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Evolution of Tachyoryctoidinae (Rodentia, Mammalia): evidences of the Oligocene and Early Miocene of Mongolia

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(With 9 figures, 5 tables)

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Abstract

Tachyorytoidinae were subterranean rodents of the Late Oligocene and Early Miocene of Central and Eastern Asia. The remarkably rich fossil collection from the Valley of Lakes in Mongolia comprises eight species, of which two are new. *Tachyoryctoides bayarmae* nov. spec., *Tachyoryctoides radnai* nov. spec., *Tachyoryctoides obrutschewi* Bohlin, 1937 and *Tachyoryctoides tatalgolicus* Dashzeveg, 1971 are evidenced from the Late Oligocene (biozones C to C1). *Tachyoryctoides* sp. bridges the Oligocene/Miocene boundary (biozones C1 to C1/D). Finally, *Tachyoryctoides kokonorensis* Li & Qiu, 1980, *Tachyoryctoides engesseri* Wang & Qiu, 2012 and *Ayakozomys* sp. from the Early Miocene (biozone D) of Mongolia are youngest. The bono-lophodont, low crowned molars of *T. radnai* and *T. bayarmae* suggest that *Tachyoryctoides* originated from a hitherto unknown rodent group with "cricetoid" molar pattern. Based on size-increase, modification toward lophodont molar pattern, and moderate hypsodonty during the course of the Late Oligocene to the Early Miocene, we consider that *T. radnai – T. obrutschewi – T. kokonorensis* represent a phylogenetic line.

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

Kurzfassung

Die Tachyoryctoidinae waren im Boden lebende Nagetiere, die im Ober-Oligozän und Unter-Miozän in Central- und Ostasien beheimatet waren. Die reichhaltige Fossiliensammlung aus dem Tal der Gobissen in der Mongolei umfasst acht Arten, davon wurden zwei Arten neu beschrieben: *Tachyoryctoides bayarmae* nov. spec., *Tachyoryctoides radnai* nov. spec., *Tachyoryctoides obrutschewi* Bohlin, 1937 und *Tachyoryctoides tatalgolicus* Dashzeveg, 1971 sind aus dem Ober Oligozän

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(Biozonen C und C1) nachgewiesen. *Tachyoryctoides* sp. überdauerte die Oligozän/Miozän-Grenze (Biozonen C1 bis C1/D). *Tachyoryctoides kokonorensis* Li & Qiu, 1980, *Tachyoryctoides engesseri* Wang & Qiu, 2012 and *Ayakozomys* sp. aus dem Unter Miozän (Biozone D) sind die jüngsten Arten aus der Mongolei. Die buno-lophodonten, niedrigkronigen Molaren von *T. radnai* und *T. bayarmae* lassen darauf schließen, dass *Tachyoryctoides* von einer bisher unbekannten Nagetiergruppe mit "cricetoidem" Molarenmuster abstammt. Unter Berücksichtigung der Zunahme von Größe, Lophodontie und Hypsodontie der Molaren vom Ober-Oligozän bis zum Unter-Miozän, sehen wir in der Entwicklung *T. radnai – T. obrutschewi – T. kokonorensis* eine phylogenetische Linie.

Schlüsselwörter: Tachyoryctoidinae, Paläogen, Neogen, Taxonomy, Biostratigraphy, Tal der Gobiseen.

Introduction

Tachyoryctoidinae are endemic rodents of Cenozoic deposits in Central and Eastern Asia. Early findings from the Late Oligocene of Shargaltein-Tal (Gansu Province in China) gave name to the genus *Tachyoryctoides*, Bohlin 1937 and to three attributed species, *Tachyoryctoides obrutschewi* Bohlin, 1937, *Tachyoryctoides pachygnathus* Bohlin, 1937 and *Tachyoryctoides intermedius* Bohlin, 1937. Recognition of *Tachyoryctoides tatalgolicus* Dashzeveg, 1971 from Late Oligocene fossil beds of Tatal Gol (Valley of Lakes in Mongolia) and *Tachyoryctoides kokonorensis* Li & Qiu, 1980 from the Early Miocene of Xieija (Xining Basin in China) was followed more recently by the description of the Early Miocene *Tachyoryctoides engesseri* Wang & Qiu, 2012 from Qu-jiachuan and *Tachyoryctoides minor* Wang & Qiu, 2012 from Dui-ting-gou (Gaolan County in the Lanzhou Basin of China). Meanwhile, numerous new findings of *Tachyoryctoides* have been reported from Late Oligocene and Early to Middle Miocene deposits in China (Bohlin 1946; Wang & Qiu 2000; Wang & Qiu 2012), Kazakhstan (Kordikova & de Bruijn 2001; Lopatin 2004; Bendukidze *et al.* 2009) and Mongolia (Mellett 1968; Kowalski 1974; Höck *et al.* 1999; Daxner-Höck & Badamgarav 2007). So far, most of the respective fossil sites provide very incomplete findings (a lower jaw and/or some isolated teeth); only from the Xining and Lanzhou Basins in China are partial skulls and lower jaws with complete tooth-rows available (Li & Qiu 1980; Wang & Qiu 2012). Currently, however, the fossil collection from the Valley of Lakes in Mongolia comprises the greatest number (more than 250 specimens) of *Tachyoryctoides* remains.

The fossils were collected during Mongolian-Austrian joint projects in the Uvurkhangai Aimag, Valley of Lakes (Central Mongolia) in the years 1995 to 2011. The study area ranges from Luuny Yas in the west to Ikh Argalatyn Nuruu in the east. Here, Tachyoryctoidinae fossils were collected from paleosol horizons of Late Oligocene to Early Miocene sediment sequences.

Material and methods

The isolated teeth were found by wet screening of sediment from twenty-four fossil layers along ten sections and fossil sites (Tab. 1). Moreover, about seventy fragmentary

lower jaws and twenty cranial fragments were collected from the surface, laterally of the investigated sections. These badly damaged, deformed, and partly incrusted fossils mostly stem from weathered and reworked caliche layers of the Hotuliin Teeg (HTE*, HTE-012), Unkheltseg (UNCH-A/3+4), Toglorhoi (TGW-A/3+4) and Taatsiin Gol (TGR-C/1+2) sections.

This material requires careful preparation and detailed analysis of cranial- and mandibular morphology, and will be the subject of a separate paper at a later date. At present we focus on the molar morphology of the well-preserved fossils, which were selected from the washed residue of bulk samples. All SEM-images were taken at the University of Vienna. To facilitate comparisons, all right-side teeth are figured as mirror images (reversed) and their figure numbers are underlined. The illustrated, measured and described fossils are housed in the collection of the Natural History Museum Vienna (coll. NHMW 2012/0062 to 2012/0066, 2012/0068, 2012/0069, 2013/0233, 2013/0244, 2013/0245, 2013/0247, 2013/0445 to 2013/0464); some fossils from the collection of the Mongolian Paleontological Center are considered in the present issue. They are marked in the material lists (coll. MPC). All measurements are given in millimetres. For classification above genus level we follow Mc Kenna & Bell (1997).

Abbreviations

* collected from surface

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

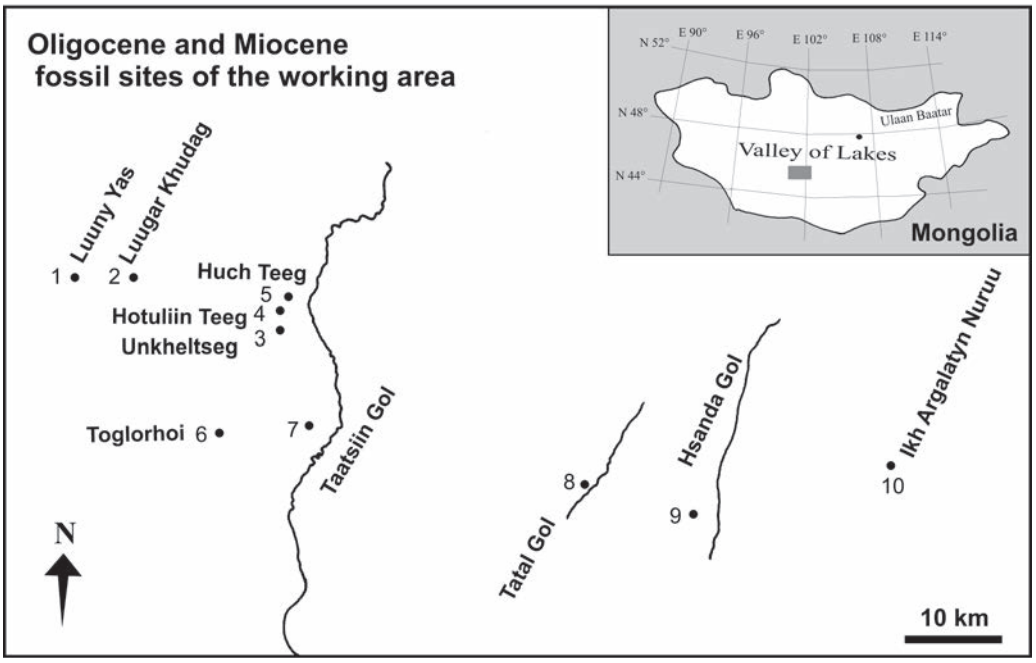
coll. MPC – collection of the Mongolian Paleontological Center, Academy of Sciences, Ulaanbaatar.

LOD – last occurrence datum

FOD – first occurrence datum

Geological setting

The Valley of Lakes is situated between the Gobi Altai Mountains in the south and the Khangai Mountains in the north and extends across ~500 km in the west-east direction in Central Mongolia. Part of it 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 are exposed along steep cliffs of mostly dry river beds. In this region several basalt layers of different age and regional extension are intercalated between fossiliferous sediments. During comprehensive geological-palaeontological investigations (1995–1997), an integrated stratigraphy of this area was elaborated (Höck *et al.* 1999). It comprises the redefinition of formations (*e.g.*, Hsanda Gol Fm. and Loh Fm.), the establishment of eight informal biozones (A, B, C,



Map 1. Studied sites in the Valley of Lakes, Mongolia. See Table 1 (opposite side) for details.

C1, D, D1/1, D1/2 and E), and $^{40}Ar/^{39}Ar$ dating of basalts I to III (Daxner-Höck *et al.* 1997; Höck *et al.* 1999; Daxner-Höck & Badamgarav 2007; Daxner-Höck *et al.* 2010). The radiometric data (whole rock samples; Höck *et al.* 1999) yielded two groups of Oligocene basalt ages, and a Middle Miocene basalt age. The older one is the Early Oligocene basalt I group around 31.5 Ma. The second is the Late Oligocene basalt II group of ages around 27–28 Ma. Finally, basalt III is of Middle Miocene age around 13 Ma (Höck *et al.* 1999: fig. 8; Daxner-Höck *et al.* 2010: 351).

Fossils indicating biozone A and B from below and above basalt I, respectively, are of Early Oligocene Age. Key fossils of biozone C were recovered below and above basalt II and are of Late Oligocene age. In the section of Unzing Khurem, basalt II (TAR M56/96: radiometric age 27.4±0.4 Ma) is situated immediately below the fossil layer TAR-A/2 containing fossils of biozone C. Basalt II of Abzag Ovo (ABO 132/97: radiometric age 27.0±0.9 Ma) is above the fossil layer ABO-A/3, which also contains the key fossils of biozone C. In the sections Tatal Gol (TAT-E) and Toglorhoi (TGW-A), sediments with index fossils of biozone C1 are immediately above biozone C, and in the Hotuliin Teeg (HTE) section fossil layers of biozone D are above biozone C1. Although no radiometric age control is available, the Mongolian biozones C1 and D correlate biostratigraphically with the Chinese mammal Ages Tabenbulukian and Xiejian, respectively. In our opinion some Mongolian mammal assemblages of biozone C1 are to be correlated with the latest Oligocene faunas of Tieersihabahe (T-I and T-II) and Suosuoquan (S-I) of the Junggar Basin (China), others with the Yantandu fauna of the Tabenbuluk region in

Table 1. Studied sites, their geographic position, stratigraphy and tachyoryctoid fauna. See opposite page for a map showing the working area.

