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The Lagomorpha genus *Bohlinotona* (Ochotonidae) from the late Oligocene of Mongolia

Margarita A. ERBAJEVA[1*], Lawrence J. FLYNN[2] & Gudrun DAXNER-HÖCK[3,4]

(with 5 figures and 3 tables)

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Abstract

Bohlinotona represents the oldest genus of the family Ochotonidae. *Bohlinotona* ranged throughout most of the late Oligocene, its earliest evidence being the species *Bohlinotona pusilla* (TEILHARD DE CHARDIN, 1926) from the locality Saint-Jacques in China. Today, the record of the genus in Mongolia is ~ 300 specimens, distributed among two species from seven localities. The rather primitive species, *B. pusilla*, is known from two Valley of Lakes localities in central Mongolia and one site in the Khaliun Basin in southwestern Mongolia. The species was first evidenced from the beginning of the late Oligocene at about 28 Ma and disappeared about one million years later when the second species, *Bohlinotona mongolica* nov. spec. had its first appearance. The latter species ranged from 27 Ma to ~ 24.5 Ma and is known from five localities in the Valley of Lakes.

Keywords: Ochotonidae, late Oligocene, Valley of Lakes, Khaliun Basin, Mongolia.

Kurzfassung

Bohlinotona ist die älteste Gattung der Familie Ochotonidae und überdauerte fast das gesamte Oberoligozän. Die Gattung wurde erstmals durch die Art *Bohlinotona pusilla* (TEILHARD DE CHARDIN, 1926) von der Lokalität Saint-Jacques in China nachgewiesen. Heute umfasst die Gattung in der Mongolei ~ 300 Funde, verteilt auf zwei Arten von sieben Lokalitäten. Die eher ursprüngliche Art *Bohlinotona pusilla* wurde von zwei Lokalitäten aus dem Tal der Gobiseen in der zentralen Mongolei und von einer Lokalität im Khaliun Becken der südwestlichen Mongolei bekannt. Sie tauchte zu Beginn des Oberoligozän, vor etwa 28 Millionen Jahren auf und

[1] Russian Academy of Sciences, Dobretsov Geological Institute, Siberian Branch, Sahianova Str. 6a, 670047 Ulan-Ude, Russia; e-mail: erbajeva@ginst.ru

[2] Harvard University, Department of Human Evolutionary Biology, 11 Divinity Avenue, Cambridge, MA 02138, USA

[3] Rupertusstr. 16, 5201 Seekirchen, Austria; e-mail: gudrun.hoeck@sbg.at

[4] Natural History Museum Vienna, Burgring 7, 1010 Vienna, Austria

***** Corresponding author

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verschwand eine Million Jahre später, als die zweite Art, *Bohlinotona mongolica* nov. spec., erstmals erschien. Letztere überdauerte den Zeitraum von 27 bis ~ 24.5 Millionen Jahren. Sie wurde aus fünf Lokalitäten im Tal der Gobiseen nachgewiesen.

Schlüsselwörter: Ochotonidae, Oberoligozän, Tal der Gobiseen, Khaliun Becken, Mongolei.

Introduction

Previously unknown in Mongolia, fossils of *Bohlinotona* de Muizon, 1977 were discovered in the course of field activities by teams of a Mongolian-Austrian research project in Mongolia working in the Taatsiin Tsagaan Nuur Basin (Valley of Lakes) and the locality Shine Us (Khaliun Basin) (Erbajeva 2007; Daxner-Höck *et al*. 2019). Throughout the past 20 years, three major Mongolia projects of complementary geo-scientific objectives have been conducted in collaboration with the Mongolian Academy of Sciences and the Natural History Museum Vienna. All investigations were funded by grants from the Austrian Science Fund (FWF-projects: P-10505-GEO, P-15724-N06 and P-23061-016; principal investigator: Gudrun Daxner-Höck).

Mongolian localities providing *Bohlinotona* fossils are Shine Us (assemblage SHU-A/1) from the Khaliun Basin in south-western Mongolia (Daxner-Höck *et al*. 2019), and seven assemblages from the Taatsiin Tsagaan Nuur Basin of the Valley of Lakes in central Mongolia: Toglorhoi (TGW-A*, assemblage TGW-A/2a+b), Taatsiin Gol south (assemblage TGR-C/1+2), Unzing Churum (assemblage TAR-A/2), Huch Teeg (assemblage RHN-A/9), Del (assemblage DEL-B/12), and Tatal Gol (assemblage TAT-055) (Daxner-Höck *et al*. 2017).

The goal of the present paper is to describe and discuss the Ochotonidae fossils of the genus *Bohlinotona*, which comprise two species, one of which is new. The stratigraphic position of the localities and the correlation of key sections and fossil horizons with the Geomagnetic Polarity Time Scale (GPTS) are given below under the section on Stratigraphy, which develops the estimated stratigraphic ranges (with numerical ages) of the two *Bohlinotona* species.

Materials and methods

The fossils were collected by screen-washing large samples in the field-camp at Taatsiin Gol and by collecting scattered fossils from sediment surfaces. The sampling result was a remarkable number of almost 300 identifiable fossils of *Bohlinotona*, and 212 of which were measured. Most identified specimens are isolated teeth; maxillary and dentary fragments are rather rare. These fossils are housed in the collections of the Geological-Palaeontological Department at the Natural History Museum in Vienna (NHMW). A second, rich Lagomorpha collection from the Valley of Lakes sites is housed in the collection of the Institute of Paleontology and Geology of the Mongolian Academy of Sciences in Ulaan Baatar. Only fossils deposited in the NHMW collection are considered in this study.

All measurements are given in Tables 1, 2 and 3 (in mm). We follow the dental terminology of López Martínez (1989).

Abbreviations

GPTS	Geomagnetic Polarity Time Scale
NHMW	collection of the Natural History Museum Vienna, Geological-Palaeontological Department
P – M	premolars and molars of the upper dentition
p – m	premolars and molars of the lower dentition
D	upper deciduous premolar
d	lower deciduous premolar
n	number of measured specimens
Ma	Million years before present
min / max range	minimum and maximum observed ranges
sd	standard deviation
L, W	length, width
l, r	left, right

Systematic Palaeontology

Class Mammalia LINNAEUS, 1758

Order Lagomorpha BRANDT, 1855

Family Ochotonidae THOMAS, 1897

Subfamily Sinolagomyinae GUREEV, 1960

Genus *Bohlinotona* DE MUIZON, 1977

Type locality: Saint-Jacques (= San-tao-ho, "couches à *Baluchitherium*"), Ordos, China; late Oligocene.

Type species: *Bohlinotona pusilla* (TEILHARD DE CHARDIN, 1926).

Emended diagnosis (after ERBAJEVA & SEN 1998): Small-sized ochotonid with rather high crowned teeth, but roots appearing in late stages of wear. The p3 has a posteroexternal reentrant filled with cement, and its anterior margin varies from rounded to almost straight. The trigonid of p4 is wide and short, its posterior wall with spur situated near the labial margin; and its talonid is oval in shape and much narrower than the trigonid.

Comments: Previously, this lagomorph was described as *Desmatolagus pusillus* by TEILHARD DE CHARDIN (1926). Later, DE MUIZON (1977) stated on the base of the teeth morphology that this taxon belongs to ochotonids and created the new genus *Bohlinotona*.

