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Rodent paleocommunities from the Oligocene of Ulantatal (Inner Mongolia, China)

HELDER GOMES RODRIGUES*, LAURENT MARIVAUX & MONIQUE VIANEY-LIAUD

Laboratoire de Paléontologie, Institut des Sciences de l'Évolution (UMR 5554, CNRS, UM2, IRD), Université Montpellier 2, cc 064, Place Eugène Bataillon, F-34095 Montpellier Cedex 05, France

** corresponding author: helder.gomes.rodrigues@gmail.com*

Abstract: The Oligocene deposits of the Ulantatal area in Inner Mongolia (China) contain among the richest mammalian faunas from Asia. To date, only some parts of the rodent faunas have been described. Here, we propose to review the rodent faunal lists for each site, including the description of a few new rodent specimens. We describe three additional rodent species: the Cylindrodontidae *Anomoemys lohiculus*, the Eomyidae *Asianeomys* sp., and the Dipodidae *Litodonomys huangheensis*. This study allows us to constrain the stratigraphic range of *Anomoemys lohiculus*, which ranged from the late Early Oligocene to the early Late Oligocene in this area. *Asianeomys* sp. and *Litodonomys huangheensis* are dated from the latest Oligocene. These Oligocene deposits consist now of more than 70 species of mammals if we include the fauna from Kekeamu. This latter corresponds to the basal part of the Ulantatal Formation and could be dated biochronologically from the earliest Oligocene. When compared to the faunas from the Valley of Lakes in Central Mongolia, the Ulantatal faunas present a great majority of rodents, and this difference can be partly explained by sampling and description biases regarding macro-mammals. This study also shows that variations existed between Inner and Central Mongolia, especially regarding the composition of the rodent paleocommunities. However, the assessment of their evolutionary history in this part of Asia with respect to the important climate and environment changes, require further precisions and more material than current data allow.

Keywords: Rodentia, Mammalia, Systematics, late Paleogene, Mongolian Plateau

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INTRODUCTION

Historical context of the Ulantatal area

The Ulantatal area is well-known for its Oligocene deposits including some of the most diversified and richest mammalian faunas (Huang, 1982). This area also encompasses Pliocene and Pleistocene deposits. Ulantatal is located about 60 km north of the small town Bayanhaote, Alxa Zuoqi County. This latter belongs to the Jilantai Basin, which is situated in Inner Mongolia (China; Fig. 1).

The first mammal fossils were unearthed in 1977 by a team of local geologists. The next year, a field campaign, led by scientists from the Institute of Vertebrate Paleontology and Paleoanthropology of Beijing (IVPP, China), established an important collection of fossils involving more than a hundred specimens (Huang, 1982). They were collected on both sides of the small valley of Ulantatal (i.e., "red river" in Mongolian), which consists of mesas alternating with isolated hills. The first relative datings indicated a "Middle Oligocene" age according to comparisons drawn with similar lithological content from the Qingshuiying Formation (Ningxia, China; Huang, 1982) and similar faunal content from the Hsanda Gol Formation (Valley of Lakes, Central Mongolia; Russell & Zhai, 1987).

In 1987, a second important expedition joining Chinese and German scientists supported by the Academia Sinica (China) and the Max Planck-Gesellschaft (Germany) allowed to investigate the Ulantatal area with precision. This expedition contributed to setting up a more accurate geological map of the region. Three stratigraphical units were defined (Ulan I, II and III), which clearly delineate the stratigraphical position of eight new localities (UTL1-8; Huang, 1992; Fig. 1). Subsequently, the study of the rodent faunas, especially the Ctenodactylidae (Vianey-Liaud *et al*., 2006) has allowed for a correlation with the contemporaneous faunas from the Valley of Lakes where deposits are dated radiometrically (^{40}Ar/^{39}Ar method; Höck *et al*. 1999; Daxner-Höck & Badamgarav, 2007). In this context, the different stratigraphical units of the Ulantatal area were dated (Schmidt-Kittler *et al*., 2007). The stratigraphical sequence of Ulantatal encompasses a series of deposits of about 60 meters in thickness, and it would extend from the late Early Oligocene to the Late Oligocene, thereby corresponding to about 8 Myr of record (see Vianey-Liaud *et al*., 2006 for more details about the geological context).

Faunal content of the Oligocene deposits from Ulantatal

The preliminary study of fossil mammals presented by Huang (1982) mentioned 30 species belonging to 18 genera, representing 16 families distributed among 7 distinct orders, and were found mainly by surface collecting. This list already emphasized the exceptional faunal richness of Oligocene sites from the Ulantatal area, which consist of a wide range of macro and micro-mammals. Since that time, many studies have significantly enhanced the number of species, and have also refined the first descriptions (e.g., Huang, 1984, 1985, 1986, 1987), but the age remains imprecise, especially concerning macro-mammals. Only some rodent faunas were described and accurately dated according to the screen-washing campaign of the eight dated sites performed during the 80's. These faunas included Dipodidae (Huang, 1992; Gomes Rodrigues *et al*., 2011), Ctenodactylidae (Vianey-Liaud *et al*., 2006, 2010), Muroidea