Locality (1–10): section – fossil layer	GPS position from west to east	Mongolian biozone	*Tachyoryctoides* species and *Ayakozomys*
1. Luuny Yas:			
LUS-027	N 45°32'05" E 100°56'50"	D	*T. kokonorensis*
LUS-29	N 45°32'03" E 100°56'52"	D	*T. kokonorensis*
2. Luugar Khudag:			
LOG-A/1	N 45°32'20" E 101°00'51"	D	*Ayakozomys* sp.
3. Unkheltseg:			
UNCH-A/3+4	N 45°27'40" E 101°12'04"	D	*T. kokonorensis*
4. Hotuliin Teeg:			
HTE-012	N 45°29'12" E 101°11'49"	D	*T. kokonorensis*
HTE-005	N 45°29'10" E 101°11'49"	D	*T. kokonorensis*
HTE-014-018	N 45°29'06" E 101°11'58"	D	*T. kokonorensis, T. engesseri*
HTE-008	N 45°29'07" E 101°11'58"	D	*T. kokonorensis, T. engesseri*
HTE-009	N 45°29'07" E 101°11'59"	D	*T. kokonorensis, T. engesseri*
HTE*	N 45°29'06-12" E 101°11'49–59"	D	*T. kokonorensis, T. engesseri, Ayakozomys* sp.
HTSE-009	N 45°28'49" E 101°11'55"	C1	*T. tatalgolicus*
HTE-057	N 45°28'54" E 101°12'17"	C1	*T. obrutschewi*
5. Huch Teeg:			
RHN-021	N 45°29'30" E 101°12'19"	C1-D	*T.* sp.
6. Toglorhoi:			
TGW-A/3+4	N 45°22'37" E 101°05'49"	C1	*T. radnai* nov. spec., *T. bayarmae* nov. spec.
7. Taatsiin Gol:			
TGR-C/1+2	N 45°23'11" E 101°14'35"	C	*T. radnai* nov. spec., *T. bayarmae* nov. spec.
8. Tatal Gol:			
TAT-E*	N 45°17'58" E 101°37'16"	C	*T. radnai* nov. spec.
TAT-042	N 45°17'57" E 101°37'14"	C	*T. radnai* nov. spec.
TAT-055	N 45°17'59" E 101°37'16"	C	*T. radnai* nov. spec.
TAT-SE*	N 45°17'46" E 101°37'57"	C-C1	*T. radnai* nov. spec., *T. bayarmae* nov. spec.
TAT-043	N 45°17'60" E 101°37'17"	C1	*T. tatalgolicus, T.* sp.
TAT-051/2	N 45°18'08" E 101°37'09"	C1	*T. obrutschewi*
TAT-E/22	N 45°18'09" E 101°37'14"	C1	*T. tatalgolicus*
TAT-E/27	N 45°18'09" E 101°37'14"	C1	*T.* sp.
TAT-052/2	N 45°18'10" E 101°37'13"	C1-D	*T.* sp.
TAT-044	N 45°17'60" E 101°37'19"	C1	*T.* sp.
9. Hsanda Gol:			
SHG-AB (top)	N 45°16'12" E 101°46'20"	C1	*T. obrutschewi*
10. Ikh Argalatyn Nuruu:			
IKH-B/5	N 45°17'32" E 102°05'34"	C1	*T. obrutschewi*

Gansu (China); the latter gives name to the Late Oligocene Chinese Land Mammal Age Tabenbulukian (Meng *et al.* 2006; Wang *et al.* 2008). Some assemblages of the Mongolian biozone D are to be correlated with the Suosuoquan faunas S-II and S-III of the Junggar Basin, and with the fauna Xiejia of Qinghai in China; the latter gives name to the Early Miocene Chinese Land Mammal Age Xiejian (Qiu *et al.* 2013; Meng *et al.* 2013).

Systematic palaeontology

Class Mammalia Linneaus, 1758

Order Rodentia Bowdich, 1821

Family Muridae Illiger, 1811

Subfamily Tachyoryctoidinae Schaub, 1958

There is no consensus among specialists about the number and identity of the genera and species of the Tachyoyctoidinae (Schaub 1958; Lopatin 2004; Bendukidze *et al.* 2009; Wang & Qiu 2012, and citations within these articles). In agreement with Wang & Qiu (2012: 125), we consider *Tachyoryctoides* Bohlin, 1937, *Ayakozomys* Tyutkova, 2000 and *Eumysodon* Argyropulo, 1939 as independent genera within the subfamily Tachyoryctoidinae Schaub, 1958.

Genus *Tachyoryctoides* Bohlin, 1937

Type species: *Tachyoryctoides obrutschewi* Bohlin, 1937

Main characters: Medium- to large-sized muroids with a myomorphous skull and sciurognathous lower jaw. The horizontal ramus of the lower jaw is robust and concave at its lingual side. The masseteric fossa extends to below m1–2, and the mental foramen is situated below the anterior root of m1. Upper and lower incisors are triangular in cross-section and have a flat labial surface. The molars are brachydont to mesodont and buno-lophodont to lophodont. All molars have a planar occlusal surface. The lophs(ids) are transverse, the entoloph and ectolophid more or less oblique. The mesoloph(id) is very weak or absent. Upper molars are tilted backward; they have three labial valleys and a forward directed sinus. Lower molars are tilted forward, they have three lingual and two labial valleys and a backward directed sinusid. Upper molars have three roots, lower molars two roots. The stratigraphic range is Late Oligocene to Early Miocene.

Discussion: *Aralomys* Argyropulo, 1939 and its two referred species *Aralomys gigas* Argyropulo, 1939 and *Aralomys glikmani* Vorontsov, 1963 from the North Aral Region (Kazakhstan) share the main dental characters with *Tachyoryctoides*. Presence or absence of the anterolophulid of m1, the size and crown height of molars, the absence or presence/length of a mesolophid, as well as narrow or wide, closed or open sinusids are considered as species characters rather than qualifying for differentiation of genera.

Consequently, we agree with other specialists (Mellett 1968; Dashzeveg 1971; Kowalski 1974; Bendukidze *et al.* 2009; Wang & Qiu 2012) to place *Aralomys* Argyropulo, 1939 into synonymy of *Tachyoryctoides*, Bohlin 1937.

Referred species /type localities:

- *T. obrutschewi* Bohlin, 1937 from Shargaltein-Tal, Gansu Province (China)
- *T. pachygnathus* Bohlin, 1937 from Shargaltein-Tal, Gansu Province (China)
- *T. intermedius* Bohlin, 1937 from Shargaltein-Tal, Gansu Province (China)
- *T. gigas* (Argyropulo, 1939) from Akespe, North Aral Region, (Kazakhstan)
- *T. glikmani* (Vorontsov, 1963) from Zherlepes, North Aral Region, (Kazakhstan)
- *T. tatalgolicus* Dashzeveg, 1971 from Tatal Gol, Valley of Lakes (Mongolia)
- *T. kokonorensis* Li & Qiu, 1980 from Xiejia, Xining Basin (China)
- *T. engesseri* Wang & Qiu, 2012 from Qu-jiachuan, Gaolan County (China)
- *T. minor* Wang & Qiu, 2012 from Dui-ting-gou, Gaolan County (China)
- *T. bayarmae* nov. spec. from Toglorhoi, Valley of Lakes (Mongolia)
- *T. radnai* nov. spec. from Taatsiin Gol, Valley of Lakes (Mongolia)

***Tachyoryctoides bayarmae* nov. spec.**

(Figs 1a–1e, Tab. 2)

2007 *Tachyoryctoides* sp. 1. – Daxner-Höck & Badamgarav: 17, tab. 3.
2010 *Tachyoryctoides* sp. 1. – Daxner-Höck *et al.*: 359, tab. 4.
2013 *Tachyoryctoides* sp. 1. – Daxner-Höck *et al.*: 488, tab. 20/4.

Derivatio nominis: In honour of B. Bayarmaa, Mongolian member of the team.

Type locality: Toglorhoi (TGW-A/3+4), Uvurkhangai, Mongolia.

Type stratum: red silty clay of the Hsanda Gol Fm.; Late Oligocene (biozone C1).

Holotype: Fragmentary left lower jaw with m1–3 (NHMW 2012/0063/0001). Measurements (length × width in mm): m1: 2.65 × 2.06; m2: 2.76 × 2.47; m3: 2.65 × 2.41).

Paratypes: 2 fragmentary right lower jaws with m1–3 (NHMW 2012/0063/0002, …/0003), right M2 (NHMW 2012/0063/0004), fragmentary left M2 (NHMW 2012/0063/0005), left M3 (NHMW 2012/0063/0006).

Further material: Late Oligocene (biozone C): Taatsiin Gol: TGR-C/1: fragmentary left lower jaw with m1–3 (NHMW 2012/0062/0001), fragmentary left lower jaws with m3 (NHMW 2012/0062/0002), right m1–3 (Coll. MPC).

Late Oligocene (biozone C1): Toglorhoi: TGW-A/3+4: cast of fragmentary left lower jaw with m2–3 (NHMW 2012/0063/0007). Original: (Coll. MPC). Tatal Gol: TAT-SE*: fragmentary left lower jaw with m3 (NHMW 2012/0064/0001).

Diagnosis: The molars are small, have low crowns and a buno-lophodont pattern. The drop-shaped lingual conids of lower molars are merged with the short metalophid and hypolophid. The labial conids are triangular with rounded labial corners. The cones/

conids and lophs/lophids are separated by wide, shallow valleys. The entoloph of M2–3 is longitudinal, the ectolophid of m1–3 is slightly oblique. The mesoloph/mesolophid is short or absent. There is no anterolophulid of m1. The anterior border of m1 is rounded and terminated by an indistinct anteroconid or by an anterolophid. The m2 has a posterior arm of protoconid. M2–3 have three roots, m1–3 have two roots.

Differential diagnosis: *Tachyoryctoides bayarmae* nov. spec. differs from almost all *Tachyoryctoides* species and from *Ayakozomys* by smaller and lower molar crowns, by more rounded cones/conids, and by the longitudinal entoloph and the less oblique ectolophid. It is as small as *Tachyoryctoides minor* Wang & Qiu, 2012 and *Eumysodon spurius* Argyropulo,1939, but differs by the low buno-lophodont molars. *Tachyoryctoides bayarmae* differs in being significantly smaller than *Tachyoryctoides radnai*, which also has brachydont and buno-lophodont molars.

Description of the holotype (Fig. 1a): The drop-shaped lingual conids of lower molars are merged with the short metalophid and hypolophid. The labial conids are triangular with rounded labial corners. The metalophid and hypolophid are connected with the anterior arms of the protoconid and hypoconid, respectively. The mesolophid of m1 is short; it is absent in m2–3. The m2 has a posterior arm of protoconid. The ectolophid of m1 is more or less longitudinal; it is slightly oblique in m2–3. The backward directed sinusid is wide and shallow in m1, extends as far as the median line in m2–3. The m1 displays no anterolophulid and no anteroconid, but a continuous anterolophid extends from the protoconid along the anterior edge toward the metaconid. The labial and a lingual anterolophid of m2–3 and the anterosinusid and protosinusid are of almost equal length and size, respectively. The mesosinusid of m1–2 is wide, but narrow in m3. The posterosinusid of m3 is the smallest sinusid.

Description of paratypes and further materials (Figs 1b –1d):

Lower jaw (Figs 1b, 1e): The diastema is concave, the mandibular ramus is high. The masseteric fossa extends to below m1–2. The lower ridge of the fossa is pronounced, and its anterior extension is as far as m1. The mental foramen is situated below the anterior root of m1. The dental pattern of m1–3 resembles the holotype. The brachydont lower tooth-row (Fig. 1e) is shown in labial view. The lower tooth-row (m1–3) is 7.20–7.90 mm long.

Table 2. Measurements of *Tachyoryctoides bayarmae* nov. spec.

	length (mm)			width (mm)	
	range	mean	N=20	range	mean
M2	2.35 – 2.47		2		2.35
M3		1.71	1		2.06
m1–3	7.20 – 7.90		3		
m1	2.53 – 2.76	2.65	3	1.94 – 2.24	2.09
m2	2.47 – 2.94	2.63	6	2.35 – 2.82	2.50
m3	2.29 – 2.76	2.51	8	2.18 – 2.65	2.38

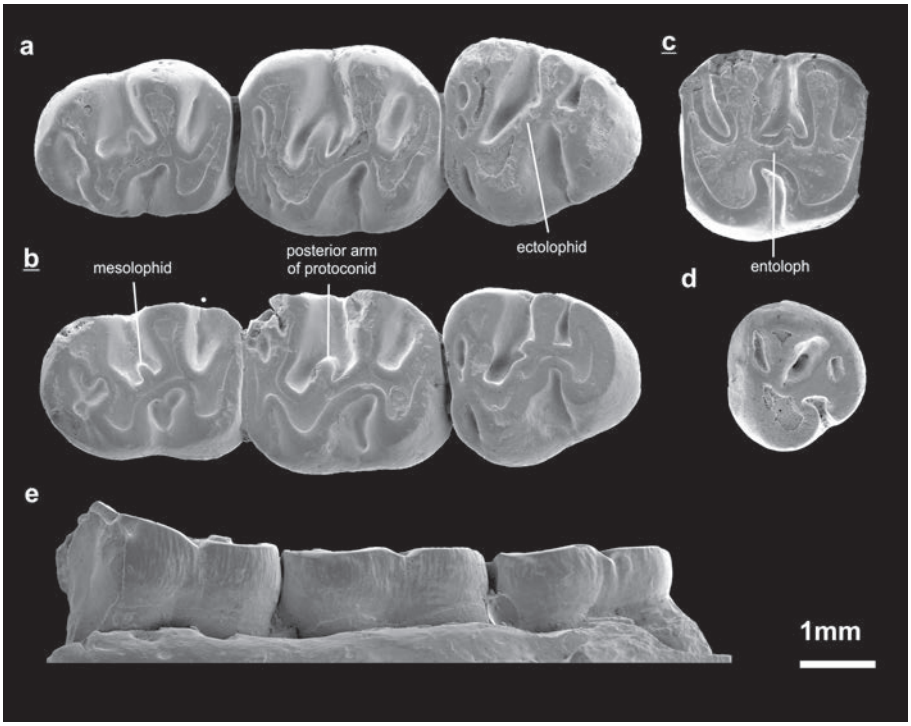


Fig. 1. *Tachyoryctoides bayarmae* nov. spec. from the Valley of Lakes, Mongolia. Late Oligocene (biozones C to C1). All specimens from the NHMW collection.
a: left m1–3, holotype (NHMW 2012/0063/0001) from Toglorhoi (TGW-A/3+4), biozone C1.
b: right m1–3, paratype (NHMW 2012/0063/0002) from Toglorhoi (TGW-A/3+4), biozone C1.
c: right M2, paratype (NHMW 2012/0063/0004) from Toglorhoi (TGW-A/3+4), biozone C1.
d: left M3, paratype (NHMW 2012/0063/0006) from Toglorhoi (TGW-A/3+4), biozone C1.
e: left m1–3, labial view (NHMW 2012/0062/0001) from Taatsiin Gol (TGR-C/1–2), biozone C.

