Fossil vertebrates from the late Miocene of Builstyn Khudag (Valley of Lakes, Central Mongolia)

Gudrun Daxner-Höck [1, 2] *, Andrej Čerňanský [3], Lawrence J. Flynn [4] & Wilma Wessels [5]

(with 15 figures and 7 tables)

Abstract

Cenozoic sediments of the Taatsiin Tsagaan Nuur region in the Valley of Lakes are known for their exceptional fossil content of the Oligocene and early Miocene, whereas, until now, middle and late Miocene records are very poor. Here, we report the late Miocene vertebrate fauna of Builstyn Khudag. Wet screening of large samples from the upper part of section BUK-A (from BUK-A/12 +14) display a rich fossil collection, comprising three lizard and five snake taxa, and sixteen small mammal species in nine families: Ochotonidae, Erinaceidae, Soricidae, Sciuridae, Eomyidae, Cricetidae, Zapodidae, Dipodidae and Gerbillidae. Surface findings of bones and teeth of large mammal families, Rhinocerotidae and Gomphotheriidae, complete the collection. The structures and the included fossils assume floodplain environments with locally dense vegetation and laterally dry open areas.

Stratigraphically, we correlate the Builstyn Khudag fauna with the early late Miocene, specifically with the early part of the Asian Bahean LMS/A and with the European Mammal Zone MN9 of the early Vallesian.

Key words: Reptilia, Mammalia, Environment, Miocene, Bahean, Vallesian.

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

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

[3] Department of Ecology, Laboratory of Evolutionary Biology, Faculty of Natural Sciences, Comenius University in Bratislava, Mlynská dolina, 842 15, Bratislava, Slovakia; e-mail: cernansky.paleontology@gmail.com

[4] Department of Human Evolutionary Biology, Harvard University, 11 Divinity Avenue, Cambridge, MA 02138, USA; e-mail: ljflynn@fas.harvard.edu

[5] Utrecht University, Department of Earth Sciences, Vening Meinesz Gebouw A, Princetonlaan 8A, 3584 CB Utrecht, The Netherlands; e-mail: w.wessels@uu.nl

* Corresponding author

Zusammenfassung

Känozoische Sedimente aus der Taatsiin Tsagaan Nuur Region im Tal der Gobiseen sind für ihren außergewöhnlichen Reichtum an oligozänen und untermiozänen Fossilien bekannt, während mittel- und obermiozäne Nachweise bisher selten sind. Hier berichten wir über die obermiozäne Wirbeltierfauna von Builstyn Khudag. Durch nass sieben der Großprobe BUK-A/12+14 aus dem oberen Teil des Profils BUK-A wurde eine reiche Fossilsammlung gewonnen. Sie umfasst 3 Echsenarten, 5 Schlangenarten und 16 Kleinsäugetierarten von 9 Familien: Ochotonidae, Erinaceidae, Soricidae, Sciuridae, Eomyidae, Cricetidae, Zapodidae, Dipodidae und Gerbillidae. Oberflächenfunde von Knochen und Zähnen der Großsäugerfamilien Rhinocerotidae und Gomphotheriidae komplettieren die Sammlung. Sedimentstrukturen und Fossilien weisen auf Aulandschaften mit dichter Vegetation hin und auch auf trockene offene Bereiche abseits des Flusses. Zeitlich korrelieren wir die Fauna mit dem frühen Obermiozän, genauer, mit dem Asiatischen unteren Bahean (LMS/A) und mit der Europäischen Säugetierzone MN9 des frühen Vallesium.

Schlüsselwörter: Reptilien, Säugetiere, Lebensraum, Miozän, Bahean, Vallesium.

Introduction – Study Area

The locality Builstyn Khudag is placed in the Taatsiin Tsagaan Nuur Basin, which is part of the Valley of Lakes in Central Mongolia. The Valley of Lakes is an intermontane basin, bounded by the Khangai Mountains in the north and the Gobi Altai Mountains in the south. It is composed of several depressions placed along of a NW – SE striking axis and extends for *ca.* 600 km from the Beger depression in the west to the Ulaan Nuur depression in the east, with the Taatsiin Tsagaan Nuur Basin in its middle part (Fig.1).
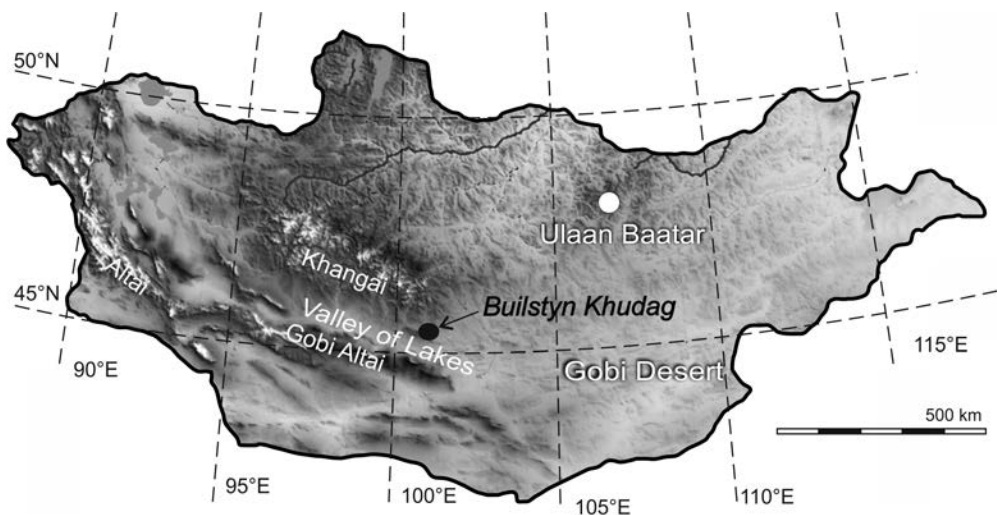

Fig. 1. Topographic map of Mongolia. The position of the locality Builstyn Khudag is marked with a black circle. Modified from Harzhauser *et al.* (2016: fig. 1)

From the locality Builstyn Khudag, scattered vertebrate fossils were found during an excursion of the International Geoscience Programme (IGCP, Project 326) in 1993. Later, in the course of two field campaigns of the Mongolian-Austrian joint project (FWF-project: P-10505-GEO) a rich fossil collection was excavated in the summers of 1995 and 1996. The vertebrate assemblage yielded lizards, snakes, and manifold mammals indicating an early late Miocene age. The present paper provides information about both the described taxa (Daxner-Höck 2001; Erbajeva 2003; Ziegler *et al.* 2007; Göhlich 2007; Heissig 2007; Maridet *et al.* 2014a, 2014b, 2015; Čerňanský & Augé 2019) and the previously undescribed but listed fossil groups (Höck *et al.* 1999; Daxner-Höck *et al.* 2013a) of this assemblage. All these data are discussed in the present paper.

Gological setting

The Valley of Lakes is filled by Mesozoic and Cenozoic sediment sequences immediately above a Proterozoic to Permian basement (Höck *et al.* 1999). The locality Builstyn Khudag is located close to the northern margin of the Valley of Lakes, where both the crystalline basement (Figs 2, 3 A) and the Mesozoic and Cenozoic basin fill (Fig. 3 B–E)
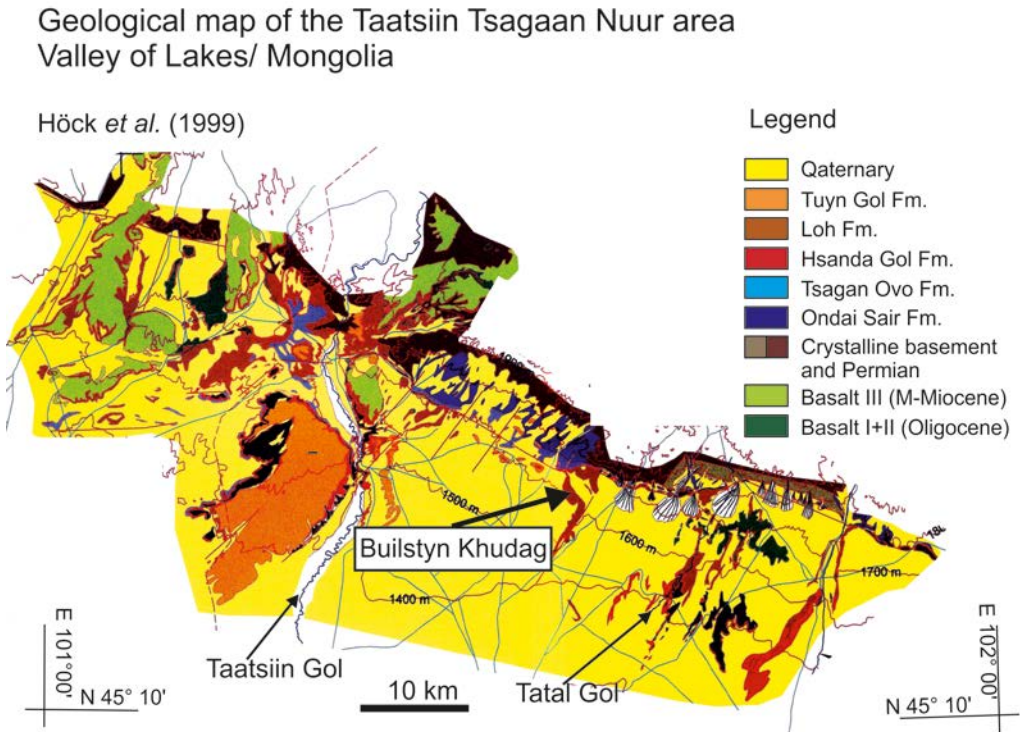

Fig. 2. Geological map of the Taatsiin Tsagaan Nuur area in the Valley of Lakes showing the location of Builstyn Khudag close to the northern basin margin. Modified from Höck *et al.* (1999).

are visible. Here, from north to south four lithologic units of the basin fill are exposed: the lower Cretaceous sediments of the Ondai Sair Formation, the Eocene Tsagan Ovo Fm., the Oligocene Hsanda Gol Fm., and the Late Miocene sequence of the Loh Fm.

The Ondai Sair Formation (Fig. 3 B) directly overlies the crystalline basement along steep dipping contacts. The formation was defined by Berkey & Morris (1927). In the Builstyn Khudag region the Ondai Sair Formation contains loose, yellowish brown, poorly consolidated gravels. These are interbedded with dark brownish, white, and grey clay layers, which are disturbed by faulting and tilting. Distinct cobble horizons with maximum particle size of up to 10 cm occur, and sometimes sediment structures like trough cross-bedding and imbrications are observable. From fine sandy layers of this formation, root traces, plant fossils, and bones of Dinosauria were found in the Builstyn Khudag region (Höck *et al*. 1999).

The boundary between the Ondai Sair and the overlying Tsagan Ovo Fm. (Fig. 3 C) is tectonic. The lower part of the latter is dominated by massive gravel beds, mostly without any visible structures. The hanging parts are generally finer clastic, they are dominated by alternating grey, green-grey, white gravels and sand layers, partly cross-bedded. In general, bed thicknesses are smaller than in the footwall parts. Three sections of the Tsagan Ovo Fm. (BUK-D, BUK-C, BUK-B) were studied in this region (Höck *et al*. 1999: pp. 92–95, figs 3–5, supplement 3). The total sequence displays a maximum thickness of > 150 m. Its upper part (BUK-B) correlates with the Tsagan Ovo sequence from the Taatsiin Gol (section TGR-A), where magnetostratigraphic data (Sun & Windley 2015) evidence a late Eocene age. No fossils were found from the Tsagan Ovo Fm.

In Builstyn Khudag no direct contact of Tsagan Ovo and Hsanda Gol Fms is visible. Nevertheless, brick red hills of the Hsanda Gol Fm (Fig. 3 D) are exposed south-west of the light-coloured sediments of the Tsagan Ovo Formation. Hsanda Gol beds are indicated by poorly sorted clay and silty clay, with locally embedded sand lenses and caliche layers. The rich fossil content evidences an Oligocene age.

Towards the south from the northern basin margin a *ca.* 36 m more or less horizontally bedded sediment sequence of the Loh Fm. (Fig. 3 E) follows. It was studied along section BUK-A (Höck *et al*. 1999: supplement 3).

Description of the section, layers BUK-A/1–17 from bottom to top: The lowermost part of the sediment sequence consists of 4 m brick red sandy silt (layers BUK-A/13). The following lower sandstone is composed of 2 m cross-bedded coarse sandstone of light-brown to rose colour, containing gravels up to 10 cm, rounded basalt clasts and bone fragments (layers BUK-A/4–5). Upsection, 10 m red sandy silt alternates with layers of red-brown sand (layers BUK-A/6–9). It is followed by the upper sandstone of 8 m thickness and is rose-beige in colour. This upper sandstone is composed of coarse sand and gravel layers, partly cross-bedded in the lower part, and in the upper part a fining upward trend is visible (layers BUK-A/10–11). From this upper part large mammal fossils were sporadically found (layer BUK-A/11). The light coloured second sandstone (BUK-A/10–11) is topped by 3 m red to orange fine clayey silt with clay clasts and small
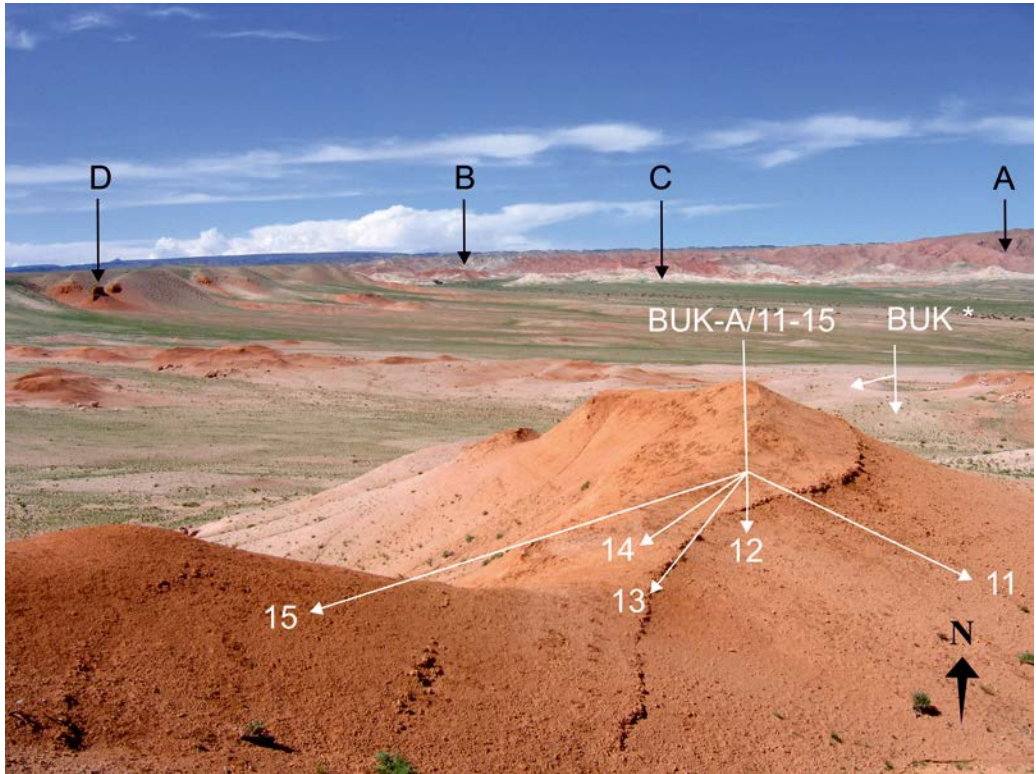
Fig. 3. Locality Builstyn Khudag at the northern margin of the Taatsiin Tsagaan Nuur area, central part of the Valley of Lakes in Mongolia. From north towards south, sediments of four stratigraphic units are exposed (marked by black arrows and letters **A–D**). The crystalline basement (**A**), followed by grey and red sequences of the Ondai Sair Formation of the lower Cretaceous (**B**). Immediately southwards, the whiteish coloured Tsagan Ovo Formation of the Eocene is exposed (**C**). On the left side, the isolated brick-red hills of the Oligocene Hsanda Gol Formation are visible (**D**). In front the orange coloured sediments of the late Miocene, parts of the Loh Formation show sediment layers BUK-A/11–15 (including the fossil beds BUK-A/12+14) and BUK *. White arrows mark BUK * and numbers of sediment layers 11–15 of section BUK-A. Coordinates of section BUK-A are: basal part: N 45°23'01", E 101°30'45.8"; upper part: N 45°23'03", E 101°30'44". Photo: G. Daxner-Höck, 2011.

vertebrate fossils embedded in the uppermost 10 cm thick layer (layer BUK-A/12). It is topped by a pronounced carbonate layer of 3–10 cm thickness (layer BUK-A/13). Immediately above the carbonate, about 10 cm fossil rich silty orange clay follows (layer BUK-A/14). The fossil content of these subsequent layers 12–14 is in agreement; therefore, we treat it as one fauna BUK-A/12+14. Upwards, the number of clay clasts and clay layers imbedded into the clayey silt increases and the colour changes to red-rose (layer BUK-A/15). Finally, a white to rose, 1 m thick clay follows (layer BUK-A/16). The uppermost part of the section is built by 3–4 m coarse sand, gravels, and pebbles of the Pleistocene (layer BUK-A/17).

From the flat area close to the base of section BUK-A, scattered bones of rhinos and proboscideans were collected (BUK*). The origin of these fossils is not clear, likely it is one of the two sandstone beds, which comprise bone fragments of large mammals.

Material and methods

The presently investigated fossils stem from the Loh Fm. of the locality Builstyn Khudag (section BUK-A). After the first findings of fossils (1993), the geological investigation of section BUK-A and wet screening of palaeontological test samples followed (1995). Resulting from these tests, rich fossil layers along the section were found, and systematic wet screening of large bulk samples followed in 1996.

The investigated fossils were collected from three main concentrations:

1. Scattered bones of rhinos and proboscideans were collected from the surface of a flat area NE but close to the base of section (BUK*). The published specimens (HEISSIG 2007; GÖHLICH 2007) are housed in the NHMW collection in Vienna.

2. A mandible of a rhino was found in the upper part of the upper sandstone (layer BUK-A/11) during the international IGCP-excursion 1993 (the specimen is housed in the PIN collection in Moscow). Aside from that, scattered bone fragments of large mammals were collected from this horizon.

3. Abundant small vertebrate fossils stem from two fossil layers (BUK-A/12 and BUK-A/14) immediately below and above of the distinct carbonate layer (BUK-A/13). There, small bones and mandibles of small vertebrates were surface-collected from an area of several m^2 (excursions 1993, 1995). Later (1996), large bulk samples (BUK-A/12+14) produced a rich collection of lower vertebrate and small mammal fossils. The samples were wet-screened in the Valley of Lakes field-camp at Taatsiin Gol. The total amount was *ca.* 5000 kg sediment yielding >1000 identifiable fossils (mainly teeth) and many bone fragments. The fossils are housed in the NHMW collection in Vienna, and in the MPC-collection in Ulaanbaatar. All published specimens are housed in the NHMW collection.

Fossil record

The following fossils were described prior to the present paper: The lacertids Eremiadini indet. (ČERŇANSKÝ & AUGÉ 2019), snakes *Eryx* sp. 1 and sp. 2, Colubrinae 1 and 2, "Natricinae" indet. (BÖHME 2007), the lagomorphs *Ochotona minor* and *O. lagreli* (ERBAJEVA 2003), the insectivores *Parvericius buk* and *Builstynia fontana* (ZIEGLER *et al.* 2007), the rodents *Tamias ertemtensis* and ?*Atlantoxerus* sp. (MARIDET *et al.* 2014b), *Nannocricetus* aff. *primitivus* (MARIDET *et al.* 2014a), *Ombomys builstynensis* (MARIDET *et al.* 2015), the rhino cf. *Iranotherium* sp. (HEISSIG 2007), and the proboscidean Gomphotheriidae indet. (GÖHLICH 2007).

Fossil groups described in the present paper complete the description of the Builstyn Khudag assemblage. These are: the skinks cf. *Ophiomorus* sp. and Squamata indet.

(by Čerňanský), the rodents Zapodidae gen. et spec. indet., *Eozapus intermedius*, *Lophocricetus xianensis*, *Paralactaga parvidens*, *Plesiodipus robustus* (by Daxner-Höck), *Myocricetodon* cf. *plebius*, *Paracricetulus schaubi*, and cf. *Abudhabia baheensis* (by Wessels). Eggshells and isolated bones of birds, bones of lower vertebrates and small mammals were sorted from sample BUK-A/12+14 but hitherto not described in detail.

The squamate specimens were photographed under a scanning electron microscope (SEM; FEI Inspect F50) at the Slovak Academy of Sciences in Banská Bystrica (Slovakia). The lateral surface of the specimen NHMW 2019/0138/0002 was photographed using a Leica M125 binocular microscope with axially mounted DFC500 camera (LAS software [Leica Application Suite] version 4.1.0 [build 1264]). The standard anatomical orientation system is used throughout this paper. The image processing program ImageJ was used for measurements.

For comparison, the following *Ophiomorus* specimens are used in this paper: *Ophiomorus punctatissimus* (NHMW 23527), *O. tridactylus* (NHMW 10396), *O. raithmai* (UF 86251, 86262, 86274, 86290, and 86291). For other skinks, see ČERŇANSKÝ & SYROMYATNIKOVA (2021) and ČERŇANSKÝ *et al.* (2020).

Opinions differ in regards to higher level systematics of jumping mice, birch mice, and jerboas. We follow the palaeontologists SIMPSON (1945), DAXNER-HÖCK (1999), QIU & LI (2016), and QIU (2017) in grouping these rodents in the superfamily Dipodoidea FISCHER, 1817 distributed in two subfamilies: Zapodidae COUES, 1875 (for jumping mice and birch mice) and Dipodidae FISCHER, 1817 (for jerboas).

Scanning electron microscope images (SEM) of Rodentia were taken by D. Gruber and E. Höck (Biocenter, University Vienna), and those of Erinaceidae and Soricidae by K. Wolf-Schwenninger (Staatliches Museum für Naturkunde, Stuttgart).

Underlines of figure numbers indicate that figured specimens were mirrored (*e. g.*, Fig. 10 C shows a right m2, but the m2 is figured as if it were from the left side).