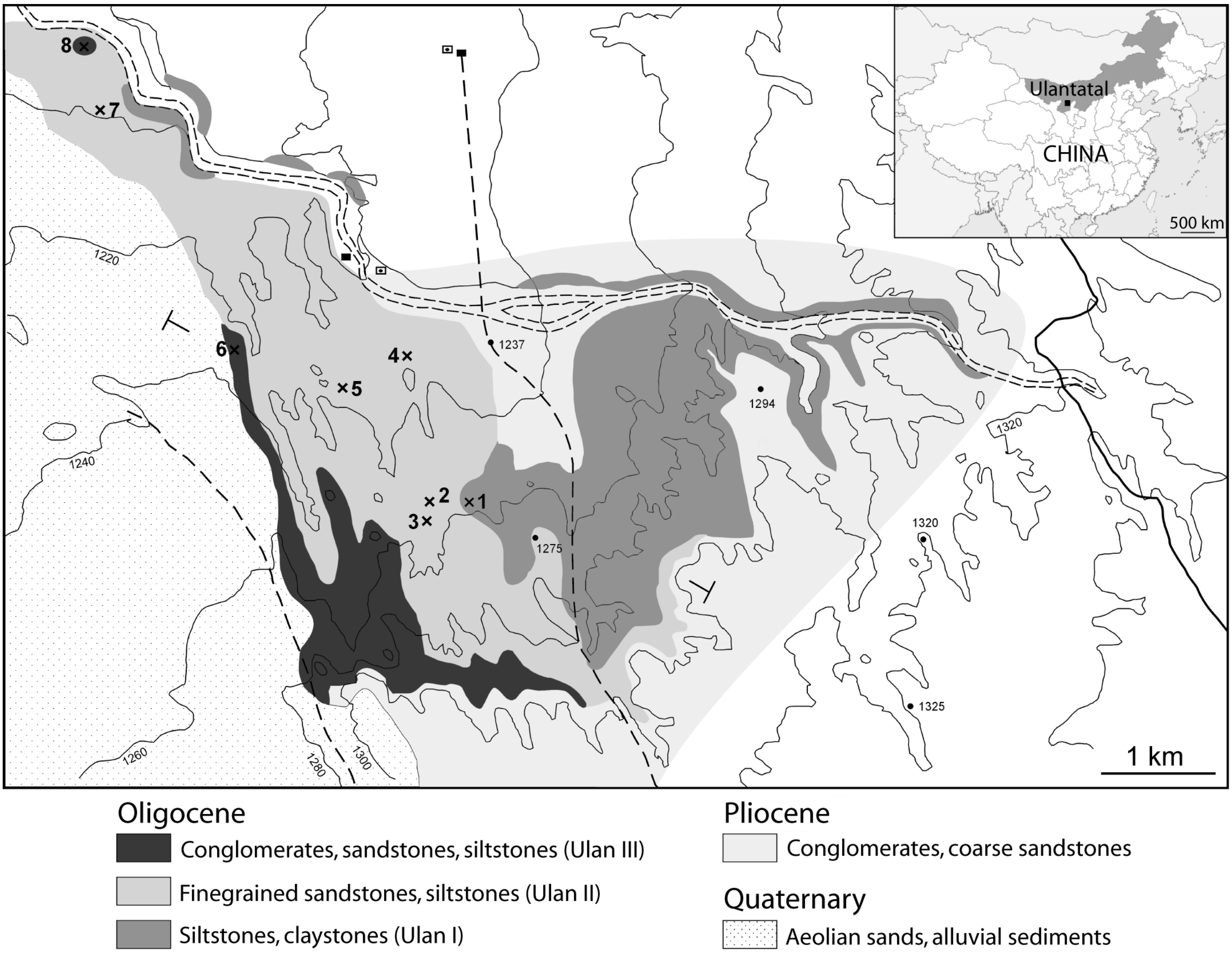

Figure 1. Map showing the location and the geology of the Ulantatal area in Inner Mongolia, China (from Vianey-Liaud *et al*., 2010 and Gomes Rodrigues *et al*., 2012a). Numbers correspond to UTL sites.

(Gomes Rodrigues *et al*., 2012a), and a few Aplodontoidea and Sciuridae (Vianey-Liaud *et al*., 2013). To date, no revised faunal lists have been erected since the description of these new fossils, including specimens from Kekeamu, which is a small branch of the Ulantatal valley investigated twice by Chinese scientists in 1988 and 1989 (Wang & Wang, 1991).

The aim of this paper is to describe the additional rodent specimens and to make an overall review of the Oligocene mammalian faunas from Ulantatal. Such a review will be necessary for further discussions about the evolution of the main rodent paleocommunities from the Mongolian Plateau (i.e., Northern China and Central Mongolia).

MATERIAL AND METHODS

The dental material was described following the classical rodent nomenclature of Wood & Wilson (1936) involving a few modifications depending on the group investigated (Wang & Emry, 1991; Marivaux *et al*., 2004; Gomes Rodrigues *et al*., 2012a; Fig. 2). Specimens were listed according to the IVPP system. Measurements were made at 0.01 mm with a measuroscope Nikon 10 linked to a digital counter Nikon CM-6S.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821

Family CYLINDRODONTIDAE Miller & Gidley, 1918

Anomoemys Wang, 1986

Anomoemys lohiculus (Matthew & Granger, 1923)

(Fig. 3A-L)

Holotype. AMNH 19100, left maxillary with P3-M2.

Type Locality. Oligocene, Hsanda Gol Formation, Loh, Mongolia.

Emended Diagnosis. Cheek teeth unilaterally hypsodont; on upper molars, main transverse lophs salient and almost equal in height to each other; protocone mesio-distally elongated, hypocone small and nearly indistinct from the protocone within the primitive endoloph; paracone and metacone incorporated in transverse lophs; metaloph retroverse and incomplete; presence of longitudinal crests connecting the protoconule, metaconule and posteroloph; P4 with strong parastyle; dp4 with marked mesoconid and strong hypoconulid; p4 with complete metalophulid II, ectolophid straight, entolophid connected to