He referred it to the subfamily Lagomyinae Lilljeborg, 1866 (= Ochotoninae Thomas, 1897). However, *Bohlinotona* is characterized by peculiar archaic features such as the presence of three roots on upper molariform teeth, two small buccal, and one large lingual, as in the Paleogene genus *Desmatolagus*. Some upper teeth conserve a crescentic valley on the occlusal surface as the paleolagins. Moreover, as in the leporid upper tooth row dentition, *Bohlinotona* retains M3, even if it is very small, which is otherwise absent in ochotonids. All these primitive characters allow *Bohlinotona* to be placed in the subfamily Sinolagomyinae (Erbajeva & Sen 1998).

Bohlinotona pusilla (Teilhard de Chardin, 1926)
(Fig. 1, Tab. 1)

p.p. 1926 *Desmatolagus pusillus* – Teilhard de Chardin: 23, figs 11 A, B, 12 B.
p.p. 1977 *Bohlinotona pusilla* – de Muizon: 272, fig. 3b, c, d.
1998 *Bohlinotona pusilla* – Erbajeva & Sen: 98, figs 2–3, tab. 1.
2017 *Bohlinotona* cf. *pusilla* – Daxner-Höck *et al*.: 136.
2019 *Bohlinotona* cf. *pusilla* – Daxner-Höck *et al*.: 204, figs 6 A–G, tab. 1.

Occurrences of *Bohlinotona pusilla* in Mongolia: Valley of Lakes, Hsanda Gol Formation of Tatal Gol (TAT-055) and Toglorhoi (TGW*), and Beger Formation of the Khaliun Basin, Shine Us (SHU-A/1). Originally, in the localities Tatal Gol (TAT-055) and Toglorhoi (TGW*) *Bohlinotona* was represented mostly by isolated teeth and was recognized as *B.* cf. *pusilla.* Later, abundant specimens discovered in the Shine Us site were analysed and it was established that they are all morphologically similar and belong to one species – the nominative species *Bohlinotona pusilla.* As a result, the morphological descriptions of the species and their measurements are given for the specimens from the three combined localities.

Stratigraphic range: Late Oligocene, *Amphechinus taatsiingolensis* Abundance Zone (= letter zone C).

Material (inventory numbers):

Valley of Lakes:

Tatal Gol (TAT-055): 1 P4 (NHMW 2014/0268/0001), 1 M2 (NHMW 2014/0268/0002), 1 p3–m2 (NHMW 2014/0268/0003), and 1 P3 (damaged, NHMW 2014/0268/0004).

Toglorhoi (TGW-A*): 1 P4–M2 (NHMW 2019/0149/0001), and 1 M1 (NHMW 2019/0149/0002). Collected from surface, age determination likely but not confirmed.

Khaliun Basin:

Shine Us (SHU-A/1): 14 p3 (NHMW 2013/0113/0001, …/0030 to …/0041, …/0091), 2 p4 (NHMW 2013/0113/0092, …/0093), 1 m1 (NHMW 2013/0113/0085), 5 m2 (NHMW 2013/0113/0002, …/0086 to …/0089), 1 P2 (NHMW 2013/0113/0003), 12 P3 (NHMW 2013/0113/0004, …/0016, …/0022 to …/0029, …/0042 to …/0043), 22 P4 (NHMW 2013/0113/0005, …/0015, …/0044 to …/0063), 15 M1 (NHMW

2013/0113/0006 to …/0008, …/0010, …/0019, …/0064 to …/0073, …/0094), 6 M2 (NHMW 2013/0113/0009, …/0074 to …/0078), 1 p4–m1 (NHMW 2013/0113/0012), 2 p3–m2 (NHMW 2013/0113/0011, …/0017), 1 p4–m2 (NHMW 2013/0113/0018), 1 P3–P4 (NHMW 2013/0113/0020), 1 P3–M1 (NHMW 2013/0113/0021), 1 P4–M3 (NHMW 2013/0113/0014), 3 D4 (NHMW 2013/0113/0011 to …/0013), 1 d3 (NHMW 2013/0113/0014), and 1 incisor (NHMW 2013/0113/0015). Additional specimens were recently selected from residuals of previously wet-screened samples (NHMW 2013/0113/0095 to …/0220). Moreover, the collection includes fragments of premolars, molars, deciduous teeth and incisors (NHMW 2013/0113/0000).

Measurements: see Tab. 1.

Description: Small-sized and rooted ochotonid with high crowned teeth. The teeth structures and the size of all specimens from the three studied localities are essentially similar. Upper cheek teeth, except P2, are transversely curved and have three roots, two

Table 1. Tooth measurements (mm) and descriptive statistics of *Bohlinotona pusilla* (TEILHARD DE CHARDIN, 1926) from the Valley of Lakes (TAT-055, TGW*) and the locality Shine Us (SUH-A/1), southwestern Mongolia.

Specimens (n = 125)	length (mm)			width (mm)	
	range	mean	n	range	mean
P3–M1		3.5	1		
P3–P4	2.25–2.35	2.3	2		
P4–M3		3.5	1		
P4–M2	3.2–4.30	3.25	2		
P4–M1	2.4–3.20	2.7	3		
P2		0.65	1		1.25
P3	1.00–1.25	1.10	14	1.85–3.70	2.50
P4	1.00–1.65	1.15	24	1.80–5.50	2.58
M1	0.90–1.50	1.09	17	2.50–4.70	3.23
M2	0.80–1.25	0.92	8	1.70–4.00	2.50
M3		0.50	1		1.25
p3–m2	4.75–6.00	5.25	3		
p3–m1	3.50–4.70	4.15	3		
p3–p4	2.35–3.00	2.60	3		
p4–m2	3.90–4.75	4.38	3		
p4–m1		2.90	1		
p3	0.80–1.20	0.98	17	0.90–1.30	1.15
p4	1.35–1.50	1.45	5	1.25–1.70	1.52 trig
				1.05–1.25	1.14 tal
m1	1.15–1.50	1.41	7	1.50–2.00	1.66 trig
				0.85–1.30	1.10 tal
m2	1.35–1.75	1.56	9	1.40–1.60	1.56 trig
				1.00–1.25	1.07 tal