The M2 (Fig. 1c) is almost square in outline. It is strongly worn. The labial and lingual pairs of cones are in opposite position and the direction of protoloph and metaloph is transverse. There is a strong labial anteroloph. The mesoloph is short. The direction of the entoloph is longitudinal. Anterosinus and posterosinus are almost equally sized. The mesosinus is wider and deeper. The sinus is slightly directed forward.

The M3 (Fig. 1d) is the smallest tooth. It displays two pronounced cones (paracone and protocone) and four labial lophs (labial anteroloph, protoloph, metaloph and the small posteroloph). The hypocone is small, the metacone reduced. The mesoloph is absent. There are three labial fossettes; the sinus is lingually open.

Remarks: *Tachyoryctoides bayarmae* nov. spec. is the smallest, most primitive and stratigraphically oldest species of *Tachyoryctoides*. It displays some primitive "cricetoid" molar features such as the buno-lophodont pattern, low molar crowns and the longitudinally directed entoloph. These features resemble the considerably larger species

Tachyoryctoides radnai nov. spec. *Tachyoryctoides bayarmae* and *Tachyoryctoides radnai* co-occur in some Mongolian localities and fossil layers of the Late Oligocene.

Stratigraphic range: Late Oligocene (biozones C–C1).

***Tachyoryctoides radnai* nov. spec.**

(Figs 2a–2e, Table 3)

1997 *Tachyoryctoides* (small spec.). – Daxner-Höck *et al.*: 172.
1999 *Tachyoryctoides obrutschewi*. – Höck *et al.*: 116.
2007 *Tachyoryctoides obrutschewi* p.p. – Daxner-Höck & Badamgarav: 17, tab. 3.
2010 *Tachyoryctoides obrutschewi* p.p. – Daxner-Höck *et al.*: 359, tab. 4.
2013 *Tachyoryctoides obrutschewi* p.p. – Daxner-Höck *et al.*: 488, tab. 20/4.

Derivatio nominis: In honor of Yo. Radnaa, Mongolian member of the field-team.

Type locality: Taatsiin Gol (TGR-C/1-2), Uvurkhangai, Mongolia.

Type stratum: reworked caliche layer of the Hsanda Gol Fm.; Late Oligocene (biozone C).

Holotype (Fig. 2a): Fragmentary right lower jaw with m1–3 (NHMW 2013/0445/0001). Measurements (length × width in mm): m1: 3.41 × 2.76; m2: 3.53 × 3.35; m3: 3.65 × 3.24).

Paratypes (all specimens from the type locality – Figs 2b–2e): 2 fragmentary left lower jaws with m1–3 (NHMW 2013/0445/0002, …/0003), 2 fragmentary right lower jaws with m1–3 (NHMW 2013/0445/0004, …/0005), 1 right m1 (NHMW 2013/0445/0006), 1 left M1 (NHMW 2013/0445/0007), a fragmentary skull with right and left M1–2 (NHMW 2013/0445/0008), a fragmentary skull with right I, M1–3 and left M1–3 (NHMW 2013/0445/0009), 3 right fragmentary lower jaws with m1–3 (Coll. MPC).

Further material: Late Oligocene (biozone C): Tatal Gol: TAT-E*: left m1 (NHMW 2013/0446/0001); TAT-055: left lower jaw with m1–2 (Coll. MPC); TAT-042: right m2–3 (Coll. MPC).

Late Oligocene (biozone C1): Tatal Gol: TAT-SE*: fragmentary right lower jaw with m3 (NHMW 2013/0447/0001). Toglorhoi: TGW-A/3+4: fragmentary skull with left and right I and left M1 (NHMW 2013/0448/0001).

Diagnosis: *Tachyoryctoides radnai* nov. spec. is one of the medium-sized *Tachyoryctoides* species. The upper incisor has a triangular cross-section and a flat labial side. The molars have low crowns of buno-lophodont pattern. The cones/conids and lophs/lophids are separated by wide valleys. The direction of protoloph and metaloph of M1–3 is transverse. The direction of entoloph/ectolophid of M1–3/m1–3 is longitudinal/oblique. The trigonid of m1 is short. The anterolophid of m1 in which the anteroconid is merged terminates the trigonid-basin anteriorly. A weak anterolophulid can be present. The mesoloph/mesolophid is short or absent. A short ectomesolophid of m1 can be present. M1–3 have three roots; m1–3 have two roots.

Differential diagnosis: The tooth structures of *Tachyoryctoides radnai* nov. spec. differ from almost all *Tachyoryctoides* species and from *Ayakozomys* by lower molar crowns, the short trigonid of m1, the less lophodont molar pattern, the more symmetric position of cones/conids, the longitudinal entoloph, the less oblique ectolophid, the frequently occurring mesolophid, and the sporadic occurrence of an ectomesolophid of m1. Beyond these dental features *Tachyoryctoides radnai* differs by its smaller size from all large-sized species, and by significantly larger size from the small species *Tachyoryctoides minor* and *Tachyoryctoides bayarmae*. The dental pattern of *Tachyoryctoides radnai* is most similar with *Tachyoryctoides bayarmae. Ayakozomys* sp., *Tachyoryctoides obrutschewi* and *Tachyoryctoides tatalgolicus* are also of medium size, but *Tachyoryctoides radnai* differs from these three taxa by buno-lophodont molar features, the wide valleys and lower molar crowns.

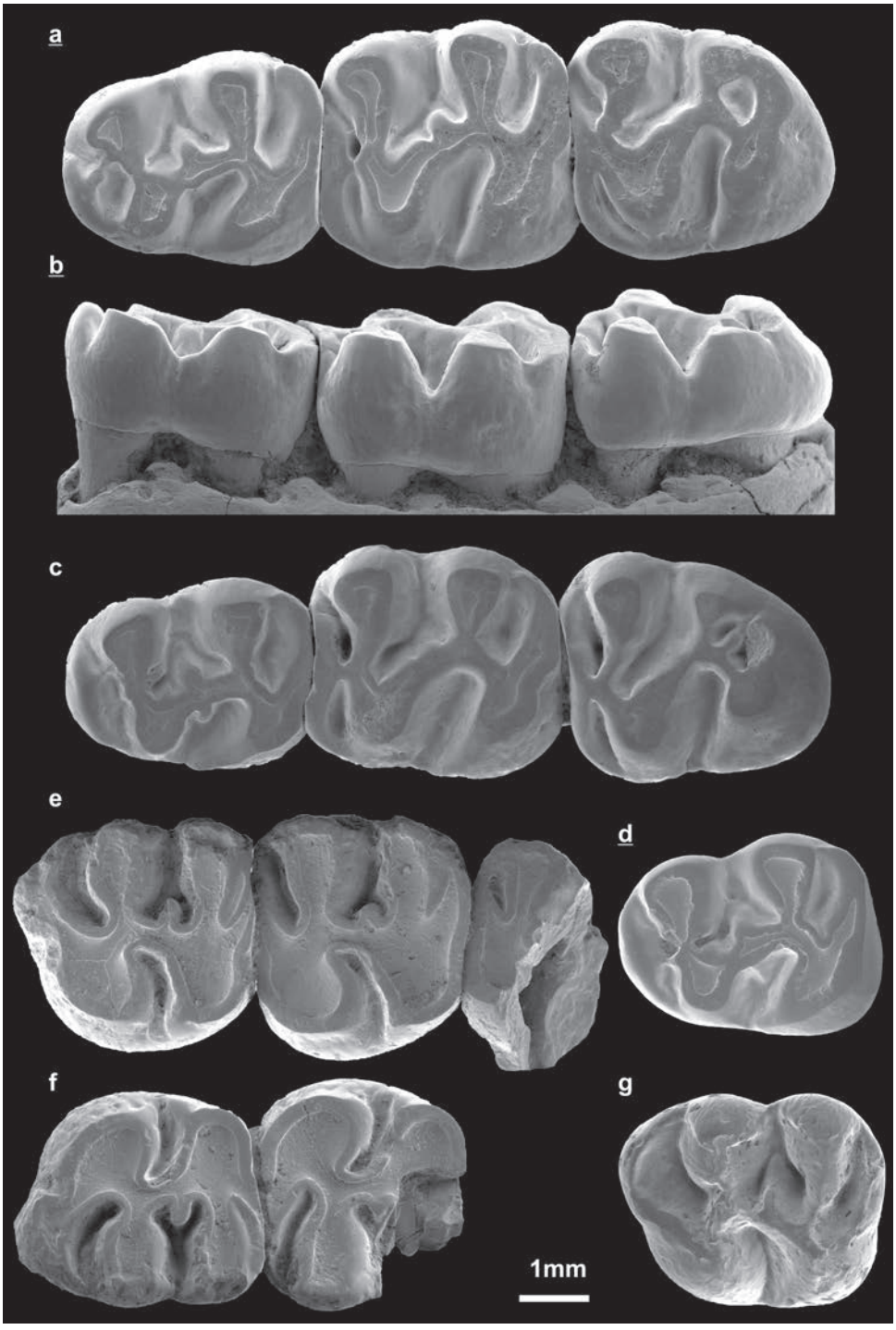
Description of the holotype (Figs 2a, 2b): The drop-shaped lingual conids of lower molars are merged with the short metalophid and hypolophid. The labial conids are triangular with rounded labial corners. The metalophid and hypolophid are connected with the anterior arms of protoconid and hypoconid, respectively. The mesolophid of m1–2 is short; it is absent in m3. The ectolophid of m1–3 is slightly oblique. The backward directed sinusid is wide and shallow in m1, extending as far as the median line in m2–3. The m1 displays a labial anterolophid and a weak anterolophulid connecting anteroconid and metalophid. The labial anterolophid of m2–3 is longer than the lingual one. The anterosinusid and protosinusid are almost equally sized. The mesosinusid of m1–2 is wide, but narrow in m3. The posterosinusid of m3 is small and rounded.

Description of paratypes and further materials (Figs 2c–2g):

Lower jaw: The diastema is concave. The masseteric fossa extends to below m1–2. The lower ridge of the fossa is pronounced, and its anterior extension is as far as m1. The mental foramen is situated below the anterior root of m1. The dental pattern of m1–3 resembles the holotype. The lower tooth- row (m1–3) is 10–11 mm long. The m1 (Fig. 2c) shows a short ectomesolophid.

Table 3. Measurements of *Tachyoryctoides radnai* nov. spec.

	length (mm)			width (mm)	
	range	mean	N=40	range	mean
M1–3	10.09 mm		1		
M1	3.35 – 3.94	3.65	6	2.94 – 3.12	2.97
M2	3.12 – 3.53	3.29	4	3.06 – 3.24	3.15
M3		2.59	2	2.35 – 2.53	
m1–3	10.00 – 11.00		3		
m1	3.12 – 3.65	3.43	8/9	2.47 – 2.76	2.65
m2	2.94 – 3.53	3.24	10	2.94 – 3.41	3.12
m3	3.12 – 3.65	3.30	9	2.76 – 3.24	3.00



Upper dentition (Figs 2e–2g): There are three badly damaged skull fragments, which will be described and illustrated elsewhere. The upper incisor has a triangular cross-section and a flat anterior surface. The lingual side of the upper molars is higher than the labial side. The upper tooth-row (M1–3) is 10.9 mm long. The M1–3 have rounded cones and short transverse lophs. The entoloph is longitudinal. The mesoloph of M1–2 is short; it is absent in M3. The long anteroloph of M1 extends along the anterior margin of the tooth as far as the antero-labial edge. M2–M3 have a shorter labial anteroloph than M1. The sinus of M1–3 is narrow, shallow, and turns forward. Protosinus, mesosinus and posterosinus of M1–M3 are transverse. M1 is the largest, M3 the smallest of upper molars. M1–3 have three roots (two labial, one lingual); m1–3 have two roots.