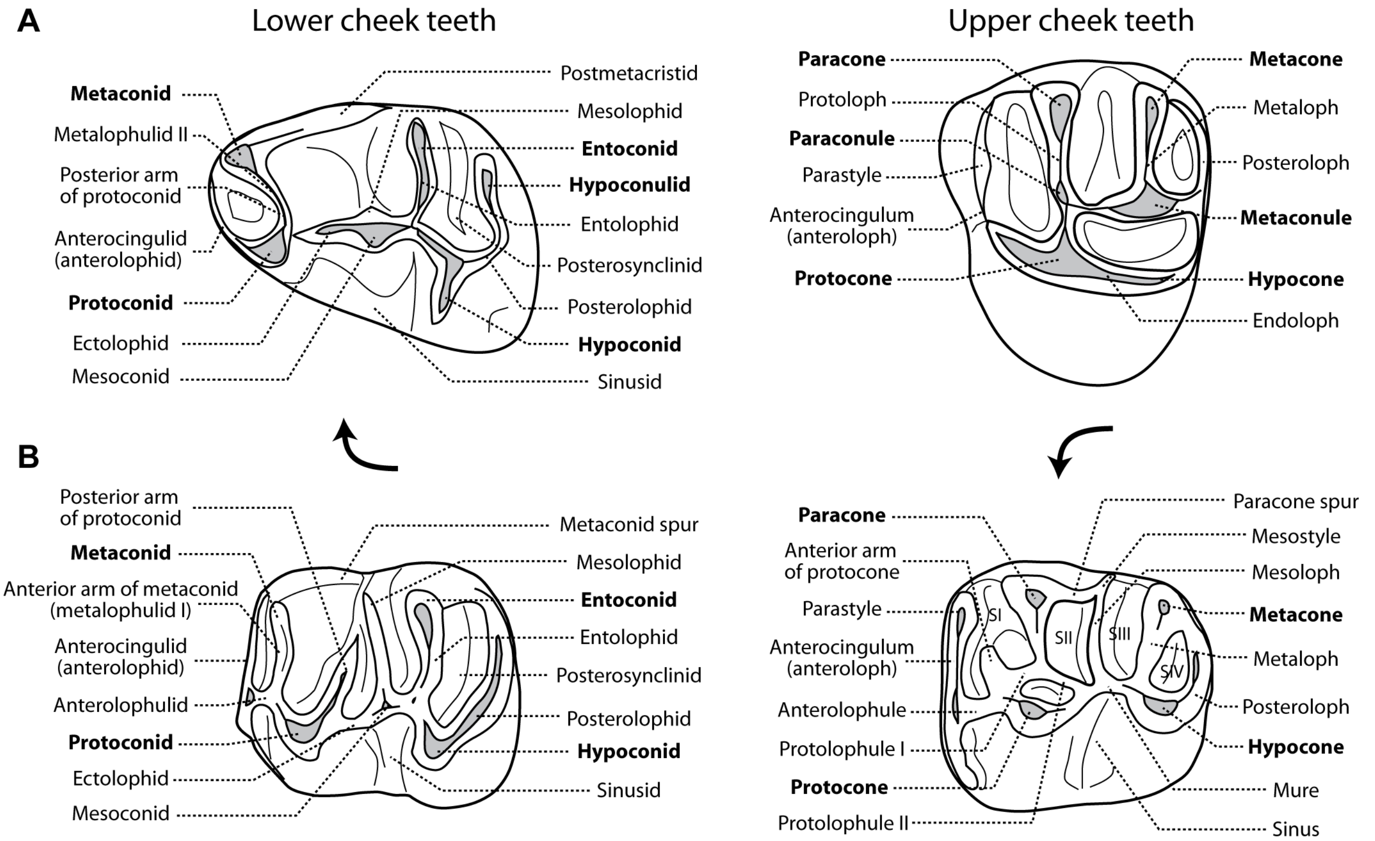

Figure 2. Dental nomenclatures used in this study. **A**: dp4 and P4 for cylindrodontids. **B**: m2 and M2 for dipodids and eomyids. SI to SIV correspond to synclines I to IV.

mesoconid or to hypoconulid, hypoconid salient and developed mesio-externally, hypoconulid distinct.

Material. see Table 1.

Stratigraphical Range. UTL1 (Ulan I) and UTL4 (Ulan II), late Early Oligocene and early Late Oligocene, respectively.

Description

The lower and the upper cheek teeth are lophodont and high crowned except deciduous premolars.

Lower teeth

On dp4, the protoconid and metaconid are both small (Fig. 3A, D). They are linked by a low anterocingulid and by a well-developed metalophulid II. The metaconid is mesially located compared to the protoconid. A large postmetacristid, probably including an indistinct mesostylid because of high wear, starts from the distal part of the metaconid and extends along the lingual side of the tooth toward the entoconid. The mesolophid is very low and reduced. A low spur starts from the mesial part of the metalophulid II and runs toward this mesolophid. The entolophid meets the mesoconid distally. It includes a hardly distinct entoconid, which is mesiodistally compressed and as high as the hypoconid, and is located on the distal border of the tooth. The hypoconid continues as a strong posterolophid, which is dominated by a mesiodistally compressed and moderately high hypoconulid. The posterosynclinid is open lingually between the hypoconulid and entoconid. Central synclinids are wide and deep.

The p4s are wider than large due to the asymmetrical hypsodonty affecting mostly the region of the hypoconid (Fig. 3B-C, E-F). These teeth are also strongly heavily worn as shown by their smoothed border. They have two roots. Lophids include faintly protruding cuspids. The protoconid and metaconid are linked by a short anterolophid. The observation of dp4 is important for the interpretation of homologies, especially for the mesial part of p4. As a result, a complex cristid constituted by a proverse lingual branch of the mesolophid joins the mesial-most part of the metalophulid II. A lingual cristid starting from the mesial border of the entoconid reaches the mesostylid. In the talonid of one tooth (Fig. 3B), the entolophid is connected to the central part of the ectolophid. On the other one (Fig. 3C), the entoconid is more distal, and the entolophid does not reach the ectolophid, but it is connected to a reduced hypoconulid via a mesio-distal cristid dividing the posterior synclinid in two parts. The posterolophid closes the posterosynclinid and joins the entoconid.

The m1s and m2s are tetralophodont and possess two mesial roots and one distal (Fig. 3G-H). The anterior synclinid is the most elongated, while the others are equal in size. Homologies can be observed between a pristine tooth (Fig. 3H), and dp4 and p4 morphologies. The mesial synclinid is closed lingually by a cristid linking the metaconid to the mesostylid. Mesially, the anterolophid links both the protoconid and metaconid. The second lophid could be the result of the addition of the posterior arm of the protoconid and the lingual part of a lingual mesolophid. The central and distal synclinids are opened lingually. The entoconid is included in the entolophid, as the metaconid in the anterolophid. The ectolophid is complete and the entolophid reaches a minute mesoconid labially. On the pristine tooth, the hypoconulid is clearly visible on the posterolophid. This lophid does not reach the distal base of the entoconid.

Table 1. Dental measurements for specimens of *Anomoemys lohiculus* (in mm).

UTL1 (IVPP V17669.1 to 18)		UTL4 (IVPP V17670.1 and 2)	
dp4	2.24 x 1.64	M1 or 2	2.39 x 2.63
dp4	-	M3	2.14 x 2.16
p4	2.28 x 2.35		
p4	2.38 x 2.21		
m1 or 2	2.72 x 2.86		
m1 or 2	2.58 x 2.29		
m1 or 2	-		
P4	2.66 x 3.40		
P4	-		
M1 or 2	2.05 x 2.77		
M1 or 2	2.14 x 3.08		
M1 or 2	2.20 x 3.17		
M1 or 2	2.11 x 2.69		
M1 or 2	2.06 x -		
M1 or 2	-		
M1 or 2	-		
M1 or 2	-		
M3	2.3 x 2.72		

Upper teeth

P4s have a strong parastyle, which is elongated transversally (Fig. 3I). The main four lophs have nearly the same height. A short anteroloph joins the prominent protocone. This latter is larger than wide, and it is fused with a minute hypocone on which the posteroloph is connected. The protoconule is reduced and only developed in its mesial part. The metaconule is reduced, but less than the protoconule, and laterally compressed; it is connected to the protoconule mesially and to the posteroloph distally. The paracone and metacone are incorporated in the protoloph and metaloph, respectively, but remain distinct. The metaloph is interrupted in its lingual part, since there is no connection between the hypocone and metaconule. All the synclines are deep and open, except the more distal. Labially, there is neither ectoloph nor mesostyle, but only a weak mesio-labial crest starting from the metacone and reaching the base of the paracone.