Abbreviations

NHMW	collection of the Natural History Museum Vienna (Austria)
UF	collection of the University of Florida, Florida Museum of Natural History (USA)
PIN	collection of the Paleontological Institute of the Russian Academy of Sciences, Moscow
MPC	collection of the Institute of Paleontology and Geology of the Mongolian Academy of Sciences, Ulaanbaatar.
P – M	premolars and molars of the upper dentition
p – m	premolars and molars of the lower dentition

I – i   upper and lower incisors

C – c   upper and lower canines

D   upper deciduous premolar

d   lower deciduous premolar

n   number of specimens

LMS/A   Chinese Neogene Land Mammal Stage/Age

MN   European Neogene Mammal Zone

Ma   Million years

Systematic Palaeontology

Order Squamata OPPEL, 1811

Family Scincidae GRAY, 1825

Genus *Ophiomorus* DUMÉRIL & BIBRON, 1839

cf. *Ophiomorus* sp.
(Fig. 4 A–D)

M a t e r i a l from sample/layer BUK-A/12+14 (3 specimens): 2 left dentaries (NHMW 2019/0138/0001, …/0002) and 1 right dentary (NHMW 2019/0138/0003).

D e s c r i p t i o n o f d e n t a r i e s : The description is based on three fragments of dentaries which all represent more or less posterior portions of this jaw element (Fig. 4 A–D). The high dental crest supports teeth, however the tooth row is largely incomplete. The dentary has a long portion without dentition posterior to the tooth row. Here, the coronoid process starts to rise dorsally – this large process is distinctly elevated posteriorly (Fig. 4 A). It reaches a much higher dorsal level than tooth apices of the preserved teeth. In regards to two additional ventral processes, the surangular process is best preserved in NHMW 2019/0138/0003. It is triangular and pointed, but reaches much less posteriorly than the coronoid process (Fig. 4 B). However, it should be noted that its ventral portion appears to be damaged. In the specimen NHMW 2019/0138/0001, the surangular process is broken off (Fig. 4 A), but when complete, posteriorly it could approach the level of the dorsally located coronoid process. In the same specimen, the root portion of the angular process is preserved. It is large and it can be estimated that when complete, it overreached the coronoid process posteriorly. In medial view, the Meckel's groove is fully open and wide in the posterior region, but it markedly narrows anteriorly. The alveolar foramen is well-developed (Fig. 4 C), located at the level between the 2nd and 3rd tooth position (counted from posterior). The intramandibular septum, which separates the alveolar canal medioventrally from the Meckelian cartilage, is completely fused to the lateral wall of the bone without free ventral portion. Meckel's groove is roofed by the
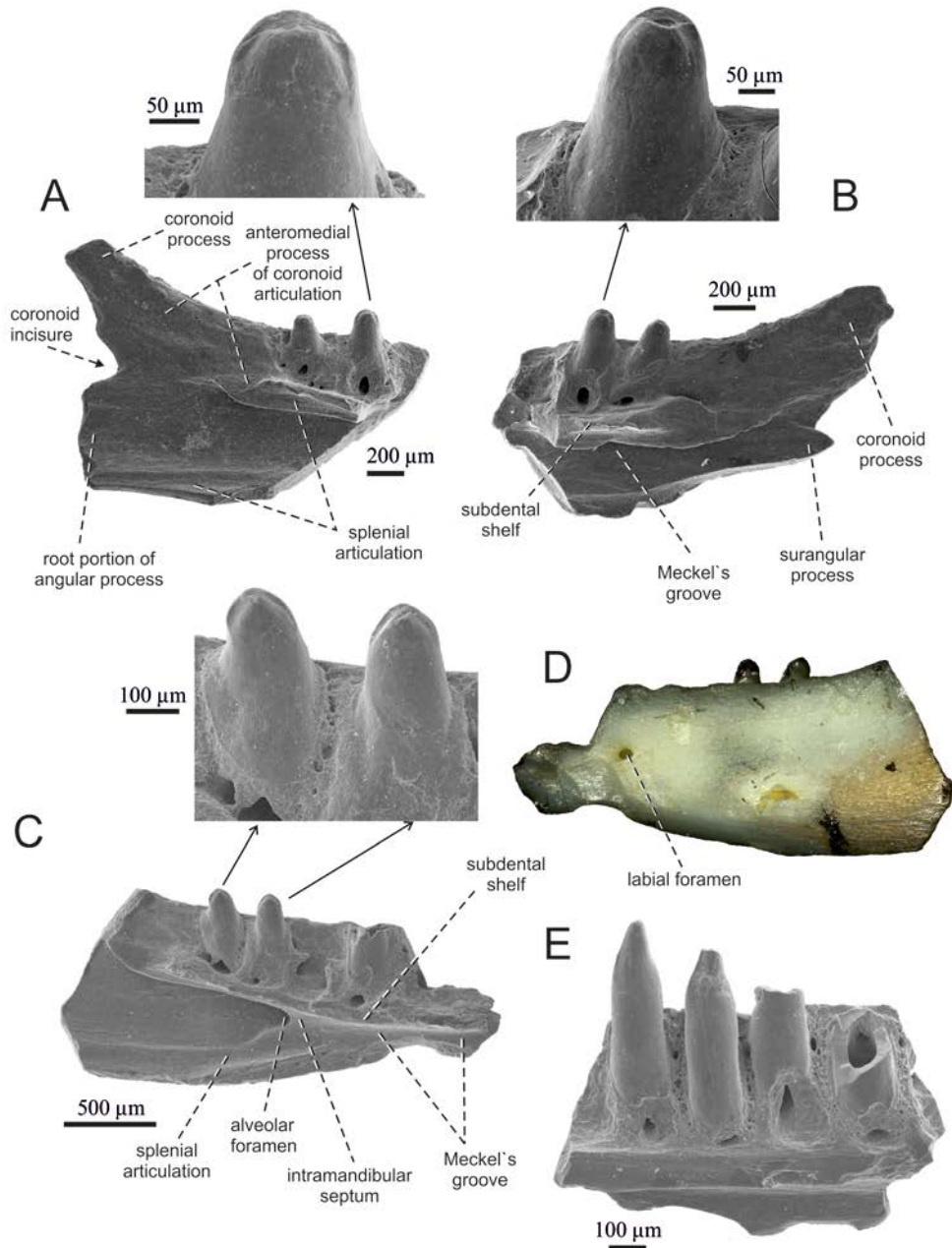
Fig. 4. Squamata from the Builstyn Khudag locality (assemblage BUK-A/12+14), Taatsiin Tsagaan Nuur area, Valley of Lakes, Mongolia, Loh Fm., late Miocene, letter zone E, Bahean LMS/A. cf. *Ophiomorus* sp. **A**: left dentary, medial view with detail of tooth (NHMW 2019/0138/0001), **B**: right dentary, medial view with detail of tooth (NHMW 2019/0138/0003), **C**: left dentary, medial view with detail of teeth (NHMW 2019/0138/0002), **D**: left dentary, lateral view (NHMW 2019/0138/0002). Squamata indet. **E**: right dentary, medial view (2019/0139/0001).

subdental shelf. The posteriormost region of the shelf and posterior area on the coronoid process form an articulation facet for the anteromedial process of the coronoid; the facet is located posterior to the tooth row. Anteroventral to it, there is an articulation facet for the splenial. On the ventromedial margin of the subdental shelf, this facet reaches the level of the 2nd or 3rd tooth position (the section is partly damaged). The facet for the splenial on the ventral margin of the bone reaches the level of the 3rd tooth position (counted from posterior).

The lateral surface of the bone is smooth. The surface is pierced by labial foramina; but only one foramen is preserved. It is visible in the specimen NHMW 2019/0138/0002 (Fig. 4 D). The foramen is located at the level of the 4th tooth position (counted from posterior). Two other specimens have smooth surfaces, but note that they both represent more posterior portions of the dentaries.

Description of the dentition: The implantation is pleurodont, with the tooth bases ankylosed to their sockets and surrounded by a ring of bony tissue. The maximum preserved tooth positions, five, are present in the specimen NHMW 2019/0138/0002. Teeth are robust, but rather small in the posterior region. However, a preserved ventral half of the 4th tooth (counted from posterior) in the specimen NHMW 2019/0138/0002 gives an estimation of the presence of higher teeth further anteriorly than those preserved in the posteriormost region. The last posterior tooth is usually smaller (in two of three available specimens here). The tooth crowns are blunt and rounded, in some cases they form blunt triangles. The crowns appear to be transversally bicuspid; there is a less distinctive lingual cusp and sharper labial cusp. No striation is recognized and was most likely absent. Ventral to the tooth crown, the tooth neck gradually widens at the base. The bases are pierced by resorption pits of various sizes.

Taxonomic allocation of NHMW 2019/0138/0001–0003: The dentary specimens NHMW 2019/0138/0001–0003 exhibit fully open Meckel's groove (although it narrows anteriorly, the morphology of the specimen NHMW 2019/0138/0003 supports the statement that it was not closed). Among skinks, fully open Meckel's groove is present in members of the Scincidae clade (*sensu* HEDGES 2014; Scincinae sensu ESTES *et al*. 1988) and in *Ateuchosaurus* (see ČERŇANSKÝ *et al*. 2020). The enclosure is present in members of Acontidae, Sphenomorphidae, Eugongylidae, Lygosomidae, Egerniidae, and Mabuyidae (see GREER 1970, 1974; RIEPPEL 1981; ESTES 1983; EVANS 2008; HUTCHINSON & SCANLON 2009; GAUTHIER *et al*. 2012; ČERŇANSKÝ & SYROMYATNIKOVA 2021; ČERŇANSKÝ *et al*. 2020).

Only the posterior dentary portions are preserved in the Builstyn Khudag material and the allocation of such fragmentary material always needs to be met with caution. These portions of dentaries share the following combination of features with those of the recent living genus *Ophiomorus* (see ČERŇANSKÝ *et al*. 2020): (1) small size; (2) open Meckel's groove, being wide in the posterior region, but markedly narrow anteriorly; (3) large coronoid process; and (4) the alveolar foramen is located at the level of the posterior teeth – more precisely at the level between the 2nd and 3rd tooth position (counted from

posterior; this can slightly vary among extant *Ophiomorus* species, a condition similar to that exists in fossil species, *e. g.*, in *O. tridactylus*.

Among here studied species of *Ophiomorus*, the preserved portions of the dentaries strongly resemble the morphology present in the species *O. punctatissimus*: (1) the dentition with blunt and transversally bicuspid tooth apices (see CAMAITI *et al.* 2019); (2) the facet for anteromedial process of coronoid reaching at the level posterior to the tooth row; (3) facet for splenial reaching at the level of the last posterior teeth; (4) posterior to the tooth row, there is a long area without dentition; and (5) the posterior end of the dentaries appears to possess three distinct posterior processes, where the coronoid process gradually starts to rise dorsally, and is markedly dorsally elevated. In *O. tridactylus* and *O. raithmai*, the coronid process is not so markedly dorsally elevated as that in *O. punctatissimus* (see also ČERŇANSKÝ *et al.* 2020).

If correctly allocated, the Mongolian material represents the first and thus also oldest evidence of the *Ophiomorus* lineage (for the Pleistocene record, see VILLA *et al.* 2020). Moreover, it shows the occurrence of this skink lineage in Asia during the late Miocene (*ca.* 9 Ma) and it potentially forms its easternmost distribution (Mongolia). However, the similarities to *O. punctatissimus* is rather unexpected, because this taxon represents the westernmost extant species of the genus, and the only one occurring exclusively in Europe. Previously, the Turkish populations were considered as *O. punctatissimus* (POULAKAKIS *et al.* 2008), but currently have been redescribed as *O. kardesi* by KORNILIOS *et al.* (2018). According to POULAKAKIS *et al.* (2008), it seems that *O. punctatissimus* is an old eastern Mediterranean species and possibly the ancestral form of *O. punctatissimus* invaded the Aegean region from Anatolia. But this can be particularly interesting from the viewpoint of previously reported faunal relationship of another Asian Miocene locality (Baikal Lake) to European sites, highlighting the astonishing high similarity of faunas (RAGE & DANILOV 2008; ČERŇANSKÝ *et al.* 2020).

There is, however, at least one difference between the Mongolian material and extant *O. punctatissimus*; the surangular process of the latter one is long, posteriorly overreaching the coronoid process. Thus, it seems more probable that the morphological similarities might be caused by convergent evolution reflecting environmental preferences or they are simply plesiomorphic among *Ophiomorus* species. But as mentioned above, the Mongolian late Miocene material studied here is incomplete and it does not allow strong taxonomical and palaeobiogeographical conclusions. Moreover, the dentary morphology of many *Ophiomorus* representatives is unknown.

R e m a r k s : The nocturnal burrowing skink genus *Ophiomorus* currently consists of 12 extant species (KAZEMI *et al.* 2011; UETZ & HOŠEK 2018; KORNILIOS *et al.* 2018), ranging from south-eastern Europe (Greece) to extreme north-western India (ANDERSON & LEVITON 1966). Today, the genus *Ophiomorus* includes species of elongated skinks with greatly reduced appendages; ranging from species having short limbs and a reduced number of fingers to completely limbless forms. The representatives of this genus usually live under rocks (GREER & WILSON 2001). In fact, they exhibit two major adaptive trends,

based on which two groups were identified (ANDERSON & LEVITON 1966). The western group (the areas from Greece to the Zagros Mountains of Iran: *O. punctatissimus*, *O. latastii*, and *O. persicus*), with elongated cylindrical bodies and the greatest degree of limb reduction, is adapted to a life under rocks or borrows in the loose soil. The eastern group (the desert areas from Iran through southern Afghanistan and Pakistan to the Punjab: *O. tridactylus*, *O. raithmai*, *O. nuchalis*, *O. blanfordi*, *O. chernovi*, *O. streeti*, and *O. brevipes*) consists of sand dune dwellers.

Squamata indet.
(Fig. 4 E)

M a t e r i a l from sample/layer BUK-A/12+14 (1 specimen): One right dentary (NHMW 2019/0139/0001).

D e s c r i p t i o n o f t h e d e n t a r y : Only a fragment of the right dentary is preserved. It is small in size, obviously belonging to a tiny lizard. It bears four tooth positions (Fig. 4 E); two and half teeth are still attached (in the 4th one, only the tooth base is preserved). The dental crest is high. The subdental shelf is narrow in the preserved section. It is straight and shallow dorsally, the sulcus dentalis is absent here. Meckel's groove is fully open, but the ventral portion of the dentary is largely damaged. The intramandibular septum is horizontal. The lateral surface is smooth, pierced by one small labial foramen at the level between the 2nd and 3rd preserved tooth positions.

D e s c r i p t i o n o f t h e d e n t i t i o n : The implantation is pleurodont. Teeth are high with monocuspid crowns. The tooth crowns are pointed, markedly narrow (they are constricted) and slightly recurved relative to the tooth necks. The anterior and posterior cutting edges appear to be present. The lingual side of the crowns possesses very fine apicobasal striations. The cylindrical tooth necks gradually continue to the tooth bases. The bases are pierced by large resorption pits about their midregions.

T a x o n o m i c a l l o c a t i o n of NHMW 2019/0139/0001: The specimen NHMW 2019/0139/0001 represents an animal of very small body size. Unicuspid, recurved teeth are often present in burrowing skinks (and in the anterior region of many lacertids and teiids; see KOSMA 2004). The tooth shape slightly resembles *e. g.*, *Ophiomorus tridactylus* (for this taxon, see ČERŇANSKÝ *et al.* 2020), but unfortunately only a small dentary fragment is preserved. Thus, there is a lack of potential diagnostic features and in fact, the allocation of this specimen to any taxon would be doubtful. We can exclude gekkotans, acrodont lizards, and *e. g.*, lacertids, but not other groups, such as, *e. g.*, skinks and anguimorphs. But it should be noted that the latter group is less probable because of the position of the resorption pits. The position indicates that the tooth replacement pattern does not resemble that of modern anguimorphs, where the interdental type is present (MCDOWELL & BOGERT 1954). Further, more complete material of this form from this locality is therefore needed for a more precise allocation. In any case, the specimen NHMW 2019/0139/0001 shows that another lizard occurred in the late Miocene environment of the Builstyn Khudag locality.

Family Lacertidae Oppel, 1811

Tribe Eremiadini Shcherbak, 1975

Eremiadini indet.

2019   Eremiadini indet. – Čerňanský & Augé: 829–832, figs 13–17.

M a t e r i a l from sample/layer BUK-A/12+14 (19 specimens): 1 premaxilla (NHMW 2016/0208/0001), 4 right maxillae (NHMW 2016/0208/0002 to …/0005), 2 left maxillae (NHMW 2016/0208/0006, …/0007), 4 left dentaries (NHMW 2016/0208/0008 to …/0011), 4 right dentaries (NHMW 2016/0208/0012 to …/0015), 3 vertebrae (NHMW 2016/0208/0016 to …/0018), 1 frontal (NHMW 2016/0208/0019).

M a i n c h a r a c t e r i s t i c s a n d r e m a r k s : The rich material, which consists of premaxilla, maxillae, frontal, dentaries and vertebrae, is allocated to the tribe Eremiadini by Čerňanský & Augé (2019). Although fragmentary, the material represents the oldest evidence of this tribe in the area of East Asia [for detailed description, figures and discussions see Čerňanský & Augé (2019: pp. 829–832, figs 13–17)].

Suborder Serpentes Linnaeus, 1758

Family Boidae Gray, 1825

Subfamily Erycinae Bonaparte, 1831

Eryx sp. 1 and *Eryx* sp. 2

2007   *Eryx* sp. 1 – Böhme: 47, tabs 1–2, textfig. 2/1.
2007   *Eryx* sp. 2 – Böhme: 47, tabs 1–2, textfig. 2/1a–d.

M a t e r i a l from sample/layer BUK-A/12+14 (3 specimens): Several vertebrae of *Eryx* sp. 1 (NHMW 2007/0059/0001, …/0002) and *Eryx* sp. 2 (NHMW 2007/0058/0001).

For short descriptions and interpretations see Böhme (2007).

Family Colubridae Oppel, 1811

Subfamily Colubrinae Oppel, 1811

Colubrinae 1 and Colubrinae 2

2007   Colubrinae 1 – Böhme: 47, tabs 1–2, textfig. 1/3.
2007   Colubrinae 2 – Böhme: 47, tabs 1–2, textfig. 1/4.

M a t e r i a l from sample/layer BUK-A/12+14 (2 specimens): Several vertebrae of Colubrinae 1 (NHMW 2007/0056/0001) and Colubrinae 2 (NHMW 2007/0057/0001, …/0002).

For short descriptions and interpretations see Böhme (2007).

Subfamily "Natricinae" Bonaparte, 1831

"Natricinae" indet.

2007   Natricinae indet. – Böhme: 47, tabs 1–2, textfig. 2/2.

M a t e r i a l from sample/layer BUK-A/12+14 (1 specimen): 1 trunk vertebra of a juvenile natricine individual (NHMW 2007/0060/0001).

For short descriptions and interpretations see Böhme (2007).

O v e r v i e w o f S q u a m a t a : The lizard diversity in the available Builstyn Khudag material is relatively low, but three lineages can be identified: Eremiadini (Lacertidae, the most successful and abundant clade here, see Čerňanský & Augé 2019), cf. *Ophiomorus* sp. (Scincidae), and Squamata indet. The presence of members of the tribe Eremiadini suggests an arid paleoenvironment in the Builstyn Khudag locality during the late Miocene (Čerňanský & Augé 2019; nowadays, members of this clade usually inhabit desert and steppe regions, see *e. g.*, Arnold *et al.* 2007). The presence of cf. *Ophiomorus* might support this statement. As for snakes, Böhme (2007) identified and briefly discussed three clades: Erycinae, Colubrinae, and Natricinae. She stated that the semi-fossorial sand boas indicate a dry and open environment, although probably with some water sources (the presence of natricines).

Class Mammalia Linnaeus, 1758

Order Lagomorpha Brandt, 1855

Family Ochotonidae Thomas, 1897

Genus *Ochotona* Link, 1795

Ochotona lagreli Schlosser, 1924

2003   *Ochotona lagreli* – Erbajeva: 216–219, tab.1, fig. 2/A, C, D, E, G, H.

T y p e l o c a l i t y : Ertemte 2, Inner Mongolia, China

S t r a t u m t y p i c u m : Ertemte Formation, late Miocene, Baodean LMS/A, MN 13

S t r a t i g r a p h i c r a n g e : late Miocene to Pleistocene (Qiu 1987)

P u b l i s h e d m a t e r i a l from sample/layer BUK-A/12+14 (*ca.* 28 specimens): 1 p3 (NHMW 2001/0029/0001), 1 P2 (NHMW 2001/0029/0002), 1 P3 (NHMW 2001/0029/0003), 1 M1 (NHMW 2001/0029/0004), 1 M2 (NHMW 2001/0029/0005), 1 M2 (NHMW 2001/0029/0006), 2 P3, 3 P4, 4 M1, 6 M2, 1 frag. Maxilla (P4–M1), 2 I sup., 3 p4, 1 m1, 2 m2, 1 i inf. (NHMW 2001/0029/0000). Erbajeva (2003: tab. 1, fig. 2).

S o f a r u n p u b l i s h e d m a t e r i a l from sample/layer BUK-A/12+14 (*ca.* 30 specimens): 4 maxillary fragments with teeth (right P4–M1, left P4–M2, left P2–M2, left

P3–M2), 26 deciduous and permanent cheek teeth, diverse fragments and incisors (NHMW 2001/0029/0000). This material was not yet available when ERBAJEVA (2003) described *O. lagreli* from Builstyn Khudag.

R e m a r k s : In the present paper we follow the descriptions, measurements, and interpretations of ERBAJEVA (2003: pp. 216–219, tabs 1–2, fig. 2), however, since sorting of residuals from screen-washed sediments was recently completed, the number of Lagomorpha specimens from BUK-A/12+14 increased significantly. Therefore, a future revision of the Lagomorpha group is in preparation.

Ochotona minor BOHLIN, 1942

2003   *Ochotona minor* – ERBAJEVA: 219–221, tabs 3–4, fig. 3.

T y p e l o c a l i t y : Ertemte, Inner Mongolia, China

S t r a t u m t y p i c u m : Ertemte Formation, late Miocene, Baodean LMS/A, MN 13

S t r a t i g r a p h i c r a n g e : late Miocene to Pleistocene (QIU 1987)

P u b l i s h e d m a t e r i a l from sample/layer BUK-A/12+14 (11 specimens): 1 P3 (NHMW 2001/0030/0001/1; ERBAJEVA 2003: tab. 3, fig. 3/A); 1 M2 (NHMW 2001/0030/0001/2; ERBAJEVA 2003: tab. 3, fig. 3/B); 1 p3 (NHMW 2001/0030/0001/3; ERBAJEVA 2003: tab. 3, fig. 3/C); 1 P4, 3 M1, 2 p4, 1 m1, 1 m1–2 fragm., 2 I (NHMW 2001/0030/0001/0000). See ERBAJEVA (2003: tab. 3).

So far u n p u b l i s h e d m a t e r i a l from sample/layer BUK-A/12+14 (*ca.* 40 specimens): 1 left mandible (m1–3) and 39 upper and lower cheek teeth (NHMW 2001/0030/0000). This material was not yet available when ERBAJEVA (2003) described *O. minor* from Builstyn Khudag.