Remarks: *Tachyoryctoides radnai* nov. spec. is most similar with the smaller species *Tachyoryctoides bayarmae*, especially as concerns its primitive cricetoid molar features (*e.g.*, the buno-lophodont pattern, low crowns, longitudinal direction of the entoloph of upper molars). *Tachyoryctoides radnai* and *Tachyoryctoides bayarmae* provide the oldest records of *Tachyoryctoides* in Mongolia and co-occur in identical fossil beds (TGR-C/1, TGW-A/3+4). *Tachyoryctoides radnai* is well represented by fragmentary skulls, fragmentary lower jaws and by isolated teeth. Detailed analyses and the reconstruction of the cranial morphology will be presented later in a special issue.

The stratigraphic range is Late Oligocene (biozones C–C1).

Tachyoryctoides obrutschewi BOHLIN, 1937
(Figs 3a–3e)

2007 *Tachyoryctoides obrutschewi* p.p. – DAXNER-HÖCK & BADAMGARAV: 17, tab. 3.
2010 *Tachyoryctoides obrutschewi* p.p. – DAXNER-HÖCK *et al.*: 359, tab. 4.
2013 *Tachyoryctoides obrutschewi* p.p. – DAXNER-HÖCK *et al.*: 488, tab. 20/4.

Type locality: Shargaltein-Tal, Gansu Province (China).

Type stratum: Late Oligocene.

Occurrences of *Tachyoryctoides obrutschewi* (Valley of Lakes, Uvurkhangai):

Late Oligocene (biozone C1): Hotuliin Teeg: HTE-057: left fragmentary jaw with m2–3 (NHMW 2013/0449/0001; m2: 3.30 × 3.35 mm; m3: 3.50 × 2.95 mm), left M3 (2 NHMW 2013/0449/0002; 2.53 × 3.12 mm). Tatal Gol: TAT-051/2: right fragmentary jaw with m1–2 (NHMW 2013/0450/0001; m1: 3.53 × 3.12 mm; m2: 3.24 × 3.10 mm). The

◀ Fig. 2. *Tachyoryctoides radnai* nov. spec. from Taatsiin Gol (TGR-C/1–2), Valley of Lakes, Mongolia. Late Oligocene (biozone C). All specimens from the NHMW collection.
a: right m1–3, occlusal view, holotype (NHMW 2014/0445/0001). **b**: right m1–3, labial view, holotype (NHMW 2014/0445/0001). **c:** left m1–3, paratype (NHMW 2014/0445/0004). **d**: right m1, paratype (NHMW 2014/0445/0006). **e**: left M1–3 (of skull fragment), paratype (NHMW 2014/0445/0008). **f**: right M1–2 (of skull fragment), paratype (NHMW 2014/0445/0008). **g**: left M1, paratype (NHMW 2014/0445/0007).

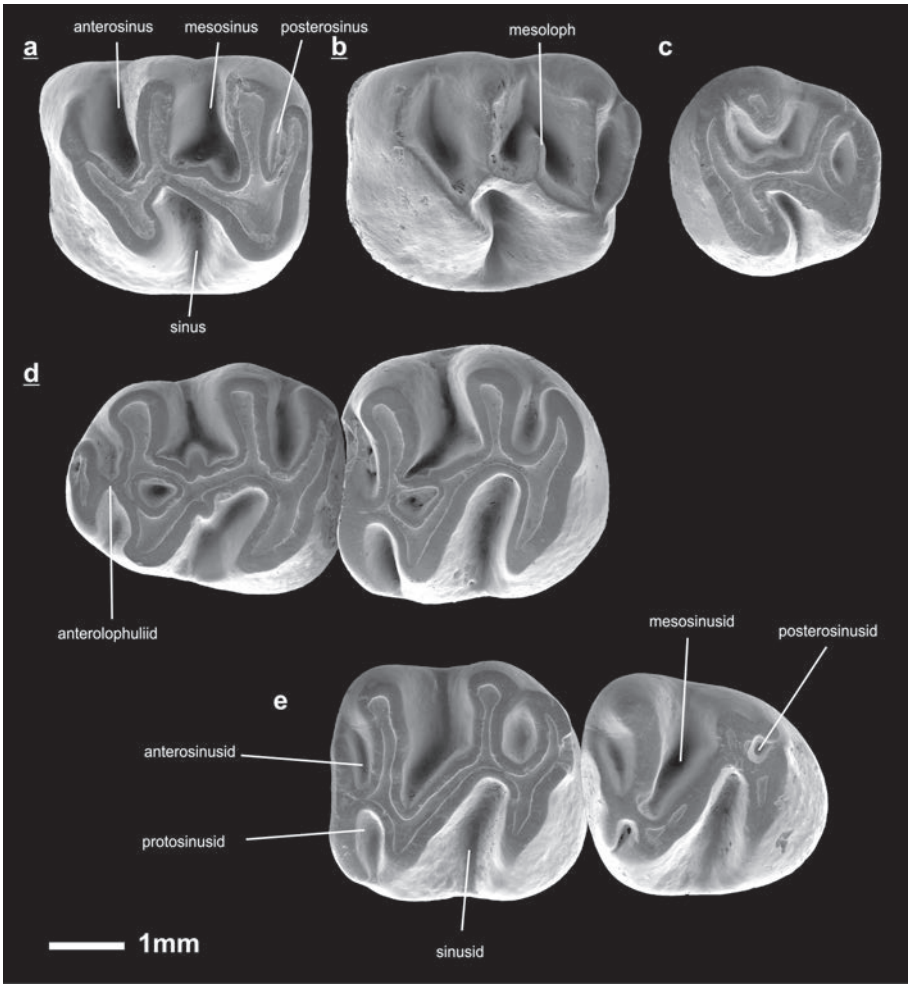


Fig. 3. *Tachyoryctoides obrutschewi* Bohlin, 1937 from the Valley of Lakes, Mongolia. Late Oligocene (biozone C1). All specimens from the NHMW collection.
a. Right M1 (NHMW 2013/0451/0001) from Ikh Argalatyn Nuruu (IKH-B/5).
b. Right M1 (NHMW 2013/0452/0001) from Hsanda Gol (SHG-AB/top of the section).
c. Left M3 (NHMW 2013/0449/0002) from Hotuliin Teeg (HTE-057).
d. Right m1–2 (NHMW 2013/0450/0001) from Tatal Gol (TAT-052/1).
e. Left m2–3 (NHMW 2013/0449/0001) from Hotuliin Teeg (HTE-057).

estimated length of the tooth-row is ~ 10–11 mm. Ikh Argalatyn Nuru: IKH-B/5: left M1 (NHMW 2013/0451/0001; 3.82 × 3.53 mm). Hsanda Gol: SHG-AB* (top of the section): right M1 (NHMW 2013/0452/0001; 3.53 × 2.94 mm).

Description: The masseteric fossa of the jaw extends to below the anterior part of m2 and is marked by pronounced upper and lower ridges. The position of the mental foramen is below m1. The molars are brachydont to mesodont and have a lophodont pattern.

The length of a composed lower tooth-row (m1–3) is ~10–11 mm. The m1 (Fig. 3d) has anteroconid and anterolophulid. The anterosinusid and protosinusid are open toward lingual and labial sides, respectively. A fossettid is enclosed by metalophid I, metalophid II and the anterior and posterior arm of protoconid. The ectolophid is slightly oblique. Mesolophid and ectomesolophid of m1 are extremely short. All sinusids of m1 are open. The m2 (Fig. 3d) displays also a closed fossettid, but no mesolophid or ectomesolophid. The labial and lingual anterolophid of m2 are of almost equal length, anterosinusid and protosinusid are open. The m2–3 of a second specimen (Fig. 3e) have no fossettid nor mesolophid. Anterosinusid, protosinusid and sinusid are open, but posterosinusid is closed.

The occlusal outline of M1 (Figs 3a–3b) is trapezoidal. There are four labial lophs and a short mesoloph, three labial valleys and the lingual sinus. Labial and lingual cones merge with the lophs. The labial valleys and lophs are transverse. The anteroloph is slightly oblique; it is merged with the anterior arm of the protocone end extends as far as the antero-labial corner of the tooth. The posterior arm of the protocone is connected with protoloph and entoloph. From this connection the protoloph extends transversely toward the labial border, and the entoloph extends obliquely toward the hypocone at the lingual border. The metaloph is connected with the hypocone. The oblique sinus is directed forward. No M2 is available. The M3 (Fig. 3c) is almost square in outline, but the anterior portion is wider than the posterior. There are three labial lophs. The labial anteroloph merges with the protocone. The metacone is isolated. The sinus is directed forward. The posterosinus is closed. The upper molars have three roots, the lower molars two roots.

Remarks: The mental foramen of *Tachyoryctoides obrutschewi* is below the posterior root of m1. Other *Tachyoryctoides* species studied by us have the mental foramen below the anterior root of m1. The dental features and size of *Tachyoryctoides obrutschewi* are transitional between the smaller, low crowned, buno-lophodont molars of *Tachyoryctoides radnai* and the larger, mesodont, lophodont molars of *Tachyoryctoides kokonorensis*. Moreover, these three species occur in Mongolia in a stratigraphic sequence. In our opinion they represent a phylogenetic line, from the most primitive *Tachyoryctoides radnai* of the Late Oligocene (biozones C–C1), to the transitional *Tachyoryctoides obrutschewi* (biozone C1), to the advanced *Tachyoryctoides kokonorensis* of the Early Miocene (biozone D).

The stratigraphic range is Late Oligocene (biozone C1).

Tachyoryctoides tatalgolicus DASHZEVEG, 1971

(Figs 4a–4d)

1971 *Tachyoryctoides tatalgolicus* sp. nov. – DASHZEVEG, D.: 69, fig. 1.

Type locality: Tatal Gol, Mongolia.

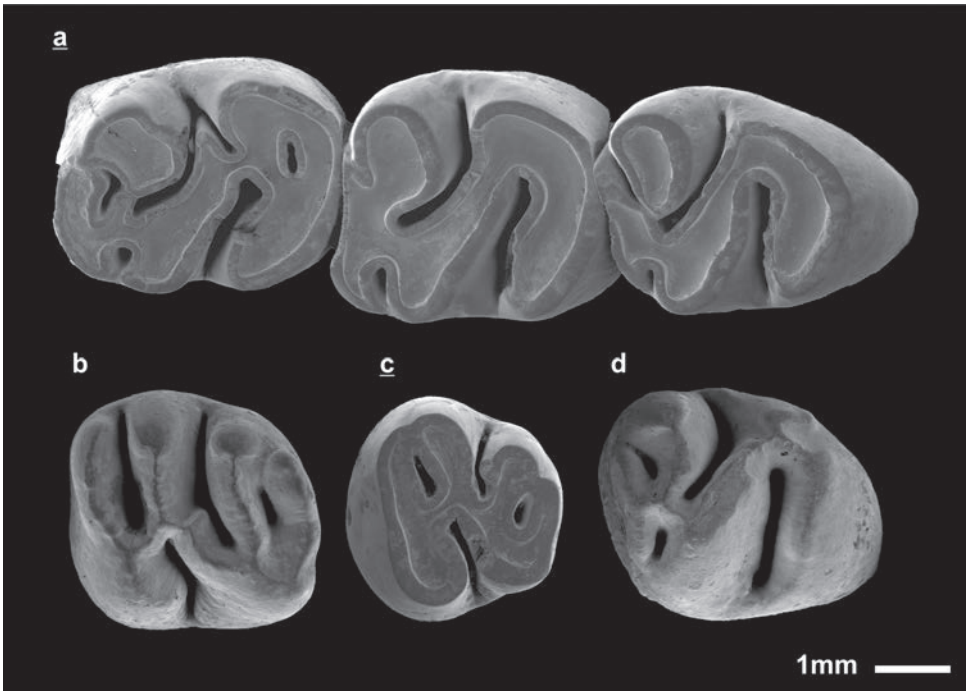


Fig. 4. *Tachyoryctoides tatalgolicus* DASHZEVEG, 1971 from the Valley of Lakes, Mongolia. Late Oligocene (biozone C1). All specimens from the NHMW collection.
a. Right m1–3 (NHMW 2013/0453/0001) from Tatal Gol (TAT-043).
b. Left M2 (NHMW 2013/0453/0004) from Tatal Gol (TAT-043).
c. Right M3 (NHMW 2013/0454/0001) from Tatal Gol (TAT-E/22).
d. Left m3 (NHMW 2013/0453/0003) from Tatal Gol (TAT-043).