The morphology of M1s and M2s (Fig. 3J-K) is close to that of P4s. However, the parastyle is reduced, elongated, and included in the anteroloph. The paracone and metacone are less distinct. The protocone is less wide and the metacone has a more distal position.

M3s are not greatly elongated distally (Fig. 3L). The metacone is indistinct and the metaloph is lower than other lophs.

Remarks. Although the size of some lower molars appears greater than the size of the holotype (Matthew & Granger, 1923; Kowalski, 1974), these specimens are assigned to *A. lohiculus*. Huang (1993a) already described some specimens of *A. lohiculus* from the Ulantatal area, but the material lacked good provenance. Some of these cylindrodontids from Ulantatal could be the first confirmation of this family in the Late Oligocene of Asia. To date, the only cylindrodontid attributed to the Late Oligocene is the doubtful *Sespemys thurstony* from North America (Walsh & Storer, 2008).

Family DIPODIDAE Fischer von Waldheim, 1817

Litodonomys Wang & Qiu, 2000

Litodonomys huangheensis Wang & Qiu, 2000

(Fig. 3M-N)

Holotype. one right m2 (IVPP V11768.1).

Type Locality. Late Oligocene, GL 9601B in Shangxigou of Lanzhou Basin, Lower Member of the Xianshuihe Formation, Gansu, China.

Material. 1 M3 (IVPP V17663.1, 0.96x0.95), 1 m3 (IVPP V17663.2, 1.19x1.02).

Stratigraphical Range. UTL6 (Ulan III), latest Oligocene.

Description

Lower teeth

The m3 is short and pear-shaped. The anterolophid is present, while the anterolophulid is missing. The protoconid and metaconid are linked via a transverse metalophulid I. The distal spur of the metaconid is marked and nearly reaches the minute entoconid. The ectolophid starts from the posterior arm of the protoconid and reaches the entoconid. As a result, the sinusid is wide and more distally protruding, while the mesolophid is missing. The hypoconid is marked but included in the posterolophid, which is fused with the entolophid.

Upper teeth

The M3 is rounded. The anteroloph is marked, while the anterolophule is central and reaches the lingual part of the elongated paracone. This cusp is stronger than the protocone, which is small and conical. They are connected by a short protolophule II. The mure is faintly developed, as the endoloph, and it joins the protolophule II. The hypocone is strongly reduced. The metaloph can be either missing or merged with the strong posteroloph. The central syncline is very wide due to the absence of both metacone and mesoloph.

Remarks. These specimens can be attributed to the species *Litodonomys huangheensis*, because there is no significant difference with respect to the first fossils described from Shangxigou (Eastern Gansu, Xianshuihe Formation; Wang & Qiu, 2000), except the presence of anterolophid on m3. However, the M3 from UTL 6 differs from other material from the Valley of Lakes (Daxner-Höck *et al*., 2014) in having a mure, and its lingual part of the anteroloph clearly separated from the protocone. In general, the specimens found in the Valley of Lakes appear slightly smaller than most of the hypodigm. Such differences could also represent intraspecific variation, which is to date poorly known, but is generally important for third molars in rodents. These m3 and M3 from UTL6 also differ from those of *Litodonomys xishuiensis* (Wang, 2003), *Litodonomys lajeensis* (Li & Qiu, 1980; Daxner-Höck *et al.*, 2014), and *Litodonomys minimus* (Kimura, 2010) in being larger, with the distal part far less reduced. Moreover, the material from Ulantatal is contemporaneous with that excavated in Shangxigou (Wang & Qiu, 2000a), in Yandantu (Wang, 2003), and in the Valley of Lakes (Daxner-Höck *et al*., 2014).

Family EOMYIDAE Winge, 1887

Asianeomys Wu *et al*., 2006

***Asianeomys* sp.**

(Fig. 3O-P)

Material. 1 P4 (IVPP V17671.1, 0.91x0.97), 1 M1 or M2 (IVPP V17671.2, 0.92x1.14)