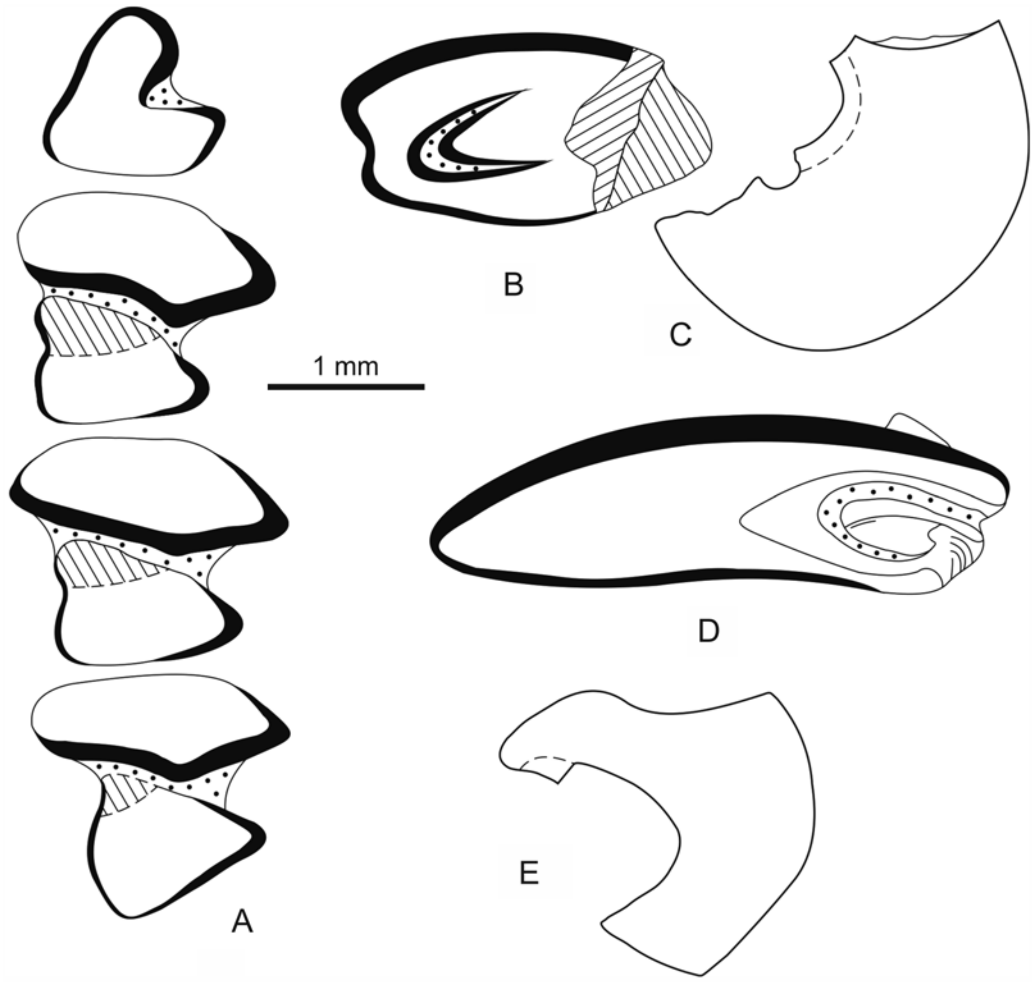


Fig. 1. *Bohlinotona pusilla* (Teilhard de Chardin, 1926). **A**: Right p3–m2, (NHMW 2014/0268/0003) from Tatal Gol (TAT-055), occlusal view. **B, C**: Right P4 (NHMW 2014/0268/0002) from Tatal Gol (TAT-055), occlusal (B) and dorsal (C) views. **D, E**: Right M2 (NHMW 2014/0268/0001) from Tatal Gol (TAT-055), occlusal (D) and dorsal (E) views.

small lateral roots and one large permanent internal root. In old individuals the internal root remains open. Accordingly, the occlusal surface of strongly worn teeth is very wide.

P2: The tooth is columnar, slightly curved antero-posteriorly, and has one root. The occlusal surface is oval in shape. Two shallow anterior reentrants, one extending to the root (paraflexus) are filled with a small amount of cement. The anterior margin of the tooth is covered by an enamel band (Daxner-Höck *et al*. 2019: fig. 6 B, B1).

P3: In young individuals it has an oval occlusal outline, with three lobes separated by anterior reentrants. The deep anteroexternal reentrant (paraflexus) is filled with cement, the shallow internal (hypostria) lacks cement (DAXNER-HÖCK *et al*. 2019: fig. 6 D) and disappears early in wear. The internal protocone continues with anteroloph, the large middle lobe (paracone) is bulbous in outline, the external metacone is small and very short. Worn teeth gradually become wider (DAXNER-HÖCK *et al*. 2019: fig. 6 A). The anteroloph and the lingual part of the paracone are separated by the reentrant but stay in place throughout wear. The enamel band covers mainly the lingual margins of the tooth.

P4: The tooth of young individuals is rectangular in occlusal outline, and has a crescentic central valley filled with cement (Fig. 1 B, C), which disappears in advanced wear stage. The tooth is relatively long externally, shorter internally. The internal border gradually becomes angled, the lateral margin, often slightly broken, remains relatively straight (DAXNER-HÖCK *et al*. 2019: fig. 6 A, D).

Worn M1 and M2 show a similar trend, although M2 has slightly sharper, more angular internal and external edges. Moreover, the anterior margin of M2 is wider than the posterior one (Fig. 1 D, E; DAXNER-HÖCK *et al*. 2019: fig. 1 A). M3 is not yet known.

The mandible is relatively robust below p4. The lower incisor extends posteriorly as far as the end of m1 and develops visible tubercles on both the lingual and labial sides of the mandibular ramus. The foramen mentale is located below p3.

The p3 is triangular in occlusal outline, has smooth rounded edges, and the posteroexternal fold contains a small amount of cement (Fig. 1 A; DAXNER-HÖCK *et al*. 2019: fig. 6 E, F1). The posterior border of p3 is straight. The entire tooth crown is covered by enamel.

The p4–m2 have angular external and rounded internal edges. The enamel band is well developed on the external and posterior margins of the trigonid and talonid, which are connected by cement. The trigonids are much wider than talonids, and are longer externally with expanded anterior and posterior borders. The talonid is oval, sharper externally, and even triangular in m2 (Fig. 1 A, Tab. 1, DAXNER-HÖCK *et al*. 2019: fig. 6 E).

The m3 has not yet been found, but the mandible displays a round alveolus for m3.

Discussion: *Bohlinotona pusilla*, known from the localities TAT-055 and TGW* (Tatal Gol and Toglorhoi, Valley of Lakes) and SHU-A/1 (Shine Us, Khaliun Basin), represents the nominative species. Our material shows three roots, the same morphological structure of teeth as the type material from Saint-Jacques, China, and it is similar in size. Previously, scarce ochotonid fossils from the Shine Us site were recognized as *B.* cf. *pusilla* (DAXNER-HÖCK *et al*. 2019). The greatly expanded sample from Shine Us confirms assignment as the nominative taxon.

***Bohlinotona mongolica* nov. spec.**

(Figs 2–4, Tabs 2, 3)

2007 *Bohlinotona* sp. (small) – ERBAJEVA: tab. 1
2014 *Bohlinotona* cf. *pusilla* – ERBAJEVA & DAXNER-HÖCK: 234, fig. 12.
2017 *Bohlinotona* cf. *pusilla* – DAXNER-HÖCK *et al*.: tab. 9

Derivatio nominis: after Mongolia, where the fossils were collected.

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

Stratum typicum (Fig. 5): Hsanda Gol Formation, late Oligocene, *Amphechinus taatsiingolensis* Abundance Zone (Harzhauser *et al.* 2017), corresponds to letter zone C (Daxner-Höck *et al.* 2017).

Type material: Holotype (Fig. 3 A, E): Fragment of the left mandible with p3–m3 (NHMW 2013/0354/0001). Measurements (Tab. 3); lower cheek tooth row length, p3–m3 = 5 mm. Paratypes (Fig. 3 B): additional specimens from the type locality Taatsin Gol: TGR-C/1+2: 1 p3–p4r, 1 P4–M1l, 1 P3r, 1 P4r, 1M1l, 1 M1r,1 M2 l, 1 m1–m2l, 1 p4r, 1 m1r, 1 m2l (NHMW 2013/0354/0002 to …/0012).

