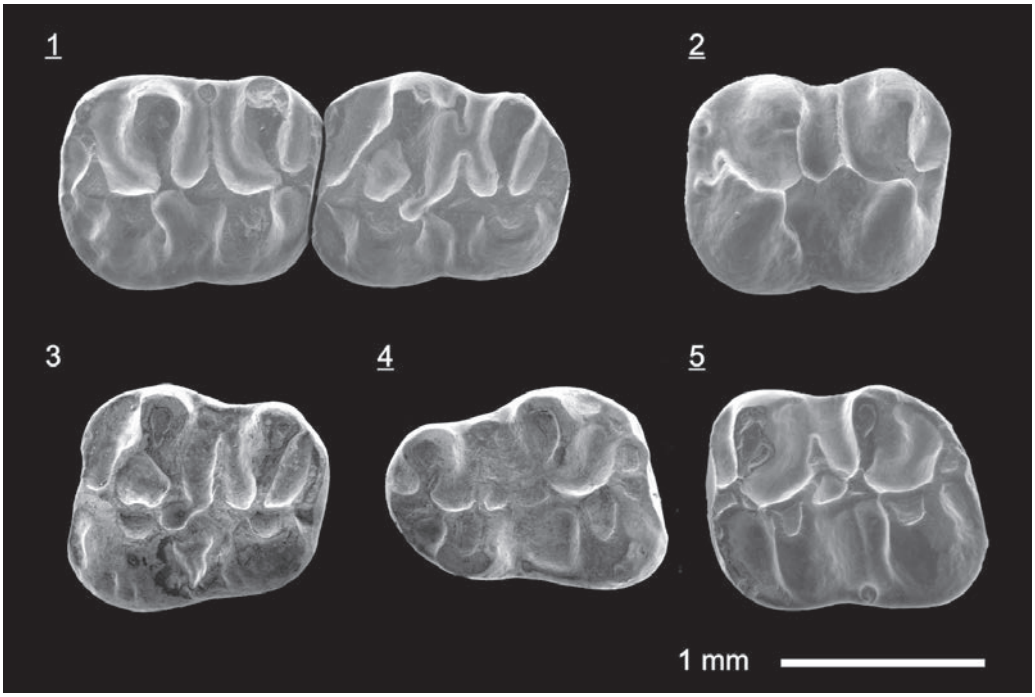


Fig. 24. *Heterosminthus* cf. *lanzhouensis* WANG & QIU, 2000 from the Valley of Lakes, Mongolia. Late Oligocene (biozone C1) to the Oligocene-Miocene transition (biozone C1–D). All specimens from the NHMW collection. **1**: right M1–2 (NHMW 2013/0259/0001) from Huch Teeg (RHN-021; biozone C1–D). **2**: right M1(NHMW 2012/0067/0001) from Huch Teeg (RHN-023; biozone C1). **3**: left M2 (NHMW 2013/0260/0001) from Hotuliin Teeg (HTS-056/1+2; biozone C1–D). **4**: right m1 (NHMW 2013/0260/0002) from Hotuliin Teeg (HTS-056/1+2; biozone C1–D). **5**: right m2 (NHMW 2013/0260/0003) from Hotuliin Teeg (HTS-056/1+2; biozone C1–D).

Late Oligocene (biozone C1) fossil horizons yielded isolated teeth, which are slightly larger than *Heterosminthus firmus*, otherwise their morphology seems to fit the variability described. We consequently refer this material as *Heterosminthus* cf. *firmus*.

Heterosminthus cf. *lanzhouensis* WANG & QIU, 2000

(Figs 24/1–5, Tab. 20)

2001 *Heterosminthus* cf. *firmus* p.p. – DAXNER-HÖCK: 370–371, pl. 5, figs 1–4, tabs 8, 10.

Type locality: GL 9601B Shanxigou, Lanzhou Basin (China). Late Oligocene.

Occurrences of *H.* cf. *lanzhuensis* in Mongolia (Valley of Lakes, Uvurkhangai): Late Oligocene to the Oligocene-Miocene transition (C1 to C1–D).

Late Oligocene (biozone C1):

- Huch Teeg: RHN-023: 1 M1r (NHMW 2012/0067/0001), Huch Teeg: RHN-023: P4–M2l (coll. MPC).