R e m a r k s : In the present paper we follow the descriptions, measurements, and interpretations of ERBAJEVA (2003: p. 219, tab 3, fig. 3). The small species, *O. minor*, from Builstyn Khudag was described on the basis of a few fossils only. Meanwhile the available material increased and a future revision of the Lagomorpha group is in preparation.

Order Erinaceomorpha GREGORY, 1910

Family Erinaceidae FISCHER, 1817

Genus *Parvericius* KOERNER, 1940

Parvericius buk ZIEGLER, DAHLMANN & STORCH, 2007
(Fig. 5 A–I)

2007   *Parvericius buk* nov. spec. – ZIEGLER *et al.*: 109–113, tabs 12, 15, fig. 14/1, 14/4–9, 14/11–12.

T y p e l o c a l i t y : Builstyn Khudag (BUK-A/12+14), Valley of Lakes, Mongolia

S t r a t u m   t y p i c u m : Loh Formation, late Miocene, letter zone E (Höck *et al*. 1999)

S t r a t i g r a p h i c   r a n g e : early to late Miocene

P u b l i s h e d   m a t e r i a l from sample/layer BUK-A/12+14: (94 specimens; collection numbers: NHMW 2005/0215/0001 to …/0094):

H o l o t y p e **:** Left m1 (NHMW 2005/0215/0001, Fig. 5 B).

P a r a t y p e s **:** Left p4 (NHMW 2005/0215/0003, Fig. 5 A), left m2 (NHMW 2005/0215/0004, Fig. 5 C), right m3 (NHMW 2005/0215/0005, Fig. 5 D̲), right P3 (NHMW 2005/0215/0006, Fig. 5 E̲), left P4 (NHMW 2005/0215/0007, Fig. 5 F), right M1 (NHMW 2005/0215/0008, Fig. 5 G̲), left M2 (NHMW 2005/0215/0009, Fig. 5 H), right M3 (NHMW 2005/0215/0002, Fig. 5 I̲). Additional material: Left and right dentary fragments with p4–m1, a left maxillary fragment with M2–M3, and 83 isolated teeth (NHMW 2005/0215/0010 to …/0094).

S o f a r u n p u b l i s h e d   m a t e r i a l from sample/layer BUK-A/12+14 (> 100 specimens, recently sorted from screen-washed residuals): Fragmentary mandibles and numerous isolated teeth (NHMW 2005/0215/0000). These fossils were not yet available for the description by Ziegler *et al*. (2007).

O t h e r   o c c u r r e n c e s : Olon Ovoony Khurum (ODO-A/2) from the early Miocene (biozone D1/1) and Loh (LOH-A/2) from the middle Miocene (biozone D1/2). Both localities are situated in the Valley of Lakes, Mongolia (Ziegler *et al*. 2007).

D i f f e r e n t i a l   d i a g n o s i s : *"The genus Parvericius differs from all other erinaceines in the anteroposteriorly compressed trigonid of the m1 and m2. Parvericius buk differs from the only other species of the genus*, *P. montanus* Koerner, *1940*, *in the less marked ectocingulids of the lower molars*, *in the P4 being distinctly shorter than the M1*, *and in the metaconule on M1 and M2*, *which is indicated as swelling in the termination of the postparacrista."* Ziegler *et al*. (2007: p. 109)

R e m a r k s : In the present paper we follow the description and measurements of Ziegler *et al*. (2007: p. 109, tab. 12), and the figures (Fig. 5 A–I̲) are from Ziegler *et al*. (2007: fig. 14/1, 14/4–9, 14/11–12). While the genus *Parvericius* ranges back to the Oligocene, the species *P. buk* has a Miocene range Ziegler *et al*. (2007: p. 113). The erinaceid *P. buk* is very well represented in the late Miocene Builstyn Khudag assemblage, predominantly by isolated teeth. Occurrences from the early and middle Miocene are comparably rare.

Fig. 5. *Parvericius buk* Ziegler, Dahlmann & Storch, 2007 from the Builstyn Khudag locality (assemblage BUK-A/12+14), Taatsiin Tsagaan Nuur area, Valley of Lakes, Mongolia, Loh Fm., late Miocene, letter zone E, Bahean LMS/A. **A**: p4 left, (NHMW 2005/0215/0003), **B**: m1 left, holotype (NHMW 2005/0215/0001), **C**: m2 left (NHMW 2005/0215/0004), **D̲**: m3 right (NHMW 2005/0215/0005), **E̲**: P3 right (NHMW 2005/0215/0006), **F**: P4 left (NHMW 2005/0215/0007), **G̲**: M1 right (NHMW 2005/0215/0008), **H**: M2 left (NHMW 2005/0215/0009), **I̲**: M3 right (NHMW 2005/0215/0002). All figured specimens from Ziegler *et al*. (2007: fig. 14/1, 14/4–9, 14/11–12).
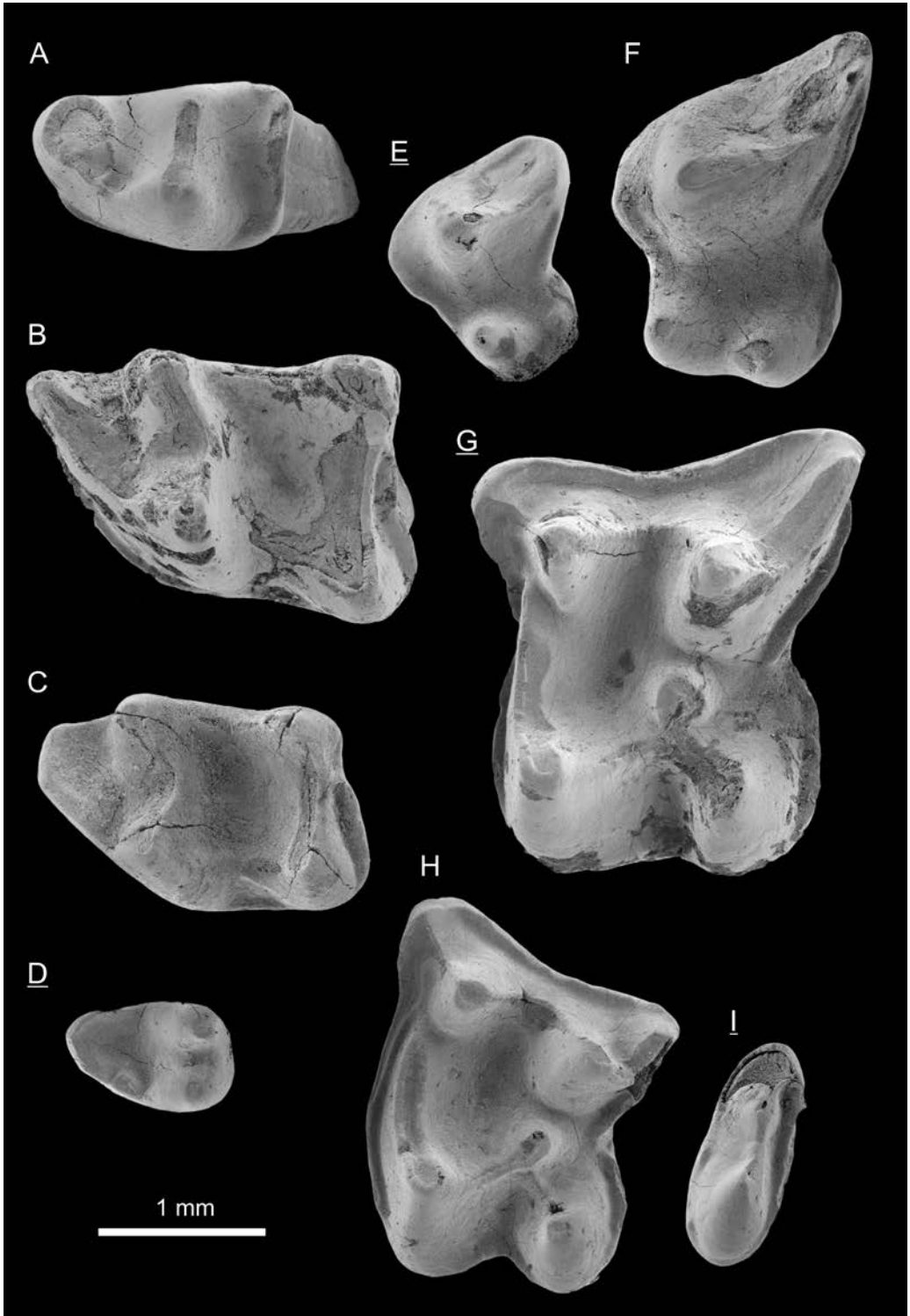
Order Soricomorpha GREGORY, 1910

Family Soricidae FISCHER,1814

Genus *Builstynia* ZIEGLER, DAHLMANN & STORCH, 2007

Builstynia fontana ZIEGLER, DAHLMANN & STORCH, 2007
(Fig. 6 A – G2)

2007   *Builstynia fontana* nov. gen. nov. spec. – ZIEGLER *et al.*: 138–142, tabs 14, 15, fig. 26/1–9.

T y p e   l o c a l i t y : Builstyn Khudag (BUK-A/12+14), Valley of Lakes, Mongolia

S t r a t u m   t y p i c u m : Loh Formation, late Miocene, biozone E (HÖCK *et al.* 1999)

S t r a t i g r a p h i c   r a n g e : late Miocene; at present restricted to the type locality.

P u b l i s h e d   m a t e r i a l from sample/layer BUK-A/12+14 (27 specimens; collection numbers: NHMW 2006/0054/0001 to …/0027).

H o l o t y p e : Right mandibular fragment with distal part of incisor, a1, p4, m1 (NHMW 2006/0054/0001, Fig. 6 G1–G2).

P a r a t y p e s : Left I sup. (NHMW 2006/0054/0002, Fig. 6 A), right I sup. (NHMW 2006/0054/0003, Fig. 6 B), right M1 (NHMW 2006/0054/0004, Fig. 6 C), left M2 (NHMW 2006/0054/0005, Fig. 6 D), right i inf. (NHMW 2006/0054/0006, Fig. 6 F1–F2), left m2 (NHMW 2006/0054/0007, Fig. 6 E), left mandibular fragment with m1–2 (NHMW 2006/0054/0008), left mandibular fragment with m3 (NHMW 2006/0054/0009)**.** Additional material:1 mandibular fragment with p4–m2, 1 mandibular fragment with m2, 4 I sup, 1 A sup., 1 M1, 8 i inf., 2 m1 (NHMW 2006/0054/0010 to …/0027)**.**

Hitherto u n p u b l i s h e d   m a t e r i a l from the type locality BUK-A/12+14 (*ca.* 40 specimens): some mandibles and numerous isolated teeth (NHMW 2006/0054/0000; partly tooth fragments). These fossils were recently sorted from old residuals of sample BUK-A/12+14, consequently they were not yet available for the description by ZIEGLER *et al.* (2007: pp. 138–142, fig. 26/1–9, tab. 14).

D i a g n o s i s : *"I sup. not fissident; upper molars broad with strongly emarginated distal margin and relatively narrow hypoconal flange, distal cingulum interrupted at the*

Fig. 6. *Builstynia fontana* ZIEGLER, DAHLMANN & STORCH, 2007 from the Builstyn Khudag ▶ locality (assemblage BUK-A/12+14), Taatsiin Tsagaan Nuur area, Valley of Lakes, Mongolia, Loh Fm., late Miocene, letter zone E, Bahean LMS/A. **A**: I left (NHMW 2006/0054/0002), **B**: I right (NHMW 2006/0054/0003), **C**: M1 right (NHMW 2006/ 0054/0004), **D**: M2 left (NHMW 2006/0054/0005), **E**: m2 left (NHMW 2006/0054/0007), **F1**: i right, buccal view (NHMW 2006/0054/0006), **F2**: i right, lingual view (NHMW 2006/0054/0006), **G1**: right mandibular fragment with distal part of incisor, a1, p4, m1, holotype, occlusal view (NHMW 2006/0054/0001), **G2**: right mandibular fragment with distal part of incisor, a1, p4, m1, holotype, buccal view (NHMW 2006/0054/0001). All figured specimens from ZIEGLER *et al.* (2007: fig. 26/1–7).
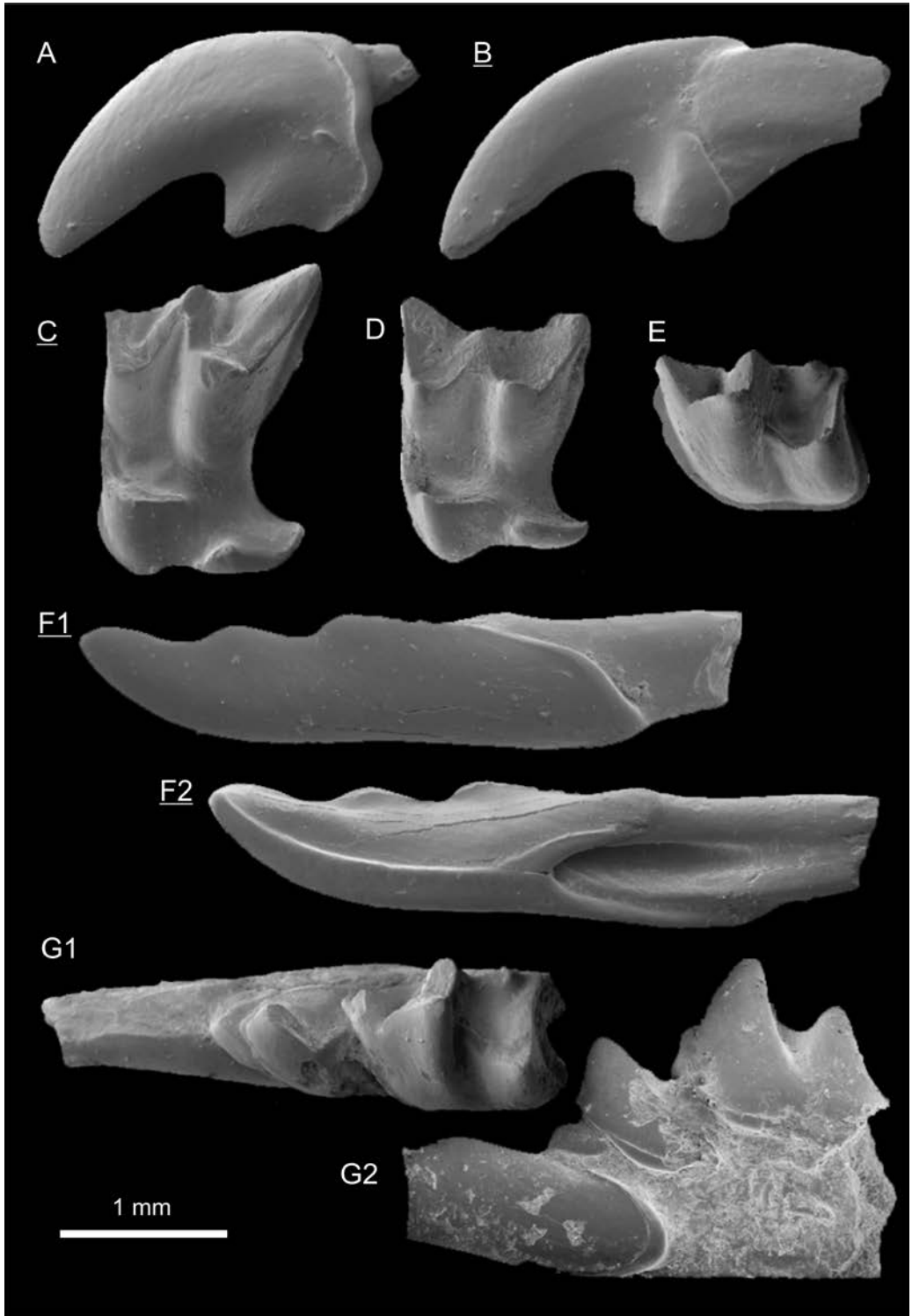
deepest point of the distal emargination; i inf. bicuspid; a1 reduced in size as compared to p4; m1−2 relatively broad with shallow hypoflexid, relatively short talonid, weak entoconid and low or moderate entocristid; labial basis of m1 strongly inclined disto-ventrally in labial view; m3 talonid reduced in size and morphology; condylus with narrow and high interarticular area and broad lower articular facet (in lingual view ending in line with distal margin of internal temporal fossa). Coronoid process somewhat tilted laterally, condyles medially." ZIEGLER *et al*. (2007: p. 138)

R e m a r k s : In the present paper we follow the description and measurements of ZIEGLER *et al*. (2007: pp. 138−142, tabs 14, 15) and the figures (Fig. 6 A−G2) are from ZIEGLER *et al*. (2007: fig. 26/1−7). *Builstynia* differs from all other genera of the tribe Neomyini by a not fissident upper incisor and the shortened talonid of m1−2. The monospecific genus *Builstynia* is only known from the late Miocene at Builstyn Khudag in Mongolia. There it is well represented by *ca.* 70 mandibles and isolated teeth.

<div align="center">

Order Rodentia BOWDICH, 1821

Family Sciuridae FISCHER, 1817

Genus *Tamias* ILLIGER, 1811

Tamias ertemtensis (QIU, 1991)

</div>

1991   *Eutamias ertemtensis* – QIU: 225.
2007   *Prospermophilus* cf. *orientalis* – DAXNER-HÖCK & BADAMGARAV: 16, tab. 3.
2014b   *Eutamias* cf. *ertemtensis* – MARIDET *et al*.: 278−279, tab. 2, fig. 4.
2016   *Tamias ertemtensis* – QIU & LI: 536−538.

T y p e   l o c a l i t y : Ertemte 2, Inner Mongolia, China (QIU 1991)

S t r a t u m   t y p i c u m : Ertemte Formation, late Miocene, Baodean LMS/A, MN 13

S t r a t i g r a p h i c   r a n g e : late Miocene to early Pliocene

M a t e r i a l from sample/layer BUK-A/12+14 and measurements (3 specimens): 1 left M1/2 (NHMW 2013/0405/0001; 1.29 × 1.63 mm), 1 left p4 (NHMW 2013/0405/0002; 1.17 × 0.94 mm), 1 left dp4 (NHMW 2013/0405/0003; 1.07 × 0.90 mm)

For description and figures see MARIDET *et al*. (2014b: p. 278, fig. 4).

R e m a r k s : The teeth are characterized by small dimensions. The occlusal surface of M1/2 is of sub-square shape, the protoloph without protoconule, the protoloph and metaloph converge towards the protocone. The metaloph is constricted at its contact with the protocone. A small metaconule exists. The Mongolian teeth fall within the range of *Tamias ertemtensis*, in both, dimensions and molar morphology. The species is very common during the Neogene of Central Nei Mongol and other regions in China, and its dental pattern stays rather stable from the Miocene to the Pliocene (QIU & LI 2016: p. 545).

Genus *Atlantoxerus* FORSYTH MAJOR, 1893

Atlantoxerus sp.
(Fig. 7 A−D, Tab. 1)

2007   Sciuridae indet. 4 − DAXNER-HÖCK & BADAMGARAV: 16, tab. 3.
2014b   ? *Atlantoxerus* sp. − MARIDET *et al.*: 285−288, tab. 2, fig. 7.

M a t e r i a l from sample/layer BUK-A/12+14 (7 specimens): 1 left D4 (NHMW 2013/0411/0001; lingual part broken), 1 left M1/2 (NHMW 2013/0411/0002, Fig. 7 A), 1 left M1/2 (NHMW 2013/0411/0003, Fig. 7 B), 1 right M3 (NHMW 2013/0411/0004, Fig. 7 C), left maxilla fragment with P4−M3 (NHMW 2013/0411/0005), left m1/2 (NHMW 2013/0411/0006, Fig. 7 D), right m1/2 (NHMW 2013/0411/0007; lingual posterior corner broken).

For description see MARIDET *et al.* (2014b: pp. 285−288, fig. 7, tab. 2). The figured specimens (Fig. 7 A−D) are identical with those figured by MARIDET *et al.* (2014b: fig. 7 a−d).

R e m a r k s : The teeth from BUK-A/12+14 follow the main characteristics of *Atlantoxerus* and *Heteroxerus* in dental pattern, but are larger than most *Heteroxerus* species. They have unilateral hypsodont cheek teeth with strong cusps and crests. Upper molars have no protoconule on the long protoloph, the metaloph of M1/2 is of medium length, has a metaconule and a weak connection to the posteroloph (one of two specimens, Fig. 7 A). The metaloph has no lingual connection to protocone. M1/2 have a small mesostyle. M3 has a distinct metaloph and a metaconule (Fig. 7 C). The lower m1/2 (Fig. 7 D) have distinct lophids, of them hypolophid is of medium length and without buccal connection to hypoconid or posterolophid. These characters are typical of *Atlantoxerus*, however, the Mongolian teeth are smaller than comparable *Atlantoxerus* occurrences from the late Miocene of Nei Mongol in China (QIU & LI 2016). At present a reliable species identification is not possible based on the few specimens available.

Tab. 1. Measurements of *Atlantoxerus* sp. from BUK-A/12+14 (MARIDET *et al.* 2014b).

Atlantoxerus sp.	length (mm)	width (mm)
D4 l (NHMW 2013/0411/0001)	1.81	−
M1/2 l (NHMW 2013/0411/0002)	2.14	2.66
M1/2 l (NHMW 2013/0411/0003)	2.01	2.65
M3 r (NHMW 2013/0411/0004)	2.33	2.10
P4 l (NHMW 2013/0411/0005)	1.59	1.93
M1 l (NHMW 2013/0411/0005)	1.80	2.55
M2 l (NHMW 2013/0411/0005)	1.93	2.33
M3 l (NHMW 2013/0411/0005)	1.33	2.09
m1/2 l (NHMW 2013/0411/0006)	2.12	2.00
m1/2 l (NHMW 2013/0411/0007)	2.38	−

Fig. 7. *Atlantoxerus* sp. from the Builstyn Khudag locality (assemblage BUK-A/12+14), Taatsiin Tsagaan Nuur area, Valley of Lakes, Mongolia, Loh Fm., late Miocene, letter zone E, Bahean LMS/A. **A**: M1/2 left (NHMW 2013/0411/0002), **B**: M1/2 left (NHMW 2013/0411/0003), **C**: (NHMW 2013/0411/0004), **D**: m1/2 left (NHMW 2013/0411/0006). The figured specimens are identical with MARIDET *et al*. (2014b: fig. 7/a–d).

Family Eomyidae Linnaeus, 1758

Genus *Ombomys* Maridet, Daxner-Höck, Badamgarav & Göhlich, 2015

Ombomys builstynensis Maridet, Daxner-Höck, Badamgarav & Göhlich, 2015
(Fig. 8 A–D)

2007   Eomyidae indet. 4 – Daxner-Höck & Badamgarav: 16, tab. 3.
2013a   Eomyidae indet. 4 – Daxner-Höck *et al.*: 487, tab. 20.4.
2015   *Ombomys builstynensis* sp. Nov. – Maridet *et al.*: 221–226, tabs 5–6, figs 8 a–j, 9 a–e.