Additional material studied:

Amphechinus taatsiingolensis Abundance Zone (= letter zone C):

Toglorhoi: TGW-A/2a: 1 P3–M3r (NHMW 2013/0353/0001), 2 P3l (NHMW 2013/0353/0002, …/0003), 1 p3l, 1 p3r (NHMW 2013/0353/0004, …/0005), 1 p4r (NHMW 2013/0353/0006), 1 m1r, 1 m1l (NHMW 2013/0353/0007, …/0009), and 1 m2r (NHMW 2013/0353/0008); TGW-A/2b: P3–M1r (NHMW 2013/0353/0010), 2 P3l (NHMW 2013/0353/0011, …/0016), 1 P4l, 1 P4r (NHMW 2013/0353/0012, …/0013), 1M1r (NHMW 2013/0353/0014), 1 M2l (NHMW 2013/0353/0015), and 1 p4l (NHMW 2013/0353/0017); TGW-A/1: 1 M2l (NHMW 2013/0353/0019); TGW-surface: 1 m1r (NHMW 2013/0353/0018).

Unzing Churum: TAR-A/2: 1 P2r (NHMW 2013/0355/0001), 1 P4r (NHMW 2013/0355/0002), 1 M2l (NHMW 2013/0355/0004), 1 p4l (NHMW 2013/0355/0007), 1 m1r (NHMW 2013/0355/0003), 2 m1l (NHMW 2013/0355/0005, …/0008), and 1 m2r (NHMW 2013/0355/0006).

Yindirtemys deflexus Abundance Subzone (= letter zone C1):

Del: DEL-B/12: 2 P3l (NHMW 2013/0356/0001, …/0007), 1 P3r (NHMW 2013/0356/0006), P4–M1l (NHMW 2013/0356/0003), 1 M1r (NHMW 2013/0356/0002), 1 M1l (NHMW 2013/0356/0010), 2 M2l (NHMW 2013/0356/0011, …/0012), 1 M2r (NHMW 2013/0356/0009), 2 p4l (NHMW 2013/0356/0008, …/0013), 2 m1l (NHMW 2013/0356/0004, …/0014), 1 m1r (NHMW 2013/0356/0015), and 1 m2l (NHMW 2013/0356/0005).

Huch Teeg: RHN-A/9: 1 p4l (NHMW2013/0357/0001), 1 m1l (NHMW2013/0357/0002), and 4 trigonid fragments (NHMW2013/0357/0003 to …/0006).

Stratigraphic range of *B. mongolica* nov. spec.: Late Oligocene, *Amphechinus taatsiingolensis* Abundance Zone (= letter zone C) to *Yindirtemys deflexus* Abundance Subzone (= letter zone C1). (Fig. 5).

Measurements: see Tabs 2 and 3.

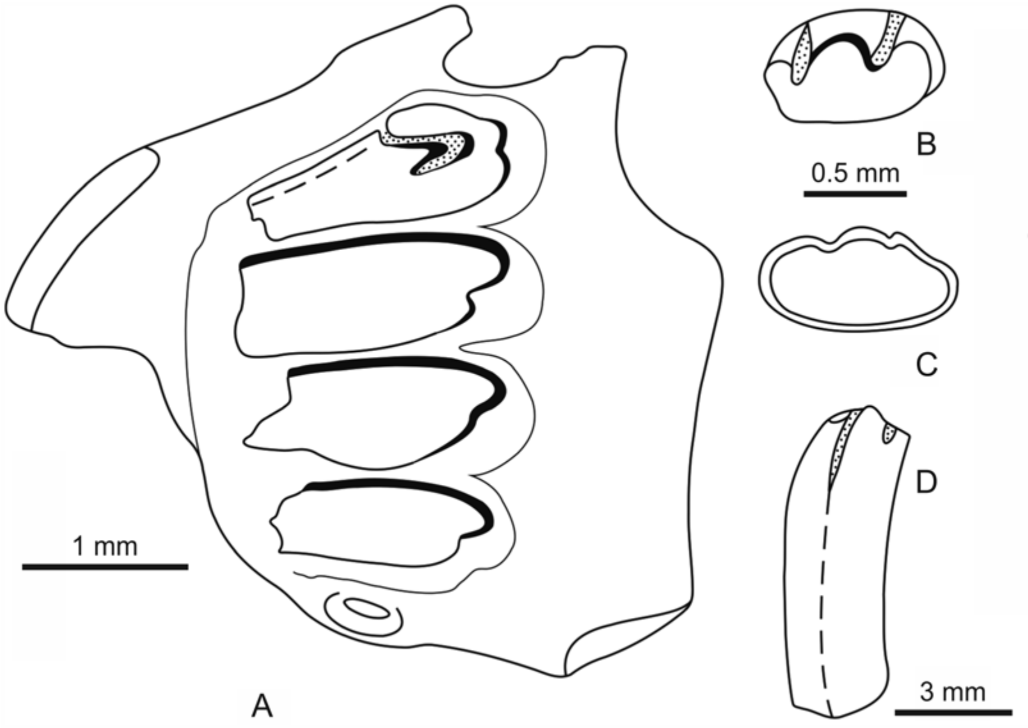


Fig. 2. *Bohlinotona mongolica* nov. spec. **A**: Right P3–M3, (NHMW 2013/0353/0001) from Toglorhoi (TGW-A/2), occlusal view. **B–D**: Right P2 (NHMW 2013/0355/0001) from Unzing Churum (TAR-A/2), occlusal (B), root (C), and frontal (D) views. 1-mm-scale bar valid for A, 0.5-mm-scale bar valid for B and C, and 3-mm-scale bar valid for D.

Diagnosis: Small-sized hypsodont ochotonid; upper cheek teeth with one large root on the lingual side and lacking buccal roots; small M3 persists; P3–M2 with shallow internal reentrant, variably developed as hypostria; p3 consists of one squared column with a posteroexternal reentrant filled with cement. Trigonids of p4–m2 are much wider than long with sharply angular external edges, rounded internally.

Differential diagnosis: *B. mongolica* nov. spec. differs from the type species *B. pusilla* in the following characters, which are considered derived: greater hypsodonty; upper molariform teeth lack buccal roots, the one internal root closes its pulp cavity with age; upper cheek teeth are much less recurved even in worn individuals; anteroconid of p3 is shorter and much wider than seen in the nominative taxon *Bohlinotona pusilla*.