Oligocene-Miocene transition (biozone C1–D):

- Huch Teeg: RHN-021: M1–2r, 1 m2r (NHMW 2013/0259/0001–0002).
- Hotuliin Teeg: HTS-056/1+2: 1 M2l, 2 m1r, 2 m2l, 2 m2r (NHMW 2013/0260/0001–0007).

Description (Figs 24/1–5): Medium-sized bunodont molars of rectangular outline. Compared to other *Heterosminthus* species, the molars are relatively wide and short and display rather primitive dental structures. Cones/conids and loph(id)s robust. M1–2 with four roots; m1–2 with two roots.

P4: one cusp and a weak posterior cingulum.

M1 (Figs 24/1–2): pairs of labial and lingual cones in opposing position; anterior arm of protocone of medium length or long, extending to antero-labial edge or to anterior cingulum; anterocone present (Fig. 24/1) or absent; protocone with weak postero-lingual crest; protoloph connected with entoloph; entoloph constricted posterior to protocone; mesoloph long, extending to labial edge; metaloph connected with posterior arm of hypocone; posteroloph strong; weak hypoconule; postero-lingual sulcus/sinus between hypocone and hypoconule; sinus directed forward.

M2 (Figs 24/2–3): main cusps in opposing position; labial anteroloph strong, lingual anteroloph weak or absent; anterocone and mesocone present; double protoloph; protoloph I connected with anterior arm of protocone; protoloph II connected with protocone or posterior arm of protocone; postero-lingual crest of protocone connected with mesocone; mesoloph long or of medium length; metaloph connected with hypocone; posteroloph with weak hypoconule; weak postero-lingual sulcus between hypocone and hypoconule; sinus shallow.

m1 (Fig. 24/4): lingual pair of main cusps situated anterior to labial ones; anteroconid strong, isolated or connected with protoconid and metaconid by two strong crests (anterior arm of protoconid and metalophid I); posterior arm of protoconid absent, or strong and building metalophid II; mesolophid of medium length, oblique, attached to the posterior arm of protoconid or basal part of metaconid; short ectolophid extends from anterior hypoconid-arm forward to basal slope of protoconid; strong mesoconid situated at the middle part of ectolophid; posterolophid robust; hypoconulid shifted toward lingual.

Table 20. Measurements of *Heterosminthus* cf. *lanzhouensis*.

	length (mm)			width (mm)	
	range	mean	N = 13	range	mean
M1	1.44 – 1.48	1.46	3	1.20 – 1.32	1.20
M2	1.41 – 1.41	1.41	3	1.20 – 1.30	1.30
m1	1.44 – 1.48		2	1.08 – 1.13	
m2	1.41 – 1.60	1.49	5	1.18 – 1.22	1.20

m2 (Fig. 24/5): lingual pair of main conids situated anterior to labial ones; double anterolophid, labial branch stronger than lingual one; anteroconid, mesoconid and hypoconulid pronounced; metalophid I and anterior arm of protoconid connected with anteroconid; posterior arm of protoconid curved and connected with basal part of metaconid; oblique mesolophid attached to the posterior arm of protoconid or absent; ectolophid short; voluminous mesoconid; anterior part of ectolophid attaches posterior slope of protoconid; hypolophid connected with mesoconid or anterior arm of hypoconid; posterolophid and hypoconulid strong; sinusid directed backward; posterior sinusid weak or absent; anterior sinusid pronounced.

Remarks: *Heterosminthus* cf. *lanzhouensis* is evidenced by fragmentary jaws and isolated molars from three fossil layers of two localities in Mongolia. The occurrences range from the Late Oligocene to the Oligocene-Miocene transition. These teeth resemble *Heterosminthus firmus* and *Heterosminthus lanzhuensis*, but the average molar sizes exceed the values of both species. However, the length-width ratio of molars and certain primitive dental characters are similar to *Heterosminthus lanzhouensis*, so we identify these teeth as *Heterosminthus* cf. *lanzhouensis*.

Heterosminthus aff. *nanus* ZAZHIGIN & LOPATIN, 2000

(Figs 25/1–2, Tab. 21)

2001 *Heterosminthus firmus* p.p. – DAXNER-HÖCK: 368–370.

Type locality: Batpaksunde (Kazakhstan); Early Miocene.