T y p e   l o c a l i t y : Builstyn Khudag, sample BUK-A/12+14, Valley of Lakes, Mongolia

S t r a t u m   t y p i c u m : Loh Formation, late Miocene, biozone E (Höck *et al.* 1999)

S t r a t i g r a p h i c   r a n g e : Late Miocene; At present restricted to the type locality

H o l o t y p e **:** right M1/2 (NHMW 2013/0076/0004)

O t h e r   m a t e r i a l (13 specimens): right D4 (NHMW 2013/0076/0001), right P4 (NHMW 2013/0076/0002, Fig. 8 A), left M1/2 (NHMW 2013/0076/0003, Fig. 8 B), right M1/2 (NHMW 2013/0076/0005), right M1/2? (NHMW 2013/0076/0006), right M3? (NHMW 2013/0076/0007), right d4 (NHMW 2013/0076/0008), left p4 (NHMW 2013/0076/0009), left p4 (NHMW 2013/0076/0010, Fig. 8 C), left p4 (NHMW 2013/0076/0011); right p4 (NHMW 2013/0076/0012); left m1/2 (NHMW 2013/0076/0013, Fig. 8 D), left m3 (NHMW 2013/0076/0014; lost).

Hitherto u n p u b l i s h e d   m a t e r i a l from the type locality: 15 isolated teeth (NHMW 2013/0076/0015 to …/0029; partly fragments). These fossils were not yet available for the first description by Maridet *et al*. (2015: pp. 222–226, tabs 5–6, figs 8–9).

We follow the description, measurements, and figures of Maridet *et al*. (2015: pp. 221–226, tabs 5–6, figs 8 a–j, 9 a–e).

D i a g n o s i s : *"Small-sized bunodont eomyid with slender tooth morphology (small cusps and cuspids, and wide synclines and synclinids), and a low crown…Upper teeth missing the mesoloph and lower teeth with very rare and weakly-developed mesolophid, the molars have only three syncline(id)s, the central one being longer and larger than the others. M1/2 has a trapezoidal outline, with the oblique and short longitudinal crest joining directly the metaloph to the posterior end of the protocone. p4s with an oblique longitudinal crest joining the hypoconid with the metalophid or even directly with the metaconid, never with the protoconid."* (Maridet *et al*. 2015: p. 221)

R e m a r k s : *Ombomys* is a monospecific genus of Eomyidae, and only known from the late Miocene of Builstyn Khudag in Mongolia so far. There it is well represented by *ca*. 30 teeth. Recently, other Eomyidae were recorded from the late Miocene of Nei Mongol (China), mainly by isolated teeth. These are occurrences of *Keramidomys fahlbuschi* Qiu, 1996 from Balunhalagen, Huitenghe, and Bilutu, of *Keramidomys magnus* Qiu & Li, 2016 from Amuwusu, Shala, and Bilutu, of *Leptodontomys gansus* Zheng & Li, 1982
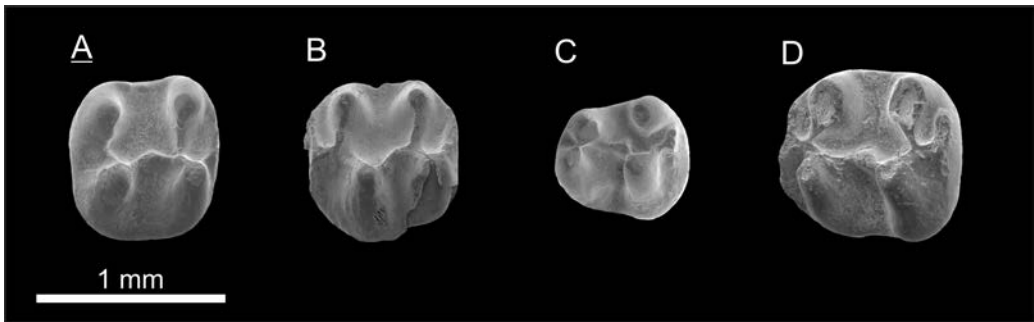
Fig. 8. *Ombomys builstynensis* MARIDET, DAXNER-HÖCK, BADAMGARAV & GÖHLICH, 2015 from the Builstyn Khudag locality (assemblage BUK-A/12+14), Taatsiin Tsagaan Nuur area, Valley of Lakes, Mongolia, Loh Fm., late Miocene, letter zone E, Bahean LMS/A. **A**: P4 right (NHMW 2013/0076/0002), **B**: M1/2 left (NHMW 2013/0076/0003), **C**: p4 left (NHMW 2013/0076/0010), **D**: m1/2 left (NHMW 2013/0076/0013). The figured specimens are identical with MARIDET *et al.* (2015: fig. 8 b, d, g, i).

from Amuwusu, Balunhalagen, Huitenghe, Shala, Bilutu, Ertemte 2, and Harr Obo 2, of *Leptodontomys lii* QIU, 1996 from Amuwusu, Balunhalagen, Huitenghe, Shala, and Bilutu, and of *Pentabuneomys fejfari* QIU & LI, 2016 from Amuwusu and Balunhalagen (QIU & LI 2016: pp. 557−562). The Mongolian eomyid *Ombomys builstynensis* MARIDET *et al.*, 2015, however, differs from all these genera and species by its small size, the reduced mesoloph(id), low cone(id)s, and wide valleys.

Family Cricetidae FISCHER, 1817

Genus *Nannocricetus* SCHAUB, 1934

Nannocricetus primitivus ZHANG, ZHENG & LIU, 2008
(Fig. 9 A−D, Tab. 2)

1999   *Allocricetus*? sp. – HÖCK *et al.*: 119, fig. 21/15.
2008   *Nannocricetus primitivus* – ZHANG *et al.*: 307−314, tabs 1−2, figs 1−2.
2014a   *Nannocricetus* aff. *primitivus* – MARIDET *et al.*: 260−263, tab. 2, figs 9−10.

T y p e   l o c a l i t y : Lantian, Shaanxi Province, China

S t r a t u m   t y p i c u m : Bahe Formation, early late Miocene (Bahean LMS/A); fossil beds palaeomagnetically dated at 8.03−10.21 Ma (KAAKINEN 2005)

O t h e r   o c c u r r e n c e s : Balunhalagen, Huitenghe, Shala, Baogeda Ula, Bilutu (Nei Mongol, China), Bahe, Shanxi, and Shengou (Qinghai, China) (QIU & LI 2016: p. 624), and Builstyn Khudag (Valley of Lakes, Mongolia)

S t r a t i g r a p h i c   r a n g e : late Miocene, Bahean to Baodean LMS/A, MN9 to MN12

Material from sample/layer BUK-A/12+14 (49 specimens + 17 fragments): 1 right maxillar fragment with M2−3 (NHMW 2013/0442/0016), 2 right mandible fragments with m1−2 (NHMW 2013/0442/0025, …/0026), 1 left mandible fragment with m2 (NHMW 2013/0442/0034), 6 left M1 (NHMW 2013/0442/0001 to …/0006), 1 right M1 (NHMW 2013/0442/0007), 1 left M2 (NHMW 2013/0442/0008), 8 right M2 (NHMW 2013/0442/0009 to …/0015, …/0042), 3 right M3 (NHMW 2013/0442/0017 to …/0018, …/0043), 1 left M3 (NHMW 2013/0442/0044), 3 left m1 (NHMW 2013/0442/0019 to …/0021), 4 right m1 (NHMW 2013/0442/0022 to …/0024, …/0045), 9 left m2 (NHMW 2013/0442/0027 to …/0033, …/0046 to …/0047), 5 right m2 (NHMW 2013/0442/0035 to …/0037, …/0040, …/0048), 3 right m3 (NHMW 2013/0442/0038 to …/0039, …/0041), 1 left m3 (NHMW 2013/0442/0049) and 17 fragmentary teeth (NHMW 2013/0442/0000).

Main characteristics and remarks: The described specimens agree with the diagnosis of *Nannocricetus* by: low-crowned molars with short or absent mesoloph(id), a bifid anterocone of M1, a narrow single or bifid anteroconid of m1, short buccally located metalophid and hypolophid of m1 and m2.

There are two species, *N. mongolicus* SCHAUB, 1934 ranging from the late Miocene to the early Pliocene, and *N. primitivus* ZHANG, ZHENG & LIU, 2008 ranging throughout the late Miocene. For description of the type material of *N. primitivus* see ZHANG *et al.* (2008: pp. 309−311, figs 1−2, tabs 1−2). Further information on the two species is provided by WU (1991) and QIU & LI (2016).

Nannocricetus mongolicus represents a progressive form in the *Nannocricetus* lineage. The older species *Nannocricetus primitivus* differs from *N. mongolicus* mainly by smaller and wider teeth, less derived dental features, *e.g.*, the short single or slightly bicuspid anteroconid of m1, a short or sometimes reduced mesoloph(id) of M1−2/m1−2, the presence of a lingual anterolophid of m2, three roots of M1 and M2, lower cusps, shallower valleys (ZHANG *et al.* 2008: p. 313; MARIDET *et al.* 2014a; QIU & LI 2016: p. 624, tabs 77−78).

Tab. 2. Measuremens of *Nannocricetus primitivus* ZHANG, ZHENG & LIU, 2008 from BUK-A/12+14 (MARIDET *et al.* 2014a: tab. 2).

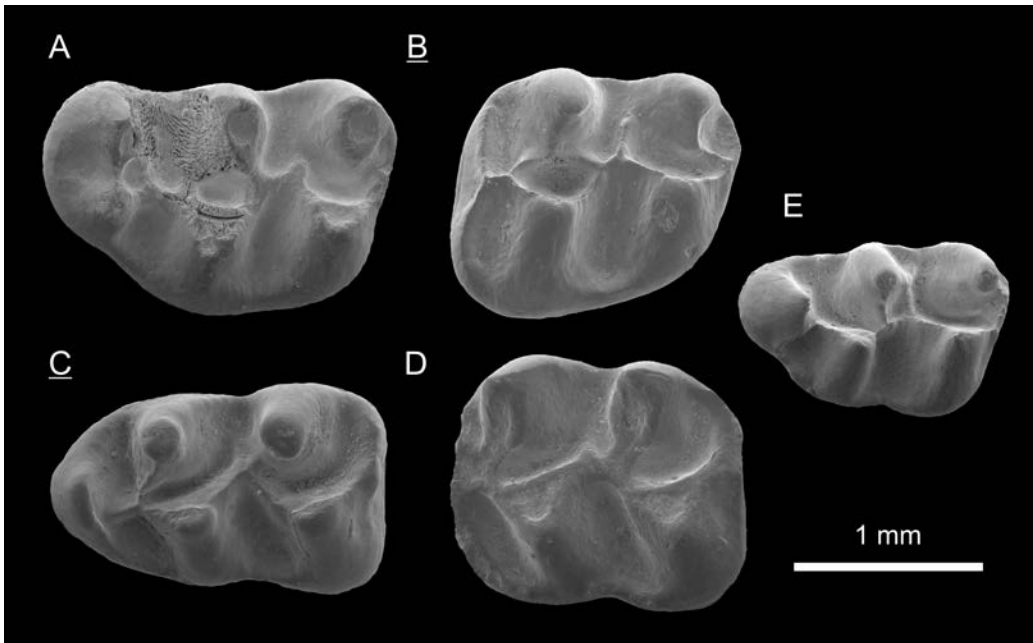| *N. primitivus*	length (mm)			width (mm)	
	range	mean	n	range	mean
M1	1.79−1.99	1.85	6	1.16−1.33	1.24
M2	1.35−1.53	1.43	9	1.19−1.34	1.23
M3	1.07−1.14	1.10	3	1.03−1.09	1.06
m1	1.63−1.77	1.71	8	0.99−1.15	1.09
m2	1.40−1.58	1.48	12	1.14−1.26	1.20
m3	1.19−1.34	1.29	4	1.05−1.07	1.06

Fig. 9. Cricetidae from the Builstyn Khudag locality (assemblage BUK-A/12+14), Taatsiin Tsagaan Nuur area, Valley of Lakes, Mongolia, Loh Fm., late Miocene, letter zone E, Bahean LMS/A. *Nannocricetus primitivus* ZHANG, ZHENG & LIU, 2008: **A**: M1 left (NHMW 2013/0442/0001), **B**: M2 right (NHMW 2013/0442/0009), **C**: m1 right (NHMW 2013/0442/0023), **D**: m2 left (NHMW 2013/0442/0028). The specimens are identical with MARIDET *et al.* (2014a: figs 9 a, 9 k, 10 b, 10 g). *Paracricetulus schaubi* YOUNG, 1927: **E**: M1 left (NHMW 2013/0441/0001).

The specimens from Mongolia (BUK-A/12+14) agree with dental features of the type material of *Nannocricetus primitivus* (ZHANG *et al.* 2008: pp. 309–311, figs 1–2, tabs 1–2), but the Mongolian specimens are slightly larger. Because of the size differences, MARIDET *et al.* (2014a) assumed that the Mongolian form might represent a higher advanced stage than the type of *N. primitivus*, and determined it as *N.* aff. *primitivus*. Presently, we identify the Mongolian occurrences as *N. primitivus*, because various late Miocene morphotypes of the species occur in other subsequent, well stratified faunas from Nei Mongol and these show a mosaic of primitive and more modern dental characters and a wide range of tooth sizes. There seems to be a trend towards increasing root numbers, losing the metaloph II in M1 and M2, reducing the mesoloph(id), gradually forming a bicuspid anterocone, and deepening anteriorly the furrow of the anteroconid in m1, gradually elongating the m1, narrowing the anteroconid of m1, and developing a double anterolophulid from a single one (QIU & LI 2016: pp. 624–625, figs 178–179, 181, tabs 77–78).

The Mongolian specimens (Fig. 9 A–D) provide more primitive than advanced molar characters, *i. e.*, three roots of all M1 and M2, the rather short M1/m1, a slightly bicuspid

anterocone(id) of M1 (90%) and m1 (50%) but no anterior furrow of the anteroconid. The mesolophid of m1 is reduced, however short mesoloph(id)s are present at M1 (90%), M2 (60%) and m2 (70%). There is also a short lingual anterolophid at m2 (60%), and the metaloph II of M1 (80%) and M2 (30%) still exists. The tooth sizes of the Mongolian material are in agreement with *N. primitivus* from Balunhalagen and Shala, they are smaller than specimens from Huitenghe but slightly larger than Baogeda and Bilutu specimens (all from Nei Mongol), and also larger than the type material from Lantian (Shaanxi Province).

The dominance of primitive dental characters suggests an early evolutionary stage of *N. primitivus* from Builstyn Khudag (Mongolia), most probably correlative with Chinese occurrences of the early late Miocene (Bahean LMS/A, MN9–10).

Genus *Paracricetulus* YOUNG, 1927

Paracricetulus schaubi YOUNG, 1927
(Fig. 9 E)

1999   *Megacricetodon* sp. – HÖCK et al.: 119, fig. 27/13.
2014a   *Megacricetodon* sp. – MARIDET et al.: 259, fig. 8.

T y p e   l o c a l i t y : Quantougou, Central Lanzhou Basin, Gansu, China.

S t r a t u m   t y p i c u m : Upper Xianshuihe Formation, Middle Miocene, middle Tunggurian.

O t h e r   o c c u r r e n c e s : Locality XJ 200617, North Junggar Basin, Xinjiang, China (middle Tunggarian).

M a t e r i a l   from sample/layer BUK-A/12+14 (2 specimens): 2 left M1 (NHMW 2013/0441/0001, …/0002).

M e a s u r e m e n t s (length × width): 1 left M1 (NHMW 2013/0441/0001) (Fig. 9 E); 1.42 × 0.93 mm[*]; 1 left M1, fragment (NHMW 2013/0441/0016); ?? × 0.92 mm.

D e s c r i p t i o n : The M1, one complete and one without the anterocone, is almost unworn (Fig. 9 E). The cusps are high and steep and the undivided anterocone is as high as the protocone. The other cusps are slightly higher. A very narrow crest running from the anterocone apex ends at the anterior base of the protocone. A short anterolophule connects anterocone and protocone. The protolophule is short and almost transverse. The longitudinal crest is semi-circular with a steep posterior part, the anterior arm of the hypocone, which continues into the labial sinus as a mesoloph. In one molar the mesoloph continues to the labial edge of the sinus. In both molars the paracone spur is connected to the mesoloph, creating a small square shaped valley. A metalophule is absent, the hypocone is connected to the metacone by the posteroloph, a high ridge on the posterior side of the metacone.

---

* Measurement from MARIDET et al. (2014a: p. 259).

R e m a r k s : Qɪᴜ (2001a), emended *Paracricetulus schaubi* and provided detailed descriptions based on more specimens from the type-locality Quantougou. Morphology and size both show a large variation. The morphological characteristics of the two BUK specimens fit the morphological variation described by Qɪᴜ (2001a) and they fall in the lower range of the measurements.

Paracricetulus schaubi is only known from two assemblages, the Tunggurian Quantougou Fauna in the central Lanzhou Basin of China (Qɪᴜ 2001a), considered 11.7 Ma or 12.8 Ma by Zʜᴀɴɢ *et al.* (2020) and the North Junggar Basin, China, dated middle Tunggurian (Wᴜ *et al.* 2009).

Genus *Plesiodipus* Yᴏᴜɴɢ, 1927

Plesiodipus robustus Qɪᴜ & Lɪ, 2016
(Fig. 10 A−C, Tab. 3)

2013a   *Prosiphneus* sp. – Dᴀxɴᴇʀ-Höᴄᴋ *et al.*: 488, tab. 20.4.

T y p e l o c a l i t y : Balunhalagen, Sonid Zouqui, Nei Mongol, China

S t r a t u m t y p i c u m : Balunhalagen bed of the late Miocene; discordant on top of the Aoerban Fm. (uppermost middle Miocene)

O t h e r o c c u r r e n c e s : Huitenghe and Bilutu in Nei Mongol (China), and Builstyn Khudag (Mongolia)

S t r a t i g r a p h i c r a n g e : late Miocene, Bahean to Baodean LMS/A

M a t e r i a l from sample/layer BUK-A/12+14 (3 specimens): 3 isolated teeth (NHMW 2018/0128/0001 to …/0003)

D e s c r i p t i o n : Large sized species of *Plesiodipus* with very robust lophodont, high crowned molars. The molars have obliquely compressed main cusps, which are fused with the lophs/lophids, forming three rows of oblique ridges. Upper M2 has no protosinus. The lingual valley (sinus) and two buccal valleys (anterosinus and mesosinus) are in W-shaped arrangement. Lower m2 with two lingual valleys (mesosinusid and posterosinusid) and two buccal valleys (protosinusid and sinusid). Positions of sinusid and posterosinusid are opposite to mesosinusid and posterosinusid.

Tab. 3. Measurements of *P. robustus* Qɪᴜ & Lɪ, 2016 from BUK-A/12+14.

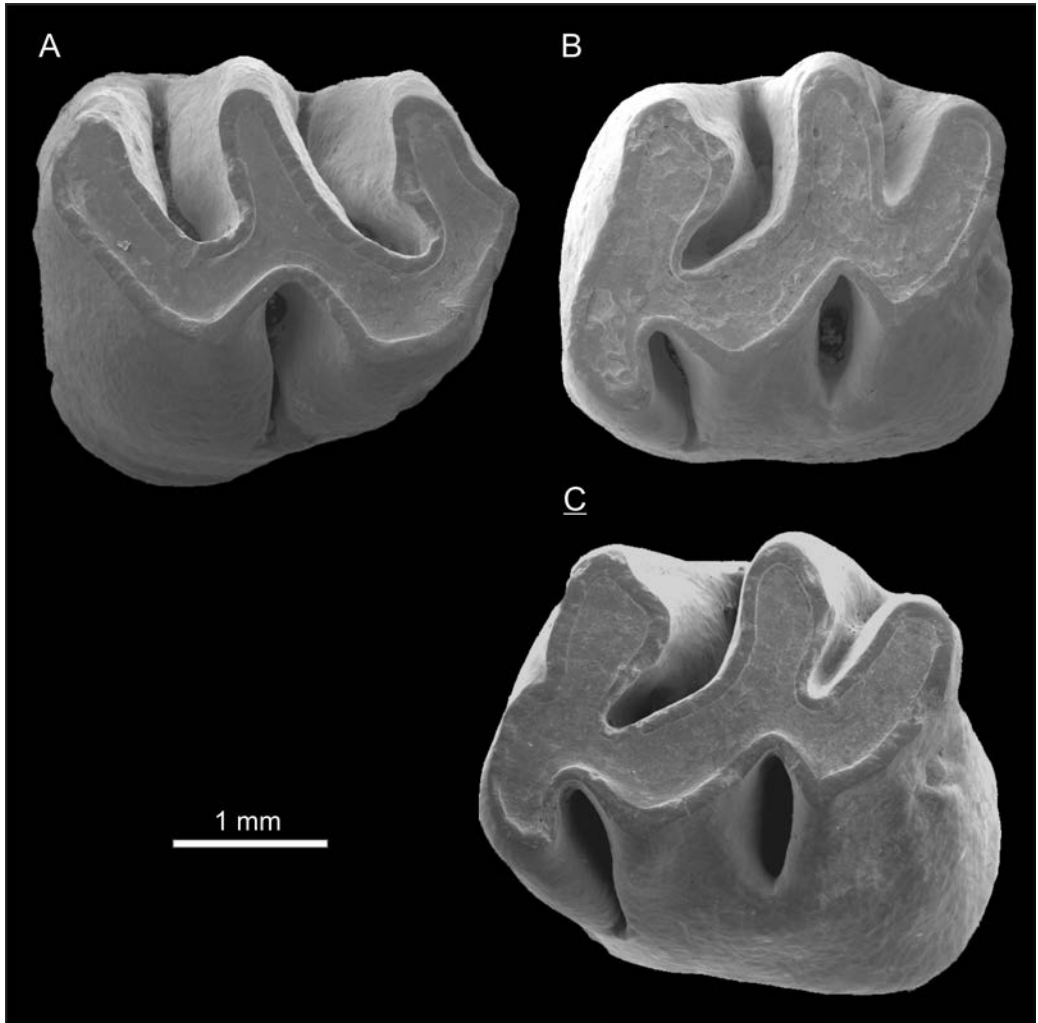| *Plesiodipus robustus*	length (mm)	width (mm)	hight (mm)
right m2 (NHMW 2018/0128/0001)	2.97	2.24	2.55
left m2 (NHMW 2018/0128/0002)	2.97	2.30	2.55
left M2 (NHMW 2018/0128/0003)	2.85	2.36	2.12

Fig. 10. *Plesiodipus robustus* QIU & LI, 2016 from the Builstyn Khudag locality (assemblage BUK-A/12+14), Taatsiin Tsagaan Nuur area, Valley of Lakes, Mongolia, Loh Fm., late Miocene, letter zone E, Bahean LMS/A. **A**: M2 left (NHMW 2016/0128/0003), **B**: m2 left (NHMW 2016/0128/0002), **C**: m2 right (NHMW 2016/0128/0001).