Type stratum: Hsanda Gol Fm., Late Oligocene.

Occurrences of *Tachyoryctoides tatalgolicus* in Mongolia (Valley of Lakes, Uvurkhangai):

Late Oligocene (biozone C1): Tatal Gol: TAT-043: right fragmentary jaw with m1–3 (NHMW 2013/0453/0001). Measurements: toothrow m1–3 = 12 mm; m1: 4.10 × 3.60 mm; m2: 3.85 × 3.60 mm; m3: 4.00 × 3.40 mm), 1 right fragmentary m1 (NHMW 2013/0453/0002), 1 left m3 (NHMW 2013/0453/0003; 4.10 × 3.15 mm), 1 left M2 (NHMW 2013/0453/0004; 3.20 × 3.10 mm). TAT-E/22: 1 right M3 (NHMW 2013/0454/0001; 2.67 × 3.00 mm). Hotuliin Teeg: HTSE-009: 1 left m2 (NHMW 2013/0455/0001; 3.90 × 3.80 mm).

Description: The masseteric fossa of the jaw (NHMW 2013/0453/0001) extends to below the anterior part of m2 and is marked by pronounced upper and lower ridges. The position of the mental foramen is below the anterior root of m1. The occlusal surface of molars is planar. The molars are larger than those of *Tachyoryctoides obrutschewi*, have

mesodont crowns, thick enamel, voluminous lophs/lophids and extremely narrow, deep valleys extending across the teeth beyond the median line. M3 has three roots, the lower molars two roots.

The lower tooth-row (m1–3) is 12 mm long. The m1 (Figure 4a) has a rectangular occlusal outline. The trigonid is wide. It displays a labial and lingual anterolophid. An indistinct anterolophulid connects the lingual anterolophid and the metaconid. The mesolophid is of medium length. Metalophid and hypolophid are very short. The metalophid is cut off from the large, rounded metaconid. The oblique ectolophid extends from the protoconid in postero-lingual direction beyond the median line of the tooth. Anterosinusid and protosinusid are closed. The mesosinusid is narrow and oblique. The posterosinusid is closed (= posterofossettid). The sinusid is narrow, directed backward and extends beyond the median line of the tooth. The m2–3 have no mesolophid. Labial and lingual arms of the anterolophid are present. The short metalophid of m3 is cut off from the metaconid (Fig. 4a), and the hypolophid is merged with the entoconid. The ectolophid is strong, oblique and long. Sinusid and mesosinusid are also long, narrow, oblique and extend beyond the median line. The posterosinusid is absent (Fig. 4a) or very shallow (Fig. 4d).

There is only one unworn M2 (Fig. 4b): It has a lophodont pattern (conids are merged with the lophids), a high crown, four labial oblique lophs and three narrow labial valleys. From the lingual margin, the narrow oblique sinus extends in an anterolabial direction as far as the median line. A small mesoloph is visible. The posterosinus is shallow and tends to be closed.

The M3 (Fig. 4c) is the smallest molar, but resembles M2. It has no mesoloph, a closed anterosinus and posterosinus.

Remarks: *Tachyoryctoides obrutschewi* and *Tachyoryctoides tatalgolicus* are similar, but not identical. *Tachyoryctoides tatalgolicus* shows more advanced dental features such as: the higher tooth crowns, extremely narrow valleys, diagonal loph/lophids and the more oblique sinusid. The deep and narrow valleys extend beyond the median line of the tooth; thus, lingual and labial ones overlap. These differences seem to be beyond the range of individual variation, and therefore we do not agree with KOWALSKI (1974), LOPATIN (2004) and WANG & QIU (2012) to put *Tachyoryctoides tatalgolicus* into synonymy with *Tachyoryctoides obrutschewi*. The presently studied material comprises, in our opinion, both *Tachyoryctoides* species from the Tatal Gol sections. We found *Tachyoryctoides obrutschewi* from layer TAT-051/2 and *Tachyoryctoides tatalgolicus* from the layers TAT-043 and TAT-E/22. All three fossil layers are of Late Oligocene age (biozone C1). Earlier findings of *Tachyoryctoides* from Tatal Gol area were identified as *Tachyoryctoides obrutschewi*, *Tachyoryctoides pachygnathus* and *Tachyoryctoides tatalgolicus* (MELLETT 1966; DASHZEVEG 1971; KOWALSKI 1974).

We think that the dental morphology and size of *Tachyoryctoides tatalgolicus* is most similar to *Tachyoryctoides glikmani* from the Aral region (VORONTSOV 1963; LOPATIN 2004). However, the main reason for the diverging taxonomical interpretations is the unknown variation of dental characters, because the type material of these species is

limited to a single lower jaw or to a very few specimens. The age of *Tachyoryctoides tatalgolicus* is Late Oligocene (biozone C1).

Tachyoryctoides kokonorensis Li & Qiu, 1980

(Figs 5a–5f, 6a–6h, Tab. 4)

1997 *Tachyoryctoides pachygnathus*. – Daxner-Höck *et al.*: 172.
1999 *Tachyoryctoides kokonorensis*. – Höck *et al.*: 118.
2007 *Tachyoryctoides kokonorensis*. – Daxner-Höck & Badamgarav: 17, tab. 3.
2013 *Tachyoryctoides kokonorensis*. – Daxner-Höck et al.: 482, 488, 490, tab. 20/4.

Type locality: Xiejia (China).

Type stratum: Early Miocene.

Occurrences in Mongolia (Valley of Lakes, Uvurkhangai):

Early Miocene (biozone D): Hotuliin Teeg: HTE*: Left lower jaw fragment with m1–2 (NHMW 2013/0456/0001), 1 left m3 (NHMW 2013/0456/0002), 1 left m1 (NHMW 2013/0456/0003), 1 left M1 (NHMW 2013/0456/0004), 1 right M2 (NHMW 2013/0456/0005),1 left M3 (NHMW 2013/0456/0006), 10 skull fragments, 43 fragmentary lower jaws, with partial tooth-rows, isolated molars, incisors and bones (NHMW 2013/0456/0007 to …/0060) and 30 jaws and teeth (Coll. MPC); HTE-012:

Table 4. Measurements of *Tachyoryctoides kokonorensis* from Hotuliin Teeg (HTE) and Unkheltseg (UNCH).

	length (mm)			width (mm)	
HTE:	**range**	**mean**	**N=143**	**range**	**mean**
M1–3	10 – 11 mm				
M1	4.12 – 4.71	4.44	13	3.29 – 4.41	3.79
M2	3.00 – 3.88	3.49	27	3.53 – 4.29	3.86
M3	2.06 – 3.06	2.64	18	2.65 – 3.82	3.33
m1–3	11 – 13 mm				
m1	3.35 – 4.53	4.02	21	2.88 – 3.65	3.30
m2	3.06 – 4.12	3.71	40	3.18 – 4.12	3.65
m3	2.94 – 4.29	3.75	24	2.65 – 3.94	3.38
UNCH:	**range**	**mean**	**N=68**	**range**	**mean**
M1–3	11 – 12 mm				
M1	4.41 – 5.29	4.68	12	3.53 – 4.29	3.98
M2	3.53 – 4.88	3.70	12	3.76 – 4.29	4.02
M3	2.47 – 3.29	2.75	9	2.94 – 4.00	3.37
m1–3	11 – 13 mm				
m1	3.53 – 4.82	4.11	12	2.94 – 3.65	3.38
m2	3.24 – 4.12	3.76	15	3.29 – 4.00	3.71
m3	3.82 – 4.59	4.12	8	2.94 – 3.59	3.29