Stratigraphical Range. UTL6 (Ulan III), latest Oligocene

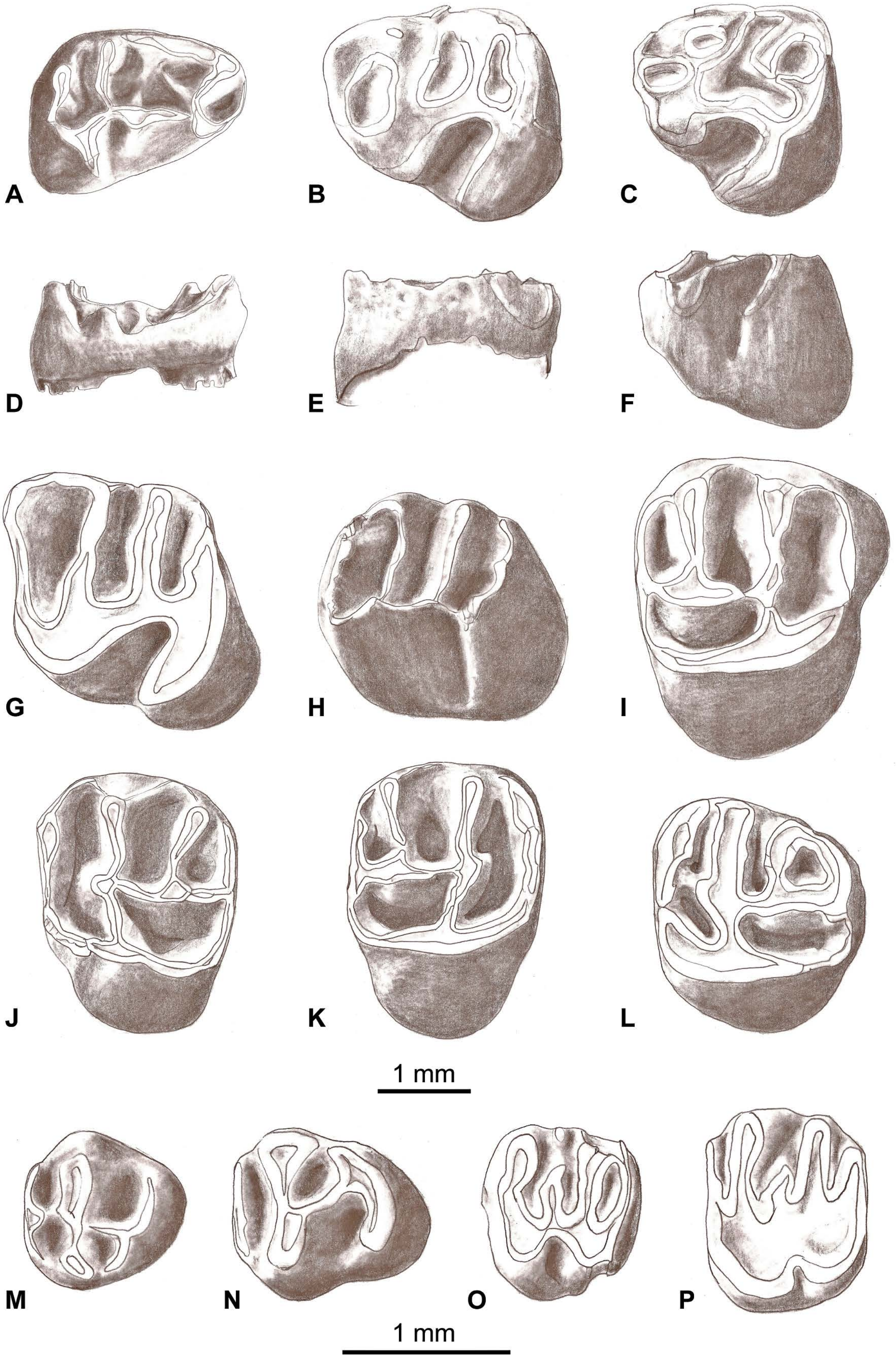

Figure 3. Dental illustrations of *Anomoemys lohiculus*, *Litodonomys huangheensis* and *Asianeomys* sp. **A-L**: *Anomoemys lohiculus* UTL1. **A**, occlusal and **D**, lingual sides of right dp4; **B**, occlusal and **E**, lingual sides of left p4; **C**, occlusal and **F**, labial sides of left p4; **G-H**, occlusal sides of left M1 or M2; **I**, occlusal side of right P4; **J**, occlusal side of left M1 or M2; **K**, occlusal side of right M1 or M2; **L**, occlusal side of left M3. **M-N**: *Litodonomys huangheensis*, UTL6; occlusal sides of left M3 and m3. **O-P:** *Asianeomys* sp., UTL6; occlusal sides of left DP4 and M1.

Description

Upper teeth

The P4 is worn. The anteroloph is rudimentary and the syncline I is absent. The protolophule I, which links the protocone and paracone, is curved mesiodistally. The mesoloph is moderately enlarged and distally curved. It extends the mesial part of the mure. The syncline II is narrow. The mesostyle is distinct but poorly developed. The transverse metaloph links the anterior arm of the hypocone. The paracone and metacone are transversally elongated. The posteroloph joins the base of the metacone and closes the syncline IV. The sinus is slightly proverse.

The M1 or M2 (extremely worn) is wider than large. The anteroloph reaches the labial side. The syncline I is open. The protoloph I joins the protocone and paracone. A crest distally starting from the paracone follows the labial margin toward the metacone. The mesoloph is curved toward the distal part of the tooth. The mesostyle is absent. The transverse metaloph meets the anterior arm of the hypocone. The metacone is distinct, but included in the strait metaloph. The posteroloph does not reach the base of the metacone and the syncline IV remains open as a result.

Remarks. *Asianeomys* sp., like other *Asianeomys* samples, has a bunolophodont pattern with highly developed lophs, with rudimentary to absent anteroloph and syncline I on P4, and with the mure connected to the distal arm of the the protoloph. It presents the same size as the Chinese *Asianeomys asiaticus* (Wang & Emry, 1991), *Asianeomys dangheensis* (Wang, 2002; Maridet *et al*., in press) and *Asianeomys junggarensis* (Wu *et al*., 2006), while it is slightly smaller than *Asianeomys engesseri* (Wu *et al*., 2006), and greater than *Asianeomys fahlbuschi* (Wu *et al*., 2006) and the Kazak *Asianeomys bolligeri* (Lopatin 2000, 2004; Maridet *et al*., in press). It differs from *Asianeomys asiaticus* in having a shorter prelobe and a mesoloph on P4, and in the presence of a distal paracone crest and the absence of mesostyle on M1-2. It differs from *Asianeomys junggarensis* and *Asianeomys dangheensis* in having a syncline I absent on P4 and shorter mesoloph. It differs from *Asianeomys engesseri* and *fahlbuschi* in having a transverse metaloph on M1 or M2. It also differs from *Asianeomys bolligeri* in having a curved mesoloph, and in not having a lingual arm of anteroloph on M1-2. Most of the characters discussed here are frequently highly variable, and it cannot be excluded that *Asianeomys* sp. actually belongs to one of these species, an issue which can be addressed only when additional material will be found.

DISCUSSION

Updated mammalian faunal lists of Ulantatal

Kekeamu corresponds to the basal part of the Ulantatal Formation (Wang & Wang, 1991). This fauna includes 11 species encompassing 10 families (Tables 2 and 3). Among them, rodents are predominantly represented and include one cylindrodontid, one aplodontid, one dipodid, two muroids, and two ctenodactyloids, which need re-examination because some species were not precisely assigned. Two Kekeamu taxa have been described: the ctenodactyloid, *Ageitonomys neimongoliensis* (Wang, 2010) and *Ardynomys* sp. (Wang & Meng, 2009). According to the presence of *Karakoromys*, which is a rodent typical of these biozones (Schmidt-Kittler *et al*., 2007), it could be dated from the Early Oligocene. But, it could more precisely be from the earliest part of the Oligocene due to the occurrence of *Ardynomys* (Wang & Meng, 2009). Even if it is a genus more frequently found in Eocene strata, it is also found in the informal biozone A of the Valley of Lakes (Fig. 4).

To date, the different faunas from the Oligocene deposits of Ulantatal include more than 70 species encompassing 8 orders of mammals. Among them, there is an impressive majority of micro-mammals, especially rodents, which encompass at least 50 species belonging to 9 different families (Tables 2 and 3). Some fossils, including notably macro-mammals (i.e., Perissodactyla, Cetartiodactyla, Carnivora and Creodonta) and some small squamates, still remain in the collection of the IVPP to be described and given accurate locality data. Indeed, macro-mammals and a few micro-mammals (i.e., Eulipotyphla, Lagomorpha and Didymoconida) unearthed during the first expeditions (Huang, 1982) were dated imprecisely as "Middle Oligocene", and thus need to be reconsidered (Table 3). The real total number of macro-mammals is low (12 species) and probably underestimated when compared to the number of rodents, which might be due to the differential sampling between the field campaigns. Moreover, although the number of all the Oligocene species of rodents is very close between the Ulantatal area and the Valley of Lakes (more than 50 and 60 species, respectively), the abundance of macro-mammals strongly differs (at least more than 10 and 40 species, respectively; Daxner-Höck *et al*., 2010, 2014; Maridet *et al*. 2014a, b, in press). For instance, Cetartiodactyla appear much more abundant in the Valley of Lakes (21 species; Daxner-Höck *et al*., 2010), than in Ulantatal (3). There are also strong differences regarding other micro-mammals such as Eulipotyphla and Lagomorpha. These observations are likely the result of incomplete data due to sampling bias, even if differential geographical distribution cannot be excluded for the moment. The last point concerns the occurrence of some species during the Late Oligocene at Ulantatal (e.g., *Anomoemys lohiculus*, *Cricetops dormitor*, *Eucricetodon asiaticus*, and *Ulaancricetodon badamae*), which are only present during the Early Oligocene in the Valley of Lakes. Unfortunately, this issue will be tackled only when all the rodent faunas are described, in order to know if it is a question of dating of UTL sites from Unit II or a matter of differential stratigraphic ranges regarding rodents from Inner and Central Mongolia.