Description of the holotype: The holotype is an adult mandible bearing full cheek tooth dentition. The p3 is small, square in shape, has smooth rounded edges, anterior margin with shallow deepening without cement, lingual border almost straight, deep posteroexternal fold filled with cement (Fig. 3 A–D). p4–m2 have sharp, angular external and rounded internal edges (Fig. 3 A, B, F). Trigonid is connected to the much

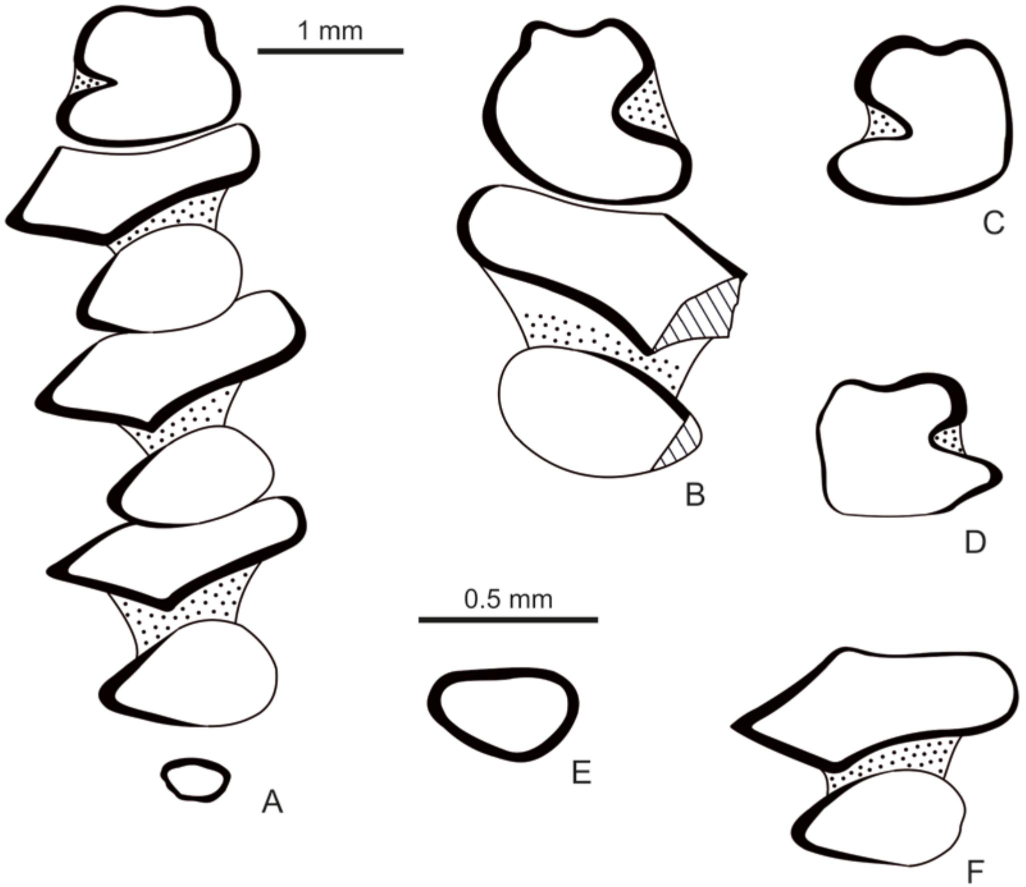


Fig. 3. *Bohlinotona mongolica* nov. spec. **A, E**: Left p3–m3, Holotype (NHMW 2013/0354/0001) from Taatsin Gol (TGR-C/1-2), occlusal view (A), m3 enlarged (E). **B**: Right p3–p4 (NHMW 2013/0354/0002) from Taatsin Gol (TGR-C/1-2), occlusal view. **C**: left p3 (NHMW 2013/0353/0005) from Toglorhoi (TGW-A/2a), occlusal view. **D**: Right p3 (NHMW 2013/0353/0004) from Toglorhoi (TGW-A/2a), occlusal view. **F**: Left p4 (NHMW 2013/0356/0008) from Del (DEL-B/12), occlusal view. 1-mm-scale bar valid for all figures except E.

narrower talonid by cement. Externally, the antero-posterior dimension of the trigonid is greater than the rounded internal portion due to the expanded anterior and posterior borders. Talonids are oval in shape. The oval m3 is very small; enamel covers its entire margin (Fig. 3 A, E).

Description of additional material: P2 is small, slightly curved antero-posteriorly, outline of tooth is oval, two shallow anterior flexuses contain some cement (external one is less persistent, internal fold, slightly longer, extends downwards up to 1/4 of tooth height and disappears, see Fig. 2 B–D).

