New discoveries of Sciurids (Rodentia, Mammalia) from the Valley of Lakes (Central Mongolia)

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(With 7 figures and 2 tables)

Abstract

The present publication reports new discoveries of sciurid rodents from the Taatsiin Gol area (Valley of Lakes) in Mongolia. The fossil sciurids recovered in this area include only dental and fragmentary jaws remains. Specimens have been found from early Late Oligocene (local biozone C) to the Late Miocene (local biozone E). Although the material is scarce and often poorly preserved in the localities of the Valley of Lakes, six taxa belonging to five genera have been identified in the scope of the Austrian-Mongolian project: ?*Eutamias* sp*., Eutamias* cf. *ertemtensis*, *Plesiosciurus* aff. *sinensis*, *Kherem shandgoliensis,* ?*Atlantoxerus* sp. and Pteromyini indet. Among these taxa from the Valley of Lakes, Pteromyini indet. might be the only strictly forest-dweller taxon. Despite an extensive sampling, sciurid rodents seem to be totally missing from the Early Oligocene fossil record of the Valley of Lakes.

Key-words: Sciuridae, Rodentia, Oligocene, Miocene, Mongolia, Valley of Lakes, Systematics

Introduction

A joint Austrian-Mongolian project was carried out in the Taatsiin Gol area in Mongolia starting with three field seasons, from 1995 to 1997. At that time the primary objectives were to focus on geological mapping, concurrent age dating of the basalts, and sedimentologic, paleontologic and stratigraphic studies in Oligocene and Miocene sediments. This continental sequence allowed a precise stratigraphic adjustment based on the evolution of mammals and the age determination of basalts as elaborated by Daxner-Höck *et al.* (1997) and Höck *et al.* (1999). Between 2001 and 2012 several additional field investigations were conducted and more fossil specimens where sampled,

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especially thousands of specimens of Oligocene and Miocene mammals. A part of the mammalian fossil record has already been studied in detail such as Ruminantia (VISLO-BOKOVA & DAXNER-HÖCK 2002), Rhinocerotidae (HEISSIG 2007), Proboscidea (GÖHLICH 2007), Marsupiala, Erinaceomorpha and Soricomorpha (ZIEGLER *et al.* 2007), and part of Rodentia (*e.g.*, DAXNER-HÖCK 2000; DAXNER-HÖCK 2001; DAXNER-HÖCK & WU 2003; SCHMIDT-KITTLER *et al.* 2007). Moreover, preliminary results are available on Didymo-conidae, Creodonta and Carnivora (*e.g.*, MORLO & NAGEL 2006; MORLO & NAGEL 2007; NAGEL & MORLO 2003) and Lagomorpha (*e.g.*, ERBAJEVA 2007). In this publication we carry on the study of rodents by presenting a detailed description of the sciurid rodents from diverse layers of early Late Oligocene to Late Miocene age.

Material and methods

The material of sciurid recovered in the Taatsiin Gol area comes mostly from screen washings of individual layers identified in each locality. It comprises 36 specimens, and consists predominantly of isolated teeth and a few fragmentary jaws remains. They are deposited in the paleontological collection of the Natural History Museum in Vienna (NHMW), Austria, and are catalogued with the numbers: NHMW 2013/0397/0001 to 2013/0413/0001.

Observations and measurements were done with a binocular microscope Leica WILD M8 allowing precision to 0.01 mm. The terminology used to describe molars and the measurement method follow CUENCA BESCOS (1988). A clear distinction between the first and second molars was not always possible; both teeth are not separated and named as M1/2 and m1/2. For each measureable tooth the length and width are provided under the form: 'length'×'width'. All the measurements are given in millimetres.

Abbreviations

L o c a l i t i e s : BUK = Builstyn Khudag; HTE = Hotuliin Teeg; LOH = Loh; ODO = Olon Ovoony Khurem; TGW = Toglorhoi; UNCH = Unkheltseg; UTO = Ulaan Tolgoi. See DAXNER-HÖCK & BADAMGARAV (2007, fig. 1) for a map presenting the geographic distribution of the localities.

I n s t i t u t i o n : NHMW = Naturhistorisches Museum Wien.

T e e t h : DP, dp = deciduous premolar; P, p = premolar; M, m =Molar. Upper-case letters indicate upper teeth, whereas lower case letters indicate lower teeth.

Geologic and chronologic framework

All the specimens described below have been collected in the area of the "Valley of Lakes" in Central Mongolia. This area is in the Pre-Altai depressions which are situated in West-ern and South-Central Mongolia between the Mongolian Altai and the Gobi Altai Moun-tains in the south and the Khangai Mountains in the north. Here, above the Proterozoic
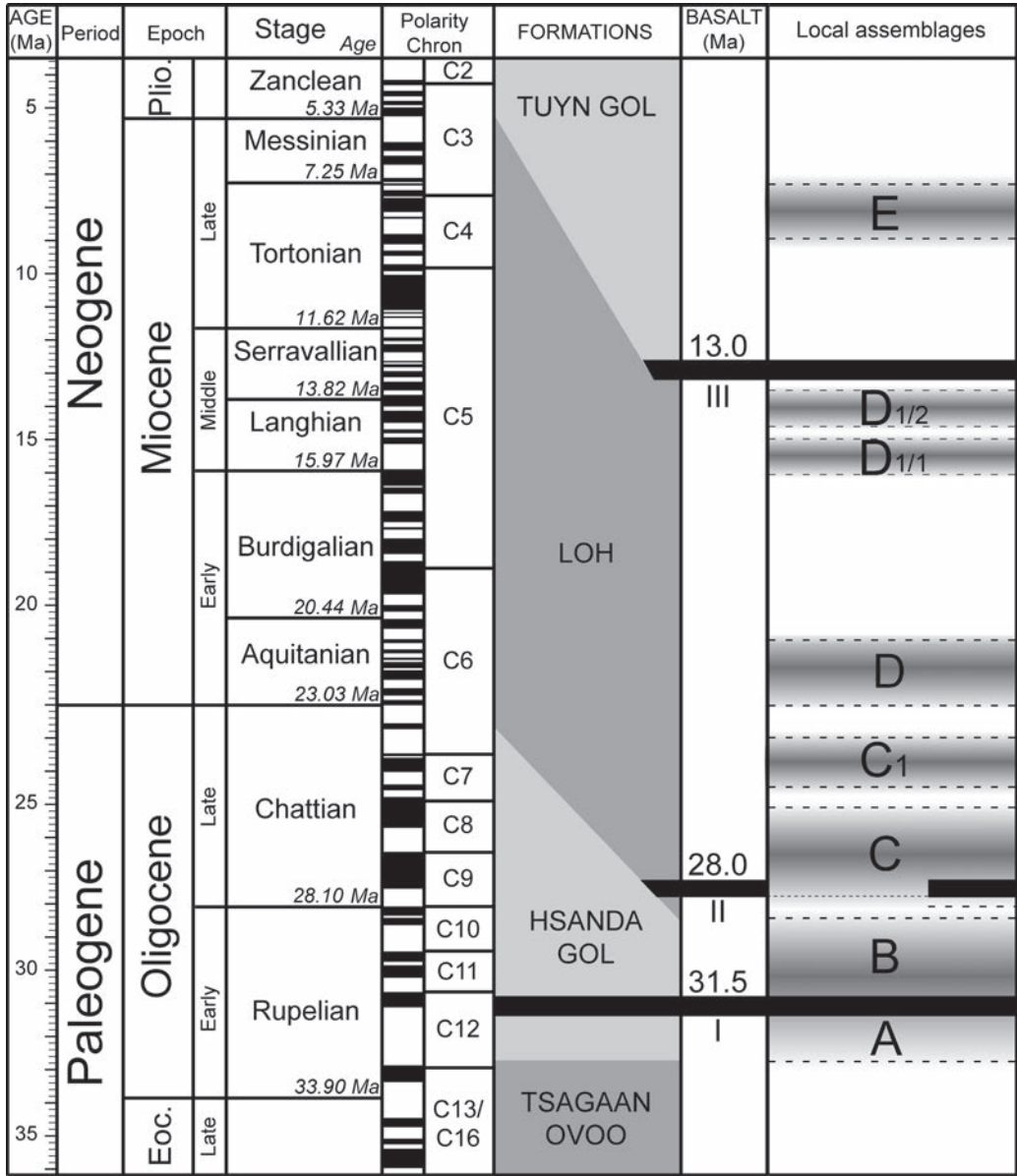
Fig. 1. Sedimentary formations and correlation chart of the Mongolian rodent assemblages with the Geological Time Scale, modified after DAXNER-HÖCK *et al.* (2013) and GRADSTEIN *et al.* (2012). Local Oligocene-Miocene chronology is based on informal biozones and basalt datings. See HÖCK & BADAMGARAV (2007) and DAXNER-HÖCK *et al.* (2013) for a detailed presentation of the regional geology and biochronological framework, and MARIDET *et al.* (2014) for a recent update on the Miocene biozones.