M2 (Fig. 10 A) has three buccal lophs (1. Anteroloph, 2. Fused paracone + protoloph, 3. Fused metacone + metaloph + posteroloph), but no mesoloph. Lingually there are two wide cones (protocone and hypocone). The protocone continues anteriorly with the anteroloph. The hypocone is continuous with loph 3. The position of the sinus is opposite to loph 2. The sinus is rather shallow. The buccal valleys (anterosinus and mesosinus) are deep and turning backwards. They extend lingually across the median line of the M2. The position of the two buccal valleys is opposite to protocone and hypocone. There is no protosinus and no posterosinus.

The m2 (Fig. 10 B–C) has a very deep mesosinusid extending labially across the median line of the tooth. The posterosinusid, protosinusid and sinusid are shallow. The pronounced labial anterolophid connects lingually to the fused metalophid + metaconid. The three lingual lophids are: 1. The fused metaconid + metalophid, 2. The fused entoconid + hypolophid, and 3. The posterolophid. The tooth crown is longer than high. The width is less than the height and the length.

R e m a r k s : The large sized *Plesiodipus robustus* derived from the much smaller middle Miocene species *P. leei* Young, 1927 as shown by Qiu & Li (2016). *P. robustus* was first evidenced from locality Balunhalagen (Bahean). Additional occurrences in China are the late Miocene faunas of Huitenghe (Bahean) and Bilutu (Baodean) (Qiu & Li 2016). The specimens from the latter two localities are slightly larger and have stronger crests than the type specimens, presumably more advanced features (Qiu & Li 2016: p. 615).

The specimens from Builstyn Khudag (Mongolia) are within the morphological and metric variation of the type material from Balunhalagen in Nei Mongol (China).

<div align="center">

Superfamily Dipodoidea Fischer, 1817

Family Zapodidae Coues, 1875

Genus *Lophocricetus* Schlosser, 1924

Lophocricetus xianensis Qiu, Zheng & Zhang, 2008
(Fig. 11 A–F, Tab. 4)

</div>

1982   *Protalactaga* cf. *tunggurensis* – Zheng: textfig. 4A and 4B.
1996   *Lophocricetus gansus* – Qiu: 190.
1999   *Lophocricetus* cf. *gansus* – Höck *et al.*: 120, fig. 27/12.
2001   *Heterosminthus gansus* – Daxner-Höck: 371–373, tabs 12–13, pl. 7, figs 1–15.
2016   *Lophocricetus xianensis* – Qiu & Li: 591.

T y p e   l o c a l i t y : Lantian, Shaanxi Province, China

S t r a t u m   t y p i c u m : Bahe Formation, early late Miocene, Bahean LMS/A

S t r a t i g r a p h i c   r a n g e : early late Miocene

P u b l i s h e d   m a t e r i a l from sample/layer BUK-A/12+14: (280 specimens)

13 maxilla fragments with teeth (NHMW 2001/0039/0001, …/0002, …/0008, …/0021 to …/0026, …/0061 to …/0065), 10 fragmentary mandibles with teeth (NHMW 2001/0039/0006, …/0007, …/0015, …/0121 to …/0124, …/0161, …/0163, …/0191) and 257 isolated teeth (NHMW 2001/0039/0003 to …/0005, …/0011, …/0009 to …/0014, …/0016, …/0017 to …/0020, …/0027 to …/0060, …/0066 to …/0120, …/0125 to …/0127, …/0129 to …/0131, …/0133 to …/0160, …/0162, …/0164 to …/0190, …/0192 to …/0264, …/0266 to …/0280); Daxner-Höck (2001: fig. 1/1–15).

S p e c i m e n s figured in the present paper: Left maxilla fragment with M1–M2 (NHMW 2001/0039/0023, Fig. 11 A–B), left M3 (NHMW 2001/0039/0116, Fig. 11 C), left m1 (NHMW 2001/0039/0158, Fig. 11 D), left m2 (NHMW 2001/0039/0214, Fig. 11 E), left m3 (NHMW 2001/0039/0232, Fig. 11 F)

So far u n p u b l i s h e d m a t e r i a l from sample/layer BUK-A/12+14 (60 specimens): 3 maxilla fragments, 1 fragmentary mandible, 56 isolated teeth (NHMW 2001/0039/0281 to …/0340). The latter fossils were not yet available for the description by DAXNER-HÖCK (2001).

D e s c r i p t i o n a n d m a i n c h a r a c t e r i s t i c s: Medium sized zapodid with low crowned buno-lophodont molars. Molar sizes decrease from anterior to posterior (M1 to M3/ m1 to m3). The buccal and lingual cusps are obliquely aligned. The cusps of upper molars tilt backwards, those of lower molars forwards.

M1 (Fig. 11 A) has seven distinct cusps, *i. e.*, the four main cones (paracone, metacone, protocone, and hypocone) and the mesocone, protostyle, and posterocone (the latter almost replacing the posteroloph). The entoloph is short and connects to the protoloph, the posterocone connects to the metaloph. Mesoloph of M1 is usually short. M2 (Fig. 11 B) has a long mesoloph, mesocone, and protostyle are small. The anteroloph is single or double. The elongated hypocone connects to the transverse metaloph and posteriorly it is continuous with the posteroloph. M3 (Fig. 11 C) is small, triangular-rounded in shape, with two lingual cusps and four buccal lophs. m1–m2 have moderately developed cingulids and weak ectostylids, no mesolophid. m1 (Fig. 11 D) with a pronounced ectomesolophid and mesoconid. The hypoconid connects to the mesoconid and/or posterolophid or posteroconid, respectively. The hypolophid is transverse and connects to the mesoconid. m2 (Fig. 11 E) has four strongly alternating main cusps, the lingual ones are anterior to the buccal ones. Protoconid is usually without a posterior arm. The labial anterolophid is crescentic and contacts the buccal base of the protoconid. m3 (Fig. 11 F) is small, and has a simplified pattern of m2. M1–2 have four, M3 three roots. Lower molars have two roots, except for m2, occasionally with three roots, two

Tab. 4. Measurements of *Lophocricetus xianensis* QIU, ZHENG & ZHANG, 2008 from BUK-A/12+14 (DAXNER-HÖCK 2001: tab. 12).

L. xianensis	length (mm)			width (mm)	
	range	mean	n	range	mean
P4	0.45–0.73	0.57	17	0.45–0.68	0.59
M1	1.48–1.95	1.71	67	1.00–1.25	1.13
M2	1.20–1.59	1.35	34	0.86–1.14	1.00
M3	0.68–0.80	0.72	11	0.66–0.77	0.73
m1	1.20–1.68	1.44	75	0.86–1.14	0.98
m2	1.23–1.52	1.34	65	0.86–1.36	1.04
m3	0.80–0.93	0.89	15	0.68–0.77	0.72

anterior and one posterior. Detailed descriptions of maxilla-, mandible- and molar morphology, and figures are given in DAXNER-HÖCK (2001: pp. 371–373, pl. 7, figs 1–15).

R e m a r k s : New additional fossil material from BUK-A/12+14 and increasing information about related taxa allow a revision of the Zapodidae originally assigned as *Heterosminthus gansus* ZHENG, 1982 by DAXNER-HÖCK (2001).

The dental characters are transitional between the genera *Heterosminthus* SCHAUB, 1930 and *Lophocricetus* SCHLOSSER, 1924. In 2001 the fossil evidence of *H. gansus* and two other species of similar dental morphology was very poor. *H. gansus* was known by a left mandible with m1–2, and a left m2, *Protalactaga* cf. *tunggurensis* was known by a left fragmentary maxilla with P4–M1 and a left M1, and *Heterosminthus simplicidens* was known by a left m2, a right m1 and a left M3 (all three species described from the type locality Tianzhu, Loc.80007, Gansu by ZHENG 1982). The latter two taxa were synonymized with *H. gansus* by QIU (1985). Finally, *H. gansus* was transferred to the genus *Lophocricetus* by QIU (1996: p. 190). Other than that, ZAZHIGIN & LOPATIN (2000a: p. 322) and DAXNER-HÖCK (2001: p. 373) emphasized significant differences from the type species *Lophocricetus grabaui* SCHLOSSER,1924 and suggested *H. gansus* would be the most advanced species of *Heterosminthus*.

The type species *Lophocricetus grabaui* SCHLOSSER, 1924 is a progressive form in the *Lophocricetus* lineage. It is characterized by larger size, distinctly developed protostyles but no mesoloph on M1 and M2, and by connection of the entoloph to the paracone and the posteroloph to the metacone on M1.

The species *Lophocricetus xianensis* QIU *et al.*, 2008 from Lantian (Shaanxi Province, China) is less derived than *L. grabaui*. It possesses a suite of transitional characters. It retains some typical features of *Heterosminthus*, *e. g.*, the presence of mesoloph on M1 and M2, the entoloph extending to protoloph on some M1, the occasional presence of double anteroloph on M2, the connection between hypoconid and mesoconid, and remnants of "pseudomesolophid" and posterior crest of protoconid on some m1s, the presence of posterior arm of protoconid and even the connection between the posterior arm of protoconid and the mesoconid on some m2s. However, it also has significant features of the type species *L. grabaui*, *e. g.*, the distinct protostyle or posterolingual rib of protocone on M1 and M2, the entoloph extending to paracone on some M1s, the developed ectostylids and cingulids on m1 and m2, the strong ectomesolophid, and the connection between hypoconid and entoconid on some m1s, and the absent posterior arm of protoconid in the majority of m2s (QIU & LI 2016: pp. 590–591). *L. xianensis* is a distinctive species of the late Miocene. It was described by QIU & LI (2016) from Balunhalagen, Huitenghe, Shala, Baogeda Ula, and Bilutu (Nei Mongol, China), with Balunhalagen being oldest (early Bahean) and Bilutu youngest (late Baodean).

In accordance with QIU & LI (2016: p. 591) we consider, that the Mongolian specimens from Builstyn Khudag best agree with *Lophocricetus xianensis*, both in size and molar morphology, and, therefore, the Mongolian specimens, previously described as *H. gansus* by DAXNER-HÖCK (2001), are to be transferred to *L. xianensis*. Moreover, concerning
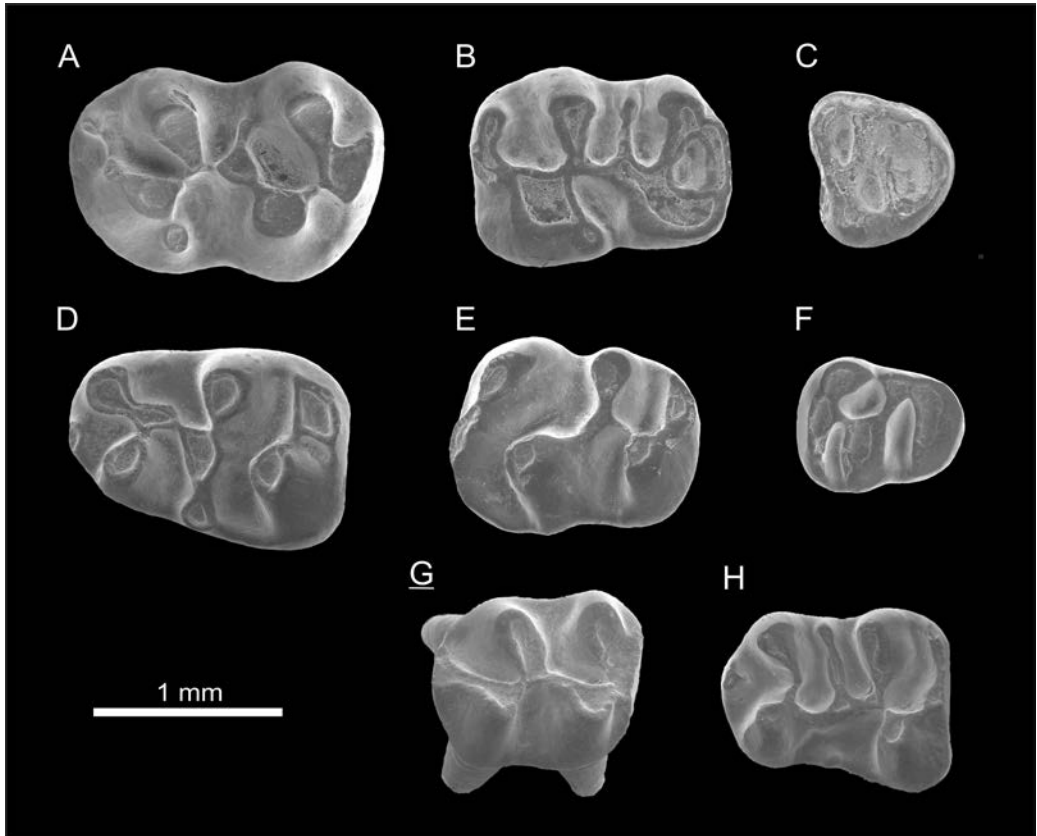
Fig. 11. Zapodidae from the Builstyn Khudag locality (assemblage BUK-A/12+14), Taatsiin Tsagaan Nuur area, Valley of Lakes, Mongolia, Loh Fm., late Miocene, letter zone E, Bahean LMS/A. *Lophocricetus xianensis* QIU, ZHENG & ZHANG, 2008: **A**: M1 left (NHMW 2001/0039/0023), **B**: M2 left (NHMW 2001/0039/0023), **C**: M3 left (NHMW 2001/0039/0116), **D**: m1 left (NHMW 2001/0039/0158), **E**: m2 left (NHMW 2001/0039/0214), **F**: m3 left (NHMW 2001/0039/0232). Zapodidae gen. et sp. indet.: **G**: M1 right (NHMW 2016/0125/0001). *Eozapus intermedius* (BACHMAYER & WILSON, 1970): **H**: m1 left (NHMW 2020/0043/0001).

tooth sizes and molar morphology they better correlate with the older occurrences (early Bahean) than with younger occurrences (late Baodean) from Nei Mongol (China).

The species *gansus* from Tianzhu (Gansu, China), however, has fewer *Lophocricetus* characters and differs from *L. xianensis* in its missing protostyle of M1−M2, weak posterostyle of M1, shorter M1/m1, double anterolophid of m2, and missing ectostylids at m1−2. Its generic assignment is still questionable (QIU & LI 2016: p. 589). Other transitional species from Kazakhstan, Russia, and Ukraine (*H. saraicus*, *L. minuscilus*, *L. vinogradovi*, *L. saraicus*, *L. complicidens* and *L. reliquus*) and their generic assignment were discussed by ZAZHIGIN et al. (2002), ZAZHIGIN & LOPATIN (2002), and by QIU & LI (2016).

Occurrences of *Lophocricetus xianensis* were described from the type locality Lantian (Shaanxi Province, China; late Bahean,), Shengou (Qinghai), the localities Balunhal-agen, Huitenghe, Shala, Baogeda Ula, and Bilutu (Nei Mongol, China) and Builstyn Khudag (Valley of Lakes, Mongolia). The species range is: early late Miocene (lower Bahean LMS/A MN9) to late late Miocene (lower Baodean LMS/A).

Zapodidae gen. et sp. indet.
(Fig. 11 G)

L o c a l i t y : Builstyn Khudag locality (assemblage BUK-A/12+14), Taatsiin Tsagaan Nuur area, Valley of Lakes, Mongolia, Loh Fm., late Miocene, letter zone E.

M a t e r i a l from sample/layer BUK-A/12+14 and measurements (length × width) (2 specimens): 1 right M1 (NHMW 2016/0125/0001; Fig. 11 G), 1.07 × 0.86 mm; 1 fragmentary M2 l (NHMW 2016/0125/0002), ?? × 0.88 mm.

D e s c r i p t i o n : The two teeth (M1 and M2) are small, low crowned, of buno-lophodont shape, of rectangular outline, lingual and buccal cones in alternating position (the lingual cones anterior to the buccal ones) and have four roots.

M1 (Fig. 11 G) has four main cusps, the buccal paracone and metacone, and the lingual protocone and hypocone. There is no mesoloph. Protoloph and metaloph are very short and directed backwards. Protoloph connects with the entoloph posterior to protocone, and metaloph connects with the posteroloph posterior to hypocone. A pronounced anterior arm of protocone is continuous with the anteroloph and the indistinct anterocone. The entoloph is short and aligned along of the longitudinal axis of the tooth. The posteroloph has lingual and buccal branches. Between lingual posteroloph and hypocone there is a posterior sulcus.

M2 is corroded and fragmentary. It also has four main cusps, no mesoloph, short and backwards directed protoloph and metaloph. There is a pronounced protocone in lingual position. It is continuous with the lingual anteroloph. The anterior part of the tooth is wider than the posterior one. The strongly damaged posterior part preserves a strong hypocone. Metacone and posteroloph are damaged.

R e m a r k s : These two teeth cannot to be correlated with any of the known genera and species of Zapodidae so far.

Eozapus intermedius (Bachmayer & Wilson, 1970)
(Fig. 11 H)

L o c a l i t y : Builstyn Khudag locality (assemblage BUK-A/12+14), Taatsiin Tsagaan Nuur area, Valley of Lakes, Mongolia, Loh Fm., late Miocene, Mongolian letter zone E

M a t e r i a l from sample/layer BUK-A/12+14 and measurements (length × width) (1 specimen): 1 left m1 (NHMW 2020/0043/0001; Fig. 11 H), 1.21 × 0.88 mm

T y p e l o c a l i t y : Kohfidisch, Austria

Stratum typicum: Gbely Formation, late Miocene, upper Pannonian, MN 11

Stratigraphic range: late Miocene, Bahean LMS/A, MN9–MN11

Description: The m1 is small, low-crowned and of buno-lophodont shape, of rectangular outline, with two roots. In its posterior part it is wider than anterior. It has four main cusps, the drop shaped lingual metaconid and entoconid and the buccal more rounded protoconid and hypoconid. Additionally, there are small conulids at the margin of the crown, the anteroconid, ectoconulid, posteroconid (= hypoconulid in Daxner-Höck *et al.* 2014: fig. 3), and the mesoconid at the mesolophid-ectolophid connection. The five lophids are: a long mesolophid, the V-shaped metalophid, short hypolophid, long posterolophid, and the longitudinal-obliquely aligned ectolophid. The ectolophid-hypoconid connection of this specimen is constricted (Fig. 11 H).

Remarks: This unspecialised pattern of m1 commonly occurs in the Oligocene and Miocene zapodid genera *Heosminthus*, *Bohlinosminthus*, *Plesiosminthus*, and *Eozapus*. Of these four genera only *Eozapus* is known to range to modern times, the others being extinct much earlier. The oldest occurrences of *E. intermedius* are Richardhof-Golfplatz and Götzendorf in Austria (Daxner-Höck & Höck 2015: p. 62, plates 67–68). The species ranges from MN9 to MN11 all over Europe, and was also evidenced in Russia (Saray 1, Olkhon Island, Baikal Region; Daxner-Höck *et al.* 2013b: pp. 511–512, pl. 22.1, fig. 20a–20b). The range of *E. intermedius* corresponds with the early late Miocene (Bahean LMS/A in Asia). *E. intermedius* and the younger Chinese species *E. similis* Fahlbusch, 1992 (known from the late latest Miocene, Baodean LMS/A faunas of Ertemte and Harr Obo in China) and *E. setchuanus* (still living in China) show size increase from the stratigraphically older to youngest occurrences. Morphological differences are of minor importance. The fourth species *E. major* Qiu & Li, 2016 from Balunhalagen in Nei Mongol (Bahean LMS/A) differs from all former discussed species by a distinct lophodont molar pattern (Qiu & Li 2016: fig. 98).

The m1 of *Sinozapus parvus* Qiu & Li, 2016 from Amuwusu (Qiu & Li 2016: fig. 99 F and 100) differs from *E. intermedius* by smaller size and a strong longitudinal crest connecting metalophid and mesolophid.

Family Dipodidae Fischer, 1817

Genus *Paralactaga* Young, 1927

***Paralactaga parvidens* Qiu & Li, 2016**
(Fig. 12 A–H, 13 A–F, Tab. 5)

1999   *Paralactaga* sp. – Höck *et al.*: 120, fig. 27/14.
2013a   *Protalactaga* sp. – Daxner-Höck *et al.*: 488, tab. 20.4.

Type locality: Shala, Sonid Youqi (IM 9610)

Stratum typicum: Baogeda Ula Formation, late Miocene, Bahean LMA/S, MN10

S t r a t i g r a p h i c   r a n g e : late Miocene, Bahean to Baodean (LMS/A Chinese mammal ages)

O t h e r   o c c u r r e n c e s : Baogeda Ula and Bilutu, Inner Mongolia (China), Builstyn Khudag, Valley of Lakes (Mongolia)

M a t e r i a l from sample/layer BUK-A/12+14 (31 specimens + 9 fragments): 1 right maxilla fragment with P4–M3 (NHMW 2016/0126/0001), 1 right maxilla fragment with M1 (NHMW 2016/0126/0027), 1 right mandibular fragment with m1 (NHMW 2016/0126/0021), 4 P4 (NHMW 2016/0126/0005, …/0007, …/0031, …/0032), 1 left M1 (NHMW 2016/0126/0008), 3 right M1 (NHMW 2016/0126/0004, …/0006, …/0029), 1 left M2 (NHMW 2016/0126/0009), 1 right M2 (NHMW 2016/0126/0003), 3 left M3 (NHMW 2016/0126/0002, …/0010, …/0026), 4 left m1 (NHMW 2016/0126/0011, …/0022 to …/0024), 5 right m1 (NHMW 2016/0126/0015, …/0016, …/0018 to …/0020), 4 left m2 (NHMW 2016/0126/0012, …/0013, …/0025, …/0030), 1 left m3 (NHMW 2016/0126/0014), 1 right m3 (NHMW 2016/0126/0017), 9 tooth fragments (NHMW 2016/0126/0028, …/0033 to …/0040).

D e s c r i p t i o n : Compared with other Alactaginae, the teeth of the Mongolian species are of small size and have rather low crowns. Young, unworn upper and lower M1–2/m1–2s show four pronounced cones(ids) which are higher than the loph(id)s. Consequently, young teeth have a buno-lophodont pattern. The lophodont character is visible in a later stage of wear. The crown of upper molars is lingually higher than buccally ("lingual mesodonty"). Lower molars are lingually almost as high as buccally. P4 has one root, M1–2 have four, M3 three, and the lower molars m1–3 have 2 roots.

Tab. 5. Measurements of *Paralactaga parvidens* Qiu & Li, 2016 from BUK-A/12+14.