Occurrences of *H.* aff. *nanus* in Mongolia (Valley of Lakes, Uvurkhangai): Early Miocene (biozone D).

- Hotuliin Teeg: HTE-014–018: m1–3r (NHMW 2013/0261/0001); HTE-005: 1 M1l (NHMW 2013/0262/0001).
- Unkheltseg: UNCH-A/3: 1 M2r, P4–M2r, M1–2r, 2 m2l, 1 m2r (NHMW 2001/0036/0001/77–78,80, 91–93).

Description (Figs 25/1–2): Smallest *Heterosminthus*-species with most primitive dental structures. Ungrooved upper incisor; molars rectangular in outline.

Table 21. Measurements of *Heterosminthus* aff. *nanus*.

	length (mm)			width (mm)	
	range	mean	N = 12	range	mean
M1	1.06 – 1.16	1.09	3	0.92 – 0.96	
M2		1.06	1/3	0.82 – 0.89	
m1		1.11	1		0.87
m2	1.08 – 1.15	1.12	4	0.82 – 0.89	0.86
m3		0.82	1		0.71

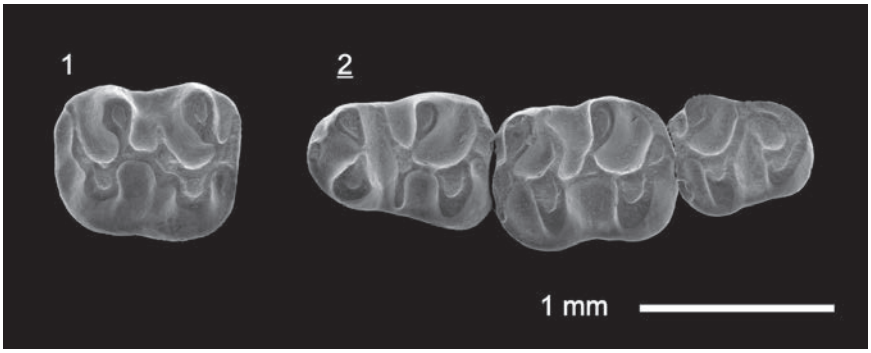


Fig. 25. *Heterosminthus* aff. *nanus* Zazhigin & Lopatin, 2000 from Hotuliin Teeg (HTE-005 and HTE-014–018) in the Valley of Lakes, Mongolia. Early Miocene (biozone D). All specimens from the NHMW collection. **1**: left M1 (NHMW 2013/0262/0001) from HTE-005. **2**: right m1–3 (NHMW 2013/0261/0001) from HTE-014–018.

M1 (Fig. 25/1): labial and lingual pair of main cones slightly alternating; anterior arm of protocone long, extending to labial corner; it can be connected with weak anterior cingulum; postero-lingual crest of protocone absent; protoloph II short, connected with entoloph; metaloph short, connected with hypoconule; mesoloph of medium length, connected with small mesocone; posteroloph strong with almost equal labial and lingual arms; hypoconule pronounced; posterosinus present; sinus wide, directed forward.

M2: labial anteroloph strong, lingual one weak or absent; protoloph II connected with entoloph close to mesocone; metaloph connected with entoloph halfway between mesocone and hypocone; mesoloph long, extending from mesocone toward abial edge; posteroloph extending from hypocone to postero-labial part of metacone; hypoconule and posterior sinus absent; sinus directed forward.

m1 (Fig. 25/2): slender, low crowned molar; metaconid and protoconid in opposing position, connected by a weak metalophid; anteroconid isolated; entoconid shifted forward; ectolophid extremely short, interrupted anterior to mesoconid; mesolophid and ectomesolophid long, extending to lingual and labial edge, respectively; hypolophid connected with mesoconid; posterolophid strong; hypoconulid shifted toward lingual.

m2 (Fig. 25/2): labial pair of main conids posterior to lingual ones; labial anterolophid present; lingual anterolophid weak or absent; metalophid I connected with strong anteroconid; posterior arm of protoconid curved, connected with basal part of metaconid; mesolophid absent; ectolophid short; strong or weak mesoconid situated in the middle part of ectolophid; hypolophid connected with mesoconid; posterolophid strong, with hypoconulid; sinusid symmetrical; anterior sinusid present.