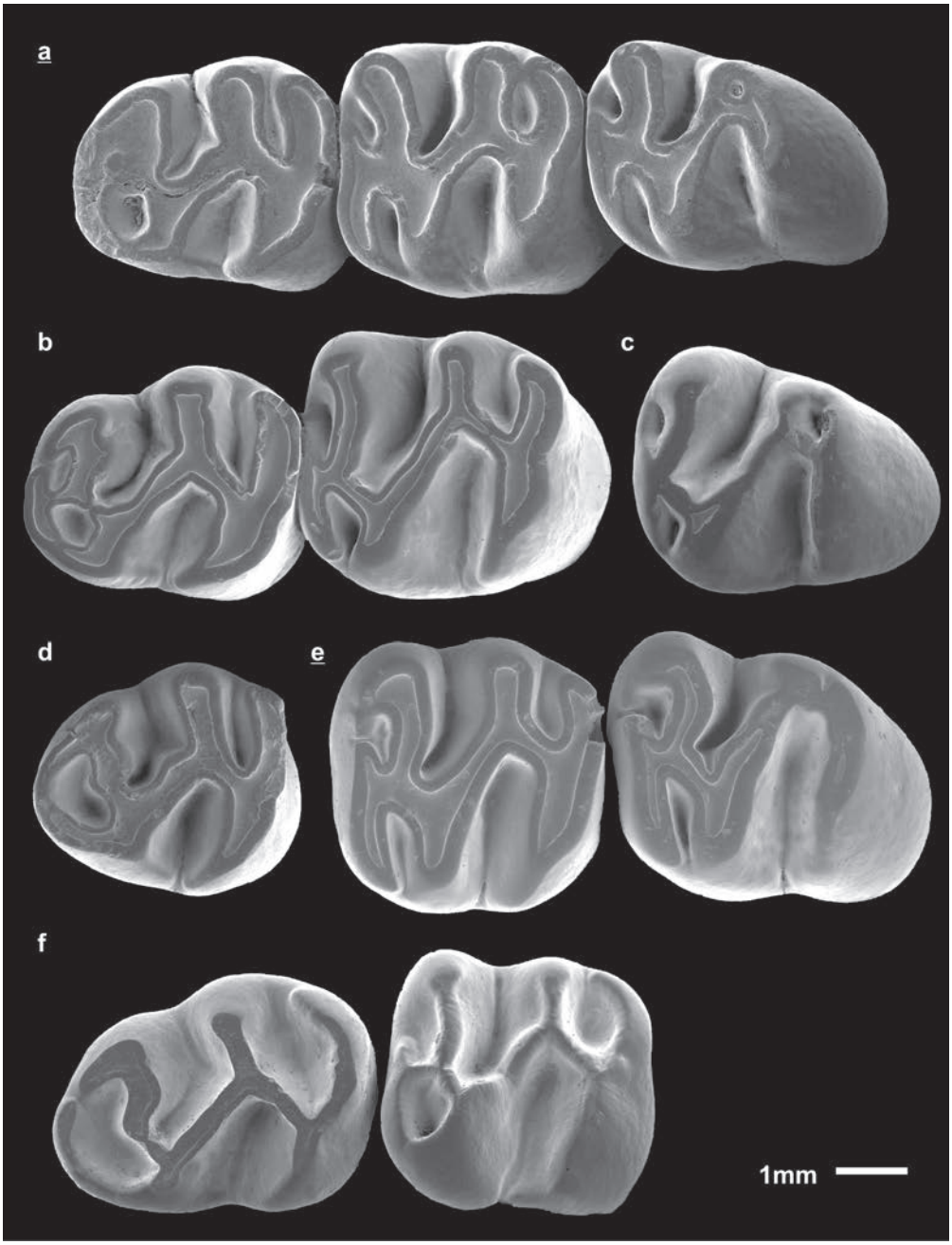


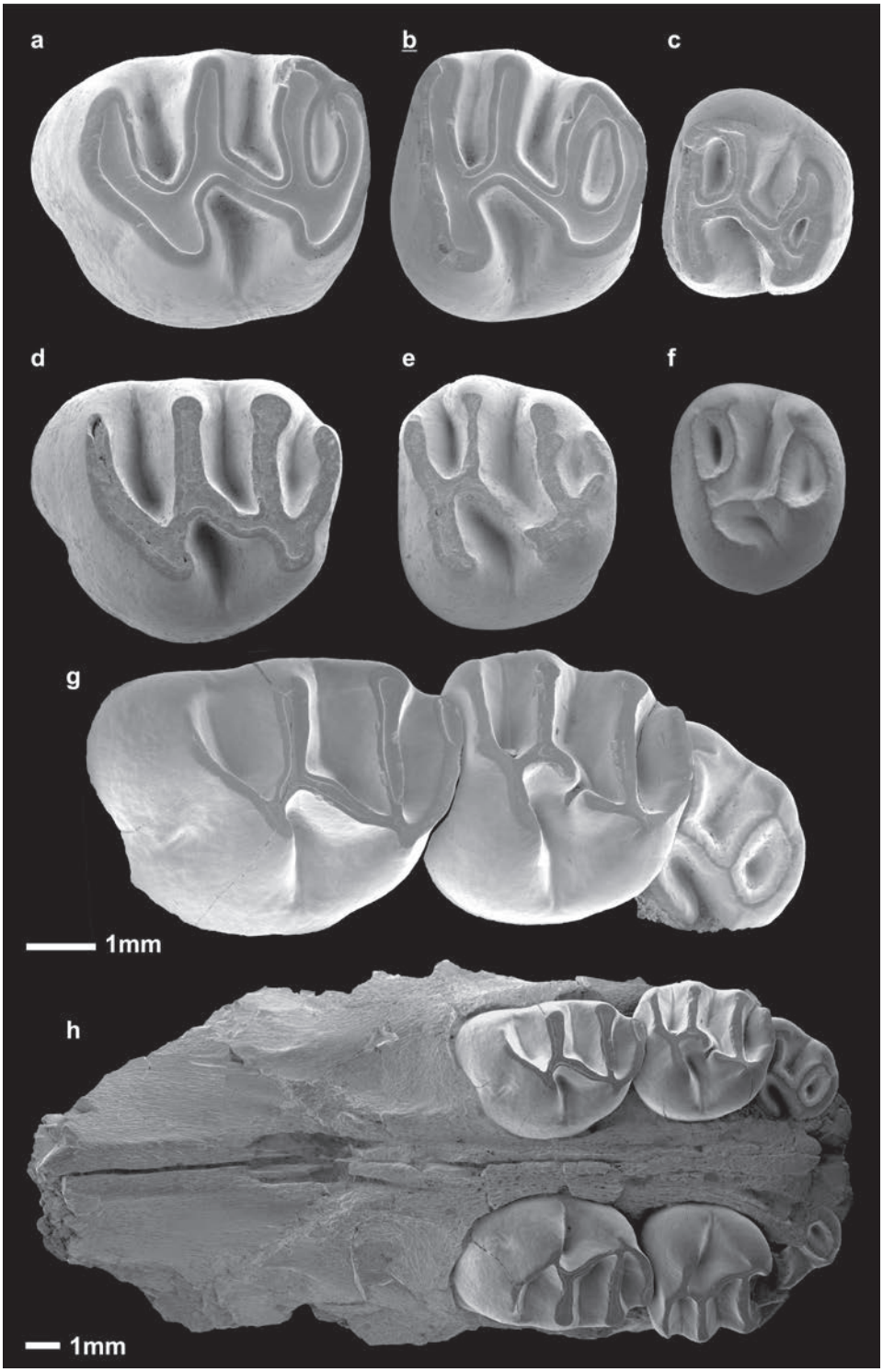
Fig. 5. *Tachyoryctoides kokonorensis* LI & QIU, 1980 from Hotuliin Teeg (HTE) and Unkeltseg (UNCH), Valley of Lakes, Mongolia. Early Miocene (biozone D). All specimens from the NHMW collection. **a**. Right m1–3 (NHMW 2013/0457/0001) from HTE-012. **b**. Left m1–2 (NHMW 2013/0456/0001) from HTE*. **c**. Left m3 (NHMW 2013/0456/0002) from HTE*. **d**. Left m1(NHMW 2013/0456/0003) from HTE*. **e**. Right m2–3 (NHMW 2013/0460/0001) from UNCH-A/3+4. **f**. Left m1–2 (NHMW 2013/0460/0002) from UNCH-A/3+4.

fragmentary right lower jaw with m1–3 (NHMW 2013/0457/0001),1 left M1(NHMW 2013/0457/0002), 1 left M2 (NHMW 2013/0457/0003), 1 left M3 (NHMW 2013/0457/0004), 2 skull fragments, 16 isolated molars, 9 fragmentary lower jaws, numerous incisors and bones (NHMW 2013/0457/0027), HTE-005: 3 molars (NHMW 2013/0458/0001 to …/0003), HTE-009: a right m3, 9 incisors (NHMW 2013/0459/0001 to …/010); HTE-014-017: 5 molars, 2 incisors (Coll. MPC). Unkheltseg: UNCH-A/3+4: Right lower jaw fragment with m2–3 (NHMW 2013/0460/0001), left lower jaw fragment with m1–2 (NHMW 2013/0460/0002), fragmentary skull with right and left M1–3 (NHMW 2013/0460/0003), 16 lower jaws with partial dentition, 7 skull fragments partly with teeth and 5 isolated molars (NHMW 2013/0460/0004 to …/0028). Luuny Yas: LUS-027: Left and right lower jaw partially with teeth (NHMW 2013/0461/0001). LUS-029: Left m2 (NHMW 2013/0462/0001).

Description: The jaws and molars are large, but more delicate than the respective bones and teeth of *Tachyoryctoides engesseri* and *Tachyoryctoides pachygnathus*. The masseteric fossa of the jaw extends to below the anterior part of m2 and is marked by pronounced upper and lower ridges (the lower ridge is longer than the upper one). The position of the mental foramen is below the anterior root of m1. Upper and lower incisors are triangular in cross-section and have a flat labial surface. The "schmelzmuster" of lower incisors is uniserial of type 3a, and the molars have a highly derived molar "schmelzmuster" of C-type (Koenigswald & Kalthoff 2007: tab.1, fig. 4c). The molars are brachydont to mesodont, lophodont, and the occlusal surface is planar. The lingual wall of upper molars is higher than the labial wall. Upper molars are tilted backward, lower molars forward. The molars are large but have rather thin enamel.

Lower molars (Fig. 5): The lower tooth-row (m1–3) is 11–13 mm long. The m1 shows two different morphotypes, morphotype A and morphotype B. In morphotype A (Figs 5a–5b) the anterolophulid separates anterosinusid and protosinusid. This m1 of type A is rather short and wide. In morphotype B (Fig. 5f) the anterolophulid is absent, and the trigonid basin (fused anterosinusid and protosinusid) is enclosed by anterolophid, protoconid, metalophid and metaconid. This m1 of type B is in most cases longer and relatively slender; it is the more advanced type. There is, however, a wide field of morphological variability between the two main morphotypes (Fig. 5). The mesolophid is very short or absent. The mesosinusid, posterosinusid and sinusid are open. The ectolophid extends obliquely from the protoconid toward the hypolophid, and turns

Fig. 6. *Tachyoryctoides kokonorensis* Li & Qiu, 1980 from Hotuliin Teeg (HTE) and Unkeltseg (UNCH), Valley of Lakes, Mongolia. Early Miocene (biozone D). All specimens from the NHMW collection. **a**. Left M1 (NHMW 2013/0456/0004) from HTE*. **b**. Right M2 (NHMW 2013/0456/0005) from HTE*. **c**. Left M3 (NHMW 2013/0456/0006) from HTE*. **d**. Left M1 (NHMW 2013/0457/0002) from HTE-012. **e**. Left M2 (NHMW 2013/0457) from HTE-012. **f**. Left M3 (NHMW 2013/0457/0004) from HTE-012. **g**. Left M1–3 (NHMW 2013/0460/0003; part of 6 h) from UNCH-A/3+4. **h**. Fragmentary skull with right and left M1–3 (NHMW 2013/0460/0003) from UNCH-A/3+4. ▶



in a right angle toward the hypoconid. The rectangular m2 is wider than m1, and its structures are similar to m1. The metalophid and hypolophid are transverse. The labial anterolophid is slightly stronger than the lingual one. Anterosinusid and protosinusid are almost equal. The m3 is similar to m2, but its posterior part is reduced (the entoconid is merged with hypolophid and posterolophid) and the posterosinusid is absent or very small.

Upper molars (Fig. 6): The upper tooth-row (M1–3) is 11–12 mm long. The outline of M1 is trapezoidal with rounded corners. There are four labial transverse lophs separated by three deep valleys, and the lingual sinus. The sinus, anterosinus and mesosinus of M1–2 are open, the posterosinus is open or closed. A short mesoloph can be present. The posteroloph is shorter than the metaloph. The M2 is shorter but wider than M1. Frequently, the anterosinus is compressed in antero-posterior direction; it is shorter and shallower than the mesosinus. The occlusal outline of M3 is rounded. The M3 resembles M2, but the anterosinus and posterosinus are smaller and closed. All upper molars have three roots (the lingual root is wide); the lower molars have two roots.

Remarks: The collections from Hotuliin Teeg and Unkheltseg comprise numerous skull fragments and badly damaged lower jaws partly with, partly without teeth. At present we assume that they mostly belong to *Tachyoryctoides kokonorensis*, but we cannot exclude that some skull fragments stem from *Tachyoryctoides engesseri* (both species are recorded from Hotuliin Teeg). The cranial morphology will be analysed and published later in a special issue. The molar pattern of the Mongolian specimens is most similar to *Tachyoryctoides kokonorensis* from the type locality Xiejia. There is, however, a wide variability of molar morphology and size, *e.g.*, morphotype A and morphotype B of lower m1. The short m1 (morphotype A) resembles the type material from Xieija rather than the longer m1 (morphotype B). Morphotype A predominantly occurs in the lower part of the Hotuliin Teeg section, whereas morphotype B dominates in Unkheltseg, which is the youngest of the mammal assemblages of biozone D in Mongolia. The age of both assemblages is Early Miocene (biozone D).

Tachyoryctoides engesseri Wang & Qiu, 2012

(Figs 7a–7f, Tab. 5)

Type locality: GL 199708, Qu-liachuan, Gaolan County (China).

Type stratum: Xianshuihe Fm., Early Miocene.

Occurrences in Mongolia (Valley of Lakes, Uvurkhangai): Hotuliin Teeg (HTE-008, HTE-009, HTE*); Early Miocene (biozone D).

Hotuliin Teeg: HTE-008: left and right hemi-mandibles (probably from one individual): left m1–3 (NHMW 2013/0463/0001), right m1–3 (NHMW 2013/0463/0002), 1 left m2 (NHMW 2013/0463/0003), 2 right m3 (NHMW 2013/0463/0004, …/0005), I inf. (NHMW 2013/0463/0006); HTE-009:1 right m2, 3 Inc. (NHMW 2013/0464/0001 to …/0004); HTE*: 1 right m1 (NHMW 2012/0068/0001), 1 left M1 (NHMW 2012/0068/0002),1

right M2 (NHMW 2012/0068/0003), 1 left M1 (NHMW 2012/0068/0004), 1 left M2 (NHMW 2012/0068/0005), 1 left M3 (NHMW 2012/0068/0006), 3 right M1 (NHMW 2012/0068/0007 to …/0009), 1 left M1 (NHMW 2012/0068/0010), 1 left M2 (NHMW 2012/0068/0011), 1 left m1 (NHMW 2012/0068/0012), 1 right m1 (NHMW 2012/0068/0013), 2 right m2–3 (NHMW 2012/0068/0014, …/0015), 1 left m2–3 (NHMW 2012/0068/0016); HTE-016-017: 6 molars (coll. MPC).

Description: The jaws are very robust, and the teeth have thick enamel. The mandibular ramus is high (13 mm).The masseteric fossa extends to below the anterior part of m2 and is marked by pronounced upper and lower ridges; the lower ridge is longer than the upper one. The position of the mental foramen is below the anterior root of m1. The lower incisor is triangular in cross-section (4 × 4 mm) and has a flat anterior surface. The molars are the largest of all *Tachyoryctoides* species known from Mongolia; they are larger than *Tachyoryctoides kokonorensis* and resemble *Tachyoryctoides engesseri* from the Lanzhou Basin (type locality).

The massive molars are brachydont to mesodont, lophodont, tilted backward/forward in upper/lower molars, respectively. The occlusal surface is planar. The m1 is higher crowned than the m3. All valleys are wide and open toward labial or lingual. The lower tooth-row (m1–3) is 15–16 mm long, the upper tooth-row (M1–3) 13–15 mm long.

The molar pattern resembles the type material (WANG & QIU 2012) by the m1 having no anterolophulid and no mesolophid, by the trigonid basin being labially open and lingually closed or open (Figs 7a, 7d). The trigonid basin is built by fusion of anterosinusid and protosinusid. The metaconid is larger than the protoconid. The metalophid is constricted in its middle part and can be interrupted. All lingual and labial valleys are open. The sinusid and ectolophid are oblique. The m2 is rectangular, wider than m1, its structures are similar to m1. The metalophid and hypolophid are transverse, the labial anterolophid is strong, the lingual one small, sometimes almost absent. There is a tiny anterosinusid but a much larger protosinusid (Fig. 7b). The m3 is similar to m2, but its posterior part is reduced (the entoconid is merged in hypolophid and posterolophid) and the posterosinusid is very small or absent.