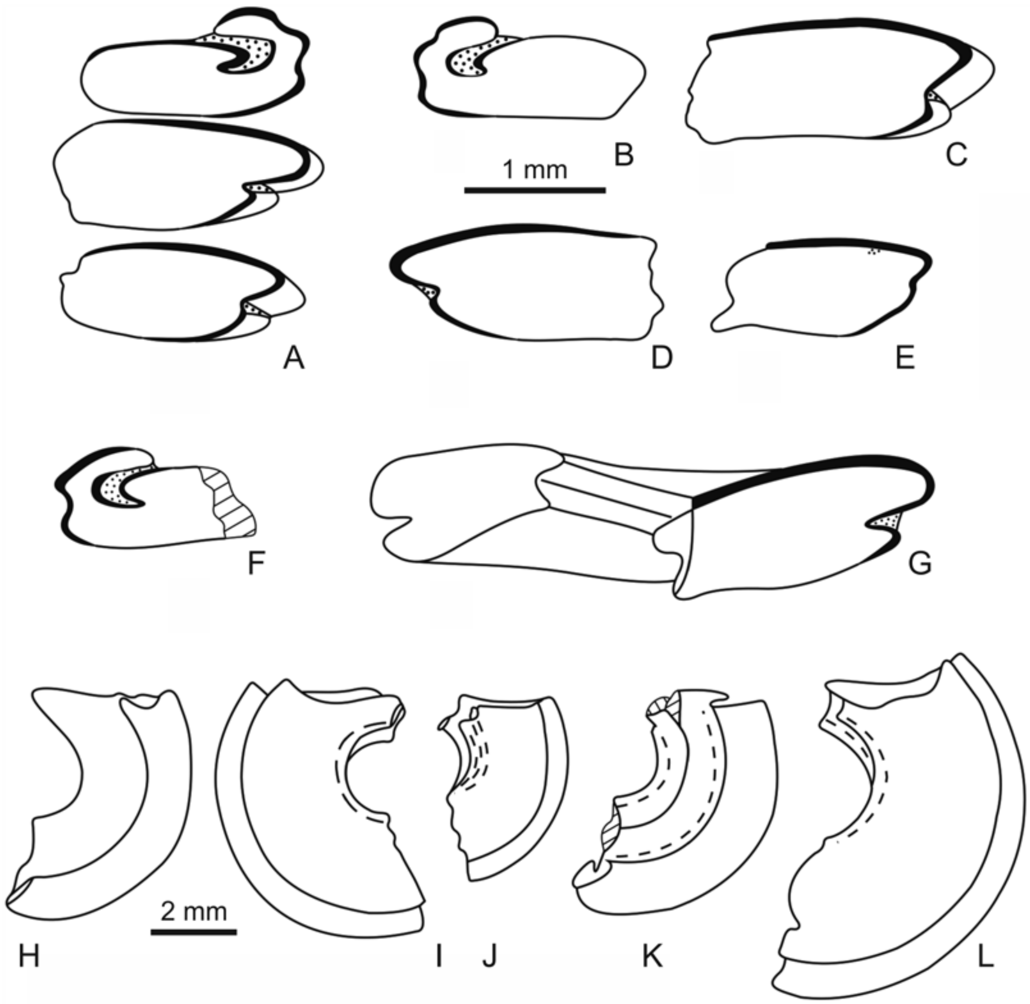


Fig. 4. *Bohlinotona mongolica* nov. spec. **A**: Right P3–M1 (NHMW 2013/0353/0010) from Toglorhoi (TGW-A/2b), occlusal view. **B, H**: Left P3 (NHMW 2013/0353/0011) from Toglorhoi (TGW-A/2b), occlusal (B) and frontal (H) views. **C**: Right P4 (NHMW 2013/0353/0013) from Toglorhoi (TGW-A/2b), occlusal view. **D, I**: Left P4 (NHMW 2013/0353/0012) from Toglorhoi (TGW-A/2b), occlusal (D) and dorsal (I) views. **E, J**: Right M1 (NHMW 2013/0353/0014) from Toglorhoi (TGW-A/2b), occlusal (E) and dorsal (J) views. **F, K**: Left P3 (NHMW 2013/0353/0002) from Toglorhoi (TGW-A/2a), occlusal (F) and frontal (K) views. **G, L**: Right P4 (NHMW 2013/0355/0002) from Unzing Churum (TAR-A/2), occlusal (G) and dorsal (L) views. 1-mm-scale bar valid for A to G, 2-mm-scale bar valid for H to L.

All upper teeth (P3–M2) are much wider than long. Their external border is irregular, probably due to the loss of buccal roots, making the external border of tooth fragile and often damaged. Tooth pulp cavity closed. Enamel band covering anterior and internal margins of tooth is lacking posteriorly and buccally. Shafts are recurved, less so in young individuals and slightly more strongly in adult individuals. Tooth width is rather stable throughout wear in contrast to that of *B. pusilla*. Even greatly worn teeth do not converge on a full circle.

In P3, the paraflexus is relatively deep in young individuals, with some cement. The lingual border is smooth with shallow deepening without cement, covered by thick enamel. P3 is represented by a number of specimens of different individual age (Fig. 4 A, B, H, F, K). In contrast to the nominative taxon, in P3 of *B. mongolica* the middle cusp (paracone) is probably united with the external one (metacone) as in advanced ochotonids. The internal protocone–anteroloph structure is rather short, crossing 1/3 of tooth width.

P4–M2 are of similar structure, anterior border of teeth is covered by thick enamel, which thins internally, and is greatly diminished buccally and posteriorly.

P4 is the largest tooth, rectangular in occlusal outline, significantly wider anteriorly due to the expanded protocone (Fig. 4 C, D, G, I). Lingual border is rounded in adults and slightly sharper in young individuals. Gradually with age, hypostria deepens and fills with cement (Fig. 4 G, L).

M1 smaller than P4, small hypostria lacking cement.

M2 much smaller than M1 and P4, hypostria is shallow, no cement, lingual and lateral borders are oblique, tooth trapezoidal in shape (Fig. 4 E, J).

Table 2. Descriptive statistics of upper tooth measurements (mm) of *B. mongolica* nov. spec. from the localities of the Valley of Lakes, Central Mongolia.

Specimens (n = 46)	n	m	min	max	sd
P3–M3	1	5.70			
P3–M2	1	5.00			
P3–M1	2	4.20	4.00	4.30	
P3–P4	2	2.67	2.60	2.75	
P4–M1	2	2.80	2.70	2.90	
P2 L	1	0.50			
P2 W	1	0.95			
P3 L	12	1.23	1.05	1.40	0.109
P3 W	10	2.30	2.00	3.20	0.384
P4 L	8	1.40	0.95	1.55	0.235
P4 W	6	3.33	2.50	4.00	0.499
M1 L	9	1.26	1.20	1.35	0.059
M1 W	9	2.88	2.50	4.00	0.482
M2 L	10	1.20	1.00	1.25	0.093
M2 W	10	2.50	2.10	3.50	0.456
M3 L	1	0.25			
M3 W	1	0.50			

M3, the smallest tooth, is oval in shape (Fig. 2 A). Its alveolus is much smaller than that of P2.

p3 is small with smooth rounded edges, the deep posteroexternal fold is filled with cement (Fig. 3 A–D), trigonid short and wide, anterior margin with shallow deepening without cement, lingual border almost straight, with small groove in some specimens, the enamel band is continuous but variable around the tooth crown.

In p4–m2 trigonid and talonid are connected by cement. Externally, the talonid margin of p4 and m1 is sharply angular and rounded internally as seen in the holotype (Fig. 3 A, B, F). Trigonids are much wider than talonids. Externally the trigonid is longer, expanded both anteriorly and posteriorly. The enamel covers all borders of the trigonids except anteriorly, where each abuts the preceding tooth; talonids have enamel only externally. Talonid is oval in shape in p4, m1 and m2 with rather smooth internal margin; however, m2 is slightly wider because it is buccally expanded with an angular external border.

Table 3. Descriptive statistics of lower tooth measurements (mm) of *B. mongolica* nov. spec. from the localities of the Valley of Lakes, Central Mongolia.

Specimens n = 41	n	m	min	max	sd
p3–m3	1	5.00			
p3–m2	1	4.50			
p3–m1	2	3.60	3.20	4.00	
p3–p4	3	2.70	2.50	3.00	
p4–m2	2	4.00	3.65	4.35	
p4–m1	3	2.70	2.10	3.00	
p3 L	5	0.88	0.75	1.05	0.157
p3 W	5	1.14	1.00	1.40	0.167
p4 L	11	1.47	1.10	1.80	0.216
tr L	11	0.75	0.60	0.95	0.063
tr W	11	1.66	1.40	1.85	0.119
tal L	11	0.73	0.55	0.85	0.100
tal W	11	1.15	1.00	1.40	0.125
m1 L	13	1.40	1.15	1.80	0.135
tr L	13	0.75	0.55	1.00	0.097
tr W	13	1.65	1.45	1.90	0.108
tal L	13	0.68	0.55	0.95	0.082
tal W	13	1.10	1.00	1.40	0.027
m2 L	5	1.50	1.30	1.65	0.106
tr L	5	0.70	0.50	0.80	0.141
tr W	5	1.60	1.45	1.75	0.071
tal L	5	0.76	0.70	0.85	0.035
tal W	5	1.10	1.05	1.15	0.035
m3 L	1	0.35			
m3 W	1	0.45			

Discussion

Bohlinotona thrived over a relatively short time, only 3.5 million years of the late Oligocene. The initial stage in evolution of the genus (~28–27 Ma) is represented by the nominative taxon *B. pusilla* (TEILHARD DE CHARDIN, 1926) having three roots on upper molariform teeth, two small buccal roots and one well developed lingual. This early species was followed by *B. mongolica* nov. spec., which shows advanced features such as greater hypsodonty of upper teeth in contrast to the highly curved tooth in *B. pusilla* and complete reduction of the buccal roots. This species spanned about 2.5 million years (~27–24.5 Ma).

In previous publications, specimens from the localities of the Valley of Lakes and Shine Us site were referred cautiously to *B.* cf. *pusilla* (ERBAJEVA & DAXNER-HÖCK 2014; DAXNER-HÖCK *et al.* 2019). The study of greatly increased collections from Mongolia allowed us to distinguish two taxa throughout the stratigraphic range of the genus. The type species of *Bohlinotona*, *B. pusilla,* is restricted to the older localities TAT-055, TGW-A*, and SUH-A/1 of about 28–27 Ma.