m3 (Fig. 25/2): three main conids of equal size; two anterolophid-arms connected with anteroconid; short metalophid connected with anteroconid; posterior arm of protoconid long, extending obliquely toward lingual edge, where it attaches to the posterolophid;

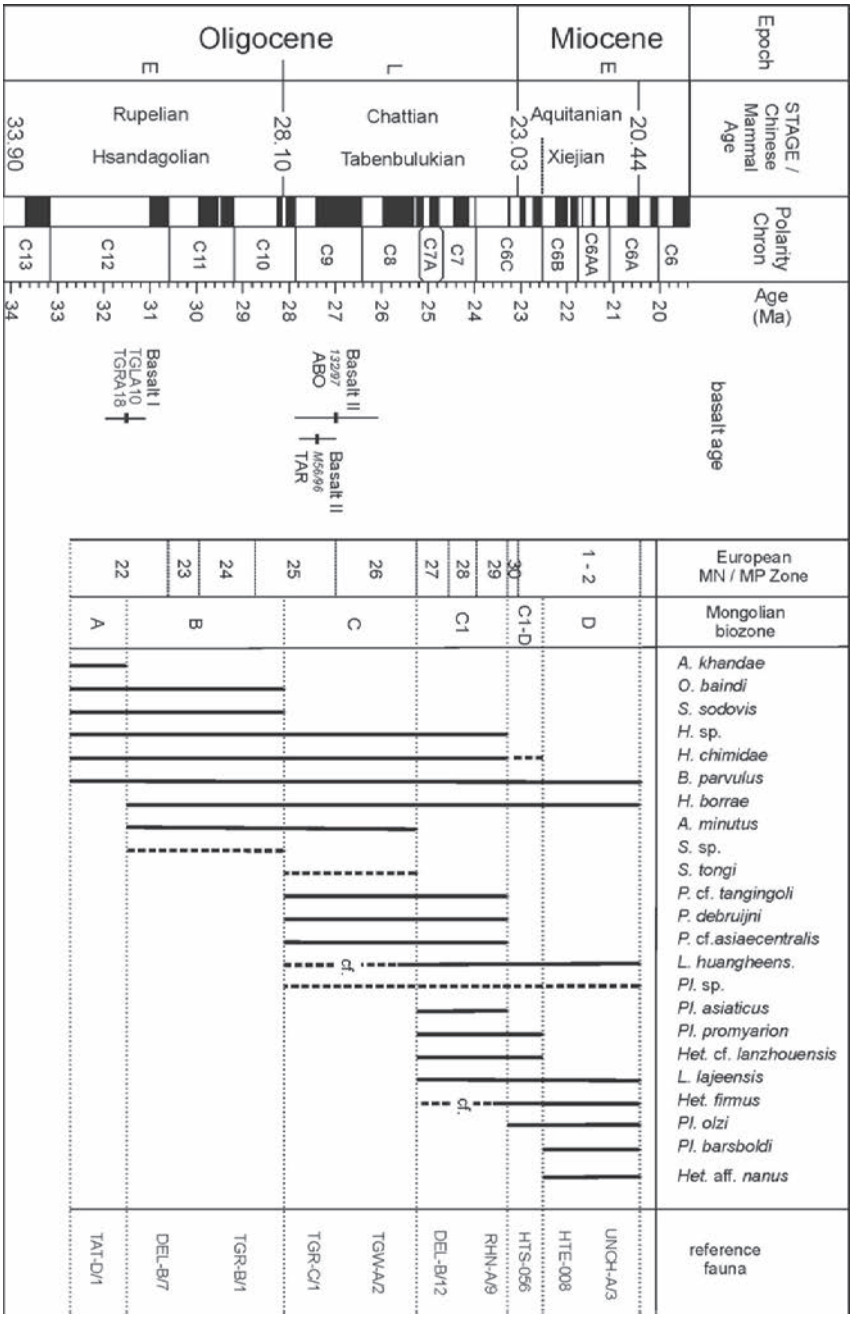


Fig. 26. Stratigraphic chart including the geologic time scale (GRADSTEIN *et al.* 2012), basalt ages and Mongolian biozones A to D (HÖCK *et al.* 1999), the European MN/MP Zones after STEININGER (1999) and LUTERBACHER *et al.* (2004), the lower boundary of the Xiejian Chinese mammal Age after MENG *et al.* (2013), the stratigraphic ranges of Dipodidae species, and reference faunas of Mongolian biozones (lower and upper part). Dot lines indicate very rare occurrences.

anterior arm of hypoconid extending obliquely in lingual direction; posterolophid long, surrounding the posterior part of m3; entoconid, hypoconulid, mesoconid, mesolophid and ectolophid absent.