and Paleozoic basement, are deposited continental sediments ranging continuously from the Cretaceous to the Quaternary. A succession of four geologic formations is recognised in this region ranging from the Late Eocene to the Late Miocene: Tsagaan Ovoo, Hsanda Gol, Loh and Tuyn Gol (see Daxner-Höck & Badamgarav 2007 for a detailed presentation of the geologic and chronologic framework). In this area the Cenozoic sedimentary sequence interlays with several basalts flaws: three coherent basaltic flows (Basalt I, II, III) of variable thickness were distinguished and dated by the 40Ar/39Ar-method (Daxner-Höck et al. 1997; Höck et al. 1999). Basalt I erupted around 31.5 Ma [range 30.4–32.1] (Early Oligocene), Basalt II is about 28.0 Ma [range 27.0–28.0] (Late Oligocene), and Basalt III about 13 Ma [range 12.2–13.2] (Middle Miocene). Basalt II is only found in the very north of the mapped area near the Unzing Khurem and the Olon Ovoony Khurem areas, its thickness also strongly varies: 5–7 m in the Unzing Khurem area whereas it can exceed 25 m in the Olon Ovoony Khurem area (Daxner-Höck & Badamgarav 2007). The rodent assemblages have been previously grouped into eight informal local biozones (Fig. 1): A and B for the Early Oligocene, C and C1 for the Late Oligocene, D for the Early Miocene, D1/1 and D1/2 for the early Middle Miocene and E for the Late Miocene. Here, we present a detailed description of the sciurid rodents yielded by diverse layers of which age span from the early Late Oligocene to the Late Miocene. Each biochronologic assemblage is presented in detail in previous publication about the Oligo-Miocene geology and fossil record of the Valley of Lakes (Daxner-Höck et al. 2007; Daxner-Höck et al. 2010) and recently updated by Daxner-Höck et al. (2013) and Maridet et al. (2014).

Systematic Palaeontology

Class Mammalia Linneaus, 1758

Order Rodentia Bowdich, 1821

Suborder Sciuromorpha Brandt, 1855

Family Sciuridae Fischer de Waldheim, 1817

Subfamily Sciurinae Fischer de Waldheim, 1817

Tribe Sciurini Fischer de Waldheim, 1817

Genus *Plesiosciurus* Qiu & Liu, 1986

Plesiosciurus aff. *sinensis* Qiu & Liu, 1986
(Fig. 2a–g)

1999 Sciuridae indet. – Höck et al., fig. 21/5, p. 119.
2007 *Spermophilinus* sp. – Daxner-Höck & Badamgarav, tab. 3, p. 91.

Localities/Stratigraphy: Toglorhoi (biozone C, early Late Oligocene); Unkheltseg and Hotuliin Teeg (biozone D, Early Miocene); Ulaan Tolgoi and Loh (biozone D1/2, early Middle Miocene)

M a t e r i a l : Biozone C: right M1/2, TGW-A/2a (NHMW 2013/0397/0001; 1.42×1.70 mm). Biozone D: right M1/2, UNCH-A/4 (NHMW 2013/0398/0001; 1.42×1.82 mm); left P4, HTE-008 (NHMW 2013/0399/0001; 1.42×1.62 mm). Biozone D1/2: right M1/2, UTO-A/5 (NHMW 2013/0400/0001; 1.37×1.78 mm); left m1/2, UTO-A/5 (NHMW 2013/0400/0002; 1.58×1.57 mm); left m1/2, UTO-A/5 (NHMW 2013/0400/0003; 1.66×1.63 mm); right m1/2, UTO-A/5 (NHMW 2013/0400/0004; 1.58×1.50 mm); left m3, UTO-A/5 (NHMW 2013/0400/0005; 1.93×1.70 mm); left M3, LOH-A/2 (NHMW 2013/0401/0001; 1.69×1.71 mm).

D e s c r i p t i o n : All molars present a slender morphology (very thin crests and large valleys) and a concave occlusal surface.

P4 – The tooth has a very thin and low anteroloph and a narrow posterosinus. The protoconule is absent whereas the metaconule is well-developed. The metaloph connects to the protocone. It has three roots.

M1/2 – The molars are characterized by a large protocone which is merging with the hypocone (the hypocone is only visible on unworn teeth). The anteroloph is thin and low compared to the protoloph, without anteroconule or parastyle; in one tooth the connection with the protocone is very weak making the anteroloph almost isolated (specimen NHMW 2013/0397/0001 from TGW-A/2a, Fig. 2b). The protoconule is missing. The metaloph always connects on the posterior end on the protocone (possibly on the hypocone); the metaconule is missing. The posterosinus is relatively narrow compared to the sinus and anterosinus. No M1/2 has the roots preserved, but what remains of the roots suggest that they probably had three of them.