A large number of specimens from a number of younger localities allow us to recognize *B. mongolica* nov. spec. The detailed morphological analysis reveals that *B. pusilla* represents an early evolutionary stage of the genus *Bohlinotona.* This taxon is characterized by archaic features: upper teeth are strongly recurved, almost circular in worn adults (Fig.1 C, E), and have three roots, two small buccal and one large lingual root. The occlusal surface of the upper teeth becomes very wide with wear (Fig. 1 D). We note that the *B. pusilla* sample from the Shine Us locality in the Khaliun Basin shows slight variation: it has a slightly smaller p3 with shorter anteroconid than seen in the Tatal Gol sites; the external border of the significantly worn upper teeth (P4, M1, and M2) are irregular, demonstrating gradual reduction of the buccal roots, and the external margins of p4–m2 become slightly more angular (Fig. 1 A).

Bohlinotona mongolica nov. spec. represents a progressive form of the genus *Bohlinotona*. It is characterized by advanced lack of buccal roots in upper teeth, a deeper hypostria with some cement in some individuals, pulp cavity of the large lingual root closed, all upper teeth are less recurved. *Bohlinotona* is a distinctive genus of the late Oligocene. It appeared at the beginning of the late Oligocene, flourished for a short time, and vanished before the end of the Oligocene. *Bohlinotona* was replaced in the region, perhaps competitively, by the more derived ochotonid *Sinolagomys*.

A case for increasingly harsh climate in the Oligocene of mid-latitude eastern Asia is gaining support (HARZHAUSER *et al.* 2017). Whether or not this indicates general growing aridity, an extended dry season was probably involved. This led to dramatic stepwise turnover and local extinction (HARZHAUSER *et al.* 2016). The brief history of *Bohlinotona* corresponds to some aspects of this climatic change.

Bohlinotona appeared in the local Mongolian record at the beginning of the late Oligocene following modest general extinction and an initial phase of faunal reorganization

(HARZHAUSER *et al.* 2016). The advanced *B. mongolica* nov. spec. displaced *B. pusilla* during the subsequent “Late Oligocene Warming”, which involved a recovery in faunal diversity. Possibly the more hypsodont dentition including sharply angular eternal walls facilitated ingestion of harsher vegetation, which is observed in modern *Lagurus lagurus*. Ultimately *Bohlinotona* disappeared by ~24.5 Ma, which was the culmination of East Asian aridification and the **L**ate **O**ligocene **E**xtinction **E**vent (LOEE) of HARZHAUSER *et al.* (2016). *Sinolagomys*, however, coped with these conditions and flourished well into the Miocene (ERBAJEVA *et al*. 2017).

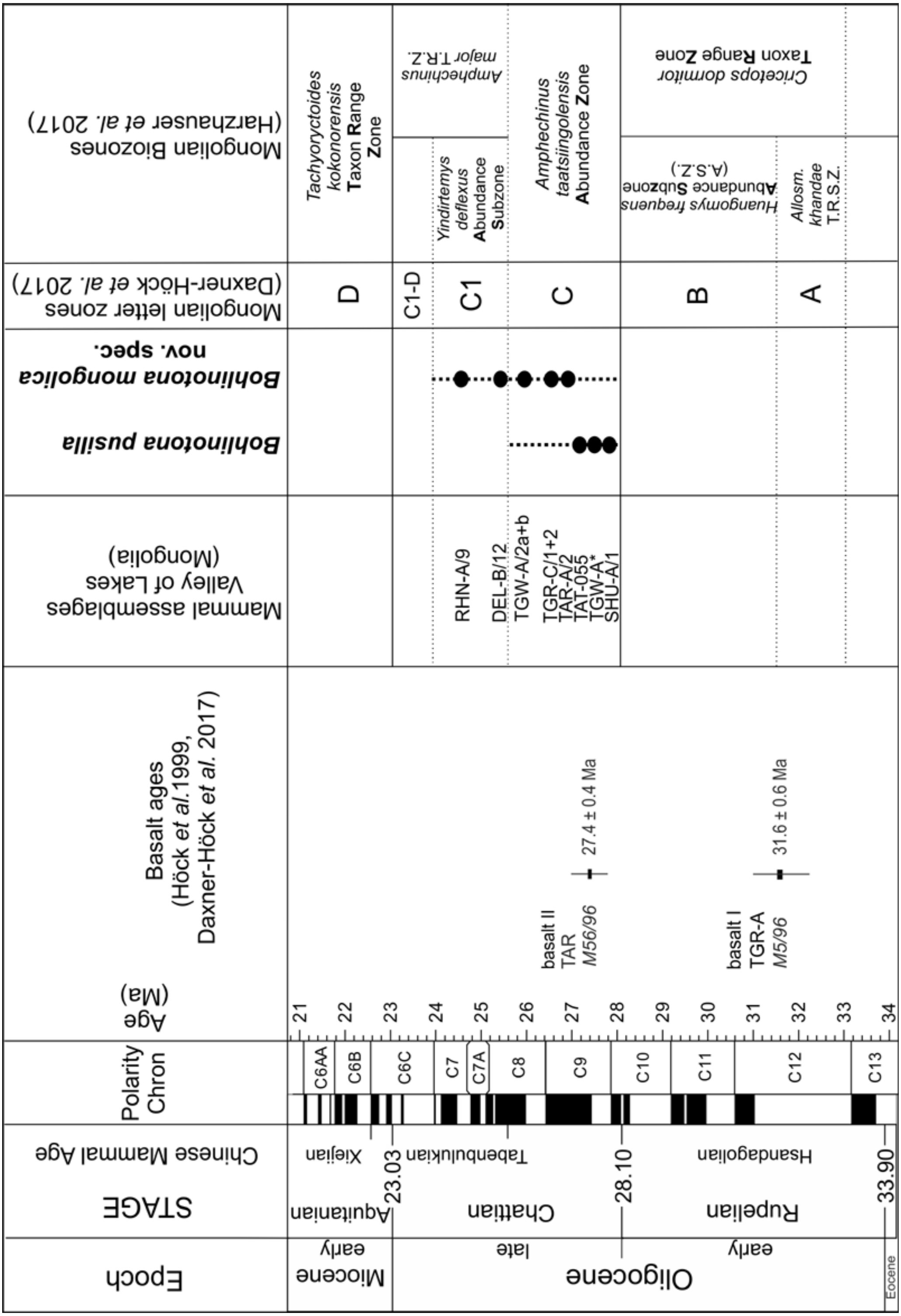
Stratigraphy (Fig. 5)

The current stratigraphic concept and age dating of mammal faunas from the Valley of Lakes (Taatsiin Gol and Taatsiin Tsagaan Nuur area in Central Mongolia) depends on two decades of geo-scientific investigations, including geology, palaeontology, biostratigraphy, $^{40}Ar/^{39}Ar$ dating of basalts, and magnetostratigraphy (HÖCK *et al.* 1999; SUN & WINDLEY 2015; DAXNER-HÖCK *et al.* 2017; HARZHAUSER *et al*. 2017). The original biozonation (letter zones A–E) proposed by DAXNER-HÖCK *et al.* (1997) and HÖCK *et al.* (1999) was based on the evolution of small mammals, faunal composition and on correlation with basalt ages. Later, these informal letter-zones were refined (DAXNER-HÖCK *et al.* 2017) and formalized as Biozones, *i. e.,* Taxon Range Zones and Abundance Zones (HARZHAUSER *et al*. 2017).