Table 5. Measurements of *Tachyoryctoides engesseri*.

	length (mm)			width (mm)	
	range	mean	N=28	range	mean
M1–3	13 – 15 mm				
M1	4.80 – 6,30	5.42	5	3.80 – 4.50	4.11
M2	4.00 – 4.55	4.11	3	4.42 – 4.55	4.51
M3		4.12	1		4.42
m1–3	15 – 16 mm				
m1	5.18 – 5.59	5.35	5	3.65 – 4.29	3.99
m2	4.88 – 5.41	5.10	7	4.41 – 4.88	4.59
m3	4.71 – 5.88	5.34	7	3.82 – 4.24	4.09

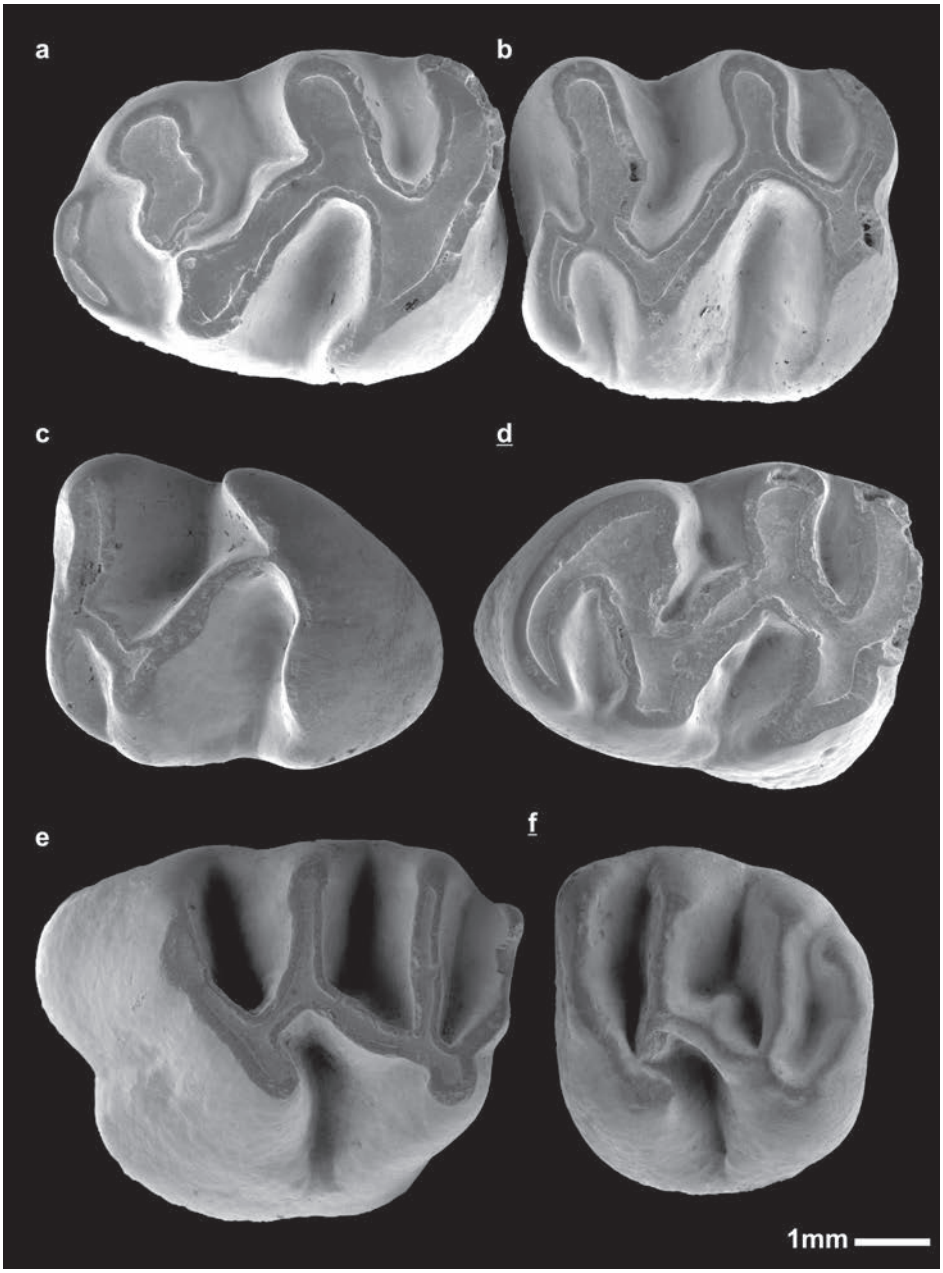


Fig. 7. *Tachyoryctoides engesseri* WANG & QIU, 2012 from Hotuliin Teeg (HTE-008, HTE*),Valley of Lakes, Mongolia. Early Miocene (biozone D). All specimens from the NHMW collection.
a. **– c**. m1–3 of left lower jaw (NHMW 2013/0463/0001) from HTE-008.
d. Right m1 (NHMW 2012/0068/0001) from HTE*.
e. Left M1(NHMW 2012/0068/0002) from HTE*.
f. Right M2 (NHMW 2012/0068/0003) from HTE*.

The outline of M1 (Fig. 7e) is trapezoidal with rounded corners. There are four labial transverse lophs separated by three deep valleys, and the lingual sinus. The labial and lingual valleys are open, except for the posterosinus, which can be closed. The mesoloph is tiny or absent. The posteroloph is shorter than the metaloph. The M2 (Fig. 7f) is shorter but wider than M1. Its anterosinus is compressed in antero-posterior direction; it is shorter and shallower than the mesosinus. The mesoloph is weak or absent. The occlusal outline of M3 is triangular with rounded corners. The M3 resembles the M2, but the posterosinus is small and closed. All upper molars have three roots (the lingual root is very wide); the lower molars have two roots.

Remarks: *Tachyoryctoides engesseri* is the largest of all *Tachyoyctoides* species from Mongolia. The jaws and teeth are more robust and larger, but the morphology of upper molars is very similar to some morphotypes of *Tachyoryctoides kokonorensis*. *Tachyoryctoides engesseri* was found from the lower part of the Hotuliin Teeg section (layers HTE-008 and HTE-009 and from the surface nearby HTE*), but not from the younger fossil beds of Unkheltseg (UNCH).

Stratigraphic range: Early Miocene (biozone D).

Tachyoryctoides sp.

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

Late Oligocene (biozone C1): Tatal Gol: TAT-043: 1 left M1-fragment, 1 right M1, 1 left M2, 1 left m2 (NHMW 2012/0069/0001 to …/0004). Measurements (M1: 4.41 × 4.53 mm, M2: 4.00 × 4.18, m2: 4.71 × 4.00). TAT-044: left jaw with m1–2 (NHMW 2013/0233/0001). Measurements (tooth-row: 13.3 mm; m1: 4.70 × 3.71, m2: 4.20 × 4.12, m3: 4.45 × 3.82). TAT-E/27: 1 left m3 (NHMW 2013/0244/0001). Measurements: (left m3: 5.12 × 4.12).

Oligocene-Miocene transition (biozone C1–D): Tatal Gol (TAT-052/2): 1 right m1, 1 left m3 (NHMW 2013/0245/0001, …/0002). Measurements (m1: 5.41 × 3.88, m3: 5.47 × 4.18). Huch Teeg (RHN-021): left M2–3 (NHMW 2013/0247/0001). Measurements (M2: 4.12 × 4.82, M3: 3.47 × ?).

Description: The right M1 (from TAT-043) is high, specifically on its lingual side. Its outline is trapezoidal with rounded corners. There are four labial transverse lophs separated by three deep valleys, and the lingual sinus. All labial and lingual valleys are open. The mesoloph is small. The posteroloph is connected with the hypocone, the metaloph is constricted. M2 is shorter than M1. Its mesoloph is weak, the posterosinus closed.

The m1 has an elliptic occlusal outline. There is a strong anterolophid, and a short anterolophulid separates anterosinusid and protosinusid (m1 from TAT-044). Moreover, m1 from TAT-052/2 has no anterolophulid but a closed trigonid basin. The mesolophid is absent, the valleys are open. The m2 is rectangular. Its structures are similar to m1. The metalophid and hypolophid are transverse. The length of labial and lingual anterolophid is almost

equal, as is also the length of anterosinusid and protosinusid. All valleys are open. The anterior part of m3 is similar to m2, but hypolophid and posterosinusid are absent.

Remarks: The molars are large and robust, in any case larger than known from the time equivalent species *Tachyoryctoides obrutschewi* and *T. Tachyoryctoides tatalgolicus*. The moderately high, lophodont molars have wide valleys (not as narrow as in *Tachyoryctoides tatalgolicus*). The pattern of m1 is similar to *Tachyoryctoides kokonorensis*, but the size, the robustness and thick enamel of teeth rather resembles *Tachyoryctoides pachygnathus* from the Late Oligocene of China and *Tachyoryctoides engesseri* from the Early Miocene of China and Mongolia. These rare specimens do not allow reliable species identification and we therefore choose open nomenclature.

Stratigraphic range: Late Oligocene (biozone C1) to Oligocene-Miocene transition (C1–D).

Genus *Ayakozomys* Tyutkova, 2000

Type species: *Ayakozomys sergiopolis* Tyutkova, 2000

Type locality: Ayaguz (Kazakhstan).

Type stratum: Early Miocene.

Dental characters: The molars are slender and small to medium sized, have moderately high crowns, a planar occlusal surface and lophodont pattern with tendencies toward prismatic structures. The cones/conids are merged with the lophs/lophids. The lophs/lophids are separated by narrow deep valleys, which are V-shaped in cross-section. The direction of labial and lingual lophs/lophids and valleys is more or less perpendicular to the longitudinal axis. Labial and lingual valleys extend beyond the median line of the tooth and overlap. Mesoloph/mesolophid and anterolophulid are absent. The M1 has four roots.

***Ayakozomys* sp.**

(Figs 8a–b)

2007 *Tachyoryctoides* sp. 2. – Daxner-Höck & Badamgarav: 17, tab. 3.
2013 *Tachyoryctoides* sp. 2. – Daxner-Höck *et al.* 488, tab. 20/4.

Occurrences in Mongolia (Valley of Lakes, Uvurkhangai):

Early Miocene (biozone D): Hotuliin Teeg: HTE*: Fragmentary left lower jaw with m1–3 (NHMW 2012/0065/0001). Measurements (length × width in mm): m1: 3.45 × 2.53; m2: 2.85 × 2.90; m3: 3.45 × ?. Length of m1–3 = 9.50 mm. Luugar Khudag: LOG-A/1: 1 right M1 (NHMW 2012/0066/0001). Measurements (length × width in mm): M1 (3.15 × 2.58).

Description: The lower tooth-row (m1–3) is 9.50 mm long. The occlusal outline of m1 is rectangular with rounded corners (W/L ratio 0.73). There are four lingual lophids (anterolophid, metalophid, hypolophid, posterolophid), three lingual transverse valleys

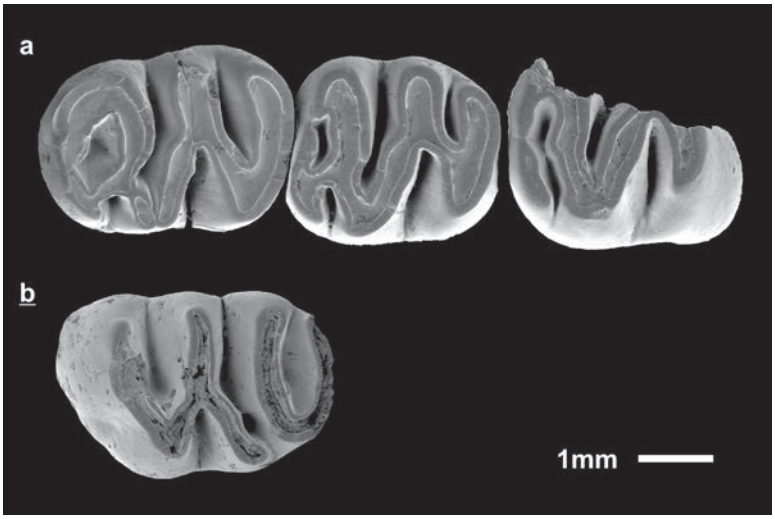


Fig. 8. *Ayakozomys* sp. from the Valley of Lakes, Mongolia. Early Miocene (biozone D). All specimens from the NHMW collection. **a**. Left m1–3 (NHMW 2012/0065/0001) from Hotuliin Teeg (HTE*). **b**. Right M1 (NHMW 2012/0066/0001) from Luugar Khudag (LOG-A/1).

(anterosinusid, mesosinusid, posterosinusid) and two labial transverse valleys (protosinusid, sinusid). The lingual and labial conids merge with the lophids. The lingual parts of the lophids are more or less transverse, the labial ones oblique. The large anterosinusid is closed, the small protosinusid open. The narrow mesosinusid extends transversely from the labial to the lingual border. Labial and lingual valleys extend beyond the median line. The hypolophid is shifted forward. The occlusal outline of m2 is also rectangular. The m2 is shorter (W/L ratio ~ 1.0), but its pattern is similar to m1. The labial anterolophid is short, the protosinusid open. The lingual anterolophid is long, the anterosinusid closed. The m3 is damaged in its postero-lingual edge. Its size and pattern resemble m2, but anterosinusid and protosinusid are fused and open labially.