M3 – It is characterized by a large protocone whereas the paracone is smaller, and the hypocone and metacone are almost undistinguishable from the posteroloph. The anteroloph is long and thin, delimiting a large anterosinus. The trigone basin is large and elongated. The M3 has three roots.

m1/2 – The teeth have a wide and rounded talonid basin. The anteroconulid is well-developed and connects to the metalophid lingually and to the protoconid labially. The metalophid is always present and complete; the mesoconid, hypoconulid, entolophid and mesostylid are always missing, and the entoconid can barely be distinguished from the posterolophid. The m1/2 has three roots.

m3 – It differs noticeably from the m1/2 in having a weakly-developed anteroconulid and having an incomplete metalophid (not reaching the metaconid), furthermore the entoconid is well-developed and distinguished from the posterolophid. The m3 has three roots.

R e m a r k s : The above described specimens differ from *Tamias* ILLIGER, 1811 and *Spermophilinus* DE BRUIJN & MEIN, 1968 in missing the mesoconid and from *Eutamias* TROUESSART, 1880 in also missing the protoconule in M1/2 (they are also smaller than *Eutamias* sp. from the biozone D). They also differ from *Sinotamias* QIU, 1991 in missing the metaconule in M1/2. QIU & LIU (1986) described a new genus of small-sized Sciuridae from Xiacaowan (Early Miocene of Jiangsu, China), *Plesiosciurus*, which also
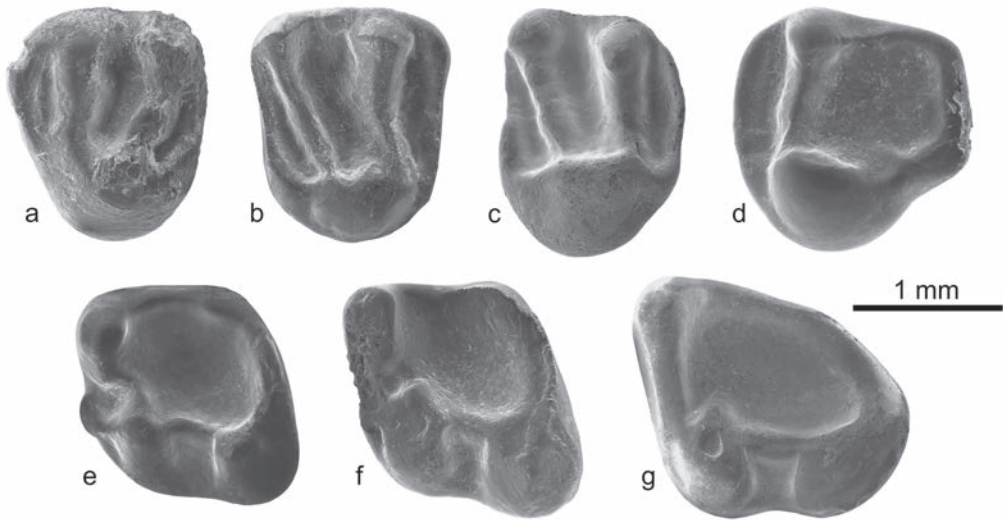
Fig. 2. *Plesiosciurus* aff. *sinensis*, from the Late Oligocene locality Toglorhoi (TGW), the Early Miocene localities Hotuliin Teeg (HTE) and Unkheltseg (UNCH), and the early Middle Miocene of Loh (LOH) and Ulaan Tolgoi (UTO), occlusal view: **a**. left P4, HTE-008 (NHMW 2013/0399/0001); **b**. right M1/2, TGW-A/2a (NHMW 2013/0397/0001); **c**. right M1/2, UNCH-A/4 (NHMW 2013/0398/0001); **d**. left M3, LOH-A/2 (NHMW 2013/0401/0001); **e**. left m1/2 (UTO-A/5, NHMW 2013/0400/0002); **f**. left m1/2 (UTO-A/5, NHMW 2013/0400/0003); **g**. left m3, UTO-A/5 (NHMW 2013/0400/0005).

differs from the above mentioned genera and is characterized by a large protocone and the absence of anteroconule, parastyle, metaconule and protoconule in M1/2, plus the absence of mesoconid in lower molars. This association of characters is also characteristic of the above described specimens. The genus comprises so far only one species, *P. sinensis*, whose size from Xiacaowan is only slightly larger than the Mongolian specimens suggesting that they might be closely related. All present specimens come from Miocene layers, except one M1/2 (Fig. 2b) which comes from the early Late Oligocene layer (TGW-A/2a). The general morphology and size of the latter is similar to that of the Miocene specimens. Despite the significant gap of time between the two records we tentatively ascribe this Late Oligocene specimen to the same species. More material will be necessary to confirm that they belong to a single lineage surviving through the Oligo-Miocene boundary.

Tribe Tamiini ILLIGER, 1811

Genus *Eutamias* TROUESSART, 1880

? *Eutamias* sp.
(Fig. 3a–c)

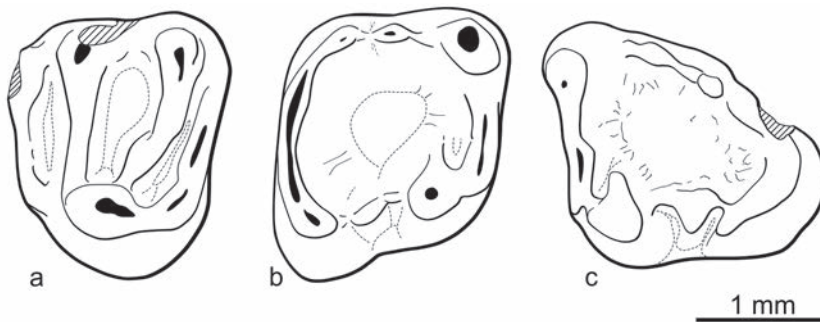2007 Sciuridae indet. 1 – DAXNER-HÖCK & BADAMGARAV, tab. 3, p. 16.

Fig. 3. ?*Eutamias* sp., from the Early Miocene localities Hotuliin Teeg (HTE) and Unkhelt-seg (UNCH), occlusal view: **a**. left P4, HTE-008 (NHMW 2013/0402/0001); **b**. right m1/2, UNCH-A/3 (NHMW 2013/0403/0001); **c**. left m3, UNCH-A/4 (NHMW 2013/0404/0001).

L o c a l i t i e s / S t r a t i g r a p h y : Hotuliin Teeg and Unkheltseg (biozone D, Early Miocene)

M a t e r i a l : Left P4, HTE-008 (NHMW 2013/0402/0001; 1.70×2.03 mm); right m1/2, UNCH-A/3 (NHMW 2013/0403/0001; 1.81×2.09 mm); left m3, UNCH-A/4 (NHMW 2013/0404/0001; 2.17×1.88 mm).