P. parvidens	length (mm)			width (mm)	
	range	mean	n	range	mean
P4	0.76–0.95	0.87	3	0.81–0.86	0.83
M1	2.19–2.50	2.35	5	1.74–1.79	1.77
M2	2.02–2.26	2.14	3	1.67–1.74	1.69
M3	1.12–1.45	1.27	4	1.26–1.50	1.38
m1	2.31–2.67	2.47	10	1.57–1.98	1.73
m2	2.38–2.50	2.42	3	1.69–1.90	1.82
m3	1.79–1.90	–	2	1.38–1.43	–

Fig. 12. *Paralactaga parvidens* Qiu & Li, 2016 from the Builstyn Khudag locality (assemblage BUK-A/12+14), Taatsiin Tsagaan Nuur area, Valley of Lakes, Mongolia, Loh Fm., late Miocene, letter zone E, Bahean LMS/A. **A**: Maxilla with P4–M3 right (NHMW 2016/0126/0001), **B**: M1 left (NHMW 2016/0128/0008), **C**: M2 left (NHMW 2016/0126/0009), **D**: M3 left (NHMW 2016/0126/0010), **E**: M1 right (NHMW 2016/0126/0004), **F**: M1 right, anterior view (NHMW 2016/0126/0006), **G**: P4 right (NHMW 2016/0126/0005), **H**: M3 left (NHMW 2016/0126/0002).
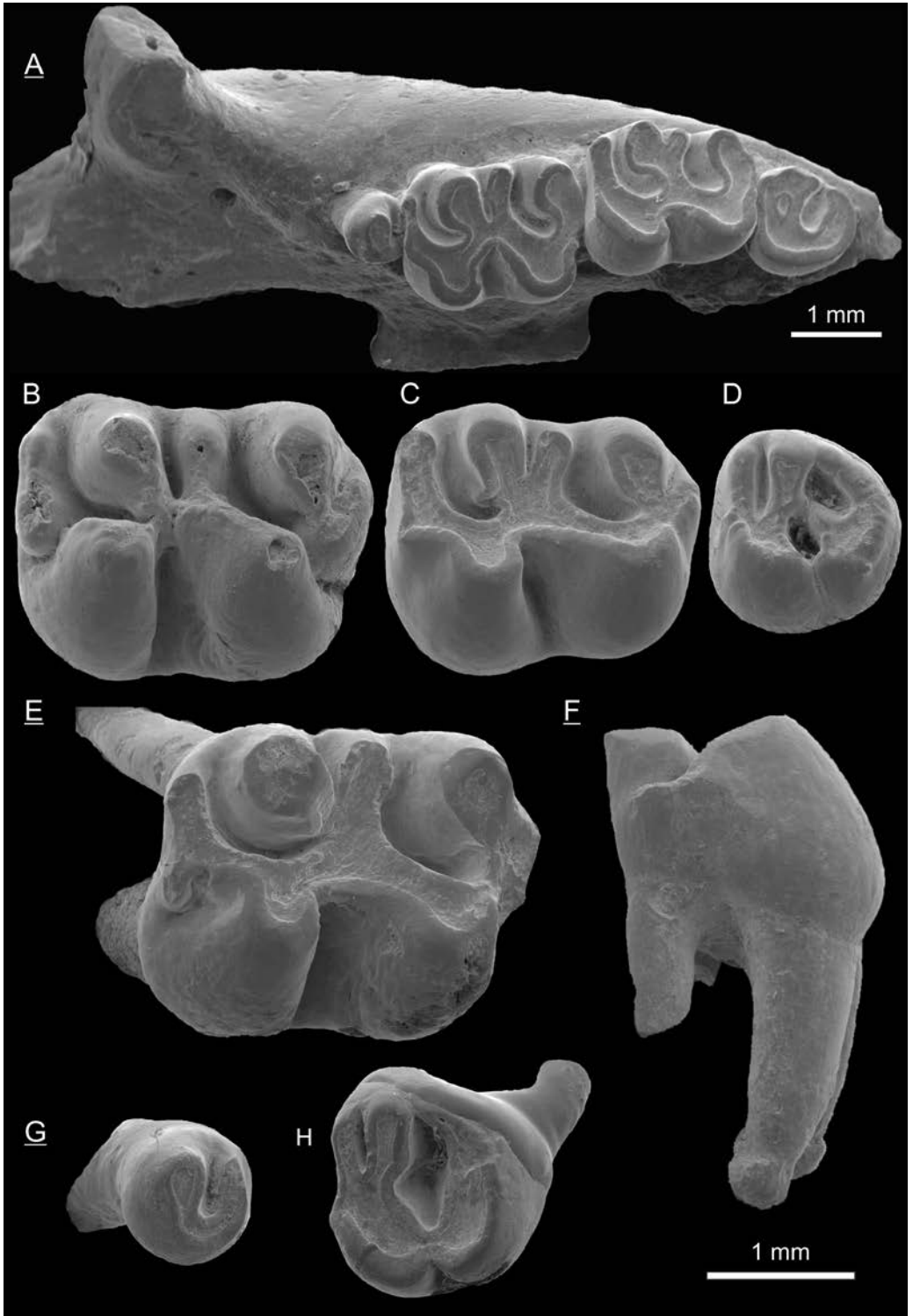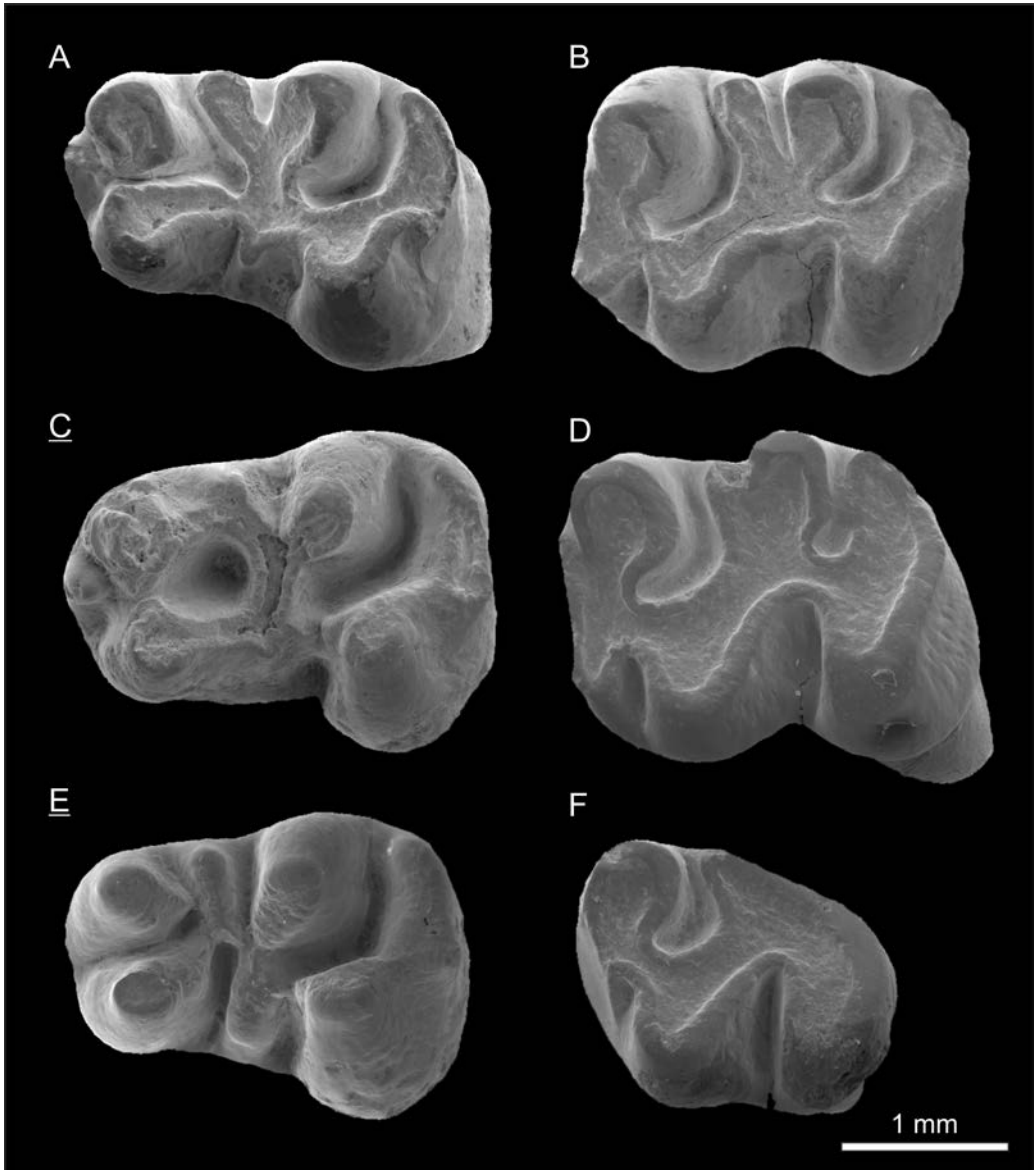
Fig. 13. *Paralactaga parvidens* Qiu & Li, 2016 from the Builstyn Khudag locality (assemblage BUK-A/12+14), Taatsiin Tsagaan Nuur area, Valley of Lakes, Mongolia, Loh Fm., late Miocene, letter zone E, Bahean LMS/A. **A**: m1 left (NHMW 2016/0126/0011), **B**: m2 left (NHMW 2016/0126/0012), **C**: m1 right (NHMW 2016/0126/0015), **D**: m2 left (NHMW 2016/0126/0013), **E**: m1 right (NHMW 2016/0126/0016), **F**: m3 left (NHMW 2016/0126/0014).

P4 consists of paracone and a crescent-shaped cingulum. The cingulum extends lingually from the paracone, then turns posteriorly and buccally (Fig. 12 G).

M1 (Fig. 12 A, B, E, F) has four pronounced cones (paracone, metacone, protocone, and hypocone) that alternate, *i. e.*, the buccal ones are positioned posterior to the lingual ones. The anteroloph is pronounced, and a small anterocone is developed in two of five M1 (Fig. 12 B). The mesoloph is always present and strong. Protoloph and metaloph are short, backwards directed and fused with mesoloph and posteroloph, respectively (Fig. 12 E). In two of five specimens protoloph and metaloph are connected to entoloph (Fig. 12 A, B). There is one lingual valley, the sinus, which is opposite to the mesoloph. The sinus is wide and deep, and almost reaches the base of the crown. The main labial valleys anterosinus and posterior mesosinus turn backwards and are shallower than the sinus (Fig. 12 A, B). The anterior mesosinus and the posterosinus (the latter is sometimes absent) are very small and shallow. The entoloph is short and without a mesocone. The M1 is buccally low, lingually it is convex and higher ("lingual mesodonty").

M2 is comparable with M1 in general shape, however, it is slightly smaller, specifically in its posterior part, and there is no distinct anterocone at the anteroloph. There is always a protoloph-mesoloph connection and a metaloph-posteroloph connection (Fig. 12 A, C).

M3 (Fig. 12 A, D, H) is rounded, has three buccal lophs and two wide cones (protocone and hypocone). The buccal lophs are: 1. anteroloph, 2. fused paracone + protoloph + mesoloph, which is connected to the protocone, and 3. fused posteroloph + metaloph + metacone continuous with hypocone. In one specimen there is a longitudinal connection between lophs 2. and 3. (Fig. 12 D).

m1 (Fig. 13 A, C, E) shows various features specifically in its anterior and middle part. The m1 narrows anteriorly and is widest in the posterior part. It has four main conids, the metaconid and protoconid in opposite position, and the entoconid and hypoconid in alternating position. A small anteroconid is present in two of eight specimens only (Fig. 13 A, C). The metaconid is either isolated (Fig. 13 A) or has a weak posterior contact with the mesolophid (Fig. 13 E). The entoconid is fused with the short forwards-directed hypolophid (Fig. 13 A, C). The protoconid is elongated along the longitudinal axis and fused with the ectolophid (Fig. 13 A, C). The hypoconid has a weak anterior contact with the ectolophid (Fig. 13 E), posteriorly it is continuous with the strong posterolophid. Posterolophid and mesolophid are present in all m1–2. The long mesolophid is always connected with the short forwards-directed hypolophid, building a Y-shaped structure (Fig. 13 A, C), which is characteristic of the genus *Paralactaga*. The ectolophid normally extends in longitudinal direction. In its middle part, where the ectolophid attaches right-angled to the mesolophid (in 6 of 8 specimens) some specimens have a small mesoconid, others a short ectomesolophid (Fig. 13 A). A few (2 of 8 specimens) have a distinct ectomesolophid running to the buccal margin of the tooth, in which case the ectolophid is S shaped not straight (Fig. 13 E).

m2 (Fig. 13 B and D) have four main conids, the lingual ones anterior to the labial ones. Mesolophid and posterolophid are the distinct lophids. Metalophid and hypolophid are very short, forwards-directed and fused with anterolophid and mesolophid, respectively. The lingual branch of anterolophid is very weak, the labial one is stronger. The sinusid is

deep, wide and directed backwards. The protosinusid is narrow and shallow. The anterior mesosinusid and posterosinusid turn forwards and are narrow. The anterior mesosinusid extends across the median line of m2. The posterior mesosinusid is narrow and shallow.

m3 (Fig. 13 F) displays three distinct conids (metaconid, protoconid, and hypoconid). Mesolophid + entoconid + hypolophid and posterolophid are fused. Anterior mesosinusid and sinusid are distinct valleys, the protosinusid is weak.

R e m a r k s : The Mongolian specimens from Builstyn Khudag (BUK-A/12+14) are of small size, and the dental features are intermediate between archaic and progressive Allactaginae. *Protalactaga* Young, 1927, predominantly occurring in the middle Miocene, represents the archaic molar type, and *Allactaga*, predominantly occurring from the Pliocene to modern times, has progressive dental features. The archaic characters are: generally small size and low crowned molars, cusp(id)s more pronounced than crests, the paracone of M1–2 joins the anterior entoloph or mesocone, ectomesolophid of m1 is pronounced, and ectolophid, mesolophid, hypolophid, and ectomesolophid of m1–2 converge at the mesoconid. The progressive dental characters are: substantially larger and higher tooth crowns, lophodont molar pattern, reduced ectomesolophid of m1, and some additional features which are characteristic of *Paralactaga* and also occur in some *Allactaga* species. The main characteristics of *Paralactaga* are: rather low crowned buno-lophodont to lophodont teeth, the protoloph joining the mesoloph and the metaloph joining the posteroloph of M1–2, and the Y shaped mesolophid and hypolophid+entoconid connection of m1–2 (Qiu & Li 2016).

Contrary to Qiu & Li (2016), *Paralactaga* was considered a synonym of *Allactaga* by Zazhigin & Lopatin (2000b: p. 560). The latter authors argue that "*Paralactaga* tooth morphotypes" would also exist among extant species of *Allactaga*. We follow the opinion of Qiu & Li (2016) that *Paralactaga* is transitional between *Protalactaga* and *Allactaga*, and shares some features with both genera. Based on the characteristics described above we consider it an independent genus. The stratigraphic range of *Paralactaga* is late Miocene to early Pliocene. *Allactaga* is younger, predominantly Pliocene to Recent.

The small sized Mongolian specimens are to be identified as *Paralactaga parvidens* on the basis of size and molar morphology. Comparison with tooth sizes of different *Paralactaga* species show, that the Mongolian material is within the size-range of *P. parvidens* from Nei Mongol (China). The molar morphology is in best agreement with *P. parvidens* from the localities Shala, Bilutu, and Baogeda Ula of the late Miocene of Nei Mongol in China (Qiu & Li 2016: p. 597, fig. 134). Other species (*P. suni*, *P. anderssoni*, *P. shalaensis*, and *P.? minor*) have distinctly larger and higher crowns (Qiu & Li 2016: fig. 132). *Proalactaga varians* Savinov, 1970 (= *Alactaga varians*; after Zhazigin & Lopatin 2000b: p. 560) from Pavlodar in Kazakhstan is also larger and differs by: a straight transverse protoloph of M1, and by the m1 metaconid isolated from the mesolophid and protoconid. *Allactaga irgizensis* Zazhigin & Lopatin, 2000b from the late Miocene of Shet-Irgiz in Kazakhstan (only 3 teeth described) is similar with *P. parvidens* in size, however, the morphology of M1 differs substantially from all Mongolian M1. For comparison see Zazhigin & Lopatin (2000b: p. 560, fig. 3).

Family Gerbillidae ALSTON, 1876

Subfamily Myocricetodontinae LAVOCAT, 1961

Genus *Myocricetodon* LAVOCAT, 1952

Myocricetodon cf. plebius QIU, 2001b
(Fig. 14 <u>A</u>−C, Tab. 6)

2013a   *Democricetodon* sp. 3 − DAXNER-HÖCK *et al.*: 488, tab. 20.4.
2013a   *Myocricetodon* sp. − DAXNER-HÖCK *et al.*: 488, tab. 20.4.

T y p e   l o c a l i t y : Quantougou, Central Lanzhou Basin, Gansu, China.

S t r a t u m   t y p i c u m : Upper Xianshuihe Formation, middle Miocene, middle Tunggurian.

M a t e r i a l from sample/layer BUK-A/12+14 (13 specimens): 1 left upper jaw fragment with worn M1 and M2 right (NHMW 2013/0441/0005) and 12 isolated molars: m1 right (NHMW 2013/0441/0002); m1 right (NHMW 2013/0441/0008) (Fig. 14 <u>A</u>); m1 right (NHMW 2013/0441/0009); m1 right (NHMW 2013/0441/0014); m1 left (NHMW 2013/0441/0006); m1 left (NHMW 2013/0441/0007); m2 right (NHMW 2013/0441/0003); m2 left (NHMW 2013/0441/0010); m2 left (NHMW 2013/0441/0013) (Fig. 14 <u>B</u>); m3 left (NHMW 2013/0441/0004) (Fig. 14 C); m3 left (NHMW 2013/0441/0011); m3 left (NHMW 2013/0441/0012).

D e s c r i p t i o n : The right upper jaw fragment has completely worn M1 and M2, only the lowermost enamel outline of the cusps is preserved. The M1 has five roots, the M2 four. The anterior root of the M1 is posterior to the zygomatic plate. The posterior point of the incisive foramen and the anterior point of palatal foramen are recognizable and the anterior enamel ridge of the M1 is in line with the posterior point of the incisive foramen and the anterior side of the M2 is in line with the anterior point of the palatal foramen. The pattern of the outline of the upper molars is in accordance with upper molars of *Myocricetodon plebius*.

Tab. 6. Measurements of *Myocricetodon* cf. *plebius* QIU, 2001 from BUK-A/12+14.

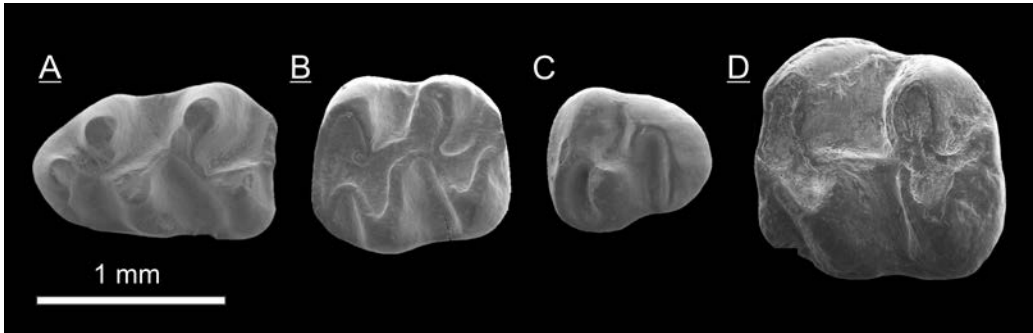| M. cf. plebius	length (mm)			width (mm)	
	range	mean	n	range	mean
M1		1.41	1		0.87
M2		0.96	1		0.84
M3			–		
m1	1.11–1.38	1.25	5	0.78–0.83	0.80
m2	0.95–1.11	1.03	3/2	0.86–0.89	0.88
m3	0.78–0.91	0.86	3	0.63–0.79	0.70

Fig. 14. Gerbillidae from the Builstyn Khudag locality (assemblage BUK-A/12+14), Taatsiin Tsagaan Nuur area, Valley of Lakes, Mongolia, Loh Fm., late Miocene, letter zone E, Bahean LMS/A. *Myocricetodon* cf. *plebius* QIU, 2001b: **A**: m1 right (NHMW 2013/0441/0008), **B**: m2 right (NHMW 2013/0441/0003), **C**: m3 left (NHMW 2013/0441/0004) and cf. *Abudhabia baheensis* QIU, ZHENG & ZHANG, 2014: **D**: m2 right (NHMW 2016/0129/0001).

The m1 has a slightly wider posterior part than the middle part. The undivided anteroconid is close to the metaconid and in all but one connected to it by a short anterior metalophulid. The anteroconid and protoconid are connected by a short, low anterolophulid in two specimens. The protoconid and metaconid are strongly connected by a short high posterior metalophulid in three specimens, weak in the other two. A lingual anterolophid is absent in all but one, in the latter a narrow lingual antero-sinusid is present. The labial anterolophid is short. The oblique longitudinal crest connects protoconid and entoconid. A very short hypolophulid connects hypoconid and entoconid. The prominent posterolophid, with a small hypoconulid, is transverse and open on its lingual edge. A very short labial branch of the posterolophid is visible in two specimens. Very small accessory cusps can be present on the edges of the labial and lingual sinusid.

The m2 is rectangular. A lingual anterolophid is absent, the metaconid is large. The labial anterolophid is not connected to the base of the protoconid. A very short anterolophulid connects anterolophid to protoconid. Protoconid and entoconid are connected by a strong oblique longitudinal ridge. A very short hypolophulid connects hypoconid and entoconid. The prominent posterolophid, with a small hypoconulid, is transverse (damaged in one).

The m3 has a rounded triangular outline. The protoconid is the most prominent cusp. The labial anterolophid is prominent in two specimens, a lingual anterolophid is absent. The protoconid is connected to the entoconid by an oblique ridge in all specimens. On the lingual edge, the metaconid and entoconid are connected by a prominent ridge which continues to the posterolabial edge of the molar, although in one not continuously. The hypoconid is incorporated into this ridge. The labial sinusid is wide and open on the labial edge of the molar.

R e m a r k s : Only three molars are allocated to *Myocricetodon plebius* by QIU (2001b). This species is not known from other faunal assemblages; thus, its size range is unknown. The BUK molars are smaller, but they have a comparable morphology. All

other *Myocricetodon* species from China are larger. *Myocricetodon plebius* is from the Quantougou Fauna, central Lanzhou Basin China, 11.7 Ma or 12.8 Ma after ZHANG *et al.* (2020).