M1–2 with four roots, m1–3 with two roots.

Remarks: *Heterosminthus* aff. *nanus* is the smallest among Mongolian *Heterosminthus* species. The small tooth sizes are equivalent with *Heterosminthus nanus*, and some dental characters resemble *Heterosminthus nanus* rather than any other species, *i.e.*, the absent postero-lingual crest of protocone and absent protostyle. However, the type material from Kazakhstan differs from the Mongolian specimens by: M1 with an entostyle connected with mesocone by a transverse crest, the ectomesolophid of m2, and the more complicated ectolophid-structures. These two very small collections, from Kazakhstan and Mongolia, do not display the full variability of dental characters, casting doubt on the species-identification of the Mongolian material.

Biostratigraphy

Dipodidae are known from all small mammal assemblages of the Oligocene and Early Miocene (Fig. 26). They display the greatest diversity of species (up to six species from one locality) and also the highest numbers of teeth.

The characteristic Dipodidae genera of the Early Oligocene in Mongolia are *Onjosminthus* (range: biozone A–B), *Allosminthus* and *Shamosminthus* (main range: biozone A–B, with rare last occurrences in the Late Oligocene / biozone C). *Heosminthus* and *Bohlinosminthus* are the long-lived genera with ranges from the Early Oligocene to the Early Miocene (biozone A–D). *Parasminthus* is documented only from Late Oligocene strata (biozone C–C1). *Litodonomys* (FOD biozone C) and *Plesiosminthus* (FOD biozone C1) range from the Late Oligocene to the Early Miocene (LOD biozone D). Finally, *Heterosminthus* is documented in Mongolia from the Late Oligocene to the Early Miocene (biozone C1–D).

The most abundant / characteristic Dipodidae-species of biozones A to D are:

Biozone A (Early Oligocene: below basalt I): *Heosminthus chimidae*, *Onjosminthus baindi*, *Shamosminthus sodovis*; FOD+LOD of *Allosminthus khandae*.

Biozone B (Early Oligocene: above basalt I): *Heosminthus chimidae*, *Heosminthus borrae*, *Allosminthus minutus*; LOD of *Onjosminthus baindi* and *Shamosminthus sodovis*.

Biozone C (Late Oligocene: below basalt II in section ABO, above basalt II in section TAR): *Heosminthus chimidae*, *Bohlinosminthus parvulus*, FOD of *Parasminthus* (3 species).

Biozone C1 (Late Oligocene: above biozone C): *Bohlinosminthus parvulus*; FOD of *Litodonomys lajeensis, Heterosminthus* and *Plesiosminthus* (2 species); LOD of *Parasminthus* (3 species).

Oligocene-Miocene transition (C1–D): *Litodonomys*; LOD of *Plesiosminthus promyarion* and *Heterosminthus* cf. *lanzhouensis*.

Biozone D (Early Miocene: above biozone C1): *Heterosminthus firmus*, *Litodonomys huangheensis*, *Litodonomys lajeensis*; FOD of *Plesiosminthus olzi*, *Plesiosminthus barsboldi* and *Heterosminthus* aff. *nanus*.

Conclusions

During eight field-campaigns from 1995 to 2012, more than four thousand teeth, numerous jaws and a few skull-fragments of Dipodidae were collected. *Heosminthus chimidae* (> 2,400 specimens) and *Bohlinosminthus parvulus* (> 800 specimens) are the prevailing species. *Heosminthus chimidae* was recovered from thirtyfour out of seventy fossil beds investigated. It ranges from the Early Oligocene to the Oligo-Miocene transition, and is the dominant Dipodidae during the Early Oligocene. *Bohlinosminthus parvulus* was recovered from twentyeight fossil beds. It ranges from the Early Oligocene to the Early Miocene and is the most numerous species of the Late Oligocene. All other species are represented by less than 150 specimens (one half by 1–50 specimens, the second half by 50–150 specimens). Except for *Heosminthus borrae* their stratigraphic ranges cover no more than one to three biozones.