D e s c r i p t i o n : P4 – The tooth is missing the protoconule but has a weakly-developed metaconule; the metaloph connects to the protocone; the hypocone is well-differentiated from the protocone; the tooth has three roots.

m1/2 and m3 –The two lower molars have a low crown, a slight ornamentation in the talonid basin, a very weakly-developed entoconid, a strong mesoconid, an interrupted metalophid, and a well-developed anteroconulid. The m1/2 has three roots but the anterior one has two pulp cavities. The roots of the m3 are not preserved.

R e m a r k s : Only three molars have been found and these are noticeably smaller than those of *Kherem shandgoliensis* Minjin, 2004, but larger than *Plesiosciurus* aff. *P. sinensis*. The general morphology and shape is characteristic of Eurasian chipmunks as indicated by the unexpended protocone and the absent or weakly-developed protoconule and metaconule in upper molars, the rhomboidal shape with rounded entoconid corner in m1/2 (Qiu, 1996). The present specimens differ from *Eutamias sihongensis* Qiu & Liu, 1986 (Early Miocene of Jiangsu, China; Qiu & Liu 1986), in being larger, having a weakly-developed metaconule and no protoconule in P4, and in having an incomplete metalophid and a strong mesoconid in lower molars. The morphology of the present specimens is otherwise similar to that of *E*. aff. *E. ertemtensis* from Tunggur (Middle Miocene of Inner Mongolia, China, Qiu 1996) but they are also noticeably smaller than the *E*. aff. *E. ertemtensis* from Tunggur. Due to their resemblance with *E*. aff. *E. ertemtensis* we tentatively ascribe these specimens to the genus *Eutamias*, but this generic identification remains uncertain due to the scarcity of the material. The above described specimens could belong to a new taxon, but due to the scanty material we only ascribe the specimen to the genus *Eutamias* and we refrain from creating a new species.
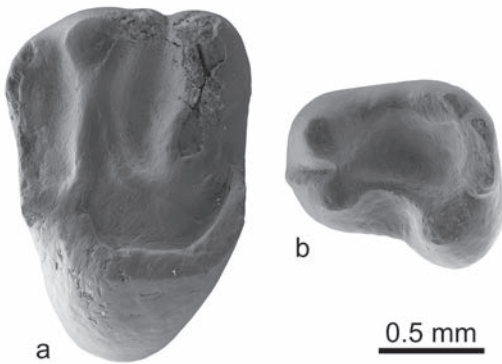
Fig. 4. *Eutamias* cf. *ertemensis* from the Late Miocene locality Builstyn Khudag (BUK-A/12+14), occlusal view: **a**. left M1/2 (NHMW 2013/0405/0001); **b**. left p4 (NHMW 2013/0405/0002).

Eutamias cf. *ertemtensis* Qɪᴜ, 1991
(Fig. 4a–b)

2007 *Prospermophilus* cf. *orientalis* – Dᴀxɴᴇʀ-Höᴄᴋ & Bᴀᴅᴀᴍɢᴀʀᴀᴠ, tab. 3, p. 16.

L o c a l i t y / S t r a t i g r a p h y : Builstyn Khudag (biozone E, Late Miocene), all specimens come from the same layer: BUK-A/12+14.

M a t e r i a l : Left M1/2 (NHMW 2013/0405/0001; 1.29×1.63 mm); left p4 (NHMW 2013/0405/0002; 1.17×0.94 mm); left dp4 (NHMW 2013/0405/0003; 1.07×0.90 mm, poorly preserved).

D e s c r i p t i o n : M1/2 – The tooth is labially-lingually elongated (much wider than long), although the tooth is strongly worn it is possible to see that it possesses a metaconule which connects to the anterior part of the hypocone; both the metacone and metaconule are large and the posterosinus is very narrow, whereas the sinus and anterosinus are large. The protoloph is very thick lingually, possibly bearing a protoconule. The posteroloph is also weakly-developed. The anteroloph is long and almost reaches the paracone labially and bears a parastyle at its extremity, but no anteroconule. The M1/2 has three roots.

p4 – It possesses a small and weakly-developed anteroconulid on the anterior border and is connected to the protoconid; the metaconid and protoconid are connected to each other by a short metalophid; the mesoconid is absent but the hypoconid, hypoconulid and entoconid are all well-developed and clearly differentiated from the posterolophid. The p4 has two roots.

dp4 – The tooth is too poorly preserved to be described, but it is possible to observe that it has two roots.

R e m a r k s : The present specimens are only slightly larger than *Eutamias ertemtensis* from Ertemte 2 (Late Miocene of Inner Mongolia, China; Qɪᴜ 1991), otherwise their morphology seems to fit the variability described by Qɪᴜ (1991). Qɪᴜ (1996) described *Eutamias* aff. *E. ertemtensis* from Tunggur (Middle Miocene of Inner Mongolia, China;

QIU 1996) and proposed that both *Eutamias* aff. *E. ertemtensis* and *Eutamias ertemtensis* could belong to one lineage. With regard to this hypothesis the specimens from Builstyn Khudag could belong to the same lineage, but more material will be necessary to secure this identification. We consequently refer our material as *Eutamias* cf. *ertemtensis*.

Tribe Pteromyini BRANDT, 1855

Pteromyini indet.
(Fig. 5a–c)

2007 Sciuridae indet. 2 – DAXNER-HÖCK & BADAMGARAV, tab. 3, p. 16.
2007 Sciuridae indet. 3 – DAXNER-HÖCK & BADAMGARAV, tab. 3, p. 16.

Locality/Stratigraphy: Unkheltseg (biozone D, Early Miocene), Olon Ovoony Khurem (biozone D1/1, early Middle Miocene).

Material: left dp4, UNCH-A/4 (NHMW 2013/0412/0001; 1.70×1.54 mm); left p4, UNCH-A/4 (NHMW 2013/0412/0002; 2.51×2.37 mm); left m1/2, UNCH-A/4 (NHMW 2013/0412/0003; 2.66×2.95 mm); left m3, ODO-B/1 (NHMW 2013/0413/0001; 3.09×3.02 mm); left m1/2 or m3 fragment, UNCH-A/4 (NHMW 2013/0412/0004; not measurable).