M1 (Fig. 8b): The occlusal outline is rectangular with rounded corners (W/L ratio 0.85). The lingual side is slightly convex, the labial side flat. The direction of valleys and labial lophs is more or less perpendicular to the longitudinal axis. There are four slender labial lophs (anteroloph, protoloph, metaloph, posteroloph), three narrow labial valleys (anterosinus, mesosinus, posterosinus) and the lingual sinus. Labial and lingual cones merge with the lophs. The deep posterosinus is labially open, lingually closed by the U-shaped connection of metaloph and posteroloph. The deep anterosinus is labially open. The mesosinus is continuous from the lingual to the labial border. The symmetrical sinus is opposite to the protoloph. The M1 has four roots: two labial, two lingual.

Remarks: So far a single species *Ayakozomys sergiopolis* TYUTKOVA, 2000 was described from the Early Miocene of Ayaguz in Kazakhstan. According to the measurements, description and drawings of the type material (TYUTKOVA 2000: 69–70; fig. 2) the

presently studied Mongolian fossils are referable to *Ayakozomys*. However, we refrain from species identification because of the scarce Mongolian material and because the type material from Kazakhstan is not available to us for comparison. Some questionable further occurrences of this rare genus in Kazakhstan and China are mentioned by Bendukidze *et al.* (2009: 535). At present we identify the Mongolian specimens as *Ayakozomys* sp. The age is Early Miocene (biozone D).

Biostratigraphy

Tachyoryctoidinae are excellent biostratigraphic markers of the Mongolian biozones C and C1 (Late Oligocene) and biozone D (Early Miocene). So far the oldest and most primitive *Tachyoryctoides* species are *Tachyoryctoides bayarmae* nov. spec. and *Tachyoryctoides radnai* nov. spec. The two species have been found in Late Oligocene deposits of the Taatsiin Gol section (layer TGR-C/1+2) associated with the entire set of key fossils of the Mongolian biozone C. The biostratigraphy and age of these deposits are evidenced by the fossil content and by the radiometric age of basalt II (~ 27 Ma; early Late Oligocene), as outlined in "Geological setting". In Toglorhoi (layer TGW-A/3+4), *Tachyoryctoides bayarmae* and *Tachyoryctoides radnai* were found in association with index fossils of biozone C1. The Toglorhoi sequence ranges from biozone C to biozone C1 (Late Oligocene).

Occurrences of *Tachyoryctoides obrutschewi* and *Tachyoryctoides tatalgolicus* are restricted to biozone C1 in the locality Tatal Gol (TAT-051/2, TAT-043, TAT-E/22). Finally, *Tachyoryctoides kokonorensis*, *Tachyoryctoides engesseri* and *Ayakozomys* sp. are associated with other index fossils of biozone D in the Early Miocene deposits Hotuliin Teeg (HTE*, HTE-009 to HTE-012), Unkheltseg (UNCH-A/3+4) and Luugar Khudag (LOG-A/1).

Index fossils (Rodentia) indicating the Mongolian biozones C, C1 and D (Daxner-Höck *et al.* 2014, Maridet *et al.* 2014, Schmidt-Kittler *et al.* 2007, Wessels *et al.* 2014):

Biozone C (lower Late Oligocene):

Tachyoryctoides bayarmae nov. spec., *Tachyoryctoides radnai* nov. spec., *Tataromys sigmodon* Matthew & Granger, 1923, *Tataromys minor longidens* Schmidt-Kittler *et al.*, 2007, *Bohlinosminthus parvulus* (Bohlin, 1946), *Heosminthus chimidae* Daxner-Höck *et al.*, 2014, *Parasminthus* Bohlin, 1946, cf. *Asianeomys bolligeri* (Lopatin, 2000), *Eucricetodon bagus* Gomes-Rodriges *et al.*, 2012, *Aralocricetodon schokensis* Bendukidze, 1993, *Coelodontomys asiaticus* Wang, 2001(LOD), *Tsaganomys altaicus* Matthew & Granger, 1923.

Biozone C1 (upper Late Oligocene):

Tachyoryctoides obrutschewi Bohlin,1937, *Tachyoryctoides tatalgolicus* Dashzeveg, 1971, *Tataromys plicidens* Matthew & Granger, 1923, *Yindirtemys deflexus* (Teilhard

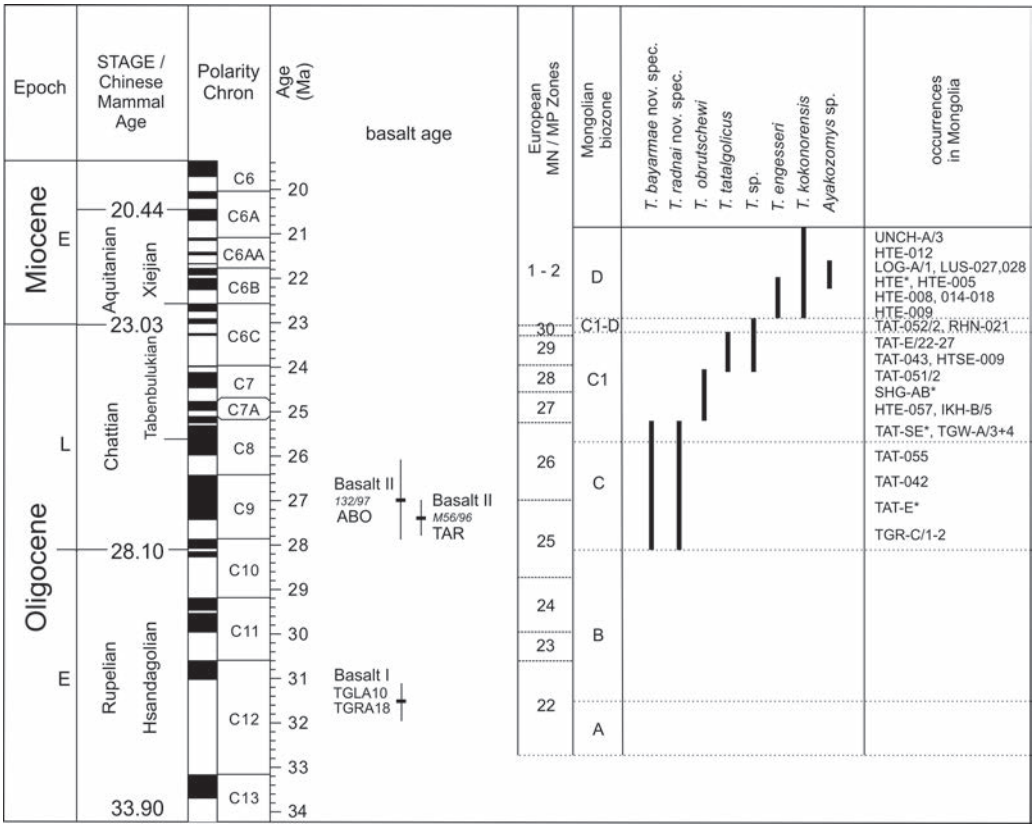


Fig. 9. Stratigraphic chart including the geologic time scale (GRADSTEIN *et al.* 2012), basalt ages and Mongolian biozones A–D (HÖCK *et al.* 1999), the European MN/MP Zones after STEININGER (1999) and LUTERBACHER *et al.* (2004), the lower boundary of the Xiejian Chinese mammal Age after MENG *et al.* (2013), the stratigraphic ranges of *Tachyoryctoides* species and *Ayakozomys* sp., and occurrences in Mongolia.

DE CHARDIN, 1926), *Bohlinosminthus parvulus* (BOHLIN, 1946), *Heosminthus chimidae* DAXNER-HÖCK *et al.*, 2014, *Plesiosminthus asiaticus* DAXNER-HÖCK & WU, 2003, *Plesiosminthus promyarion* SCHAUB, 1930, *Heterosminthus* SCHAUB, 1930 (FOD), *Asianeomys dangheensis* (WANG, 2002), *Parasminthus* BOHLIN, 1946, *Tsaganomys altaicus* MATTHEW & GRANGER, 1923 (LOD)

Biozone D (lower Early Miocene):

Tachyoryctoides kokonorensis LI & QIU, 1980, *Tachyoryctoides engesseri* WANG & QIU, 2012, *Ayakozomys* sp., *Yindirtemys suni* (LI & QI, 1980), *Distylomys* WANG, 1997 / *Prodistylomys* WANG & QIU, 1989 , *Plesiosminthus barsboldi* DAXNER-HÖCK & WU, 2003, *Plesiosminthus olzi* DAXNER-HÖCK *et al.*, 2014, *Litodonomys lajeensis* (LI & QIU, 1980),

Litodonomys huangheensis Wang & Qiu, 2000, *Heterosminthus firmus* Zazhigin & Lopatin, 2000, *Kherem shandgoliensis* Minjin, 2004, *Asianeomys dangheensis* (Wang, 2002), *Democricetodon sui* Maridet *et al*., 2011 (FOD).

Conclusions

Tachyoryctoidinae are characteristic rodents of Upper Oligocene and Lower Miocene deposits of Mongolia. Eight species from two genera were identified from twenty-three fossil layers along ten sections and fossil sites within a distance of ~ 110 km W to E and 30 km N to S (Tab. 1). The investigated area is the Taatsiin Gol and Taatsiin Tsagan Nuur region, which is part of the Valley of Lakes in Central Mongolia.

From this area we described the two oldest and most primitive species, *Tachyoryctoides bayarmae* nov. spec. and *Tachyoryctoide*s *radnai* nov. spec. The two species co-occur in some Mongolian localities, but *T. bayarmae* differs by significantly smaller molar size from *T. radnai*, which is of medium size. The age of the two species is Late Oligocene (range: biozone C to lower part of biozone C1).

Tachyoryctoides obrutschewi and *Tachyoryctoides tatalgolicus* are medium sized. The lophodont and brachydont to mesodont molars, the short mesolophid and the antero-lophulid of m1 are species characters of both *T. obrutschewi* and *T. tatalgolicus*. Nevertheless, our reason to consider *T. obrutschewi* and *T. tatalgolicus* to be independent species is that *T. tatalgolicus* has higher, more derived molar crowns with extremely narrow valleys, which extend beyond the median line. The age of the two species is Late Oligocene (range: upper part of biozone C1).

Tachyoryctoides kokonorensis and *Tachyoryctoides engesseri* are the two largest and youngest species. The lophodont, moderately hypsodont molars with rather wide valleys are characteristic of these two species. The molars of *T. engesseri*, however, are the largest and most robust, and all valleys are open. Beyond this, the molars of *T. kokonorensis* are smaller, more delicate and tend to close the trigonid-basin of m1 and the posterosinus of upper molars. More than 160 teeth, jaws and skull fragments of *T. kokonorensis* allow study of the individual variation of this species. The age of *T. kokonorensis* and *T. engesseri* is Early Miocene (biozone D).

Finally, *Ayakozomys* sp. evidences a second, rare genus of Tachyoryctoidinae. The specimens show the main genus characteristics but do not allow reliable species identification. The age is Early Miocene (biozone D).

The remarkable fossil material collected from a rather small area of ~ 3.000 km^2 in the Valley of Lakes provides insight into the local development of *Tachyoryctoides*. The buno-lophodont, low crowned molars of *Tachyoryctoides radnai* and *Tachyoryctoides bayarmae* suggest that *Tachyoryctoides* originated from a hitherto unknown rodent group with "cricetoid" molar pattern. Later, the larger, lophodont, moderately hypsodont molars developed toward more advanced species. With regard to size-increase and moderate modification of molar morphology during the Late Oligocene to the Early

Miocene, we consider that *Tachyoryctoides radnai – Tachyoryctoides obrutschewi – Tachyoryctoides kokonorensis* represent a phylogenetic line.

Investigations on the enamel microstructure of *Tachyoryctoides kokonorensis* from Unkheltseg in Mongolia show that the molars have a C-type "schmelzmuster" (*i.e.*, the Myomorpha-"schmelzmuster") and the "schmelzmuster" of the lower incisors is uniserial of type 3a (KOENIGSWALD & KALTHOFF 2007: tab.1, fig. 4c).The lower incisors with thick radial enamel and the rather large, robust, semi-hypsodont molars of *Tachyoryctoides* suggest adaptation to fossorial life (KOENIGSWALD & KALTHOFF 2007; BENDUKIDZE *et al.* 2009). This is in agreement with our observations of fossil-concentrations in paleosol horizons, which also hint at the subterranean life-style of *Tachyoryctoides*.

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