The highest species richness of Dipodidae is known in Mongolia from the Late Oligocene. The number of species is relatively low in the Early Oligocene (biozone A: six species; biozone B: eight species). They are highest in the Late Oligocene (biozone C: eleven species; biozone C1: fourteen species), and decrease again from the Oligocene-Miocene transition to the Miocene (biozone D: eight species).

The comprehensive list of all Dipodidae –taxa from the Oligocene and Early Miocene of the Taatsiin Gol area comprises nine genera and twenty species. Out of them one genus and four species are new descriptions. Only three taxa remained wothout identification on species level:

Allosminthus WANG, 1985

Allosminthus khandae (DAXNER-HÖCK, 2001)

Allosminthus minutus (DAXNER-HÖCK, 2001)

Heosminthus WANG, 1985

Heosminthus borrae nov. spec.

Heosminthus chimidae nov. spec.

Heosminthus sp.

Plesiosminthus VIRET, 1926

Plesiosminthus asiaticus DAXNER-HÖCK & WU, 2003

Plesiosminthus promyarion SCHAUB, 1930

Plesiosminthus olzi nov. spec.

Plesiosminthus barsboldi Daxner-Höck & Wu, 2003

Plesiosminthus sp.

Onjosminthus nov. gen.

Onjosminthus baindi nov. gen. nov. spec

Parasminthus Bohlin, 1946

Parasminthus cf. *asiaecentralis* Bohlin, 1946

Parasminthus cf. *tangingoli* Bohlin, 1946

Parasminthus debruijni Lopatin, 1999

Bohlinosminthus Lopatin, 1999

Bohlinosminthus parvulus (Bohlin, 1946)

Litodonomys Wang & Qiu, 2000

Litodonomys huangheensis Wang & Qiu, 2000

Litodonomys lajeensis (Li & Qiu, 1980)

Shamosminthus Huang, 1992

Shamosminthus tongi Huang, 1992

Shamosminthus sodovis Daxner-Höck, 2001

Shamosminthus sp.

Heterosminthus Schaub, 1930

Heterosminthus firmus Zazhigin & Lopatin, 2000

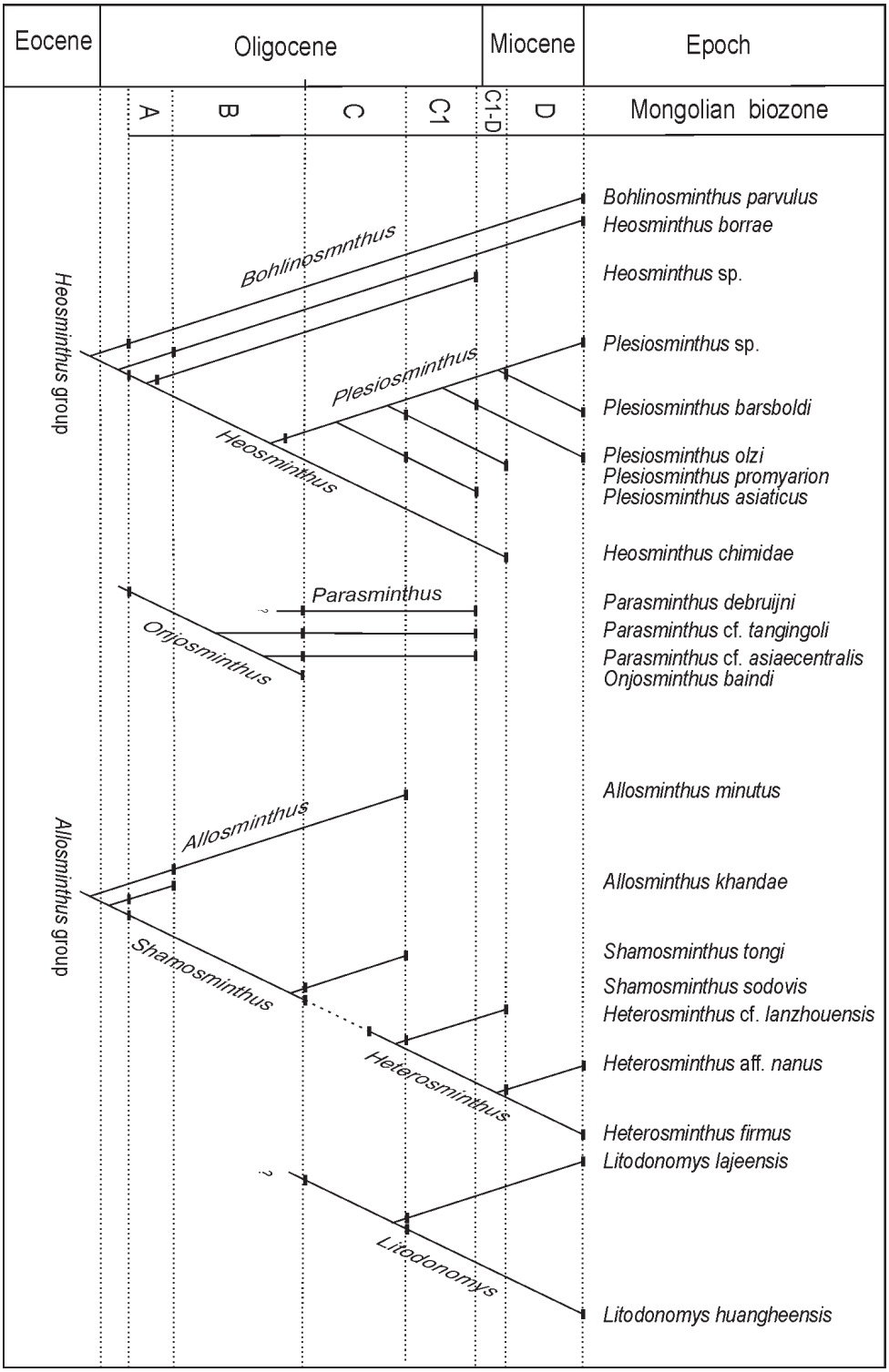
Heterosminthus cf. *lanzhouensis* Wang & Qiu, 2000