Description: The teeth are characterized by a high crown, massive cusp(id)s and deep sinus(ids), low crests, and rugose enamel in the talonid basins of the lower teeth.

dp4 – The mesotylid, entoconid and entolophid are well-developed. The metaconid is slightly anteriorly located compared to the protoconid. The dp4 has two roots.

p4 – The four main cuspids of the p4 are large, in addition the mesostylid, the mesoconid, the hypoconulid and the entolophid are also very well-developed. Like in dp4, the metaconid is slightly more anteriorly located than the protoconid, both are separated by a deep groove that opens anteriorly; they are connected by a long metalophid that skirts the groove. The mesoconid and the hypoconulid are divided by a shallow groove. Two spurs are connected to the mesostyle, one long and well-developed one forms a sharp bend and joins the metaconid, the other one is weakly developed and short and ends in the talonid basin. The p4 has two roots.

m1/2 – Like the dp4 and the p4, the m1/2 also has well-developed mesostylid, mesoconid, hypoconulid and entolophid. The metalophid forms a posterior bend delimiting a large trigonid basin. The anteroconulid is probably well-developed (the tooth is partly broken in this part) and is connected labially to the protoconid by a thick and short anterolophid. Otherwise the anteroconulid is not connected to the metalophid and the trigonid basin is open anteriorly. The m1/2 has three roots with the lingual one being clearly divided.

Fig. 5. Pteromyini indet., from the Early Miocene locality Unkheltseg (UNCH), occlusal view: **a**. left dp4, UNCH-A/4 (NHMW 2013/0412/0001); **b**. left p4, UNCH-A/4 (NHMW 2013/0412/0002); **c**. left m1/2, UNCH-A/4 (NHMW 2013/0412/0003).

m3 – The tooth is very poorly preserved and can not be described.

R e m a r k s : As stated by DE BRUIJN (1999), the association of the following characters present in the above described specimens usually indicates that the taxon can be interpreted as a flying squirrel: entoconid well-developed and well-delimited and slightly ruguose enamel. However, as argued by THORINGTON *et al.* (2005), these dental features vary widely among flying and tree squirrels so an unambiguous identification of a flying squirrel in the fossil record can only be achieved by studying the post-cranial remains. So far no post-cranial elements have been found in the Unkheltseg and Olon Ovoony Khurem localities that could be attributed to this taxon. However, if this hypothesis can be confirmed later by new materials, these specimens might represent the northernmost occurrence of a flying squirrel in Central Asia.

Among the taxa considered to be flying squirrels in the Miocene fossil record, the present specimens differ from *Petauristodon* ENGESSER, 1979, *Shuanggouia* QIU & LIU 1986, *Parapetaurista* QIU & LIU, 1986 and *Hesperopetes* EMRY & KORTH, 2007 in missing the wrinkling of the enamel in the basins and having a well-developed entolophid. They differ from *Forsythia* MEIN, 1970 and *Sciurion* SKWARA, 1986 in having a well-developed entolophid and a complete metalophid, and differ from *Blackia* MEIN, 1970 and *Pliopetes* KRETZOI, 1959 in being much larger and missing the wrinkling of the enamel. From *Albanensia* DAXNER-HÖCK & MEIN, 1975 they differ in having generally more massive cusp(id)s and a less complicated molar pattern.

So far, based on the association of features observed on the Mongolian specimens, and taking into account that the upper teeth are unknown, the European genera *Miopetaurista* KRETZOI, 1962, *Pliopetaurista* KRETZOI, 1962 and *Aliveria* DE BRUIJN *et al.*, 1980 seem to be the closest related taxa. The three lower teeth recovered from the localities Unkheltseg and Olon Ovoony Khurem are not sufficient to further identify this taxon at specific or even generic levels.

Subfamily Xerinae OSBORN, 1910

Tribe Xerini OSBORN, 1910

Genus *Kherem* MINJIN, 2004

Kherem shandgoliensis MINJIN, 2004
(Fig. 6a–g)

1999 Petauristidae indet. – HÖCK *et al.*, fig. 21/3, p. 119.
2004 *Kherem shandgoliensis* – MINJIN, fig. 1, p. 754.
2005 *Kherem asiatica* – WANG & DASHZEVEG, fig. 2, p. 90.
2007 *Kherem* sp. – DAXNER-HÖCK & BADAMGARAV, tab. 3, p. 16.

Localities/Stratigraphy: Loh (Biozone C1, Late Oligocene); Unkheltseg and Hotuliin Teeg (biozone D, Early Miocene); Ulaan Tolgoi (biozone D1/2, early Middle Miocene)

Material: Biozone D1/2: left p4, UTO-A/5 (NHMW 2013/0406/0001; 2.20×1.94 mm). Biozone D: left maxillary fragment with P4–M1, HTE-surface (NHMW 2013/0407/0001; P4 1.91×2.46 mm; M1 2.07×2.67 mm); right maxillary fragment with M1–M3, HTE-surface (NHMW 2013/0407/0002; M1 2.19×2.58 mm; M2 2.20×2.51 mm; M3 2.41×2.45 mm); right upper incisor, HTE-surface (NHMW 2013/0407/0003); left m3, UNCH-A/3 (NHMW 2013/0408/0001; 2.97×2.38 mm); left fragment mandible with p4–m2, HTE-005 (NHMW 2013/0409/0001; p4 not measurable; m1 2.53×2.58 mm; m2 2.64×2.71 mm); left DP4, UNCH-A/3 (NHMW 2013/0408/0002) (2.20×2.29 mm); right P3, UNCH-A/3 (NHMW 2013/0408/0003; 1.10×1.20 mm); left P4, HTE-005 (NHMW 2013/0409/0002; 1.91×2.48 mm); left M1/2, HTE-005 (NHMW 2013/0409/0003; 1.99×2.65 mm). Biozone C1: left M3, LOH-C/1 (NHMW 2013/0410/0001; 2.47×2.30 mm). See also table 1 for a summary of the measurement of the biozone D.

Description: The molars and premolars are characterized by being large with a high crown, and deep sinuses and sinusids.

Table 1. Measurements (in mm) of *Kherem shandgoliensis* from the localities Unkheltseg and Hotuliin Teeg (biozone D, Early Miocene). N: number of teeth measured; Min: minimum; Max: maximum.

	N	Length			Width		
		Min	Max	Mean	Min	Max	Mean
P3	1			1.10			1.20
DP4	1			2.20			2.29
P4	2	1.91	1.91	1.91	2.46	2.48	2.47
M1/2	4	1.99	2.20	2.11	2.51	2.67	2.60
M3	1			2.41			2.45
m1/2	2	2.53	2.64	2.59	2.58	2.71	2.65
m3	1			2.97			2.38

P3 – The tooth is rounded with a U-shape crest; the main cusps are indistinct. The P3 has one root.

DP4 – It is characterized by a triangular shape due to the long and curved anteroloph delimiting a large anterior sinus. The protocone is large but the hypocone is absent. The protoconule is absent whereas the metaconule is well-developed. The metaloph connects to the protocone; it is thick between the metacone and the metaconule, but very thin and low between the metaconule and the protocone. A mesostyle closes the trigone basin. The roots are not preserved.