Genus *Abudhabia* DE BRUIJN & WHYBROW, 1994

cf. *Abudhabia baheensis* QIU, ZHENG & ZHANG, 2004
(Fig. 14 <u>D</u>)

2013a   Gerbillinae indet. – DAXNER-HÖCK *et al.*: 488, tab. 20.4.

Type locality: Loc. 12, Lantian Country, Shaanxi Province, China

Stratum typicum: Bahe Formation, early late Miocene, Bahean

Other occurrences: Amuwusu (Nei Mongol); Lantan (Loc. 6, Loc. 13, Loc. 19), early late Miocene, Bahean

Material from sample/layer BUK-A/12+14 (1 specimen): 1 right m/2 (NHMW 2016/0129/0001) (Fig. 14 <u>D</u>)

Measurements (length × width): 1.32 × 1.17 mm

Description: The m2 is rectangular. The cusps have very broad bases and the sinusids are narrow. The labial anterolophid is almost cusp-like, it continues along the labial edge as a thin ridge ending at the posterolabial base of the protoconid. The protoconid and metaconid are strongly connected, as are hypoconid and entoconid. A narrow short ridge connects protoconid to hypoconid. The posterolophid is short and semi-circular.

Remarks: Morphology and size resemble *Abudhabia baheensis* as described by QIU *et al.* (2004b). However, a single m2 is not enough for a reliable species assignment.

Discussion

Biostratigraphy and Correlation

The Builstyn Khudag section does not provide any magnetostratigraphic data nor any radiometric ages, however, the small mammal species of fauna BUK-A/12+14 are relevant to biostratigraphic correlations (Fig. 15). For these correlations we selected the middle Miocene fauna Ulan Tolgoi in Mongolia and two series of intensively studied and stratified mammal faunas from Nei Mongol (Inner Mongolia) and from Lantian (Shanxi Province) in China. The first Chinese sequence comprises eleven faunas of Nei Mongol ranging from the middle to the late Miocene, with Tairum Nur being oldest (early Tunggurian LMS/A) and Ertemte and Harr Obo (late Baodean) youngest. The second comprises seven Lantian faunas (classical localities 6, 12, 13, 19, 30, 38; MS 4) of the late Miocene Bahean LMS/A (Fig. 15). Magnetostratigraphic data of these
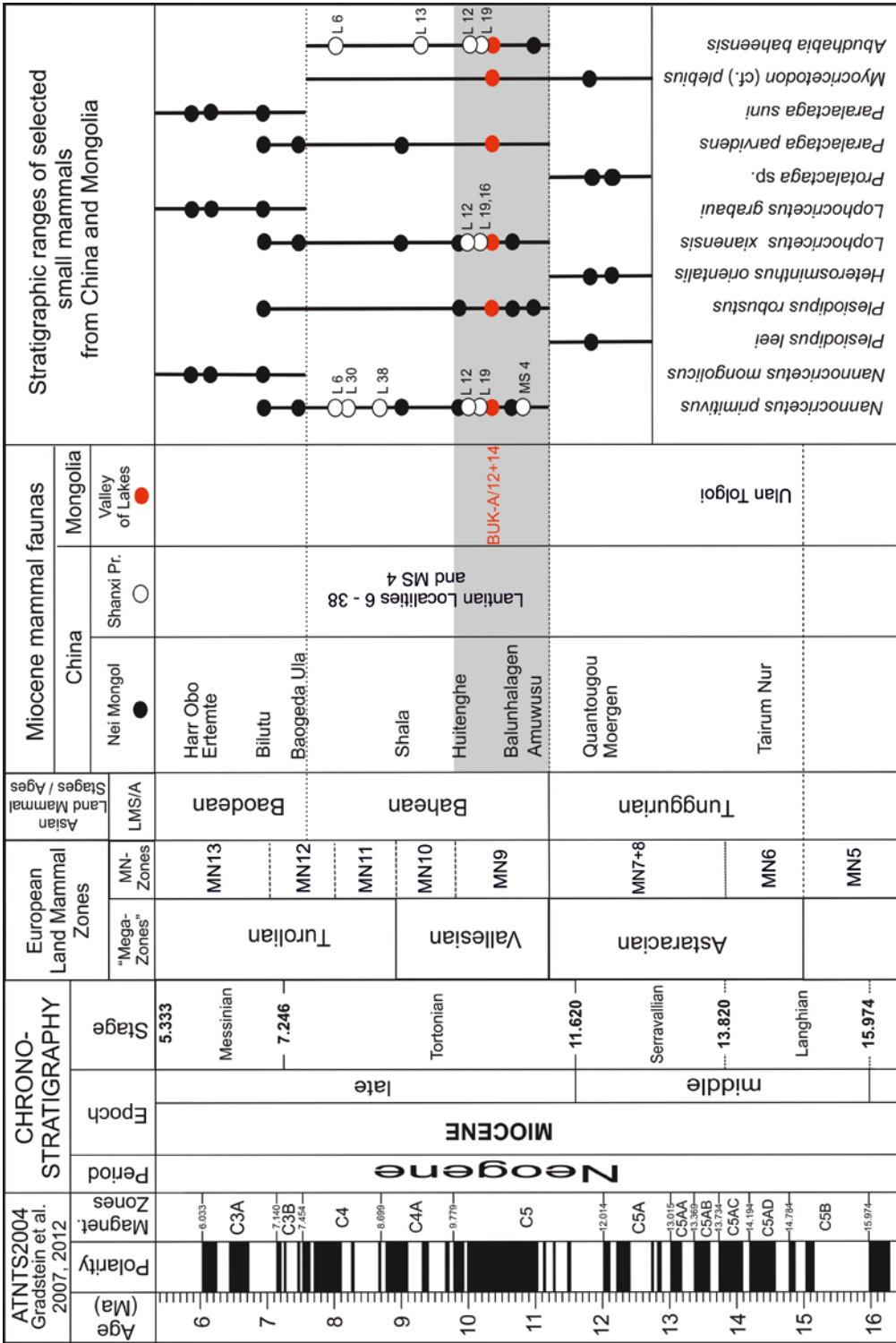
Lantian faunas indicate ages ranging from 10.8 to 8.3 Ma (KAAKINEN 2005; QIU *et al.* 2004a, 2004b, 2008; ZHANG *et al.* 2008; QIU & LI 2016; ZHANG *et al.* 2013, 2020).

Middle Miocene/Tunggurian faunas, *e. g.*, Tairum Nur, Moergen, Quantougou (QIU & LI 2016), and Ulan Tolgoi (DAXNER-HÖCK *et al.* 2013a; MENNECART *et al.* 2019) differ substantially from the late Miocene Bahean and Baodean faunas of Mongolia and China. It is evident that several middle Miocene families/genera lost their dominating role or became extinct before the middle/late Miocene transition (Distylomyidae, Tachyoryctoidinae, *Heterosminthus*, *Protalactaga*, *Gobicricetodon*, *Cricetodon*, *Democricetodon*, *Megacricetodon*, and *Alloptox*). Others survived (*Paracricetulus schaubi*, *Myocricetodon plebius*), and some developed more progressive species (*e. g.*, *Plesiodipus robustus* of the late Miocene).

Early late Miocene/Bahean faunas, such as Amuwusu, Huitenghe, Shala, Lantian (China) display both, some middle Miocene (*Plesiodipus*, *Myocricetodon*, *Paracricetulus*) and new appearing genera and species: *e. g.*, *Tamias*, *Pliopetaurista*, *Nannocricetus*, *Lophocricetus*, *Eozapus*, *Dipus*, *Paralactaga*, *Abudhabia*, *Ochotona*, and the first immigrating Murinae *Progonomy*s. The newcomers predominate in the Bahean.

In the late late Miocene/Baodean (*e. g.*, in Ertemte, Harr Obo, Bilutu, and faunas of the Yushe Basin) some Bahean genera develop progressive species, *e. g.*, *Nannocricetus mongolicus*, *Lophocricetus grabaui*, *Paralactaga suni* (Fig. 15). However, the main difference from Bahean are the significant diversifications of several groups with new genera, *e. g.*, Murinae (*Hansdebruijnia*, *Karnimatoides*, *Apodemus*, *Orientalomys*, *Micromys*), Gerbillidae (*Pseudomeriones*), Arvicolidae (*Mimomys*, *Borsodia*), Cricetidae (*Microtoscoptes*, *Microtodon*), Dipodidae (*Dipus*, *Brachyscirtes*), and the appearances of Leporidae (*Alilepus*, *Trischizolagus*) (QIU & LI 2016; FLYNN & WU 2017).

The composition of fauna BUK-A/12+14 from Mongolia (Tab. 7) is in good biostratigraphic agreement with the Bahean, specifically with lower Bahean Chinese faunas (Balunhalagen, Huitenghe, and Lantian Loc. 12, 19) (Fig. 15). It was the time of first immigrations of the murid *Progonomys* into northern China: *Progonomys sinensis* QIU, ZHENG & ZHANG, 2004 from Lantian at *ca.* 10 Ma, and *Progonomys shalaensis* QIU & LI, 2016 from Shala at *ca.* 9 Ma. The *Progonomys* immigration is an excellent time marker also in Europe, where *Progonomys hispanicus* had its first occurrences in Spain at 10.2 Ma.

Progonomys was not found in the BUK fauna. This lack may indicate a greater age than Shala and Lantian Loc. 12, or the immigration of *Progonomys* northward into the Valley of Lakes happened later than in Nei Mongol and Shanxi Province, or *Progonomys* did not reach Builstyn Khudag at all. At present we correlate the Mongolian fauna BUK-A/12+14 with the Asian early Bahean LMS/A and with the European early Vallesian Mammal Zone MN9.

◄ Fig. 15. Correlation chart including the geologic time scale (GRADSTEIN *et al.* 2007, 2012; HILGEN *et al.* 2012), the European Land Mammal Zones (STEININGER 1999), the Asian Land Mammal Stages/Ages (QIU *et al.* 2013), selected Miocene mammal faunas of China and Mongolia, and stratigraphic ranges of selected small mammals from China and Mongolia.

Palaeoenvironment

The composition of the vertebrate assemblage BUK-A/12+14 (Table 7), lithologies and sediment structures of the section allow considerations on palaeoenvironments of the Builstyn Khudag region during the basal late Miocene.

The section BUK-A displays a sequence of *ca.* 40 meters clastic sediments, mainly sandy silt, which are interbedded by two sandstone layers in the lower and middle part.

Tab. 7. Fossil assemblage BUK-A/12+14, locality Builstyn Khudag, Valley of Lakes, Mongolia, late Miocene, letter zone E.

Fossil taxa from sample BUK-A/12+14 (Fig. 3 F)	collection numbers	section/layer	specimens n = 897	Fig.
cf. *Ophiomorus* sp.	NHMW 2019/0138/0001–0003	BUK-A/12+14	3	4 A–D
Squamata indet.	NHMW 2019/0139/0001	BUK-A/12+14	1	4 E
Eremiadini indet.	NHMW 2016/0208/0019	BUK-A/12+14	19	
Eryx sp. 1	NHMW 2007/0059/0001–0002	BUK-A/12+14	2	
Eryx sp. 2	NHMW 2007/0059/0001	BUK-A/12+14	1	
Colubrinae 1	NHMW 2007/0056/0001	BUK-A/12+14	1	
Colubrinae 2	NHMW 2007/0057/0001–0002	BUK-A/12+14	2	
"Natricinae" indet.	NHMW 2007/0060/0001	BUK-A/12+14	1	
Ochotona lagreli	NHMW 2001/0029/0001–0058	BUK-A/12+14	58	
Ochotona minor	NHMW 2001/0030/0001–0051	BUK-A/12+14	51	
Parvericius buk	NHMW 2005/0215/0001–0194	BUK-A/12+14	194	5 A–I
Builstynia fontana	NHMW 2006/0054/0001–0067	BUK-A/12+14	67	6 A–G
Tamias ertemtensis	NHMW 2013/0405/0001–0003	BUK-A/12+14	3	
Atlantoxerus sp.	NHMW 2013/0411/0001–0007	BUK-A/12+14	7	7 A–D
Ombomys builstynensis	NHMW 2013/0076/0001–0029	BUK-A/12+14	29	8 A–D
Nannocricetus primitivus	NHMW 2013/0442/0001–0056	BUK-A/12+14	56	9 A–D
Paracricetulus schaubi	NHMW 2013/0441/0001, …/0016	BUK-A/12+14	2	9 E
Plesiodipus robustus	NHMW 2018/0128/0001–0003	BUK-A/12+14	3	10 A–C
Lophocricetus xianensis	NHMW 2001/0039/0001–0340	BUK-A/12+14	340	11 A–F
Zapodidae gen. et sp. indet.	NHMW 2016/0125/0001–0002	BUK-A/12+14	2	11 G
Eozapus intermedius	NHMW 2020/0043/0001	BUK-A/12+14	1	11 H
Paralactaga parvidens	NHMW 2016/0126/0001–0040	BUK-A/12+14	40	12 A–H 13 A–F
Myocricetodon cf. *plebius*	NHMW 2013/0441/0002–0016	BUK-A/12+14	13	14 A–C
cf. *Abudhabia baheensis*	NHMW 2016/0129/0001	BUK-A/12+14	1	14 D

Surface collection	collection numbers	locality/ surface	specimens n = 14	3G
cf. *Iranotherium* sp.	NHMW 2000/0160/0001–0010	BUK*	10	3 G
Gomphotheriidae indet.	NHMW 2005/0054/0001–0004	BUK*	4	3 G

Upsection, fine silty clay alternates with fossil beds and paleosol horizons. The sandstone layers consist of cross-bedded sand and gravel components, indicating high energy transport by flowing water. The upper fine clastic beds containing fossil layers hint at low energy sedimentation and dry periods. All in all, the sediment sequence evidences a fluvial system of channel fills, floodplain deposits, and palaeosol horizons.

The vertebrate assemblage BUK-A/12+14 (Fig. 3, Table 7) is composed of 24 taxa including 8 Reptilia, 2 Lagomorpha, 2 Lipotyphla, and 12 Rodentia, represented by 897 identified fossils. The two sandstone layers yielded fragmentary bones of large mammals, moreover, teeth and bones of Rhinocerotidae and Gomphotheriidae were collected from surfaces lateral to the section (Fig. 3; BUK*).

Among sqamates, both lizards (cf. *Ophiomorus* sp., Squamata indet., Eremiadini indet.) and snakes (*Eryx* sp. 1, *E.* sp. 2; Colubrinae 1, Colubrinae 2, and "Natricinae" indet.) are present, but the fossil number of three lizards and five snakes is very low (totally 30 specimens). The record of small mammals is much better: *i. e.*, 867 fossils indicating 16 species of 9 families.

Two taxa dominate by very high specimen numbers, *i. e.*, the zapodid *Lophocricetus xianensis* (340 fossils), followed by the hedgehog *Parvericius buk* (194 fossils). A second group ranges from 13 to 67 specimens, *i. e.*, the shrew *Builstynia fontana*, the pikas *Ochotona lagreli* and *Ochotona minor*, the eomyid *Ombomys builstynensis*, the cricetid *Nannocricetus primitivus*, the dipodid *Paralactaga parvidens*, and the gerbillid *Myocricetodon* cf. *plebius*. Given the large sample size from several tons of sediment, even very rare species could be found (by one to three teeth only), *i. e.*, the squirrels *Tamias* and *Heteroxerus*, the cricetids *Paracricetulus schaubi* and *Plesiodipus robustus*, the zapodids *Eozapus intermedius* and Zapodidae gen. et sp. indet., and the gerbillid cf. *Abudhabia baheensis*. (Table 7, Fig. 14).

The faunal composition of sample BUK-A/12+14 clearly shows the dominance of jumping mice (Zapodidae) and hedgehogs (*Parvericius*) providing 39 % and 22 %, respectively, among all small mammal fossils.

With reference to living relatives a ground dwelling life is assumed for the majority of represented reptile- and mammal groups. Jumping mice and birch mice inhabit riparian woodlands, or wet grassy areas, others live in open areas as well as in thickets. Today, pikas (*Ochotona*) and ground squirrels are semi-fossorial, digging burrows in soil. The ground squirrels (*Tamias* and *Heteroxerus*), gerbils (*Myocricetodon* and *Abudhabia*), and hamsters (*Nannocricetus* and *Paracricetulus*) suggest a similar lifestyle. Also, lizards (*Ophiomorus* and Eremiadini) and snakes (Erycinae and Colubrinae) shelter under stones or in burrows. On the contrary, specialists adapted to forested environments or open water are not represented in the presently studied fauna.

R e s u l t : The floodplain environments with dense vegetation, meadows and bushes provided suitable habitats for proboscideans, rhinos, jumping and birch mice. More dry open areas were inhabited by lizards, snakes and the majority of ground dwelling small mammal species.

Conclusions

Builstyn Khudag is located at the northern margin of the Valley of Lakes, where sediments of the Mesozoic and Cenozoic basin fill are exposed along a NW−SE striking fault system. Here, from north towards south Cretaceous, Eocene, Oligocene, and Miocene sediments crop out.

The present study focuses on the Miocene sequence of this region, specifically of section BUK-A. In the course of two field seasons *ca.* 5,000 kg sediment samples were collected. The result of wet screening was > 1,000 fossils of the main fossil locality BUK-A/12+14, of which *ca.* 900 fossils are described herein. This collection comprises exclusively fossil remains of smaller vertebrates: three lizards, five snakes and sixteen small mammal species. The small mammal fossils are distributed among sixteen species of nine families: Ochotonidae, Erinaceidae, Soricidae, Sciuridae, Eomyidae, Cricetidae, Zapodidae, Dipodidae, and Gerbillidae. Moreover, scattered bones and teeth of Rhinocertotidae and Gomphotheriidae were collected from surfaces close to the basis of the section (Tab. 7).

The composition of fauna BUK-A/12+14 shows that > 50 % fossils derive from two species, the zapodid *Lophocricetus xianensis* (350 specimens) and the hedgehog *Parvericius buk* (194 specimens). By contrast, lizards, snakes, shrews, pikas, and all ground dwelling rodents are not so well represented, with some being very rare.

Lithologies and sediment structures along the section indicate channel and floodplain deposits. The floodplain environments with dense vegetation, meadows and bushes assume suitable habitats for proboscideans, rhinos, jumping mice, and hedgehogs. However, lizards, snakes, and the majority of ground dwelling mammal species indicate drier habitats.

The composition of fauna BUK-A/12+14 is in good biostratigraphic agreement with the Chinese mammal faunas Balunhalagen, Huitenghe, Shala, and Lantian Loc. 12, 13, 19 of the early Bahean LMS/A (European Mammal Zones MN9−10). These faunas display some middle Miocene (Tunggurian) genera, *e. g.*, *Plesiodipus*, *Myocricetodon*, *Paracricetulus*, and new appearing taxa of the early late Miocene (Bahean), *e. g.*, *Tamias*, *Nannocricetus*, *Lophocricetus*, *Eozapus*, *Paralactaga*, *Abudhabia*, and *Ochotona*. The immigration event of the murid *Progonomys* was evidenced in China, *i. e.*, in Lantian (Loc. 12 at *ca.* 10 Ma) and Shala (at *ca.* 9 Ma), but not in Mongolia (Valley of Lakes). Unexpectedly, no Murinae tooth was found among 900 fossils from Builstyn Khudag. However, considering several possible explanations for the lack of *Progonomys* we correlate the Mongolian fauna with the lower part of the early Bahean LMS/A and with the European Mammal Zone MN9 of the early Vallesian.

Acknowledgements

References

ALSTON, E.R. (1876): On the classification of the Order Glires. – Proceedings of the Zoological Society of London, **44**/1: 61–98.

ANDERSON, S.C. & LEVITON, A.E. (1966): A review of the genus *Ophiomorus* (Sauria: Scincidae), with descriptions of three new forms. – Proceedings of the California Academy of Sciences, **33**: 499–534.

ARNOLD, E.N., ARRIBAS, O. & CARRANZA, S. (2007): Systematics of the palaearctic and oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. – Zootaxa, **1430**: 1–86.

BACHMAYER, F. & WILSON, R.W. (1970): Die Fauna der altpliozänen Höhlen- und Spaltenfüllungen bei Kohfidisch, Burgenland (Österreich). – Annalen des Naturhistorischen Museums in Wien, Serie A, **74**: 533–587.

BERKEY, C.P. & MORRIS, F.K. (1927): Geology of Mongolia: a reconnaissance report based on the investigations of the years 1922–1923. (Natural History of Central Asia, 2). – 475 pp., New York (The American Museum of Natural History).

BÖHME, M. (2007): 3. Herpetofauna (Anura, Squamata) and palaeoclimatic implications: Preliminary results. – In: DAXNER-HÖCK, G. (ed.): Oligocene-Miocene Vertebrates from the Valley of Lakes (Central Mongolia): Morphology, phylogenetic and stratigraphic implications. – Annalen des Naturhistorischen Museums in Wien, Serie A, **108**: 43–52.

BOHLIN, B. (1942): The fossil mammals from the Tertiary deposits of Taben-Buluk, Western Kansu. Part. 1. Insectivora and Lagomorpha. – Palaeontologica Sinica, New Series C, **8**: 1–113.

BONAPARTE, C.L. (1831): Saggio di una distribuzione metodica degli animali vertebrati. – 144 pp., Rome (Antonio Boulzaler).

BOWDICH, T.E. (1821): An Analysis of the Natural Classification of Mammalia for the use of Students and Travellers. – 115 pp., Paris (Smith).

BRANDT, J.F. (1855): Untersuchung über die craniologischen Entwicklungsstufen und die davon herzuleitenden Verwandtschaften und Classificationen der Nager der Jetztwelt – In: BRANDT, J.F. (ed.): Beiträge zur näheren Kenntnis der Säugethiere Russlands. (Mémoires mathématiques, physiques et naturelles, Tome 7, 1855) – pp. 125–365, St. Petersburg (Mémoires de l'Académie Impériale des Sciences).

CAMAITI, M., VILLA, A., WENCKER, L.C.M., BAUER, A.M., STANLEY, E.L. & DELFINO, M. (2019): Descriptive osteology and patterns of limb loss of the European limbless skink *Ophiomorus punctatissimus* (Squamata, Scincidae). – Journal of Anatomy, **235**: 313–345.

ČERŇANSKÝ, A. & AUGÉ, M.L. (2019): The Oligocene and Miocene fossil lizards (Reptilia, Squamata) of Central Mongolia. – Geodiversitas, **41**/24: 811–839.