Heterosminthus aff. *nanus* Zazhigin & Lopatin, 2000

It has to be emphasized that the majority of the Dipodidae species from the Oligocene and Early Miocene of Mongolia show primitive dental structures, which indicate close relationships with *Allosminthus* and *Heosminthus*. These two genera – with first occurrences of *Allosminthus* in the Middle Eocene and *Heosminthus* in the Early Oligocene – represent some of the oldest Dipodidae genera, which survived in Mongolia to the Late Oligocene and Early Miocene, respectively.

The primitive dental characters of *Allosminthus* and *Heosminthus* of the Early Oligocene can be summarizeds as follows: Small bunodont, low crowned molars; M1–2 having

Fig. 27. The stratigraphic distribution of Dipodidae species described from Mongolia, and the assumed relations between the genera *Heosminthus*, *Plesiosminthus*, *Bohlinosminthus*, *Parasminthus*, *Onjosminthus*, *Allosminthus*, *Shamosminthus*, *Heterosminthus* and *Litodonomys*. ▶



an almost square occlusal outline, a concave occlusal surface, two pairs of main cusps in opposite position and three roots (two labial, one lingual); P4 consisting of a single cone, surrounded by a posterior cingulum, and one root; upper and lower incisors having a smooth anterior surface. The two genera differ mainly by more accentuated cusps/cuspids and lophs/lophids of *Heosminthus*. Other than that, *Allosminthus* has weak crests and obtuse cusps, and m1 has frequently no anteroconid, but a pronounced mesoconid, a hypoconulid and a posterior sulcus.

We assume that *Bohlinosminthus*, *Plesiosminthu*s and *Onjosminthus* could have derived from *Heosminthus*, and that *Allosminthus* could be ancestor group of *Shamosminthus* and *Heterosminthus*.

The *Heosminthus* group and its assumed desendants:

1. The genus *Heosminthus* is evidenced in Mongolia by two independent species, *Heosminthus borrae* and *Heosminthus chimidae* and a third group, *Heosminthus* sp. (Fig. 8). *Heosminthus* sp. displays largest molar sizes, but dental characters in general are similar with *Heosminthus chimidae* and *Heosminthus borrae*. *Heosminthus borrae* (Fig. 6) is the smallest species, having the most advanced dental characters, such as pronounced high cones and lophs and narrow valleys. *Heosminthus chimidae* (Fig. 7), the most abundant of all Dipodidae species, is of varying size and generalized dental pattern.