P4 – It differs from the DP4 in having a strait anteroloph bearing a well-developed parastyle. Like in the DP4 the hypocone is indistinct, the protoconule is missing and the metaconule is well-developed. The part of the metaloph between the metaconule and the protocone is either very thin or even absent. The mesostyle can be present or absent. The P4 has 3 roots.

M1/2 – It has a long anteroloph with an always well-developed parastyle at its extremity whereas the anteroconule can be missing. The hypocone is either indistinct or small and merged with the protocone. Like in DP4 and P4, the protoconule is missing but the metaconule is well-developed. The part of the metaloph between the metacone and the metaconule is always thick, whereas the second part of the metaloph is either weakly-developed or even absent: the metaconule can be isolated (2/4), connected to the protocone (1/4) or connected to the posteroloph (1/4). The M1/2 has 3 roots.

M3 – It has a large trigone basin surrounded by a continuous crest; the hypocone and metacone are not distinguishable from this crest. One tooth has an incomplete crest in the middle of the trigone basin which seems to connect to the postero-labial border, possibly as an incomplete and weakly-developed metaloph. The second M3 is too worn to observe if this character is present. The M3 has three roots.

p4 – The metaconid and protoconid are separated by a deep groove, but they are connected by a thin metalophid which joins them posteriorly. Both the hypoconid and entoconid are very large (and higher than the anterior cusps) and connected to each other by a very thick posterolophid, the whole forming a thick crescent-like posterior border. The p4 has two roots.

m1/2 – Both teeth are worn and poorly preserved. It is still possible to observe that the anterolophid connects the metaconid to the protoconid forming a thick crescent-like antero-labial border, whereas the metalophid is comparatively less developed. The mesoconid seems absent. In both teeth the entoconid is well-developed and higher than the posteroloph. The mesostylid merges with the posterior border of the metaconid, but is separated from the entoconid by a shallow groove. One tooth has a short but complete entolophid. The m1/2 has 4 roots.

m3 – The anterolophid joins the metaconid to the protoconid and forms a thick crescent-like antero-labial border, like in m1/2. The metalophid is well-developed but not connected to the metalophid, and ends freely in the trigonid basin. Like in m1/2 the
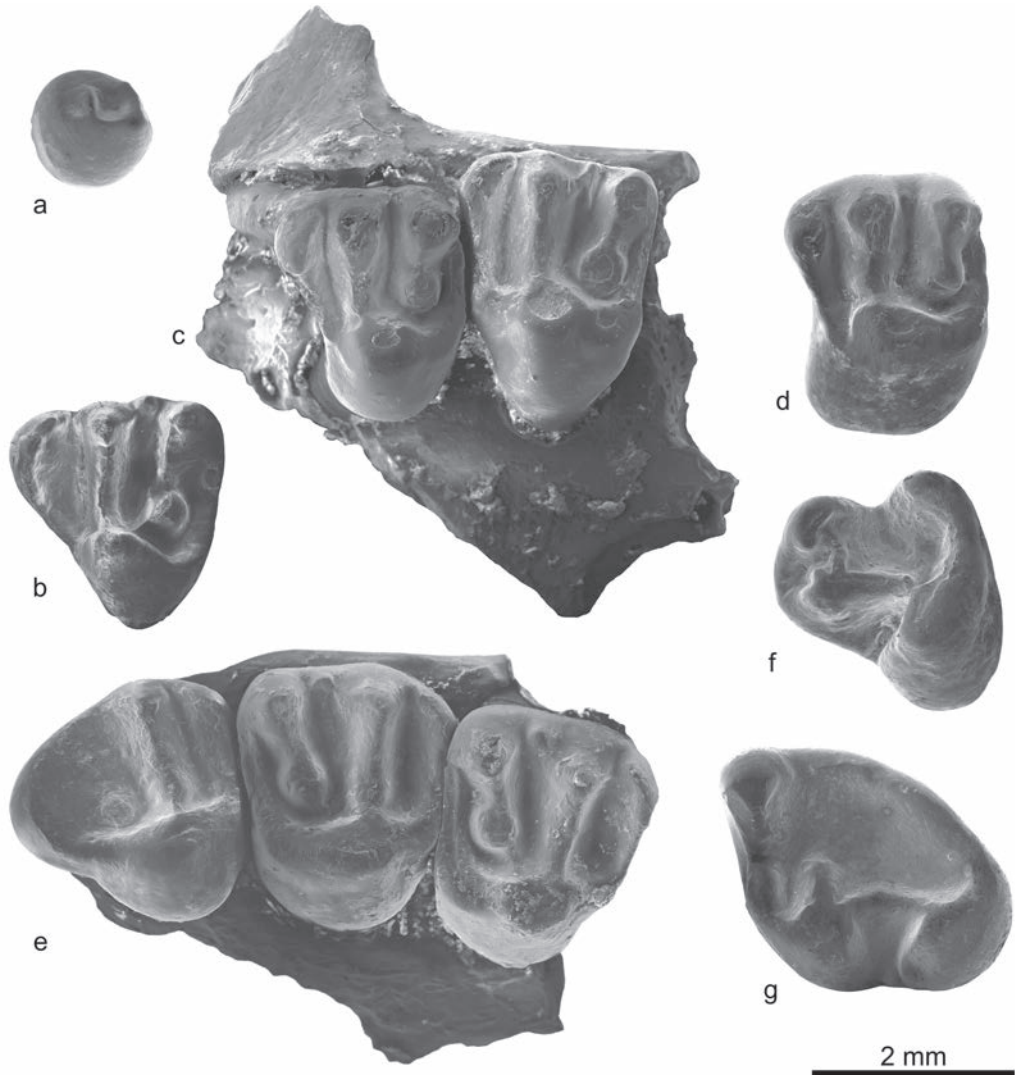
Fig. 6. *Kherem shandgoliensis*, from the Early Miocene localities Unkheltseg (UNCH) and Hotuliin Teeg (HTE), occlusal view: **a**. right P3, UNCH-A/3 (NHMW 2013/0408/0003); **b**. left DP4 (UNCH-A/3, NHMW 2013/0408/0002); **c**. left maxillary fragment with P4–M1, HTE-0 (NHMW 2013/0407/0001); **d**. left M1/2, HTE-005 (NHMW 2013/0409/0003); **e**. right maxillary fragment with M1–M3, HTE-0 (NHMW 2013/0407/0002); **f**. left p4, UNCH-A/5 (NHMW 2013/0406/0001); **g**. left m3, UNCH-A/3 (NHMW 2013/0408/0001).

entoconid is higher and slightly thicker that the posterolophid, but not as well differenti-ated as in m1/2. The m3 has three roots.