Compositions of rodent paleocommunities and ecological implications

Muroids, ctenodactyloids and dipodids are the most abundant forms among rodents at Ulantatal in representing about 98 % of the rodent specimens described. Cylindrodontids are less frequent and far less represented, while aplodontoids, eomyids and sciurids constitute the rarest groups. It appears difficult to address the case of the Tsaganomyidae from a temporal viewpoint, since there is no corresponding material known in UTL sites. The same tendencies can be observed in terms of specific richness in the Valley of Lakes, even though tsaganomyid species are as numerous as dipodids, muroids and ctenodactylids (Schmidt-Kittler *et al*., 2007; Maridet *et al*., 2014a; Daxner-Höck *et al*., 2014). Nonetheless, information is so far only partial regarding the abundance of each species in this Mongolian area, since the whole rodent material is not yet accurately described (e.g.; Dipodidae at Ulantatal, Muroidea and a few groups of rodents in the Valley of Lakes). However, while a clear biochronological framework is not yet defined for Central and Eastern Asian areas concerning the Oligocene, it is worth noting that the ctenodactylid *Karakoromys* is typical from the Early Oligocene, while the eomyid *Asianeomys*, the dipodoid *Litodonomys* and the muroid Tachyoryctoidinae are

Table 2. Rodent faunal list of the Ulantatal area detailed for each UTL site. "?" means the material is not yet described.

	Kekeamu	UTL1	UTL3	UTL4	UTL5	UTL7	UTL6	UTL8	Description
Aplodontidae									
Prosciurus sp.	+								Wang & Wang, 1991
Ninamys arboraptus (Shevyreva, 1967)								+	Vianey-Liaud *et al.*, 2013
Promeniscomys sinensis Wang, 1987								+	Vianey-Liaud *et al.*, 2013
Ctenodactyloidea									
Ageitonomys neimongolensis Wang, 2010	+								Wang, 2010
Ctenodactylidae									
Karakoromys decessus Matthew & Granger, 1923		+							Vianey-Liaud *et al.*, 2006
Karakoromys cf. *decessus* Matthew & Granger, 1924	+								Wang & Wang, 1991
Tataromys sigmodon Matthew & Granger, 1923		+		+		+		+	Vianey-Liaud *et al.*, 2006
Tataromys minor (Huang, 1985)		+	+	+	+	+	+		Vianey-Liaud *et al.*, 2006
Tataromys plicidens Matthew & Granger 1923		+		+	+	+			Vianey-Liaud *et al.*, 2006
Alashania tengkoliensis Vianey-Liaud *et al.*, 2006		+		+				+?	Vianey-Liaud *et al.*, 2006
Yindirtemys ulantatalensis (Huang, 1985)		+		+		+	+	+	Vianey-Liaud *et al.*, 2006
Yindirtemys bohlini (Huang, 1985)				+			+	+	Vianey-Liaud *et al.*, 2006
Yindirtemys shevyrevae Vianey-Liaud *et al.*, 2006		+		+		+	+	+	Vianey-Liaud *et al.*, 2006
Yindirtemys aff. *shevyrevae* Vianey-Liaud *et al.*, 2006							+		Vianey-Liaud *et al.*, 2006
Yindirtemys deflexus (Teilhard de Chardin, 1926)							+	+	Vianey-Liaud *et al.*, 2006
Huangomys frequens Schmidt-Kittler *et al.*, 2007		+	+	+	+	+		+	Vianey-Liaud *et al.*, 2006
Helanshania deserta Vianey-Liaud *et al.*, 2010		+		+					Vianey-Liaud *et al.*, 2010
Tataromyinae nov. gen., nov. sp. 2							+		Vianey-Liaud *et al.*, 2006
Tataromyinae nov. gen., nov. sp. 3								+	Vianey-Liaud *et al.*, 2006
Tataromyinae nov. gen., nov. sp. 4								+	Vianey-Liaud *et al.*, 2006
Cylindrodontidae									
Ardynomys sp.	+								Wang & Meng, 2009
Anomoemys lohiculus (Matthew & Granger, 1923)		+		+					Huang, 1993 and this paper
Dipodidae									
Heosminthus sp.	+	?			?				Wang & Wang, 1991
Parasminthus asiae-centralis Bohlin, 1946		?	+	+	?		+	+	Huang, 1992
Parasminthus tangingoli Bohlin, 1946		?	+	+	?		+	+	Huang, 1992
Bohlinosminthus parvulus Bohlin, 1946		?	+	+	?			+	Huang, 1992
Gobiosminthus qiui Huang, 1992		?		+	?	+			Huang, 1992
?*Gobiosminthus* sp. Huang, 1992		?		+	?	+	+		Huang, 1992
Shamosminthus tongi Huang, 1992		?	+	+	?			+	Huang, 1992
Ulaancricetodon badamae Daxner-Höck, 2000				+					Gomes Rodrigues *et al.*, 2011
Litodonomys huangheensis Wang & Qiu, 2000							+		This paper
Eomyidae									
Asianeomys sp.							+		This paper
Muroidea									
Eucricetodon asiaticus (Matthew & Granger, 1923)		+	+	+	+	+	+	+	Gomes Rodrigues *et al.*, 2012
Eucricetodon jilantaiensis Gomes Rodrigues *et al.*, 2012		+	+	+	+	+	+	+	Gomes Rodrigues *et al.*, 2012
Eucricetodon bagus Gomes Rodrigues *et al.*, 2012		+	+	+	+	+	+	+	Gomes Rodrigues *et al.*, 2012
Eucricetodon aff. *caducus* (Shevyreva, 1967)				+	+				Gomes Rodrigues *et al.*, 2012
Eucricetodon sp. 1		+	+						Gomes Rodrigues *et al.*, 2012
Eucricetodon sp. 2						+			Gomes Rodrigues *et al.*, 2012
Eucricetodon sp. 3	+								Wang & Wang, 1991
Bagacricetodon tongi Gomes Rodrigues *et al.*, 2012							+		Gomes Rodrigues *et al.*, 2012
Plesiodipus wangae Gomes Rodrigues *et al.*, 2012							+	+	Gomes Rodrigues *et al.*, 2012
Plesiodipus sp.		+				+			Gomes Rodrigues *et al.*, 2012
Witenia yolua Gomes Rodrigues *et al.*, 2012			+	+		+		+	Gomes Rodrigues *et al.*, 2012
Cricetops dormitor Matthew & Granger, 1923				+		+			Gomes Rodrigues *et al.*, 2012
Pseudocricetops matthewi Gomes Rodrigues *et al.*, 2012				+					Gomes Rodrigues *et al.*, 2012
Tachyoryctoidinae indet.							+		Gomes Rodrigues *et al.*, 2012
Genus indet.	+								Wang & Wang, 1991
Sciuridae									
Genus indet.								+	Vianey-Liaud *et al.*, 2013
Minimal species diversity	**7**	**15**	**11**	**24**	**7**	**15**	**18**	**21**	