ČERŇANSKÝ, A. & SYROMYATNIKOVA, E.V. (2021): The first pre-Quarternary fossil record of the clade Mabuyidae; with a comment on the enclosure of the Meckelian canal in skinks. – Papers in Palaeontology **7**/1: 195–215. https://doi.org/10.1002/spp2.1279

ČERŇANSKÝ, A., SYROMYATNIKOVA, E.V., KOVALENKO, E.S., PODURETS, K.M. & KALOYAN, A.A. (2020): The key to understanding the European Miocene *Chalcides* (Squamata, Scincidae) comes from Asia: the lizards of the East Siberian Tagay locality (Baikal Lake) in Russia. – The Anatomical Record, **303**/7: 1901–1934. https://doi.org/10.1002/ar.24289

COUES, E. (1875): Some Account, critical, descriptive, and historical, of *Zapus hudsonius*. – Bulletin of the United States Geological and Geographical Survey of the Territories, **5**: 253–262.

DAXNER-HÖCK, G. (1999): 31. Family Zapodidae. – In: RÖSSNER, G.E. & HEISSIG, K. (eds): The Miocene Land mammals of Europe. – pp. 337–342, München (Verlag Dr. Friedrich Pfeil).

DAXNER-HÖCK, G. (2001): New zapodids (Rodentia) from Oligocene-Miocene deposits in Mongolia. Part 1. – Senckenbergiana lethaea*, **81**/2: 359–389.

DAXNER-HÖCK, G. & BADAMGARAV, D. (2007): 1. Geological and stratigraphical setting. – In: DAXNER-HÖCK, G. (ed.): Oligocene-Miocene Vertebrates from the Valley of Lakes (Central Mongolia): Morphology, phylogenetic and stratigraphic implications. – Annalen des Naturhistorischen Museums in Wien, Serie A, **108**: 1–24.

DAXNER-HÖCK, G. & HÖCK, E. (2015): Catalogus Fossilium Austriae. Band 4. Rodentia neogenica. – xxvi+158 pp., Wien (Verlag der Österreichischen Akademie der Wissenschaften).

DAXNER-HÖCK, D., BADAMGARAV, D., ERBAJEVA, M.A. & GÖHLICH, U.B. (2013a): Miocene Mammal Biostratigraphy of Central Mongolia (Valley of Lakes): new results. – In: WANG, X.-M., FLYNN, L.J. & FORTELIUS, M. (eds): Fossil Mammals of Asia. – pp. 477–494, New York (Columbia University Press).

DAXNER-HÖCK, D., BÖHME, M. & KOSSLER, A. (2013b): 22. New Data on Miocene Biostratigraphy and Paleoclimatology of Olkhon Island (Lake Baikal, Siberia). – In: WANG, X.-M., FLYNN, L.J. & FORTELIUS, M. (eds.): Fossil Mammals of Asia. – pp. 508–517, New York (Columbia University Press).

DAXNER-HÖCK, G., BADAMGARAV, D. & MARIDET, O. (2014). Dipodidae (Rodentia, Mammalia) from the Oligocene and Early Miocene of Mongolia. – Annalen des Naturhistorischen Museums in Wien, Serie A, **116**: 131–214.

DE BRUIJN, H. & WHYBROW, P. (1994): A Late Miocene rodent fauna from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. – Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B, **97**/4: 407–422.

DUMÉRIL, A.M.C. & BIBRON, G. (1839): Erpétologie Générale on Histoire Naturelle Complète des Reptiles. Vol. 5. – 871 pp., Paris (Roret/Fain et Thunot).

ERBAJEVA, M.A. (2003): Late Miocene ochotonids (Mammalia, Lagomorpha) from Central Mongolia. – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **2003**/4: 212–222.

ESTES, R. (1983): Encyclopedia of paleoherpetology. (Part 10 A, Sauria terrestria, Amphisbaenia). – 248 pp., New York (Gustav Fischer Verlag).

ESTES, R., DE QUEIROZ, K. & GAUTHIER, J.A. (1988): Phylogenetic relationships within squamata. – In: ESTES, R. & PREGILL, G.K. (eds): Phylogenetic relationships of the lizard families. – pp. 119–281, Stanford (Stanford University Press).

Evans, S.E. (2008): The skull of Lizards and Tuatara. – In: Gans, C., Gaunt, A.S. & Adler, K. (eds): Biology of the Reptilia, Vol. 20 (The skull of Lepidosauria). (Contributions to Herpetology, 23). – pp. 1–347, Ithaca, NY (Society for the Study of Amphibians and Reptiles).

Fahlbusch, V. (1992): Neogene mammalian faunas of Ertemte and Harr Obo in Inner Mongolia (Nei Mongol), China. – Senckenbergiana lethaea, **72**: 199–217.

Fischer, G. (1814): Zoognosia tabulis synopticis illustrata. – xiv+465 pp., Moscow (Nicolai Sergei dis Vesevolozky).

Fischer, G. (1817): Adversaria Zoologica. – Mémoires de la Societé Impériale des Naturalistes Moscow, **5**: 357–472.

Flynn, L.J. & Wu, W.-Y. (2017): Chapter 16. Dynamic Small Mammal Assemblages of Yushe Basin. – In: Flynn, L.J. & Wu, W.-Y. (eds): Late Cenozoic Yushe Basin, Shanxi province, China: Geology and Fossil Mammals, Volume II: Small Mammal Fossils of Yushe Basin. (Vertebrate Paleobiology and Paleoanthropology). – pp. 205–215, Dordrecht (Springer). https://doi.org/10.1007/978-94-024-1050-1_16

Forsyth Major, C.I. (1893): On some Miocene squirrels, with remarks on the dentition and classification of the Sciurinae. – Proceedings of the Zoological Society of London, **1893**: 179–215.

Gauthier, J., Kearney, M., Maisano, J.A., Rieppel, O. & Behlke, A. (2012): Assembling the squamate tree of life: Perspectives from the phenotype and the fossil record. – Bulletin of the Peabody Museum of Natural History, **53**: 3–308.

Göhlich, U.B. (2007): 9. Gomphotheres (Proboscidea, Mammalia) from the Early-Miocene of Central Mongolia. – In: Daxner-Höck, G. (ed.): Oligocene-Miocene Vertebrates from the Valley of Lakes (Central Mongolia): Morphology, phylogenetic and stratigraphic implications. – Annalen des Naturhistorischen Museums in Wien, Serie A, **108**: 271–289.

Gradstein, F.M., Ogg, J.G. & Smith, A.G. (2007): A Geologic Time Scale 2007. – 160 pp., Cambridge (Cambridge University Press).

Gradstein, F.M., Ogg, J.G., Schmitz, M.D. & Ogg, G.M. (2012): The geologic time scale 2012. – 1144 pp., Oxford (Elsevier).

Gray, J. E. (1825): A synopsis of the genera of reptiles and Amphibia, with a description of some new species. – Annals of Philosophy, London, **10**: 193–217.

Greer, A.E. (1970): A subfamilial classification of scincid lizards. – Bulletin of the Museum of Comparative Zoolology at Harvard University, **139**: 151–184.

Greer, A.E. (1974): The generic relationships of the scincid lizard genus *Leiolopisma* and its relatives. – Australian Journal of Zoology, **31**: 1–67.

Greer, A.E. & Wilson, G.D.F. (2001): Comments on the scincid lizard genus *Ophiomorus*, with a cladistic analysis of the species. – Hamadryad, **26**: 261–271.

Gregory, W.K. (1910): The orders of mammals. – Bulletin of the American Museum of Natural History, **27**: 1–524.

Harzhauser, M., Daxner-Höck, G., López-Guerrero, P., Maridet, O., Piller, W.E., Richoz, S., Erbajeva, M.A. & Göhlich, U.B. (2016): The stepwise onset of the Icehouse world and its impact on Oligo-Miocene Central Asian mammals. – Nature Scientific Reports, **6**, 36169. https://doi.org/10.1038/srep36169

Hedges, S.B. (2014): The high-level classification of skinks (Reptilia, Squamata, Scincomorpha). – Zootaxa, **3765**: 317–338.

HEISSIG, K. (2007): 8. Rhinocerotidae (Perissodactyla, Mammalia). – In: DAXNER-HÖCK, G. (ed.): Oligocene-Miocene Vertebrates from the Valley of Lakes (Central Mongolia): Morphology, phylogenetic and stratigraphic implications. – Annalen des Naturhistorischen Museums in Wien, Serie A, **108**: 233–269.

HILGEN, F.J., LOURENS, L.J. & VAN DAM, J.A. (2012): The Neogene period. – In: GRADSTEIN, F.M., OGG, J.G., SCHMITZ, M.D. & OGG, G.M. (eds): The geologic time scale 2012. – pp. 923–978, Amsterdam (Elsevier).

HÖCK, V., DAXNER-HÖCK, G., SCHMID, H.P., BADAMGARAV, D., FRANK, W., FURTMÜLLER, G., MONTAG, O., BARSBOLD, R., KHAND, Y. & SODOV, J. (1999): Oligocene-Miocene sediments, fossils and basalts from the Valley of Lakes (Central Mongolia) – an integrated study. – Mitteilungen der Österreichischen Geologischen Gesellschaft, **90** (1997): 83–125.

HUTCHINSON, M.N. & SCANLON, J.D. (2009): New and unusual Plio-Pleistocene Lizards (Reptilia: Scincidae) from Wellington Caves, New South Wales, Australia. – Journal of Herpetology, **43**: 139–147.

ILLIGER, C. (1811): Prodromus systematis mammalium et avium terminis zoographicis utrisque classis. – 301 pp, Berlin (C. Salfeld).

KAAKINEN, A. (2005): A long terrestrial sequence in Lantian – a window into the late Neogene palaeoenvironment of northern China. – Unpublished PhD Thesis, 49 pp., Helsinki (University Helsinki).

KAZEMI, S.M., QOMI, F.M, KAMI, H.G. & ANDRESON, S.C. (2011): A new species of *Ophiomorus* (Squamata: Scincidae) from Maranjab Desert, Isfahan Province, Iran, with a revised key to the genus. – Amphibian and Reptile Conservation, **5**: 23–33.

KOERNER, H.E. (1940): The geology and vertebrate palaeontology of the Fort Logan and Deep River formations of Montana. Part I: New vertebrates. – American Journal of Sciences, **238**/12: 837–862.

KORNILIOS, P., KUMLUTAŞ, Y., LYMBERAKIS, P. & ILGAZ, Ç. (2018): Cryptic diversity and molecular systematics of the Aegean *Ophiomorus* skinks (Reptilia: Squamata), with the description of a new species. – Journal of Zoological Systematics and Evolutionary Research, **56**: 364–381.

KOSMA, R. (2004): The Dentition of Recent and Fossil Scincomorphan Lizards (Lacertilia, Squamata) – Systematics, Functional Morphology, Palecology. – Unpublished PhD Thesis, 187 pp., Hannover (University of Hannover).

LAVOCAT, R. (1952): Sur une faune de mammifères Miocènes découverte à Beni-Mellal (Atlas Marocain). – Comptes Rendus de l'Académie des Sciences de Paris, **235**: 189–191.

LAVOCAT, R. (1961): Le gisement de vertébrés Miocènes de Beni-Mellal (Maroc). Etude systématique de la faune de mammifères et conclusions générales. – Notes et Mémoires du service Géologique du Maroc, **155**: 29–94, 52–67, 109–144.

LINK, H.F. (1795): Über die Lebenskrafte in naturhistorischer Rücksicht und die Classification der Säugthiere. – Beiträge zur Naturgeschichte, **1**/2: 1–126.

LINNAEUS, C. (1758): Systema naturae per regna tria naturae, secundum classis, ordines, genera, species, cum characteribus differentiis, synomis, locis, I. – 841 pp. Stockholm (Laurentii Salvii).

MARIDET, O., DAXNER-HÖCK, G., BADAMGARAV, D. & GÖHLICH, U.B. (2014a): Cricetidae (Rodentia, Mammalia) from the Valley of Lakes (Central Mongolia): focus on the Miocene record. – Annalen des Naturhistorischen Museums in Wien, Serie A, **116**: 247–269.

MARIDET, O., DAXNER-HÖCK, G., BADAMGARAV, D. & GÖHLICH, U.B. (2014b): New discoveries of Sciuridae (Rodentia, Mammalia) from the Valley of Lakes (Central Mongolia). – Annalen des Naturhistorischen Museums in Wien, Serie A, **116**: 271–291.

MARIDET, O., DAXNER-HÖCK, G., BADAMGARAV, D. & GÖHLICH, U.B. (2015): The eomyid rodents (Mammalia) from the Oligocene and Miocene of the Valley of Lakes (Central Mongolia). – Paläontologische Zeitschrift, **89**: 207–228.

MCDOWELL, S.B. & BOGERT, C.M. (1954): The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. – Bulletin of the American Museum of Natural History, **105**: 1–142.

MENNECART, B., AIGLSTORFER, M., GÖHLICH, U.B. & DAXNER-HÖCK, G. (2019): On the oldest Mongolian moschids (Mammalia, Ruminantia) and the early moschid evolution. – Palaeontologia Electronica, 22.2.53A: 1–17. https://doi.org/10.26879/959

OPPEL, M. (1811): Die Ordnungen, Familien und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. – 87 pp., München (Joseph Lindauer).

POULAKAKIS, N., PAKAKI, V., MYLONAS, M. & LYMBERAKIS, P. (2008): Molecular phylogeny of the Greek legless skink *Ophiomorus punctatissimus* (Squamata: Scincidae): the impact of the Mid-Aegean trench in its phylogeography. – Molecular Phylogenetics and Evolution, **47**: 396–402.

QIU, Z.-D. (1985): The Neogene mammalian faunas of Ertemte and Harr Obo in Inner Mongolia (Nei Mongol), China. – 3. Jumping mice – Rodentia: Lophocricetinae. – Senckenbergiana lethaea, **66**/1–2: 39–67.

QIU, Z.-D. (1987): The Neogene mammalian faunas of Ertemte and Harr Obo in Inner Mongolia (Nei Mongol), China. – 6. Hares and Paikas – Lagomorpha: Leporidae and Ochotonidae. – Senckenbergiana lethaea, **67**/5–6: 375–399.

QIU, Z.-D. (1991): The Neogene mammalian faunas of Ertemte and Harr Obo in Inner Mongolia, Nei Mongol (China). – 8. Sciuridae (Rodentia). – Senckenbergiana lethaea, **71**/3–4: 233–255.

QIU, Z.-D. (1996): The Middle Miocene micromammalian fauna from Tunggur, Nei Mongol. – 216 pp. Beijing (Science Press). [In Chinese with English summary]

QIU, Z.-D. (2001a): Cricetid rodents from the Middle Miocene Quantougou fauna of Lanzhou, Gansu. – Vertebrata PalAsiatica, **39**/3: 204–214. [In Chinese with English summary]

QIU, Z.-D. (2001b): Glirid and gerbillid rodents from the Middle Miocene Quantougou fauna of Lanzhou, Gansu. – Vertebrata PalAsiatica, **39**/4: 297–305. [In Chinese with English summary]

QIU, Z.-D. (2017): Chapter 7. Yushe Dipodoidea. – In: FLYNN, L.J & WU, W.-Y. (eds): Late Cenozoic Yushe Basin, Shanxi province, China: Geology and Fossil Mammals, Volume II: Small Mammal Fossils of Yushe Basin. (Vertebrate Paleobiology and Paleoanthropology). – pp. 81–86, Dordrecht (Springer). https://doi.org/10.1007/978-94-024-1050-1_16.

QIU, Z.-D. & LI, Q. (2016): Neogene Rodents from Central Nei Mongol, China. – Palaeontologica Sinica, New Series C, **198**/30: 1–492. [in Chinese with English summary]

QIU, Z.-D., ZHENG, S.-H. & ZHANG, Z.-Q. (2004a): Murids from the Late Miocene Bahe Formation, Lantian, Shaanxi. – Vertebrata PalAsiatica, **42**/1: 67–76. [in Chinese with English summary]

QIU, Z.-D., ZHENG, S.-H. & ZHANG, Z.-Q. (2004b): Gerbillids from the Late Miocene Bahe Formation, Lantian, Shaanxi. – Vertebrata PalAsiatica, **42**/3: 193–204. [in Chinese with English summary]

Qiu, Z.-D., Zheng, S.-H. & Zhang, Z.-Q. (2008): Sciurids and Zapodids from the Late Miocene Bahe Formation, Lantian, Shaanxi. – Vertebrata PalAsiatica, **46**/2: 111–123. [in Chinese with English summary]

Qiu, Z.-X., Qiu, Z.-D., Deng, T., Li, C.-K., Zhang, Z.-Q., Wang, B.-Y. & Wang, X. (2013): Chapter 1. Neogene Land Mammal Stages/Ages of China. – In: Wang, X.-M., Flynn, L.J. & Fortelius, M. (eds): Fossil Mammals of Asia. – pp. 29–90, New York (Columbia University Press).

Rage, J.C. & Danilov, I.G. (2008): A new Miocene fauna of snakes from eastern Siberia, Russia. Was the snake fauna largely homogenous in Eurasia during the Miocene? – Comptes Rendus Palevol, **7**: 383–390.

Rieppel, O. (1981): The skull and jaw adductor musculature in some burrowing scincomorph lizards of the genera *Acontias*, *Typhlosaurus* and *Feylinia*. – Journal of Zoology, London, **195**: 493–528.

Savinov, P.F. (1970): The Dipodoidea (Rodentia, Mammalia) from the Neogene of Kazakhstan. – Materialy po evolyutsii nazemnyk pozvonochnykh (Material on the Evolution of Terrestrial Vertebrates). – pp. 91–134, Moskow (Nauka).

Schaub, S. (1930): Fossile Sicistinae. – Eclogae Geologicae Helvetiae, **23**/2: 616–637.

Schaub, S. (1934): Über einige fossile Simplicidentaten aus China und der Mongolei. – Abhandlungen der Schweizerischen Paläontologischen Gesellschaft, **54**: 1–40.

Schlosser, M. (1924): Tertiary vertebrates from Mongolia. – Palaeontologica Sinica, C, **1**/1: 1–119.

Shcherbak, N.N. (1975): Katalog Afrikanskich Jascurok (catalogue of African Eremias). – 84 pp., Kiev (N. N. Shcherbak).

Simpson, G.G. (1945): The principles of classification and a classification of mammals. – Bulletin of the American Museum of Natural History, **131**: 1–135.

Steininger, F.F. (1999): 1. The Continental European Miocene. Chronostratigraphy, Geochronology and Biochronology of the Miocene "European Land Mammal Mega-Zones" (ELMMZ) and the Miocene "Mammal-Zones (MN-Zones)". – In: Rössner, G.E. & Heissig, K. (eds): The Miocene Land Mammals of Europe. – pp. 9–24, München (Verlag Dr. Friedrich Pfeil).

Sun, J. & Windley, B.F. (2015): Onset of aridification by 34 Ma across the Eocene-Oligocene transition in Central Asia. – Geology, **11**: 1015–1018.

Thomas, O. (1897): On the genera of rodents: an attempt to bring up to date the current arrangement of the order. – Proceedings of the Zoological Society London, **1897**: 1012–1028.

Uetz, P. & Hošek, J. (2018): The Reptile Database. http://www.reptile-database.org. (Accessed May 2018).

Villa, A., Georgalis, G.L. & Delfino, M. (2020): The latest Early Pleistocene amphibians and reptiles from Kaiafas (Greece) and the first record of fossil Ophiomorus (Squamata, Scincidae). – Geobios, **62**: 79–90.

Wu, W.-Y. (1991): The Neogene mammalian faunas Ertemte and Harr Obo in Inner Mongolia (Nei Mongol), China). – 9. Hamster: Cricetinae (Rodentia). – Senckenbergiana lethaea, **71**/3–4: 257–305.

Wu, W.-Y., Meng, J., Ni, X., Bi, S-D. & Wei, Y-P. (2009): The Miocene mammals from Dingshanyanchi Formation of North Junggar basin, Xinjiang. – Vertebrata PalAsiatica, **47**/3: 208–233.

Young, C.C. (1927): Fossile Nagetiere aus Nord-China. – Paleontologica Sinica, C, **8**/3: 1–82.

Zazhigin, V.S. & Lopatin, A.V. (2000a): The History of the Dipodoidea (Rodentia, Mammalia) in the Miocene of Asia: 1. *Heterosminthus* (Lophocricetinae). – Paleontological Journal, **34**/3: 319–332.

Zazhigin, V.S. & Lopatin, A.V. (2000b): The History of the Dipodoidea (Rodentia, Mammalia) in the Miocene of Asia: 3. Allactaginae. – Paleontological Journal, **34**/5: 553–565.

Zazhigin, V.S. & Lopatin, A.V. (2002): The History of the Dipodoidea (Rodentia, Mammalia) in the Miocene of Asia: 6. Lophodont Lophocricetinae). – Paleontological Journal, **36**/2: 385–394.

Zazhigin, V.S., Lopatin, A.V. & Pokatilov, A.G. (2002): The History of the Dipodoidea (Rodentia, Mammalia) in the Miocene of Asia: 5. *Lophocricetus* (Lophocricetinae). – Paleontological Journal, **36**/2: 180–194.

Zhang, P., Ao, H., Roberts, A.P., Li, Y., Sun, Q., Zhang, J., Sun, P. & Qiang, X. (2020): Magnetochronology of Mid-Miocene mammalian fauna in the Lanzhou Basin, northeastern Tibetan Plateau: Implications for Asian mammal migration. – Geoscience Frontiers, **11**/4: 1337–1344. https://doi.org/10.1016/j.gsf.2020.01.006

Zhang, Z.-Q., Kaakinen, A., Liu, L.-P., Lunkka, J.P., Sen, S., Gose, W.A., Qiu, Z.-D., Zheng, S.-H. & Fortelius, M. (2013): Chapter 6 Mammalian Biochronology of the Late Miocene Bahe Formation. – In: Wang, X.-M., Flynn, L.J. & Fortelius, M. (eds): Fossil Mammals of Asia. – pp. 187–202, New York (Columbia University Press).

Zhang, Z.-Q., Zheng, S.-H. & Liu, L.-P. (2008): Late Miocene Cricetids from the Bahe Formation, Lantian, Shaanxi Province. – Vertebrata PalAsiatica, **46**/4: 307–316. [in Chinese with English summary].

Zheng, S.-H. (1982): Middle Pliocene Micromammals from the Tianzhu Loc.80007 (Gansu Province). – Vertebrata PalAsiatica, **20**/2: 138–147. [in Chinese with English summary]

Zheng, S.-H. & Li, Y. (1982): Some Pliocene lagomorpha and rodents from loc. 1 of Songshan, Tianzu Xiam, Gansu Province. – Vertebrata PalAsiatica, **20**/1: 35–44. [in Chinese with English summary]

Ziegler, R., Dahlmann, T. & Storch, G. (2007): 4. Marsupialia, Erinaceomorpha and Soricomorpha (Mammalia). – In: Daxner-Höck, G. (ed.): Oligocene-Miocene Vertebrates from the Valley of Lakes (Central Mongolia): Morphology, phylogenetic and stratigraphic implications. – Annalen des Naturhistorischen Museums in Wien, Serie A, **108**: 53–164.