R e m a r k s : The genus *Kherem* comprises two species, *K. shandgoliensis* MINJIN, 2004 and *K. asiatica* WANG & DASHZEVEG, 2005. The genus has been described for the first

time by MINJIN (2004) based on a single lower jaw from Tashgain Bel in the Valley of Lakes, which is another Mongolian name of the locality Unkheltseg. Later, WANG & DASHZEVEG (2005) published more material from the same locality (including two lower jaws and an upper jaw) and they ascribed it to a new species, *Kherem asiatica*. The type materials of both species stems from the locality Tashgain Bel (position: 45°27′47″ N, 101°12′11″ E; WANG & DASHZEVEG 2005: p88), which is identical with our locality Unkheltseg (position: 45°27′41″ N, 101°12′05″ E; HÖCK *et al.* 1999). Local residents informed us that the whole northern rim of the Taatsiin Gol plateau is called Tashgain Bel, and a certain part of it is Unkheltseg (UNCH).

So far the genus *Kherem* is represented only by a few specimens, and the morphological and size variability of each species remains unknown. The above described specimens present similarities with both species. Both the m1/2 and m3 are similar to that illustrated by MINJIN (2004) except that they are slightly larger, but they differ from *Kherem asiatica* in having a less developed metalophid, mesoconid and entolophid. On the other hand, the above described upper dentition is similar to that described and illustrated by WANG & DASHZEVEG (2005) except that the metaconule is only rarely connected to the posteroloph in our specimens and that they are slightly smaller. This sample seems consequently to be an intermediate between the two species. Considering that all the specimens published since MINJIN (2004) come from the same locality, we rather interpret this intermediate form as a clue that the morphology and size variability of *K. shandgoliensis* and *K. asiatica* have been underestimated and that all specimens from this locality likely belong to a single species. *K. shandgoliensis* being the first species described form this locality, we consequently refer all specimens to this species.

Discussion: MINJIN (2004) and WANG & DASHZEVEG (2005) have been likely misled by an incorrect age interpretation of the locality and they consequently compared *Kherem* with sciurids and aplodontids from the Paleogene of Asia and America only. WANG & DASHZEVEG (2005) consequently interpreted *Kherem* as belonging to the subfamily Cedromurinae, but still noticed numerous differences between this taxon and those from the Late Eocene and Early Oligocene of North America. Actually, by comparing with European Miocene ground squirrels, the morphology of *K. shandgoliensis* is overall similar to *Heteroxerus* STEHLIN & SCHAUB, 1951 *Atlantoxerus* FORSYTH MAJOR, 1893 and *Palaeosciurus* POMEL, 1853. This observation is especially true for *Heteroxerus*, as several features of the molars given in its diagnosis, emended by CUENCA BESCOS (1988), are actually also characteristic of *Kherem*, such as: the incomplete or reduced metaloph that isolates (or partly isolates) the protocone from the metaconule in upper molars; the better-developed anterior cuspids in lower molars; the well-differentiated entoconid in lower molars; the reduced metalophid (especially compared to the anterolophid); and the well-developed anteroconid. The only difference of the specimens from Mongolia seems to be the weakly developed or absent hypoconulid in lower molars and the generally more linguo-labially elongated shape of the upper premolars and molars, whereas European *Heteroxerus* upper molars are rather squared. However, it is noteworthy that the upper molars of *H. grivensis* (MAJOR, 1893), the type species,

are noticeably wider than long compared to other species attributed to the same genus which indicate that this feature is not diagnostic of the genus *Heteroxerus* as a whole. However CUENCA BESCOS (1988) did not include the morphology of the jaws and incisors in her emended diagnosis. WANG & DASHZEVEG (2005) described the morphology of the mandibles and incisors from Mongolia. For instance, the laterally compressed and oval section of the incisor is one characteristic of *Heteroxerus* (HUGUENEY 1969), but WANG & DASHZEVEG (2005) mentioned fine veins on the surface of the enamel whereas HUGUENEY (1969) stated that well-marked lateral ridges are a characteristic of the genus in Europe. WANG & DASHZEVEG (2005) also emphasized the short and shallow diastema, the deep masseteric fossa with a rounded anterior end and the large mental foramen located anterior to the p4 on the mandible from Mongolia, characteristics also described by HUGUENEY (1969) on the material of *H. paulhiacensis* BLACK, 1965 from Coderet (Early Miocene, France). However, the material from Coderet slightly differs in having the masseteric fossa end more anteriorly located, in front of the M1.

As stated by PELAEZ-CAMPOMANEZ (2001) the genera *Heteroxerus* and *Atlantoxerus* are very similar based on molars morphology. They only differ by their size and the development of the anterolophid in lower molars. So far, the only differences distinguishing *Kherem* from *Heteroxerus* and *Atlantoxerus* are the weakly developed or absent hypoconulid in lower molars, the masseteric fossa ending more posteriorly on the mandible, and the missing well-marked lateral ridges on the incisor enamel. These differences confirm anyway that *Kherem* remains a valid genus of Sciuridae with regards to European Miocene ground squirrels. But the similarities between the Mongolian taxon and European ones suggest a close relationship with the modern subfamily Xerinae rather than with a Paleogene subfamily Cedromurinae.

Genus *Atlantoxerus* FORSYTH MAJOR, 1893

? *Atlantoxerus* sp.
(Fig. 7a–d)

2007 Sciuridae indet. 4 – DAXNER-HÖCK & BADAMGARAV, tab. 3, p. 16.

Locality/Stratigraphy: Builstyn Khudag (biozone E, Late Miocene). All the specimens come from the same layer: BUK-A/12+14.

Material: left DP4? (NHMW 2013/0411/0001; lingual part broken; 1.81×- mm); left M1/2 (NHMW 2013/0411/0002; 2.14×2.66 mm); left M1/2 (NHMW 2013/0411/0003; 2.01×2.65 mm); right M3 (NHMW 2013/0411/0004; 2.33×2.10 mm); left fragment of maxilla with P4–M3 (NHMW 2013/0411/0005; teeth are very worn but measurable: P4 1.59×1.93 mm; M1 1.80×2.55 mm; M2 1.93×2.33 mm; M3 1.93×2.09 mm); left m1/2 (NHMW 2013/0411/0006; 2.12×2.00 mm); right m1/2 (NHMW 2013/0411/0007; lingual-posterior corner broken; 2.38×- mm).