not found before the Late Oligocene.

Among all rodent paleocommunities, 9 families or superfamilies have been listed (Table 2). Except for aplodontoids, eomyids and sciurids, which are scarcely present, the other groups were well represented across the Mongolian Plateau, and their stratigraphic ranges cover the entire Oligocene period. Ctenodactylids, dipodids and muroids are the most diversified taxa. While the species richness of Muroidea does not vary significantly from one area to another (considering that *Ulaancricetodon* is a dipodid; see Gomes Rodrigues *et al*., 2011), there are more Dipodidae than Ctenodactylidae in the Valley of Lakes (20 and 8 species, respectively) contrary to what it is observed at Ulantatal (9 Dipodidae and 16 Ctenodactylidae). Apart from sampling variation, such differences can emphasize geographical disparities concerning the compositions of rodent communities in the Mongolian Plateau, which could be linked to partitioning of the ecological niches likely due to small local environmental variations. More generally, the size and shape variations are important in ctenodactylids and muroids (Vianey-Liaud *et al*., 2006; Gomes Rodrigues *et al*., 2012), and trends toward increasing crown height and more developed crests potentially indicate modifications of ecological niches in

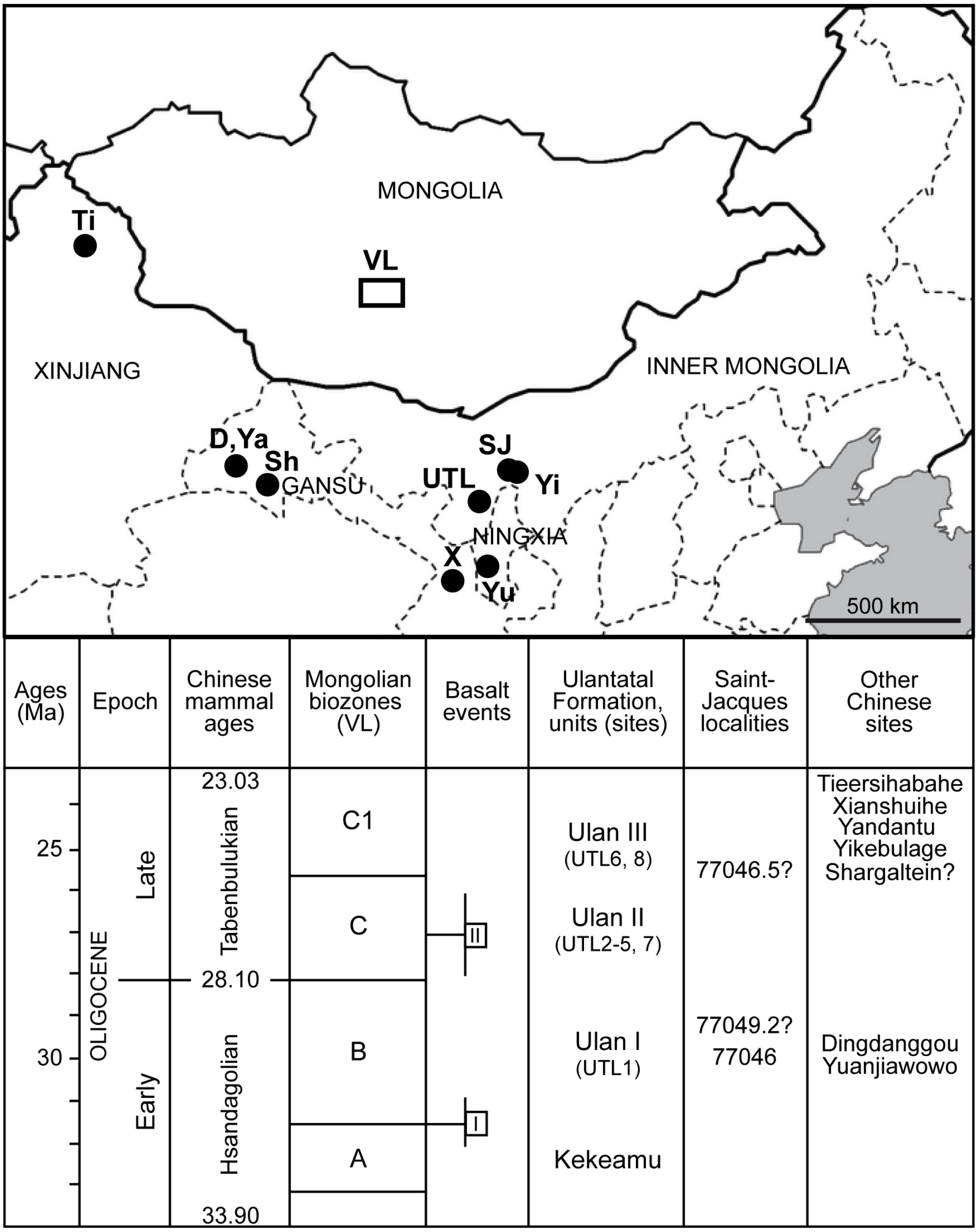

Figure 4. Location of the main Oligocene sites of Mongolia and Northern China, and biostratigraphic correlations according to local Mongolian biozones (modified after Daxner-Höck *et al*., 2010, 2014). Abbreviations: D, Dingdanggou; Ti, Tieersihabahe; Sh, Shargaltein; SJ, Saint-Jacques; UTL, Ulantatal; VL, Valley of Lakes (see Daxner-Höck *et al*., 2010 for the detail of each site); Ya, Yandantu; Yi, Yikebulage; Yu, Yuanjiawowo; X, Xianshuihue.