2. *Plesiosminthus* descended from *Heosminthus* by keeping the general molar structures, but developing its characteristic upper incisor. This tooth is laterally compressed and has a significant longitudinal groove along its anterior surface. In the course of the Late Oligocene and Early Miocene several species of *Plesiosminthus* developed, which differ in size and more or less advanced molar structures (Figs. 9–12).

3. We assume that also *Bohlinosminthus* is closely related to *Heosminthus*, because it shares the small molars, the primitive pattern, and the smooth anterior surface of upper incisors with the oldest *Heosminthus* species. However, other than *Heosminthus* and *Plesiosminthus*, *Bohlinosminthus* (Fig. 18) developed four roots of M1–2 in an early stage of evolution and consequently kept this character unchanged to the Early Miocene.

4. *Onjosminthus* shares some dental characters with the *Heosminthus* group (M1–2 having an almost square occlusal outline, two pairs of main cusps in opposite position and three roots, and a smooth anterior surface if upper incisors), however, it has significantly larger tooth sizes and some differing dental characters such as: thick wrinkled enamel; paracone spur of M1–2 connected with long mesoloph; characteristic connection between mesolophid and metaconid and posterolophid and entoconid of m1–2; accentuated mesoconid and hypoconulid (Figs.13–14).

5. The two species of *Parasminthus*, *Paraminthus* cf. *tangingoli* and *Parasminthus* cf. *asiaecentralis* (Figs. 15–16) and *Onjosminthus* are the largest Dipodidae of the Oligocene from Mongolia. *Parasminthus* displays a more advanced molar pattern than all genera discussed before. Commonly, the root numbers of M1–2 are linked with the length/

width ratio. M1–2 of square outline (*e.g.*, *Onjosminthus*) have three roots (the lingual root can be rounded, elongate in longitudinal direction or can have split tips). More advanced M1–2 of rectangular shape (*e.g.*, *Parasminthus*) have four roots. The elongation of teeth and the increase of root numbers is correlated with specific dental features, *e.g.*, the direction of protoloph and/or metaloph of M1–2 changes from transverse to oblique. The molars of *Parasminthus debruijni* share the *Parasminthus* pattern, but are significantly smaller than the other two species.

The *Allosminthus* group and its assumed desendants:

1. The genus *Allosminthus* evidences two species in Mongolia, *Allosminthus khandae* (Fig. 4) and *Allosminthus minutus* (Fig. 5). Both species are very small, but differ by M1–2 having a paracone spur, and by slightly larger tooth sizes of *Allosminthus khandae.*

2. *Shamosminthus* of the Early Oligocene has very small bunodont molars with pronounced cusps, wide valleys and weak crests and shares other dental characters of *Allosminthus*, *i.e.*, the small or absent anteroconid of m1, the pronounced mesoconid and hypoconulid, and three roots of M1–2. Later, in the course of the Early Oligocene (biozone B) *Shamosminthus sodovis* (Fig. 22/2–3) developed more advanced dental structures: M1–2 with rectangular outline, four roots, elongation of the protocone of M1 and backward directed metaloph. Finally, in the course of the Late Oligocene the much larger species *Shamosminthus tongi* (Fig. 22/1) developed.

3. The following features express the changing of the molar pattern from *Shamosminthus* to *Heterosminthus*: The tooth size and alternation of cusps increase with time. The lingual cusps shift forward, and simultaneously the direction of the lophs and valleys change from almost transverse to oblique. The originally short M1–2 become longer, the number of roots increases from three to four. The protocone of M1 elongates obliquely in antero-labial and postero-lingual direction. The size of mesoconid and hypoconulid of lower molars increases. *Shamosminthus* of the Early Oligocene had a short ectolophid of m1, which was close to the mediane line. It successively shifted in lingual direction, and became oblique or curved in *Heterosminthus* (DAXNER-HÖCK 2001: 370). The different species of *Heterosminthus* differ by molar size and dental characters (Figs 23–25).

4. The origin of *Litodonomys* and its relation to other genera is questionable. Similar to *Bohlinosminthus* it combines the small size and the more or less square outline of M1–2 with four distinct roots. However, the lophodont pattern, the strongly oblique entoloph/ectolophid, the thick enamel, and the plane occlusal surface set *Litodonomys* apart from all other Dipodidae genera studied (Figs 19–21).

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