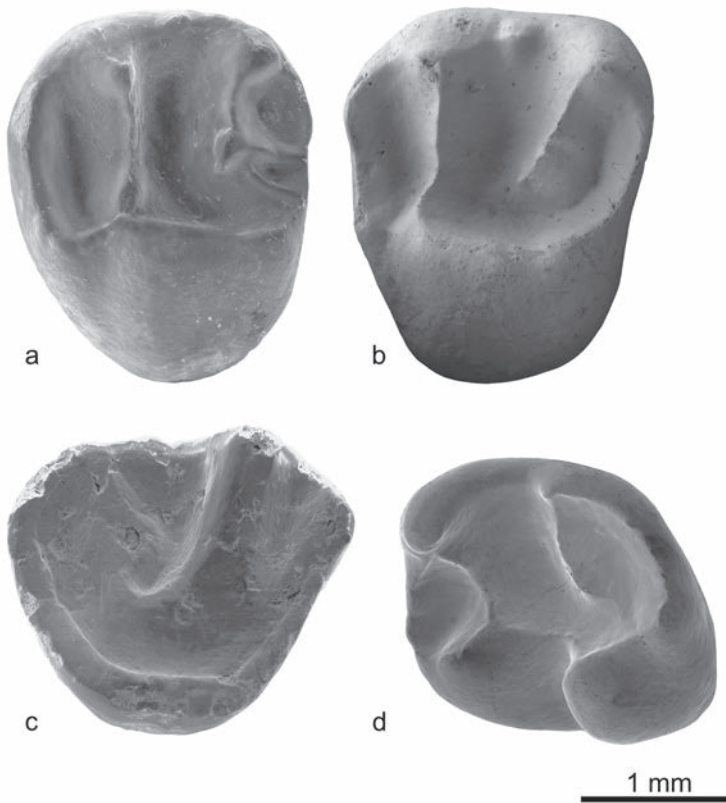Description: The teeth have a relatively high crown.

Fig. 7. ?*Atlantoxerus* sp. from the Late Miocene locality Builstyn Khudag (BUK-A/12+14), occlusal view: **a**. left M1/2 (NHMW 2013/0411/0003); **b**. left M1/2 (NHMW 2013/0411/0002); **c**. right M3 (NHMW 2013/0411/0004); **d**. left m1/2 (NHMW 2013/0411/0006).

DP4 – The broken tooth shows only from what remains of the labial part that the long and curved anteroloph reaches the paracone on the labial border and that the metaloph connects on the posteroloph. The roots are not preserved.

M1/2 – Wider than long, the hypocone is weakly developed and barely distinguishable from the protocone. Both the protocone and hypocone form a crescent-like cusp. The metaconule is present but weakly developed whereas the protoconule can be weak or absent. The metaloph is either incomplete (the metaconule is then only connected to the metacone) or connected to the posteroloph. One tooth possesses actually two crests connecting the metaconule to the posteroloph. The trigone basin is very large but it is closed labially by a well-developed mesostyle. The parastyle and anteroconule are very weakly-developed. The M1/2 has 3 roots.

M3 – Both specimens are strongly worn; it is however possible to see that the metaloph connects to the posteroloph and that the trigone basin is very large compared to the anterior and posterior sinuses. The M3 has 3 roots.

m1/2 – It has a long anterolophid and a long metalophid, both complete and delimiting a large anterior sinusid. The anteroconulid is absent. The entoconid is small and connected to the posterolophid. The entolophid is long and connects either on the hypoconulid or on the hypoconid, so the posterolophid and the entolophid delimit a very large posterior sinusid. The roots are not preserved.

R e m a r k s : The height of the crown (higher than *Kherem shandgoliensis*), the large size (similar to that of *Atlantoxerus blacki* (DE BRUIJN, 1967) from the Early Miocene of Spain) the long and complete anterolophid, metalophid and entolophid in m1/2 seem to fit the diagnosis of the genus *Atlantoxerus* as proposed by CUENCA BESCOS (1988), but the shape of the M1/2 (wider than long), the metaloph often connecting to the posteroloph and the absence the anteroconulid in m1/2 seem on the other hand to differ. However, the morphological variability for the genus might have been underestimated at the time. DE BRUIJN (1999) stated the difference between both genera is not clear, mainly based on the robustness of the cheek teeth. PELAEZ-CAMPOMANEZ (2001) also indicated that only the size and the development of the anterolophid can differentiate *Heteroxerus* from *Atlantoxerus*. The ascription of the Mongolian specimens to the genus *Atlantoxerus*

Table 2. Occurrences of the sciurid taxa in each assemblage and layer from the Late Oligocene to the Late Miocene, and their correlation with the local biochronology. Biozones correspond to the local biochronologic assemblages defined by HÖCK *et al.* (1999) and recently updated by DAXNER-HÖCK *et al.* (2013) and MARIDET *et al.* (2014).

Epoch	biozone	Layer	*Plesiosciurus* aff. *sinensis*	*Kherem shandgoliensis*	? *Eutamias* sp.	Pteromyini indet.	*Eutamias* cf. *ertemtensis*	? *Atlantoxerus* sp.
Late Miocene	E	BUK-A/12+14					+	+
Middle Miocene	D1/2	UTO-A/5	+	+				
	D1/2	LOH-A/2	+					
	D1/1	ODO-B/1				+		
Early Miocene	D	HTE-008	+		+			
	D	HTE-005		+				
	D	HTE-surface		+				
	D	UNCH-A/4	+		+	+		
	D	UNCH-A/3		+	+			
Late Oligocene	C1	LOH-C/1		+				
	C	TGW-A/2a	?					

is consequently only based on their large size and gracile morphology, whereas European species ascribed to the *Heteroxerus* are usually smaller and more robust. This generic ascription remains however uncertain.

Wu (1988) described for the first time two species of *Atlantoxerus*, *A. jungarrensis* Wu, 1988 and *A. giganteus* Wu, 1988, from the Middle Miocene of the Junggar Basin (China). These taxa for instance can have a metaloph connecting to the posteroloph and lack the anteroconulid. Likewise Qiu (1996) described a new species of *Atlantoxerus*, *A. orientalis* Qiu, 1996, from the Middle Miocene of Inner Mongolia (China) which has a wider M1/2 and a metoloph sometimes connecting to the posteroloph in M1/2.

The specimens described here are smaller than *Atlantoxerus orientalis* and much smaller than *A. jungarrensis* and *A. giganteus*. Based on the scarce material we have, it is not possible to further identify these specimens at specific level.

Conclusions

The material of Sciuridae is relatively scarce compared to other groups of small mammals found in the Valley of Lakes; it is furthermore often poorly preserved. Consequently, some taxa described above can not be fully identified at species or generic levels. However, all together six taxa belonging to five genera have been identified in the scope of the Austrian-Mongolian project (Table 2). Although the ecology of fossil sciurid rodents is difficult to infer based on dental remains, most of the taxa described above belong to the Tamiini and Xerini tribes which imply that they are mostly ground squirrels. The Sciurini *Plesiosciurus* is interepreted as intermediate between ground and tree squirrels based on its dentition (Qiu & Liu 1986). The undetermined Pteromyini might consequently be the only strictly forest-dweller, suggesting a predominance of open landscapes in the Late Oligocene and Miocene of Central Mongolia. It is noteworthy, that despite extensive sampling in the Early Oligocene layers of the Valley of Lakes, no mammalian remain has ever been found that could be referred to Sciuridae. The family Sciuridae seems consequently to be missing from the Central Mongolian Early Oligocene fossil record.

Acknowledgements

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