Table 3. Complementary mammalian faunal list for Kekeamu and surface finds for the Ulantatal areas from early field campaigns.

Area	Superfamily/family	Genus and species	References
Kekeamu	Erinaceidae	?*Tupaidon* sp.	Wang & Wang, 1991
	Palaeolagidae	*Desmatologus* sp.	Wang & Wang, 1991
	Chalicotheridae	*Schizotherium* cf. *avitum* Matthew & Granger, 1923	Wang & Wang, 1991
	Hyracodontidae	*Ardynia* cf. *mongoliensis* Matthew & Granger, 1923	Wang & Wang, 1991
Surface collecting	Feloidea	*Paleoprionodon* sp.	Huang, 1993
	Amphicyonidae	*Cynodictis elegans* Matthew & Granger, 1924	Huang, 1993
		?*Amphicynodon* sp.	Huang, 1993
	Feliformia	*Paleogale sectoria* (Gervais, 1852)	Huang, 1993
	Bovoidea	*Palaeohypsodontus* cf. *P. asiaticus* Trofimov, 1958	Huang, 1985
		Hanhaicerus qii Huang, 1985	Huang, 1985
	Cervoidea	*Eumeryx culminis* Matthew & Granger, 1924	Huang, 1985
	Hyaenodontidae	*Hyaenodon neimongoliensis* Huang & Zhu, 2002	Huang & Zhu, 2002
	Didymoconidae	*Didymoconus colgatei* Matthew & Granger, 1924	Meng & McKenna, 1998
	Erinaceidae	*Palaeoscaptor acridens* Matthew & Granger, 1924	Huang, 1984
		Paleoscaptor rectus Matthew & Granger, 1924	Huang, 1984
	Palaeolagidae	*Desmatolagus* cf. *D. gobiensis* Matthew & Granger, 1923	Huang, 1987
		Desmatolagus pusillus Teilhard de Chardin, 1926	Huang, 1987
	Ochotonidae	*Sinolagomys kansuensis* Bohlin, 1937	Huang, 1987
		Sinolagomys major Bohlin, 1937	Huang, 1987
	Leporidae	*Ordolagus teilhardi* (Burke, 1941)	Huang, 1986
	Rhinocerotidae	*Cadurcodon* sp.	Huang, 1982
		Aceratherium sp.	Huang, 1982
	Muroidea	*Selenomys mimicus* Matthew & Granger, 1923	Huang, 1982
	Tsaganomyidae	*Tsaganomys altaicus* Matthew & Granger, 1923	Wang, 2001
		Coelodontomys asiaticus Wang, 2001	Wang, 2001

a general context of global cooling (Dupont-Nivet *et al*., 2007) and local aridification and opening of environments. This is supported by dental microwear analyses in these rodents, which show an increase of the potential consumption of abrasive and fibrous plants more frequently found in open habitats (Gomes Rodrigues *et al*., 2012b).

There are a lot of species that appeared during the latest Oligocene, especially at Ulantatal (i.e., UTL6 and 8) where nearly half of the species are new. That can be explained by a slight warming event recorded at the end of the Oligocene, which could have induced a moderate faunal turnover and a slight change of environments (de Man & Van Simayes, 2003; Maridet *et al*., 2009; Gomes Rodrigues *et al*., 2012a). This is particularly shown by the concomitant occurrence of eomyids, aplodontids and sciurids specific of more forested habitats, as well as small muroids, such as *Bagacricetodon tongi*. Fossorial rodents are also well represented in the Mongolian Plateau during the Oligocene, and are notably characterized by high-crowned teeth, and “mole-rat-like” skulls observed in Tsaganomyidae. Cylindrodontids are typical of the Early Oligocene (e.g., *Ardynomys*), and only one occurrence is registered in the Late Oligocene deposits of Ulantatal (this work). Tsaganomyids are common mainly in the Early Oligocene, including specimens from Ulantatal (Wang, 2001). In the Mongolian Plateau, *Cyclomylus* and *Coelodontomys* species are specific of the Early Oligocene, while the occurrence of *Tsaganomys altaicus* extended to the Early Miocene. The decline of these groups during the Late Oligocene could be partly related to the appearance of fossorial muroids, the Tachyoryctoidinae (Wang & Qiu, 2012). Further researches are needed to address the main evolutionary, ecological and migratory events of the whole rodent paleocommunities in this part of Asia during the Oligocene to make reliable comparisons with other regions.

PROSPECTS

Contrary to the Valley of Lakes, faunal lists from other Northern Chinese areas are generally sparse, and the relative abundance of each taxon is not always specified. In this context, even if it remains premature to draw comparisons with Ulantatal, it seems important to list them to show first their geographical and chronological interests for further studies (Fig. 4). The nearest sites from Ulantatal are located at Saint-Jacques, belonging to the Wulanbulage Formation, which is well-known for having yielded abundant mammal fossils (Wang *et al*., 1981). Among the vast number of sites, the best documented are 77046, 77046.5 and 77049.2 (Wang, 1987a,b, 1997, 2001; Wang & Emry, 2001). There is also a very close site from the Yikebulage Formation (Wang *et al*., 1981). Apart from Inner Mongolia, other Northern Chinese sites bear Oligocene faunas, such as the Yuanjiawowo fauna from the Haiyuan area located in Ningxia (Wang *et al*., 1994). Not far from there, in Eastern Gansu, the lower member of the Xianshuihe Formation (Lanzhou Basin; Wang & Qiu, 2000a, b) includes deposits, which are latest Oligocene in age (Xiagou and Shangxigou). The geological area of western Gansu originally described by Bohlin (1937, 1946) and including sites from Shargaltein (Wang & Qiu, 2003) and Taben-Buluk, has been investigated recently. Taben-Buluk, currently known as the Danghe area and corresponding to the Paoniuquian Formation, consists of a lower part including the Dingdanggou fauna (Wang & Qiu 2004) and an upper part including the Yandantu fauna (Bohlin’s Yindirte fauna; Wang, 2003; Wang *et al*., 2003; Wang *et al*., 2008). In the northwestern part of China, the Tieersihabahe section of the Junggar Basin (Xinjiang) comprises a few sites accurately dated from the latest Oligocene (Meng *et al*., 2006). Because of the importance of these different Oligocene sites with distinct ages, it appears crucial to update their stratigraphic characteristics and to accurately date and describe their fauna in order to discuss the distribution of specific taxa in Central and Eastern Asia, and both the structure and evolution of the different mammal paleocommunities in a context of global climate change and local environment modifications.

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