Together, these data allow correlation of key sections and provide fossil horizons with numerical ages derived from the Geomagnetic Polarity Time Scale (GPTS) (GRADSTEIN *et al*. 2012; OGG & LUGOWSKI 2004). The mammal assemblages of Shine Us (SHU-A/1), Toglorhoi (TGW*) and Tatal Gol (TAT-055) comprising *B. pusilla* are indicative of letter Zone C (= *Amphechinus taatsiingolensis* Abundance Zone). The mammal assemblages of Unzing Churum (TAR-A/2), Taatsiin Gol south (TGR-C/1+2), Toglorhoi (TGW-A/2a+b) comprising *B. mongolica* nov. spec., also indicate letter zone C (= *Amphechinus taatsiingolensis* Abundance Zone). However, two more advanced mammal assemblages of Del (DEL-B/12) and Huch Teeg (RHN-A/9) comprising *B. mongolica* nov. spec. indicate letter zone C1 (= *Yindirtemys deflexus* Abundance Subzone, *i. e*., the lower part of the *Amphechinus major* Taxon Range Zone) (HARZHAUSER *et al*. 2017) (Fig. 5).

Stratigraphic data from two key sections in the Valley of Lakes, *i. e.*, Taatsiin Gol south (TGR-C) and Unzing Churum (TAR-A), allow correlation of the letter zones C and C1 with the GPTS and the radiometric age of basalt II.

It was demonstrated by magnetostratigraphic data (SUN & WINDLEY 2015) from the key section Taatsiin Gol south (TGR-C: lower part, including fossil layers TGR-C/1+2 of the Hsanda Gol Fm.), and by the $^{40}Ar/^{39}Ar$ data of basalt II from the Unzing Churum (TAR M56/96) section, which provided an age of 27.4+/−0.4 Ma. (HÖCK *et al.* 1999: fig. 18; DAXNER-HÖCK *et al.* 2017: p. 171, tab. 2, fig. 30), that letter zone C correlates with chrons C9n–C8n.2n.



Epoch
STAGE
Chinese Mammal Age
Polarity Chron
Age (Ma)
Basalt ages (Höck et al. 1999, Daxner-Höck et al. 2017)
Mammal assemblages Valley of Lakes (Mongolia)
Bohlinotona pusilla
Bohlinotona mongolica nov. spec.
Mongolian letter zones (Daxner-Höck et al. 2017)
Mongolian Biozones (Harzhauser et al. 2017)
Miocene
early
Oligocene
late
early
Eocene
Aquitanian
Chattian
Rupelian
23.03
28.10
33.90
Xiejian
Tabenbulukian
Hsandagolian
C6AA
C6B
C6C
C7
C7A
C8
C9
C10
C11
C12
C13
21
22
23
24
25
26
27
28
29
30
31
32
33
34
basalt II
TAR
M56/96
27.4 ± 0.4 Ma
basalt I
TGR-A
M5/96
31.6 ± 0.6 Ma
RHN-A/9
DEL-B/12
TGW-A/2a+b
TGR-C/1+2
TAR-A/2
TAT-055
TGW-A*
SHU-A/1
D
C1-D
C1
C
B
A
Tachyoryctoides kokonorensis Taxon Range Zone
Amphechinus major T.R.Z.
Yindirtemys deflexus Abundance Subzone
Amphechinus taatsiingolensis Abundance Zone
Cricetops dormitor Taxon Range Zone
Huangomys frequens Abundance Subzone (A.S.Z.)
Allosm. khandae T.R.S.Z.

Letter zone C1 correlates with chrons C8n.2n–C7n.2n (according to magnetostratigraphic data along the upper part of section TGR-C; sediments of the Loh Fm.; SUN & WINDLEY 2015). According to these data and to the biostratigraphic record, the range of letter zone C is ~ 28 to 25.6 Ma (late Oligocene, early Chattian), and the range of letter zone C1 is 25.6 to 24 Ma (late Oligocene, late Chattian, Tabenbulukian) (DAXNER-HÖCK *et al*. 2017: pp. 171–172, fig. 30).

Consequently, in Mongolia the genus *Bohlinotona* is a typical mammal of the late Oligocene. The estimated range of the older species, *B. pusilla*, is from ~28 to ~27 Ma, the stratigraphic younger species *B. mongolica* nov. spec. ranged from 27 to ~24.5 Ma (Fig. 5).

Conclusions

Lagomorph fossils of the genus *Bohlinotona* were found in Mongolia from sediments in two basins dating to the late Oligocene. Fossils of this genus are generally very scarce, known only in Asia and initially described from the Locality Saint-Jacques in China (TEILHARD DE CHARDIN 1926). Intensive investigations in Mongolia by the Austrian-Mongolian expeditions produced collections from 7 localities totaling ~300 specimens in the Valley of Lakes and Khaliun regions. Based on morphological structures of teeth and metrical data, two successive species are recognized. The older form (*B. pusilla*) shows archaic features: upper teeth are strongly recurved; there are three roots, two small buccal and a large lingual root, and in worn teeth (adult individuals) the upper teeth describe almost a full circle and the wear surface becomes very wide. Among *B. pusilla* we can trace some variation of features in upper teeth: the external border of the significantly worn upper teeth (P4, M1 and M2) in specimens from Shine Us are irregular, demonstrating a degree of reduction of the buccal roots. Moreover, the external margins of p4–m2 become slightly sharper, possibly in response to increasingly harsh vegetation.

The second, more advanced species (*B. mongolica* nov. spec.) is characterized by the loss of buccal roots and closure of the pulp cavity of the lingual root, all upper teeth less strongly recurved. The species retains the very small M3 of the genus. Lower cheek teeth have sharply angled external walls.

Bohlinotona existed over a rather short time, the late Oligocene, its history directly impacted by major climatic reorganization in the region (HARZHAUSER *et al.* 2016, 2017). Over a relatively short interval, a distinctive species replacement coincided with

◀ Fig. 5. Correlation chart showing the Geologic Time Scale, the Geomagnetic Polarity Time Scale (GPTS) (GRADSTEIN *et al.* 2012; OGG & LUGOWSKI 2004), and Chinese mammal ages. Ages of basalt I and II (HÖCK *et al.* 1999; DAXNER-HÖCK *et al.* 2017), and assemblages from the Valley of Lakes and the Khaliun Basin in Mongolia including *Bohlinotona*. The observed ranges of *B. pusilla* and *B. mongolica* are given with the refined Mongolian letter zones (DAXNER-HÖCK *et al.* 2017) and Mongolian Biozones (HARZHAUSER *et al.* 2017).

changing climatic conditions. *Bohlinotona* declined and disappeared in the late Oligocene. We consider it likely that *Sinolagomys*, which had appeared somewhat later than *Bohlinotona* and survived into the early Miocene, was better suited to harsher conditions and out-competed *Bohlinotona* during the Late Oligocene Extinction Event (Harzhauser *et al*. 2016).

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